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Shrubland Ecosystem Genetics and Biodiversity: Proceedings

Abstract

McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. **Shrubland ecosystem genetics and biodiversity: proceedings**; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 365 p.

The 53 papers in this proceedings include a section celebrating the 25-year anniversary of the Shrub Sciences Laboratory (4 papers), three sections devoted to themes, genetics, and biodiversity (12 papers), disturbance ecology and biodiversity (14 papers), ecophysiology (13 papers), community ecology (9 papers), and field trip section (1 paper). The anniversary session papers emphasized the productivity and history of the Shrub Sciences Laboratory, 100 years of genetics, plant materials development for wildland shrub ecosystems, and current challenges in management and research in wildland shrub ecosystems. The papers in each of the thematic science sessions were centered on wildland shrub ecosystems. The field trip featured the genetics and ecology of chenopod shrublands of east-central Utah. The papers were presented at the 11th Wildland Shrub Symposium: Shrubland Ecosystem Genetics and Biodiversity held at the Brigham Young University Conference Center, Provo, UT, June 13–15, 2000.

Keywords: wildland shrubs, genetics, biodiversity, disturbance, ecophysiology, community ecology

Acknowledgments

We thank the many people and organizations that assisted in the advance preparation and conduct of the symposium, anniversary celebration, and field trip. Brigham Young University President Merrill J. Bateman, Rocky Mountain Research Station Director Denver P. Burns, and Forest Service Vegetation Management and Protection Washington Office Director William T. Sommers kindly helped with the anniversary celebration. Members of the A. Perry Plummer and Howard C. Stutz families including Mrs. Blanch Plummer and Dr. Howard and Mrs. Mildred Stuz were present at the bust unveiling, which honored the contributions of Mr. Plummer and Dr. Stutz in establishment of the Shrub Sciences Laboratory. Stacia Simonsen, Von Phillips, and Rob Holcombe and other staff members of the Brigham Young University Conferences and Workshop staff were gracious, accommodating, and efficient in all aspects of the symposium and field trip preparation and conduct. Pat Ford, Geneva Ball, Stewart Sanderson, and Stan Kitchen of the Shrub Sciences Laboratory, Gary Jorgensen of the Great Basin Experimental Range, and volunteer Roberta Leslie helped with logistical and clerical support. Technical sessions were chaired by Durant McArthur, Kent Ostler, Scott Walker, Darrell Ueckert, Ann Hild, and Bruce Roundy. Daniel Fairbanks sculpted the busts and assisted the Plummer and Stutz families with the bust unveiling. Marcus Alan Vincent prepared the cover illustration with its five shrub species (black greasewood, big sagebrush, fourwing saltbush, rubber rabbitbrush, and Stansbury cliffrose). Several units of the Shrub Research Consortium made financial contributions to assist with proceedings publication costs including the Shrub Sciences Laboratory, Brigham Young University College of Biology and Agriculture and Department of Botany and Range Science, Utah State University, Utah Division of Wildlife Resources, University of Idaho, Montana State University, University of Nevada-Reno, Texas A&M System-Texas Agricultural Experiment Station, Texas Tech University, Washington State University, University of Wyoming, U.S. Department of Agriculture Agricultural Research Service-Jornada Experimental Range, Batelle Pacific Northwest Laboratories, and Bechtel Nevada. We thank the Rocky Mountain Research Station Publishing Service Unit for preparing the final publication.

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Daniel J. Fairbands
Compilers

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Shrubland Ecosystem Genetics and Biodiversity: Proceedings

Provo, UT, June 13–15, 2000

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*Charter members

The Shrub Research Consortium was formed in 1983 with five charter members (see list). Over time SRC has grown to its present size of 25 institutional members. The SRC had three principal objectives in its charter: (1) developing plant materials for shrubland rehabilitation; (2) developing methods of establishing, renewing, and managing shrublands in natural settings; and (3) assisting with publication and dissemination of research results. These objectives have been met by a series of symposia sponsored by the Consortium and partners. This publication is the 11th in the series; the previous 10 are listed on the next page. Proceedings of all publications to date have been published by the U.S. Department of Agriculture, Forest Service, Intermountain Research Station and Rocky Mountain Research Station. The executive committee has plans for additional symposia. The next one will be held in Laramie, WY, in 2002 with a shrubland ecosystem seeds and soil theme. Each symposium has had a theme, but the executive committee has encouraged attendance and participation by shrubland ecosystem biologists and managers with wider interests than any particular symposium theme—the heart of the Consortium's programs are wildland shrub ecosystem biology, research, and management.

Availability of Previous Wildland Shrub Symposia Proceedings

First: Tiedemann, A. R.; Johnson, K. L., compilers. 1983. Proceedings—research and management of bitterbrush and cliffrose in Western North America; 1982 April 13–15; Salt Lake City, UT. General Technical Report INT-152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 279 p. Out of print—available from National Technical Information Service as document PB83-261537 A13.

Second: Tiedemann, A. R.; McArthur, E. D.; Stutz, H. C.; Stevens, R.; Johnson, K. L., compilers. 1984. Proceedings—symposium on the biology of *Atriplex* and related chenopods; 1983 May 2–6; Provo, UT. General Technical Report INT-172. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 309 p. Out of print—available from National Technical Information Service as document PB85-116358 A14.

Third: McArthur, E. D.; Welch, B. L., compilers. 1986. Proceedings—symposium on the biology and management of *Artemisia* and *Chrysothamnus*; 1984 July 9–13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 398 p. Out of print—available from National Technical Information Service as document PB86-182318 A18.

Fourth: Provenza, F. D.; Flinders, J. T.; McArthur, E. D., compilers. 1987. Proceedings—symposium on plant herbivore interactions; 1985 August 7–9; Snowbird, UT. General Technical Report INT-222. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 179 p. A few copies are available from the Rocky Mountain Research Station; otherwise available from National Technical Information Service as document PB90-228578 A09.

Fifth: Wallace, A.; McArthur, E. D.; Haferkamp, M. R., compilers. 1989. Proceedings—symposium on shrub ecophysiology and biotechnology; 1987 June 30–July 2; Logan, UT. General Technical Report INT-256. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 183 p. Available from the Rocky Mountain Research Station.

Sixth: McArthur, E. D.; Romney, E. M.; Smith S. D.; Tueller, P. T., compilers. 1990. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5–7; Las Vegas, NV. General Technical Report INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 351 p. Out of print—available from National Technical Information Service as document PB91-117275 A16.

Seventh: Clary, W. P.; McArthur, E. D.; Bedunah, D.; Wambolt, C. L., compilers. 1992. Proceedings—symposium on ecology and management of riparian shrub communities; 1991 May 29–31; Sun Valley, ID. General Technical Report INT-289. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 232 p. Out of print—available from National Technical Information Service as document PB92-227784 A11.

Eighth: Roundy, B. A.; McArthur, E. D.; Haley, J. S.; Mann, D. K., compilers. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19–21; Las Vegas, NV. General Technical Report INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 384 p. Available from the Rocky Mountain Research Station.

Ninth: Barrow, J. R.; McArthur, E. D.; Sosebee, R. E.; Tausch, R. J., compilers. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23–25; Las Cruces, NM. General Technical Report INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 275 p. Available from the Rocky Mountain Research Station.

Tenth: McArthur, E. D.; Ostler, W. K.; Wambolt, C. L., compilers. 1999. Proceedings: shrubland ecosystem ecotones; 1998 August 12–14; Ephraim, UT. Proceedings RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 299 p. Available from the Rocky Mountain Research Station.

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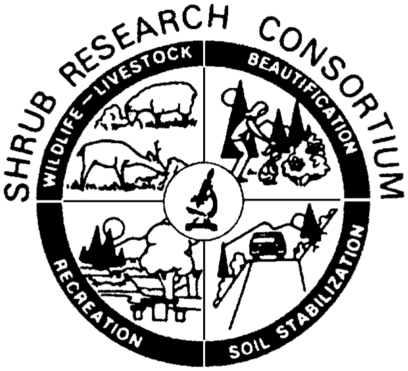


Anniversary Celebration

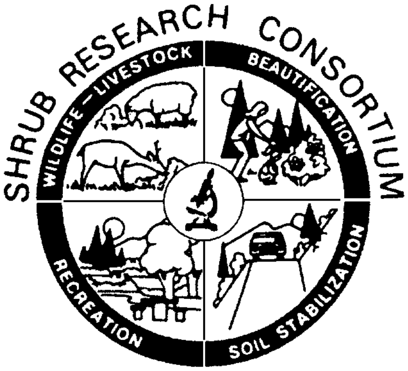
Genetics and Biodiversity

Disturbance Ecology and Biodiversity

Ecophysiology

Community Ecology

Field Trip



Anniversary Celebration

The Shrub Sciences Laboratory at 25 Years: Retrospective and Prospective

E. Durant McArthur

Abstract—The Shrub Sciences Laboratory celebrated its 25th anniversary with the symposium documented by these proceedings and a ceremony honoring people instrumental in its establishment: Mr. A. Perry Plummer represented Forest Service Research and Development and Dr. Howard C. Stutz represented Brigham Young University. The laboratory came into being because of the research foundation in Western shrub ecosystems generated by USDA Forest Service researchers and their colleagues and the need to carry on programmatic research in vast Western shrublands. Since establishment of the laboratory, dozens of scientists and professionals with technical and clerical support have conducted shrubland ecosystem research and development centered on shrubland ecosystem ecology and experimental range management, including winter livestock management on salt shrublands; seed quality testing and production and seed and seedbed ecology and adaptation; genetic variation, population biology, and systematics and taxonomy; breeding systems, hybridization, and hybrid zones; rangeland rehabilitation and restoration; equipment development, and cultural care of wildland species; soil/plant interactions, pathology, entomology, and mycorrhizae; nutritive quality, palatability, and wildlife habitat; and invasive weeds and weed biology. A continuing robust research program is anticipated that will build on previous research accomplishments, and will especially emphasize genetic variation and plant material development, fire susceptible ecosystems, invasive weed control and biology, and the ecology and restoration of ecosystems on the urban/wildland interface. Laboratory personnel and collaborators have published nearly 800 titles during the past quarter century; these are listed in the References section and in appendix A.

Origin of Laboratory

The Shrub Sciences Laboratory was officially opened with appropriate fanfare on November 4–6, 1975, with a shrub workshop for scientists and land managers; science sessions featuring contributed and invited presentations on shrub research (Stutz 1976); and a banquet, dedication, ribbon cutting, and open house. Some 350 people attended these activities, which were held at the laboratory and at the Wilkinson Student Center of Brigham Young University. Associate Deputy Chief of the Forest Service Warren T. Doolittle, Intermountain Forest and Range Experiment Station Director Roger R. Bay, and Brigham Young University President Dallin H. Oaks presided at these functions that were cosponsored by the Station, Brigham Young University, Utah Division of Wildlife Resources, Utah State University, and the Utah Section of the Society for Range Management. The program steering committee included Howard C. Stutz, Professor, Department of Botany and Range Science, Brigham Young University; James P. Blaisdell, Assistant Director, Intermountain Forest and Range Experiment Station; Cyrus M. McKell, Professor, Department of Range Science, Utah State University; and Norman C. Hancock, Chief, Game Management, Utah Division of Wildlife Resources.

The need for a laboratory dedicated to shrubland ecosystem research had been evident for some time (Blaisdell 1972). The Intermountain Forest and Range Experiment Station (now part of the Rocky Mountain Research Station) had been conducting research on the shrublands of the Colorado Plateau, Great Basin, and associated mountains beginning as early as 1912. The Intermountain Station had established three experimental ranges in central and southern Utah, Great Basin, Desert, and Benmore (Astroth and Frischknecht 1984; Clary and Holmgren 1982; Keck 1972; Kitchen and McArthur 1996; McArthur and Monsen 1996), and had active research units dealing with shrubland ecosystem research topics housed in office space with inadequate laboratory and greenhouse facilities in Ephraim and Provo. Utah and Provo are centrally located in respect to the vast shrublands of Western North America setting near the juncture of the Rocky Mountain, Colorado Plateau, and Basin and Range physiographic provinces. Within the U.S. Department of Agriculture, Forest Service Research and Development network of laboratories, the Shrub Sciences Laboratory is unique in that it is the only location out of more that 60 total research locations that is dedicated to research on shrubland ecosystems. This is appropriate because up to 40 percent (1.8×10^6 km^2) of the conterminous 17 Western United States is shrubland (Küchler 1964; McArthur and Ott 1996).

The origin of the laboratory was documented, in part, in a letter written to me on March 17, 1985, by retired (January 1, 1966) Forest Service Deputy Chief for Research V. L. Harper, triggered by my presentation, “Building on Nature’s Diversity: Western Shrubs,” in the Forest Service Washington Office Seminar Series, 1984–1985, on February 26, 1985:

> I was much interested in the item about this seminar by you in the 3-08 issue of *The Friday Newsletter*, published by the F.S.
>
> Among other things, it recalled to mind some history of the Lab’s origin. I was doing a “Research Inspection” of the Intermountain Station (about 1960) and one of the research centers which Director Joe Pechanec and I visited was the work on shrub research. After listening to the Project Leader’s [A. Perry Plummer] presentation viewing some of the field experiments, I turned to Joe Pechanec and said in effect…:

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> "Joe, maybe we ought to amend the *Ten-year Research Program* to include a new laboratory at Provo—a lab featuring shrub research including genetics, etc." Joe grinned broadly and said "I hoped you would see this need." He then produced a memo outlining the justification for such a laboratory, hopefully to be located on the grounds of Brigham Young University. He further remarked, "I have prepared a speech, which I can now cut short, giving a big pitch for the lab." I told Joe that I was personally acquainted with the president of the university [Ernest L. Wilkinson] … and had dealings with him. "Why don't we go to see him during this trip," I said. Our visit with the president was friendly and very encouraging. He offered a long-term lease—free for the site for the building and other cooperative aspects. Amending this projected research plan was not difficult. I simply added the Provo location to the list of needed lab construction. The research plan used only an overall figure for construction and I felt we would not reach that figure anyway. From then on, while I was Chief of Research, it was on the list that I gave Senator Stennis, who in turn related it to the Senate in a speech and to the Appropriation Sub-committee, at the proper time.
>
> I am glad the Shrub Sciences Laboratory, unlike some others that I got funds for from the Budget Bureau and/or Congress, has not been abandoned by the current Administration's Budget cuts.

With the impetus generated by Deputy Chief Harper and Station Director Pechanec through Forest Service administrative circles and the Congress and backed up by strong Brigham Young University support, the laboratory became a reality but not without some vicissitudes, for example, annual appropriations for construction was impounded or sequestered by the Administration until 1974 when $760,000 was authorized for construction; actual construction was begun in October 1974 (fig. 1). The Utah Congressional delegation of the time gave bipartisan support for the laboratory. Congressman Gunn McKay (D) was especially active on behalf of the establishment of the laboratory (fig. 2); Senators Frank Moss (D) and Wallace Bennett (R) and Congressmen Sherm Lloyd (R) and Wayne Owens (D) were supportive as well. The University was proactive in establishing the laboratory by providing the land for the laboratory, associated greenhouses, and support facilities both at the laboratory site on the south edge of campus (735 North 500 East) and an ancillary site at 1325 East on 820 North through long-term leases at the minimal legal cost of $1.

Originally, the laboratory was to be called the Shrub Improvement Laboratory. However, Dr. Neil C. Frischknecht, a charter Range Scientist and Team Leader in the Mineland Reclamation Research Work Unit, raised the issue of the name of the laboratory in a June 1975 memo:

> …inasmuch as shrub improvement is essentially plant breeding, it seems that one of the following titles would more nearly reflect the scope of the research that will be done at the new lab:…Shrub Research Laboratory, Shrub Science(s) Laboratory, Shrub-Range Improvement Laboratory. …I have learned that the FS plaque and letters "Shrub Improvement Laboratory" are already on hand. If a change is in order, it is far better to make it before the building is dedicated…

Dr. Frischknecht's comment was recognized as meritorious, and the more holistic name, Shrub Sciences Laboratory, was selected and mounted on the front on the laboratory. Although my discipline is genetics, I believe it was a wise decision. The steel cast letters from "improvement" not used in "sciences" were presented to Dr. Blaisdell and Mr. Plummer by Director Roger Bay, with accompanying jocular comments, in a meeting that I remember attending.

Importance of Shrubs and Shrublands

The importance of shrub species and shrubland ecosystems in the Western United States and in other semiarid areas gained considerable impetus from the activities leading up to the establishment of the Shrub Sciences Laboratory. An international symposium (Wildland Shrubs—Their Biology and Utilization) was held in July 1971, at Utah State University in Logan, drawing researchers and land managers from many countries (McKell and others 1972). I insert a personal note: I was a postdoctoral research fellow at the University of Leeds in England at the time. I recall seeing an advertising flyer for the symposium and discussing with my mentor, Mr. David Harberd, that the subject area of the symposium was interesting and it would be nice to have an

Figure 1—Laboratory under construction (left) in February 1975 and in July 1999 (right). Photo on left by Howard C. Stutz, on right by E. Durant McArthur.

opportunity to pursue a career in that area. Such are the twists of fate that I had that opportunity shortly thereafter.

The symposium was followed several years later with a textbook, *The Biology and Utilization of Shrubs* (McKell 1989). The extent, adaptation, and use of shrubs and ecosystems that they dominate together with the prospects of a laboratory dedicated to shrub research that subsequently became a reality also stimulated, in part, a series of workshops, symposia, and publications in Utah and surrounding states and formation of the Shrub Research Consortium. The Wyoming Shrub Ecology Workshop under the leadership of Drs. Herbert G. Fisser and Kendall L. Johnson of the University of Wyoming ran for at least 17 years (1972 to 1988; Fisser 1990 lists all workshops). A similar Utah Shrub Ecology Workshop, under the leadership of Drs. Kendall L. Johnson and G. Allen Rasmussen of Utah State University ran from 1981 to 1991 (Johnson 1990 lists workshops up to that time; two subsequent workshops were held but the proceedings were not published). The Shrub Research Consortium formed in 1983 with five institutional charter members has expanded to a membership of 25 institutions (McArthur and others 1999b; Tiedemann 1984) and has sponsored 11 wildland shrub symposia (more are in the planning stages) with a diversity of wildland shrub biology themes.

Other period relevant publications include *Wyoming Shrubland Ecology*, *A Chronologic Supplemented Multiple Source Annotated Bibliography* (Fisser 1987), *Shrubs of the Great Basin, A Natural History* (Mozingo 1987), *The Sagebrush Ocean, A Natural History of the Great Basin* (Trimble 1989), *The Desert's Past, A Natural Prehistory of the Great Basin* (Grayson 1993), and *Natural History of the Colorado Plateau and Great Basin* (Harper and others 1994).

Twenty-Five Year Laboratory Celebration

Two men were honored at a bust unveiling at the beginning of the symposium and 25th year anniversary documented in this publication. Mr. A. Perry Plummer (fig. 3), long-time project leader of the Shrub Improvement and Revegetation Research Work Unit (now Shrubland Biology and Restoration RWU) of the Intermountain Forest and Range Experiment Station (now Rocky Mountain Research Station) located at the Great Basin Experimental Range (= Great Basin Research Center), Ephraim, Utah (McArthur 1991; Plummer 1972; 1977; Plummer and others 1968) for many years prior to the establishment of the Shrub Sciences Laboratory, represented the USDA Forest Service. Work by him and his group, including Utah Division of Wildlife Resources collaborators, on big game range rehabilitation, especially using native wildland shrubs, gave impetus and visibility to shrub research. Dr. Howard C. Stutz (fig. 4), Emeritus Professor of Botany and Range Science, Brigham Young University, represented the University. Dr. Stutz was untiring in his efforts as a liaison between the Utah Congressional delegation, the Forest Service, and the University during the period from the addition of the laboratory to the *Ten Year Research Program* in the early 1960s until the laboratory became a reality. Dr. Stutz has a distinguished career in plant genetics including many contributions to shrub genetics, for example, Cutler 1996; Stutz 1978; Stutz and others 1975, 1979, 1987; Stutz and Sanderson 1979, 1984, 1998; Stutz and Thomas 1964.

Figure 2—Representative K. Gunn McKay (left), Intermountain Station Director Roger R. Bay (center), and Brigham Young University President Dallin H. Oaks (right), on the site of the future Shrub Sciences Laboratory in 1974. Photo by Neil C. Frischkecht.

Dr. Daniel J. Fairbanks, Professor of Botany and Range Science, Brigham Young University, sculpted the busts and unveiled them with assistance from Mrs. Blanche Plummer and her family, Dr. Howard Stutz and Mrs. Mildred Stutz and their family, Rocky Mountain Research Station Director Denver P. Burns, and Brigham Young University President Merrill J. Bateman at the 25-year anniversary ceremony at the beginning of the symposium. The busts are now displayed in the front entrance of the Shrub Sciences Laboratory. Director Burns and President Bateman honored the 25-year celebration of the laboratory and the contributions of Mr. Plummer and Dr. Stutz with appropriate remarks. An open house at the laboratory was held for those who attended the symposium as well as the general public.

Figure 3—Mr. A. Perry Plummer, Intermountain Research Station Project Leader, instrumental in establishment of Shrub Sciences Laboratory. Photo courtesy of Mrs. Blanche Plummer.

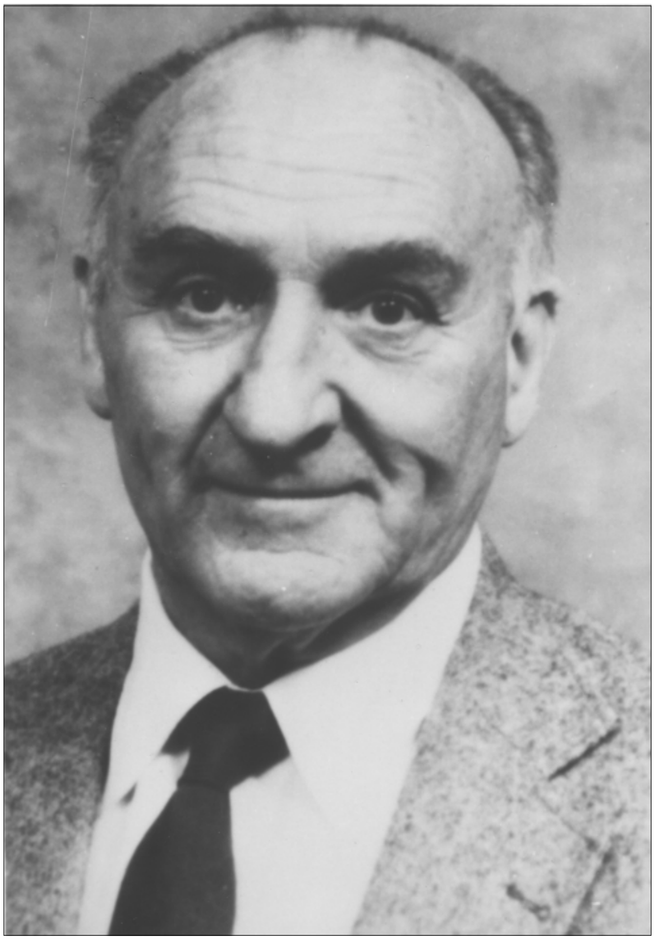

Figure 4—Dr. Howard C. Stutz, Brigham Young University Professor, tireless worker in behalf of establishment of Shrub Sciences Laboratory. Photo courtesy of Mrs. Mildred Stutz.

Staffing

At establishment time of the laboratory, the scientific staff included elements of three Forest Service Research Work Units (RWU): Shrub Improvement and Revegetation, Ecology and Management of Salt Desert Shrub Ranges, and Mined-Land Reclamation. The first two units were administered from the Shrub Sciences Laboratory, and the third was headquartered in the Forestry Sciences Laboratory in Logan, Utah, but had detached members (Neil C. Frischknecht and Robert B. Ferguson) stationed at the Shrub Sciences Laboratory until Dr. Frishcknecht retired in 1980 and Mr. Ferguson in 1983. The Ecology and Management of Salt Desert Shrub Ranges RWU continued at the Shrub Sciences Laboratory until 1984, at which time the unit was discontinued. Members of the unit were reassigned to a new RWU—Riparian Stream Ecology and Management—and moved to the Forestry Sciences Laboratory in Boise, Idaho, except for Fred J. Wagstaff who remained at the Shrub Sciences Laboratory to manage the Desert Experimental Range (DER). Dr. Wagstaff and the DER were transferred to administration of the Shrub Improvement RWU in 1986. The Shrub Improvement and Revegetation RWU changed its research emphasis to a more holistic and ecosystem approach in 1993 and captured that move with a new name—Shrubland Biology and Restoration. This unit's core work has been at the Shrub Sciences Laboratory since establishment of the lab in 1975, but some individual scientists have been in detached locations from time to time. Most notably this included Stephen B. Monsen and Nancy L. Shaw at the Boise Forestry Sciences Laboratory. Mr. Monsen transferred to the Shrub Sciences Laboratory in 1983; Dr. Shaw transferred to the Riparian Stream Ecology and Management RWU in 1986. The Shrubland Biology RWU has managed the Great Basin Experimental Range (GBER) in Ephraim Canyon of the Manti-La Sal National Forest as long as the unit and its predecessors have been in existence. At the opening of the laboratory, A. Perry Plummer and I were transferred from the Great Basin Experimental Range to the new lab, but the RWU has kept continued personnel presence at the GBER. Cooperating scientists and other personnel from the Utah Division of Wildlife Resources (UDWR) Wildlife

Habitat Restoration RWU had been closely integrated in their work assignments with the Forest Service RWU. Both units had been under the supervision of Mr. Plummer. The administration eventually separated, but coordinated research activities have continued. The UDWR Wildlife Habitat Restoration unit maintained their administrative operation in Ephraim but have also had personnel stationed at the Shrub Sciences Laboratory. Other agencies have had a presence at the lab since the beginning. Table 1 lists personnel who have been stationed at the Shrub Sciences Laboratory and its attached Desert and Great Basin Experimental Ranges during the 1975 to 2000 timeframe. The Benmore Experimental Range was deactivated as an experimental range in the early 1970s, and in any case, had no one stationed permanently on the experimental range site.

Research Accomplishments

Research at the laboratory has covered and continues to cover a broad range of topics related to wildland shrub ecosystems, which is readily apparent in the list of publications (appendix A). However, I believe that the research activities can be divided into nine principal areas of research that are briefly highlighted in this section. The literature citations for each research area are examples only and are not complete—the complete list of activities is best understood and documented by the publications listed in appendix A and summarized in table 2. These publications are principally inhouse, in other words, authored or coauthored by Shrub Sciences Laboratory personnel, but also include extramurally supported work including the integrated work of Utah Division of Wildlife Resource collaborators and a number of theses and dissertations funded and otherwise abetted by the laboratory.

Shrubland Ecosystem Ecology and Experimental Range Management

Research at the laboratory was given initial impetus by research activities on the experimental ranges and other experimental research and planting sites that preceded the establishment of the laboratory. The Great Basin Experimental Range, perhaps better known as the Great Basin Station with its ancillary outplantings and study plots, was established in 1912, and has featured research on plant adaptation, plant succession, nutrient cycling, revegetation, restoration ecology, watershed function, and game habitat improvement over its long history, including the time it has been administered out of the Shrub Sciences Laboratory (Clary and Tiedemann 1986; Keck 1972; Klemmedson and Tiedemann 1994, 1998b; McArthur and Monsen 1996; McArthur and others 1999a; Plummer and others 1968; Tiedemann and others 1987a; Tippets and Anderson 1991; Walker and others 1996). The GBER is located on the Manti-La Sal National Forest in and around the Ephraim (Cottonwood) Canyon Drainage in Sanpete County, Utah, and includes a diversity of vegetation communities over an elevational range from 6,800 to 10,000 feet.

The Desert Experimental Range was established in Pine Valley, Millard County, Utah, in 1933, with most of the area in the salt desert shrub community type, although some areas extend to higher elevations into sagebrush and pinyon-juniper communities. Research at the DER has emphasized disturbance and successional processes in North American cold desert plant communities, winter sheep management in the cold desert, rodent ecology, pronghorn biology and management, cryptobiotic soil crust ecology, desertification, and avian and mammalian population dynamics (Alzerreca-Angelo and others 1998; Anderson and others 1982a,b; Blaisdell and Holmgren 1984; Clary and Beale 1983; Clary and Holmgren 1982; Harper and others 1996; Holmgren 1975; Kitchen and McArthur 1996; O'Neal and others 1987; Tew and others 1997; Whisenant and Wagstaff 1991).

The other experimental range administratively attached to the Shrub Sciences laboratory was the Benmore Experimental Range (BER) that was deactivated as an experimental range about the time the laboratory was opened and is administered by the Spanish Fork Ranger District of the Uinta National Forest. The BER was established in the middle 1930s in a sagebrush grass community in the southeast corner of Rush Valley, Tooele County, Utah, and emphasized crested wheatgrass (*Agropyron cristatum*) seedings and livestock husbandry and production (Astroth and Frischknecht 1984).

Aside from work performed on the experimental ranges, other community and ecosystem scale research has emphasized autecology and synecology of important species and baseline community ecology, emphasizing land areas and plant and animal species for which land managers needed information (Booth and others 1990; Davis 1990; Cibils and others 1998; Ferguson and Medin 1983; Frischknecht 1975; Goodrich 1984; Grover and DeFalco 1995; Harper and others 1990a, 1992; Hegerhorst and others 1988a; Holmgren 1984; Kitchen and others 1999a; Liedolf and others 2000; McArthur 1994; McArthur and others 1989a, 1995a; McArthur and Sanderson 1992a, 1999c; Medin 1984, 1986; Medin and others 2000; Meyer 1997b; Meyer and Kitchen 1994a; Monsen and Shaw 2000; Monsen and Stevens 1999b; Pendleton and others 1995; Webb 1999; Weber and others 1985; Welch 1999; Welch and others 1995; Wood and Brotherson 1986; Woodward and others 1984).

Another major ecological research effort headquartered at the Shrub Sciences Laboratory is the Utah Division of Wildlife Resources Range Trend Project. This effort has been managed at the Shrub Sciences Laboratory since 1992. The effort is both interagency (U.S. Department of Agriculture, Forest Service, Intermountain Region, and Utah National Forests; and the U.S. Department of the Interior, Bureau of Land Management, Utah State Office and Utah Field Offices) and intra-agency (Utah Department of Agriculture and Food) in scope. The Range Trend Program monitors over 700 permanent critical habitat big game study sites on a repeating 5-year rotation. A wide range of data is collected (nested frequency and cover of vegetation, rock, litter, cryptogamic crusts, and bare ground; nested frequency, quadrat frequency and cover of grasses and forbs; cover, density, form class and vigor of shrubs and trees; effective soil depth, average soil temperature, and chemical and textural analysis of soil) as well as close-up and general view photos. Annual reports including map direction to sites, narrative, and data are prepared

Table 1—Shrub Sciences Laboratory personnel, 1975 to 2000[1].

Personnel		
Forest Service scientists		
Philip A. Barker[2]	Warren P. Clary[3]	Robert B. Ferguson[4]
Neil C. Frischknecht[2,3]	Ralph C. Holmgren[2,3]	E. Durant McArthur[2,3]
Dean E. Medin	Susan E. Meyer	Stephen B. Monsen
David L. Nelson[2,16]	Burton K. Pendleton	Rosemary L. Pendleton
A. Perry Plummer[2,3]	Arthur R. Tiedemann[3]	Charles F. Tiernan[2]
Fred J. Wagstaff	Bruce L. Welch[2]	
Professionals		
A. Clyde Blauer[5]	Sherel Goodrich	Stanley G. Kitchen
Carlos L. Lopez	Kelly L. Memmott	T. Blaine Moore[5]
Darren Naillon	Stewart C. Sanderson	
Other agency professionals		
James N. Davis[3,6]	Mark Farmer[6,7]	Bruce C. Giunta[5,6]
Ashley Green[6]	Kent R. Jorgensen[5,6]	Scott Jensen[5,6]
Richard D. Porter[8]	Clare L. Poulsen[5,6]	Richard Stevens[3,5,6]
Jason L. Vernon[5,6]	Scott C. Walker[3,5,6]	
Clerical/facilities		
Steven F. Briggs[9]	Eulala Bulow[5]	Nancy Clark
Earl Daley	Roma Jones[1]	Pat Ford[10]
Darlene Graham	Roberta Leslie[10]	Norma Nielson[2]
Carla Oskoei	Carolyn Osmond[5,6]	Charlotte Schuler
Ralph Sokolowski[10]	Karen Vance[5]	Chris Wade[5,6]
Mical Walker[10]	Sally Wolsey	
Technicians		
Stephanie L. Carlson	Suzette Clement	Susan C. Garvin
Gary L. Jorgensen[5]	John Kinney[11]	Nancy Mulligan
Ronald L. Rodriguez	Heather Schijf	Patti Schuttler
Temporaries		
Bethany Allred	David C. Anderson[11]	Kent Applegate[6]
Ganene Auger	David G. Babbel	Ben Baldwin[6]
Linda Bascom[1]	Maren C. Bauer	Juie Beckstead
Greg Begera	Barbara Behan	Wendy Bird
Rick Black[6]	Mike Carter	Joy D. Cedarleaf
Jeanne C. Chambers[11]	Dorcas Cheschelly	Vearl Christensen
Richard Clark[6]	Linda K. Cluff	Taylor Cox
Susan B. G. Debaene-Gill	Jeff Duda[11]	John Fairchild[6]
Mark C. Grover	Derek B. Hall	Lorraine Hart[11]
Gary Holmberg[6]	Jesse Hunter	Marie Jackson
Tracy L. C. Jacobson	Bethanee Johnson	David Kelley[6]
Celeste Kennard	Sharlynn King	Kim Lamb
Julia Liao	Randell L. Leonard	Bill Masslich
Thomas A. Monaco	Joann Mudge	Kathy Musso
Steve Otero	Jeffery E. Ott	Max Pierce
C. Lorenzo Pope	Heidi Pullman	Alisa P. Ramakrishnan
Doug Ramsey	Alice Rhea	Neil Roberts
Heidi Robbins	Glade Sessions	Matt Simmons
Jeffery Skousen[6]	Benton Smith	Karl Sorensen
Lans Stavast	Daniel Summers[6]	David Tarkalson
Tyler Thompson[6]	Bob Tuttle[6]	Craig Walker
Steven D. Warren[6]	Susan M. White	Amber Whitworth[6]
Jerome Willy[11]	Dan Woodruff	Roy D. Woodward
Annie Lane J. Yazzie	Carrie York	
Visiting scientists and professionals		
Phil Allen[12]	Humberto Alzerreca-Angelo[11]	Donald Beale[6,11]
Abdul H. Belal	Toupta Boguena	Dianne Delany
Max Dunford	John M. Emlen[11]	D. Carl Freeman[13]
Chu Ge-lin	John H. Graham	Ron Hacker
Roy O. Harniss[5]	Kimball T. Harper[5,11]	Mohamed Hassan
Dionne Maywald	Kathy Miglia	Gamel S. Mikel
Walter F. Muegggler[12]	Hamid Narjisse	Mohamed A. Nasr
Brian E. Norton[11]	Jordan C. Pederson[6]	Gisbert Rinschede

(cont.)

Table 1—Cont.

Personnel		
Stephen S. Rosenstock[6]	Burns R. Sabey	Dave Stricklan[14]
Avi Schmida	Courtney Smith[11]	Han Wang
SCSEPs		
Geneva Ball	Horacio Bausset	Vergie Beaudoin
Doris Curtis	Abbie Francom	Julia Golding
Esther Humphries	Lloyd Migliaccio	Lorraine Mortensen
Brian Ruck	Charles Shaw	Dick Tennent[5]
Shari Veteto		
Volunteers[15]		
Imna Alabos[11]	Monica M. Bennion	Ann Bickel
Cathleen Chamberlin-Graham	Jerry Dunifer	Scott Emlen[11]
Ursula Emlen[11]	Juan Escos[11]	Joel L. Kitchen
Ryan S. Kitchen	Mont E. Lewis[5]	Curtis D. McArthur
Ted O. McArthur	David Miglia	Alex Parent
Lynden Porter	Bettina Schultz	Alan Smith
David Smith[5]	Chatelanine Stavast	William A. Turner
Jeffery J. Vitale	Diane Wagstaff	Darren L. Welch
Michael B. Welch		
Institutional Volunteers		
Boy Scouts of America	Earthwatch	Utah Native Plant Society

[1] The list of personnel is complete for permanent employees; some of the permanent employees started in temporary employee positions. For Temporary and Senior Community Service Employment Program (SCSEP) employees the list is not complete but lists those who worked for a year or more.

[2] Employees working at the Shrub Sciences Laboratory at the time it opened.

[3] Project Leaders.

[4] Bob Ferguson was transferred to the Shrub Sciences Laboratory within a month after it opened.

[5] Great Basin Experimental Range employees. Clyde Blauer and Blaine Moore were summer employees with permanent appointments at Snow College.

[6] Utah Division of Wildlife Resources employees.

[7] Utah Department of Agriculture and Food employee.

[8] U.S. Departement of the Interior, Fish and Wildlife Service employee.

[9] Steve Briggs was a technician before he became the facilities manager.

[10] Business Managers.

[11] Desert Experimental Range employees.

[12] Phil Allen was a UDWR technician before he became a visiting scientist from Brigham Young University.

[13] Carl Freeman was FS temporary before he became a visiting scientist from Wayne State University.

[14] Dave Stricklan was a Wildlife Biologist with the Uinta National Forest with special assigment for cooperation with Shrub Sciences Laboratory Personnel.

[15] Only those volunteers who contributed at least 250 hours of time are listed, many other volunteers have made substantive contributions.

[16] Since his retirement in 1996, David Nelson has contributed thousands of hours of work.

(Davis and others 1995a,b, 1996a,b,c,d, 1998a,b,c,d,e,f, 1999a,b, 2000a,b). The Range Trend Program data is also housed on a web page: http://www.ag.state.ut.us/divisns/mkt&cons/range.htm.

Seed Quality, Testing, and Production; Seed and Seedbed Ecology and Adaptation

A principal goal of work at the Shrub Sciences Laboratory has been to provide information about seeds of plants that are used to restore or rehabilitate degraded rangeland communities. To that end the laboratory has played and continues to play an important role in setting standards for the seeds in commerce used for wildland plantings (Allen and Meyer 1986; Currans and others 1997; Meyer 1999; Meyer and Kitchen 1995; Stevens and Meyer 1990; Young and others 1995; and many publications in the *Seed Technologists Newsletter* and *Newsletter of the Association of Official Seed Analysts* senior authored by Allen, Kitchen, or Meyer). Other substantive work has emphasized seed germination, collection, storage, processing, production, and adaptation as well as seed and seedbed ecology for a wide range of shrubland ecosystem species, for example, sagebrush (*Artemisia*), saltbush (*Atriplex*), bitterbrush (*Purshia*), rabbitbrush (*Chrysothamnus*), penstemon or beardstongue (*Penstemon*), cheatgrass (*Bromus*) (Allen and Meyer 1990, 1998; Allen and others 1987, 1995; Beckstead and others 1996; Garvin and others 1996; Jacobsen and Welch 1987; Jorgensen and Davis 1984; Kitchen and Meyer 1991; Kitchen and Monsen 1994; McArthur and others 1978c, 1987a; McArthur and Young 1999; Meyer 1989, 1992; Meyer and Allen 1999a,b; Meyer and Kitchen 1992, 1994b; Meyer and Monsen 1991, 1992; Meyer and others 1987g, 1989b, 1990, 1995b, 1997, 1998; Meyer and Paulsen 2000; Meyer and Pendleton 2000; Mikhiel and others 1992; Monsen and Meyer 1990; Monsen and others 1985b; Noller and McArthur 1986; Noller and others 1984; Plummer and Jorgensen 1978; Plummer and Monsen 1977; Stevens and

Table 2—Summary of Shrub Sciences Laboratory publications, 1975 to 2000 (see appendix A for complete list).

Year	Total	Journal	Book chapter	Book	Government serial	Proceedings	Theses or dissertations	Extramural[1]
1975	14	6	3	1	0	3	1	2
1976	9	2	0	0	1	2	4	5
1977	14	4	2	0	3	1	4	2
1978	23	6	1	0	2	12	2	6
1979	20	6	1	0	3	8	2	9
1980	14	5	1	0	4	1	3	5
1981	33	16	0	0	3	9	5	8
1982	20	14	1	0	3	0	2	3
1983	53	11	1	3	9	24	5	7
1984	42	15	0	1	6	18	2	4
1985	41	17	0	1	6	15	2	8
1986	60	22	1	3	6	22	6	10
1987	47	21	2	2	2	17	3	4
1988	23	17	1	1	0	1	3	3
1989	35	18	4	2	4	7	0	2
1990	45	13	1	2	2	25	2	4
1991	12	11	0	0	1	0	0	2
1992	28	14	2	1	4	5	2	3
1993	21	7	3	0	3	7	1	4
1994	36	11	6	1	4	11	3	8
1995	34	11	1	1	4	12	5	7
1996	44	8	2	1	8	17	8	15
1997	16	8	1	0	2	2	3	3
1998	38	27	0	0	8	0	3	11
1999	48	11	1	2	4	30	0	14
2000	23	10	1	0	5	5	2	4
Total	793	311	36	22	97	254	73	152

[1] Extramural = no Shrub Sciences Laboratory Forest Service personnel authorship. Some lab personnel, for example, Steve Monsen and Stewart Sanderson, had publications that are tied into the program prior to their assignment to the Shrub Sciences Laboratory and hence some of these publications are scored as extramural or are listed in the regular reference section rather than in appendix A.

Jorgensen 1994; Stevens and others 1986, 1996; Wagstaff and Welch 1991; Welch 1995, 1996, 1997b; Welch and others 1996).

Shrub Sciences Laboratory personnel have made substantive contributions to the new *Woody Plant Seed Manual* as principal authors of more than 20 included genera (Bonner and Nisley, in review). This work has not yet been published, but the material is being made available on a Web site as it is prepared: <http:www.wpsm.net/>.

Plant Materials Development and Plant Adaptation

Development of plant materials and their site adaptation was a principal reason for the establishment of the laboratory and has remained an important part of the research effort. Laboratory scientists were instrumental in establishing various classes of wildland plant materials, source identified, tested, selected, and cultivar for use in rehabilitation plantings (McArthur 1988; Young 1995; Young and others 1995; Welch 1994). We have formally released for commercial development and use, with cooperators—mainly the Utah Division of Wildlife Resources, Utah Crop Improvement Association, Upper Colorado Environmental Plant Center, and USDA Natural Resources Conservation Service—15 separate germplasm lines:

‘Appar’ blue flax (*Linum perenne*) (1980)
‘Rincon’ fourwing saltbush (*Atriplex canescens*) (1982)
‘Ephraim’ crested wheatgrass (*Agropyron cristatum*) (1983)
‘Paiute’ orchardgrass (*Dactylis glomarata*) (1983)
‘Immigrant’ forage kochia (*Kochia prostrata*) (1984)
‘Lassen’ antelope bitterbrush (*Purshia tridentata*) (1984)
‘Hatch’ winterfat (*Ceratoides lanata*) (1985)
‘Cedar’ Palmer penstemon (*Penstemon palmerii*) (1985)
‘Summit’ Louisiana sagewort (*Artemisia ludoviciana)* (1986)
‘Hobble Creek’ mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) (1987)
‘Gordon Creek’ Wyoming big sagebrush (*A. tridendata* ssp. *wyomingensis*) (1992)
‘Pine Valley Ridge’ black sagebrush (*A. nova*) (1994)
‘Timp’ northern sweet vetch (*Hedysarum boreale*) (1994)
‘Maybell’ antelope bitterbrush (*Prushia tridentata*) (1994)
‘Umatilla’ snow buckwheat (*Eriogonum niveum*) (1997)

Several other plant materials, under current evaluation, are candidates for release for various reclamation and restoration applications including bluebunch wheatgrass (*Pesudoroegneria spicata*) (Anatone, WA); Thurber’s needlegrass (*Stipa thurberiana*) (Boise, ID), Sandberg bluegrass (*Poa secunda*) (Mountain Home, ID), additional lines of forage kochia (*Kochia prostrata*), Lewis flax (*Linum perenne*) (Scipio, UT), plains silver sagebrush (*Artemisia cana* ssp. *cana*) (Sheridan, WY), a small burnet (*Sanguisorba* *minor*) synthetic, sagebrush hybrids (*Artemisia* species and subspecies) (for fire tolerance), and several native forbs. Some of the key references for the plant material development and release are Carlson and McArthur 1985; Carlson and others 1991; Kitchen 1995; McArthur 1988; McArthur and others 1984b; Monsen and Stevens 1985; Shaw and Monsen 1986; Stevens and Monsen 1985b, 1988a,b; Stevens and others 1985a; Welch and others 1986a, 1992a, 1994; and unpublished data on file at the Shrub Sciences Laboratory.

In the process of evaluating plant materials and determining their potential for use in rehabilitation and restoration outplanting, adaptation and evaluation tests have been conducted, for example, Belal and others 1993; Davis 1983; Dewey and Plummer 1980; Ferguson 1983; Ferguson and Frischknecht 1985; Frischknecht 1983; Frischknect and Ferguson 1984; McArthur 1981, 1983; McArthur and others 1983b, 1995b, 1996; McArthur and Welch 1982; Monsen 1983, 1987; Monsen and Anderson 1993; Monsen and Christensen 1976; Monsen and Plummer 1978; Plummer 1977; Shaw and Monsen 1983b; Tiedemann and Driver 1983; Welch and McArthur 1986a. Laboratory personnel and university colleagues have been involved with a series of studies on current and predictive adaptation as determined by physiological fitness by using measures of respiration, metabolism, and temperature (Criddle and others 1994; Frank and others 1986; Jones and others 1999; McArthur and others 1998a; Monaco and others 1996; Smith and others 1999).

Genetic Variation, Population Biology, and Systematics and Taxonomy

To better manage, protect, and use wildland shrub species (and associated nonshrub species), their taxonomic status and relationships need to be understood. Many of these species were poorly defined and their inter- and intrapopulation dynamics unknown in 1975. Much progress has been made to better understand these issues by work performed by laboratory personnel and collaborators, but much work remains to be done. Many new molecular-based techniques have become available in recent years (Judd and others 1999).

Cytological research by Shrub Sciences Laboratory personnel on big sagebrush and its relatives (= subgenus *Tridentatae* of *Artemisia*) (McArthur and others 1981; McArthur and Plummer 1978; McArthur and Sanderson 1999a); other *Artemisia* (McArthur and Pope 1979), the saltbushes (*Atriplex*) (Sanderson and Stutz 1994a; Stutz and others 1979; Stutz and Sanderson 1979, 1984, 1998), greasewood (*Sarcobatus*) (Sanderson and others 1999), and spineless hopsage (*Grayia brandegei*) (Stutz and others 1987) has documented intriguing polyploidy, some of it related to habitat conditions (McArthur and Sanderson 1999a; Sanderson and others 1989). Other substantive cytological research (first or most substantive records known for the groups) has been done for bitterbrush (*Purshia*), cliffrose (*Cowania*), Apache plume (*Fallugia*), mountain mahogany (*Cercocarpus*), and other rosaceous shrubs (McArthur and others 1983c; McArthur and Sanderson 1985).

Chemotaxonomic work based on macromolecules including phenolics, terpenoids, isoenzymes, and DNA have been used to clarify population biology, species and subspecies relationships among many plant groups (Leonard and others 1981; McArthur and others 1998c) including the big sagebrush group (subgenus *Tridentatae* of *Artemisia*) (Hanks and others 1973; McArthur and others 1981, 1988b, 1998b,c; Stanton and others 2001; Stevens and McArthur 1974; Welch and McArthur 1981), rabbitbrush (*Chrysothamnus*) (Hanks and others 1975; McArthur and others 1978a; Hegerhorst and others 1987a), saltbush (*Atriplex*) (McArthur and others 1986b; Sanderson and others 1987, 1988, 1990; Sanderson and Stutz 1984), Gambel oak (*Quercus gambelii*) (Pendleton and others 1985), and rust fungi (Volger and others 1996).

Comparative studies of populations and individuals grown in uniform gardens have yielded results that have clarified variation and relationships and facilitated breeding and hybridization studies for several plant groups including sagebrush (Behan and Welch 1986; Criddle and others 1994; McArthur and Welch 1982; Welch and McArthur 1979b, 1981, 1986a), rabbitbrush (Hegerhorst and others 1987a,c; Bhat and others 1990a,b), bitterbrush and cliffrose (Criddle and others 1994; Pendleton and McArthur 1994; Welch and others 1983a), saltbush (McArthur and others 1983b; Pendleton and others 1992a, 1994; Welch and Monsen 1981, 1984), and forage kochia (Davis and Welch 1984, 1985; McArthur and others 1996; Pendleton and others 1992b; Welch and Davis 1984).

Laboratory personnel have been active in clarifying and popularizing taxonomic placement and values of shrubs and associated species in general terms in floras (Goodrich 1984; 1986a; 1986b; Goodrich and Neese 1986; Welsh and others 1987), for specific groups of plants, for example, composite (McArthur and others 1979a), chenopod (Blauer and others 1976; McArthur and Sanderson 1984; Sanderson and Stutz 1994b), and rose family (Blauer and others 1975) shrubs, willows (Goodrich 1983), sagebrush (McArthur 1979, 1983, 1994; McArthur and Goodrich 1986; McArthur and others 1981; Welch and McArthur 1990), rabbitbrush (McArthur and others 1978a; McArthur and Meyer 1987; Weber and others 1985, 1993), fourwing saltbush (Freeman and McArthur 1989), bearclaw poppies (Meyer 1997a), *Sphaeromeria* (McArthur and others 1989a, 1998c), and several other plant groups (Goodrich 1985, 1986; Goodrich and others 1985a).

Laboratory personnel have also formally named and otherwise systematically treated several plant taxa (Atwood and others 1984; Chu and others 1991; Goodrich and others 1985b; Goodrich and Welsh 1983; McArthur and others 1981; Stutz and others 1993, 1994, 1997, 1998; Stutz and Sanderson 1998; Winward and McArthur 1995).

A series of studies were performed to determine the extent and variation of resin and rubber products in rubber rabbitbrush (*Chrysothamnus nauseosus*). Populations and individuals were found to differ as were rubber and resin concentrations, on a seasonal basis (Bhat and others 1989, 1990b; Hegerhorst and others 1987b,c; 1988a,b; Weber and others 1985, 1989, 1993).

Breeding Systems, Hybridization, and Hybrid Zones

An important factor in the study of population biology, systematics, and natural hybridization and controlled hybridization is a clear understanding of breeding and pollination systems. Work at the laboratory has been fundamental in clarifying and describing breeding systems in several ecologically important wildland shrub ecosystem species complexes including sagebrush (*Artemisia*), rabbitbrush (*Chrysothamnus*), saltbush (*Atriplex*), bitterbrush-cliffrose (*Purshia-Cowania*), blackbrush (*Coleogyne*), spiny hopsage (*Grayia spinosa*), beardstongue (*Penstemon*), and flax (*Linum*) (McArthur 1989a; Pendleton and others 1989).

The big sagebrush species complex (subgenus *Tridendatae* of *Artemisia*) is perhaps the vegetation icon of the Western United States inasmuch as members of this group are widespread, dominant, and woven into history and culture (Trimble 1989). Work performed by Shrub Sciences Laboratory personnel has demonstrated that taxa (populations, subspecies, species) of these plants outcross but are also self-fertile, that hybridization has been important in evolutionary development of the group, and that hybridization may be important in management and recovery (from fire and other degradation processes) of the group (McArthur and others 1979a, 1988b, 1998b). In a series of studies examining growth and fitness in narrow hybrid zones and hybridization dynamics, laboratory personnel and colleagues have shown the likelihood that hybridization processes are important in the diversification and success of this plant group (Byrd and others 1999; Freeman and others 1991, 1995, 1999a,b; Goodrich and others 1985b; Graham and others 1995, 1999, 2001; McArthur and Goodrich 1986; McArthur and others 1988b, 1998a; McArthur and Sanderson 1999b; Messina and others 1996; Smith and others 1999; Wang and others 1997, 1998, 1999; Weber and others 1994; Winward and McArthur 1995). This series of studies has provided strong support for a hybrid zone model, *Bounded Hybrid Superiority Hybrid Zone Model* (Arnold 1997; Moore 1977), that posits the superiority of hybrid plants over parental plants but only in the hybrid zone, in contrast to competing hybrid zone models. The model can account for the abundance and apparent stability of numerous *Tridentatae* hybrid zones.

The breeding systems of chenopod family shrubs are another area in which laboratory personnel and collaborators have made fundamental discoveries and contributions to the scientific literature. Like the sagebrushes, these plants are often landscape dominants or are prominent community members and include species with wide distributions that are often important species in land management issues. These plants are monecious or dioecious and wind pollinated (McArthur and Sanderson 1984). Laboratory personnel and collaborators have shown that many saltbush species, especially fourwing saltbush (*A. canescens*) have an adaptive breeding system that incorporates environmental factors, for example, moisture and temperature into a flexible, yet genetically controlled, sexual system that enhances reproductive fitness in a patchy environment (Freeman and McArthur 1982, 1984, 1989; Freeman and others 1984, 1993a,b; McArthur 1977; McArthur and Freeman 1982; McArthur and others 1992; Pendleton and others 1992a, 1994). Knowledge of these sexual systems has practical implications in terms of nutrition, palatability, and seed production issues for management (Cibils and others 1998; Maywald and others 1998; McArthur and others 1978c; Tiedemann and others 1987b). Spineless hopsage (*Grayia brandegei*) has been shown to have an unusual breeding system, heterodichotamy, that like the trioecious system of *Atriplex canescens* (McArthur and others 1992; Freeman and others 1993b) appears to be adaptive to a patchy, resource-poor environment and may be on an evolutionary pathway to dioecy (Pendleton and others 1988, 2000b). This system may be useful in better understanding general breeding patterns in a wider context as well (Freeman and others 1981, 1997).

Breeding systems of other plants have been studied to better understand, manage, and use important shrubland ecosystem species. These include rabbitbrush (*Chrysothamus*) (McArthur and others 1978a; Meyer 1997b), bitterbrush and cliffrose (*Purshia/Cowania*) (Davis 1983; McArthur and others 1983c; Meyer and Pendleton 2000; Pendleton and McArthur 1994), blackbrush (*Coleogyne*) (Pendleton and Pendleton 1998), blue flax (*Linum perenne* and *L. lewisii*) (Kitchen 1995; Meyer and Kitchen 1994a; Pendleton and others 1993—References Section, not appendix A), and cheatgrass (*Bromus tectorum*) (Beckstead and others 1996; Hemming and others 1999; Meyer and Allen 1999a,b; Meyer and Ramakrishnan, unpublished data, Shrub Sciences Laboratory).

Rangeland Rehabilitation and Restoration, Equipment Development, and Cultural Care of Wildland Species

Techniques, demonstrations, and review for wildland rehabilitation and restoration including equipment development and use, application of herbicides, and cultural care of species used for wildland rehabilitation and restoration has been a major, continuing effort by Shrub Sciences Laboratory personnel and collaborators, especially the Utah Division of Wildlife Resources Habitat Restoration Unit. The principal efforts have been on disturbed sites such as minelands, domestic and big game rangelands, roadside disturbances, and so forth, and are documented and detailed in Blauer and others 1993; Clary and Johnson 1983; Clary and others 1985b,c,d; Davis and Harper 1990; Ferguson and Frischkneck 1981, 1985; Frischknecht 1978b; Frischknecht and Ferguson 1979; Giunta and others 1975; Hall and others 1999; Luke and Monsen 1984; McArthur and others 1978b, 1987b, 1990a, 1995b, 2000; McArthur and Sanderson 1996; Monsen 1978, 1984, 1987, 2000; Monsen and Kitchen 1994; Monsen and Meyer 1990; Monsen and Turnipseed 1990; Monsen and others 1985b, 1992, 1996; Monsen and Richardson 1984; Monsen and Shaw 1983a,b, 1986, 1996, 1999; Monsen and Stevens, in review (see References Section, not appendix A); Plummer 1976, 1977; Roundy and others 1995; Sabey and others 1990; Shaw and Monsen 1984, 2000; Skousen and others 1986; Stevens 1978, 1994, 1999a,b; Stevens and McArthur 1990; Stevens and Walker 1998; Tiedemann and Lopez 1983; Van Epps 1978; Walker and others 1995; Welch, in review (see References section, not appendix A); Whisenant and Clary 1986, 1987; and Whisenant and McArthur 1989.

Several studies have dealt with the economics of the rehabilitation processes. These have been of a general nature (Clary 1983a; Wagstaff 1983b,c,d; 1986d; Wagstaff and Pope 1987; Wagstaff and Reesman 1989) and more specific. Specific economic analyses have been presented for individual projects (Pope and Wagstaff 1987a,b), oakbrush (Wagstaff 1985), riparian (Wagstaff 1986c), pinyon and juniper (Clary and Wagstaff 1987; Wagstaff 1987), and sagebrush community management (Wagstaff 1986a), as well as for prescribed fire application (Pope and Wagstaff 1990) and big game use on private lands (Nielsen and others 1985, 1986).

Soil/Plant Interactions, Pathology, Entomology, and Mycorrhizae

Plant interactions with fungi, insects, soil, and other factors have been a continuing area of study at the Shrub Sciences Laboratory. These interactions are often positive for plants but can be negative as well. A considerable amount of work on soil crusts and mycorrhizae has demonstrated many positive interactions with microorganisms and several shrubland ecosystem plant species; these interaction are often crucial to community health (Anderson and others 1982a; Belnap 1993, 1996; Belnap and Gardner 1993; Belnap and Harper 1995; Belnap and others 1996; Buttars and others 1998; Harper and Pendleton 1993; Pendleton 2000; Pendleton and others 1999, 2000a; Pendleton and Smith 1983; Pendleton and Warren 1996). Other studies performed on plant soil interactions include some with a community focus (Klemmedson and Tiedemann 1998a,b; Kitchen and Jorgensen 1999) and on Gambel Oak (*Quercus gambelii*) (Clary and Tiedemann 1986; Tiedemann and others 1987a) and big sagebrush (*Artemisia tridentata*) (Wang and others 1998, 1999; Welch 1997b; Welch and Jacobson 1988).

Nitrogen fixation in the semiarid systems dominated by wildland shrubs is an important ecological function provided by several species. The actinorhizal (*Frankia*) relationships with antelope bitterbrush *(Purshia tridentata*), Stansbury cliffrose (*Cowania stansburiana*), curlleaf mountain mahogany (*Cercocarpus ledifolius*), and buckbrush (*Ceanothus*) have been documented by Shrub Sciences Laboratory personnel and colleagues (Nelson 1983; Nelson and Lopez 1989; Nelson and Schuttler 1984; Wood and others 1989).

A sustained effort has been made in studying wildland shrub ecosystem disease and insect relationships. Research performed on plant diseases includes work on big sagebrush (*Artemisia tridentata*) (Hess and others 1985; Nelson 1987; Nelson and Krebill 1981; Nelson and Sturgess 1986; Sturgess and Nelson 1986; Welch and Nelson 1995), antelope bitterbrush (*Purshia tridentata*) (Nelson 1987), saltbushes (*Atriplex*) (Ramsey and others 1995), Utah juniper (*Juniperus osteospermus*) (Bunderson and others 1986a), pines (*Pinus*) (Nelson 1982; Nelson and Krebill 1982), and quaking aspen (*Populus tremuloides*) (Harniss and Nelson 1984). A new series of studies is exploring the feasibility of biological control of cheatgrass (*Bromus tectorum*) by exploiting the interactions of the headsmut, *Ustilago bullata*, with cheatgrass (Meyer and others 2000b, 2001—see Reference Section not appendix A). General relationships on wildland shrub insect interactions have been reviewed (Tiernan 1978, 1980), and a general index on wildland shrub insect relationships has been published (Haws and others 1988). Specific documentation on the insects of forage kochia (*Kochia prostrata*) (Moore and others 1982), the insect-induced galls of big sagebrush (*Artemisia tridentata*) (Graham and others 2001—see Reference section not appendix A), rubber rabbitbrush (*Chrysothamnus nauseosus*) (McArthur 1986; McArthur and others 1979b), and curlleaf mountain mahogany (*Cercocarpus ledifolius*) (Tiedemann and Furniss 1985) defoliator have been provided.

Shrub die-offs, winter injury, and other environmental problems in managing and understanding wildland shrub ecosystems have been studied by laboratory personnel and collaborators. The primary causes of these phenomena are explored and documented (Haws and others 1990, 1993; McArthur and others 1988a; Nelson and others 1989, 1990a,b; Wallace and Nelson 1990; Walser and others 1990; Weber and others 1995, 1999; Van Epps 1975).

Nutritive Quality, Palatability, and Wildlife Habitat

One of the principal values of shrubs and shrubland ecosystems is habitat, including feed value for wildlife and domestic animals. Quantifying nutritive value and palatability of shrub species and other plants has been a substantive contribution of the research conducted at the Shrub Sciences Laboratory. Some early work quantifying the differential palatability of big sagebrush (*Artemisia tridentata* populations and subspecies) (Hanks and others 1971; Scholl and others 1977) stimulated followup documentation and hypothesis testing. Some general review and synthesis of nutritive quality in wildland shrub ecosystems are Belal and others 1993; Provenza and others 1987b; Tiedemann and others 1984a; and Welch 1981, 1989, 1994. Research on the preference and nutrititive quality of big sagebrush to a number of consuming animals has been completed (Elderkin and others 1986; Hobbs and others 1986; Welch 1983a, 1999; Welch and McArthur 1979b, 1981, 1986b; Welch and others 1981, 1983b, 1987, 1991; Welch and Pederson 1981; White and others 1982a). The concern that essential oils (monoterpenoids) were a serious deterrent to digestion and compromised the nutritive quality of big sagebrush has been shown to be moot inasmuch as animals such as mule deer, pygmy rabbits, sage grouse, and other herbivores are able to ameliorate the high essential oil concentrations and thereby take advantage of the species' high nutrient content (Cedarleaf and others 1983; Clary and others 1988; Cluff and others 1982; Pederson and Welch 1982; Welch and others 1982, 1983a,c; 1989; White and others 1982b). Likewise the nutritive values of black sagebrush (*Artemisia nova*) have been documented (Behan and Welch 1985, 1986; Welch and others 1981). Other species and groups of plants that have been studied by laboratory personnel from a nutrition perspective include the saltbushes (*Atriplex canescens* and other *Atriplex* species) (Cibils and others 1998; Maywald and others 1998; Sanderson and others 1987; Welch 1978; Welch and Monsen 1981, 1984), rabbitbrush (*Chrysothamnus* species) (Hanks and others 1975; Bhat and others 1990b; Goodrich and others 1999a), and several other species (Davis and Welch 1985; Monsen and others 1990; Pendleton and others 1992c; Welch and Andrus 1977; Welch and Davis 1984; Welch and others 1983b; Welch and Wagstaff 1992).

A series of reports have dealt with quality of habitats for animals, for example, the Utah Division of Wildlife Resource *Range Trend Studies* (Davis and others, several references, 1995 to 2000), pronghorn antelope (Clary and Beale 1983), salt desert game ranges (McArthur and others 1978b), mule deer (Rosenstock and others 1989), domestic sheep and elk (Beck and others 1996a,b), cattle (Vallentine and Monsen 1990), and desert tortoise (McArthur and others 1994).

Invasive Weeds and Weed Biology

Invasive weeds are a serious problem on Western wildlands. These pests may well be the most serious problem facing land managers on Western public lands (Cronk and Fuller 1995; D'Antonio and Vitousek 1992). Shrub Sciences Laboratory personnel have contributed to the understanding of this problem and are seeking solutions and facilitating scientific exchange (Buchanan and others 1978; Harper and others 1996; Kitchen and Jorgensen 1999; McArthur and others 1990b; Monsen and Kitchen 1994; Monsen 1994b; Monsen and Shaw 1997). Research has been conducted on cheatgrass (*Bromus tectorum*), bur buttercup (*Ranuculus testiculatus*), halogeton (*Halogeton glomeratus*), rush skeleton weed (*Lygodesmis juncea*), squarrose knapweed (*Centaurea virgata*), and salt cedar (*Tamarix ramosissima*). The work on cheatgrass has employed competition (Giunta and others 1975; McArthur and others 1990a; Monsen and Turnipseed 1990) as well as biocontrol (Meyer and others 2000b, 2001, see Reference section and appendix A), herbicidal control (Shaw and Monsen 2000), and wide array of germination studies (Allen and others 1995; Bauer and others 1998; Beckstead and others 1995, 1996; Meyer and Allen 1999a,b; Meyer and others 1997) of cheatgrass. Other more general work on a variety of weed problems has emphasized control through competition (Davis and Harper 1990; Stevens and McArthur 1990) and herbicides (Stevens and Walker 1998).

Technology Transfer Activities

The Shrub Sciences Laboratory has been a leader in promoting scientific exchange by sponsoring and cosponsoring symposia, workshops, seminars, tours, discussions, and lectures, and by hosting short- and long-term visits of extramural personnel (table 2) as well as sending its personnel to participate in local, national, and international science meetings and to visit other research and management sites. Several outcomes of these activities are documented by publications of these proceedings:

Johnson 1983
Tiedemann and Johnson 1983
Monsen and Shaw 1983b
Wagstaff 1983e
Johnson 1984
Tiedemann and others 1984b
Carlson and McArthur 1985
Johnson 1985
McArthur and Welch 1986b
Johnson 1987
Provenza and others 1987b
Wallace and others 1989
Johnson 1990
McArthur and others 1990b
Clary and others 1992
Monsen and Kitchen 1994
Roundy and others 1995
Barrow and others 1996
McArthur and others 1999b
Monsen and Stevens 1999b

A perusal of the publications in appendix A demonstrates that Shrub Sciences personnel have participated in many widespread venues. The laboratory serves as the headquarters of two research consortia (Shrub Research Consortium and Intermountain Consortium for Arid Land Research) that foster coordinated research (Tiedemann 1984; McArthur 1991). Personnel have a continuing history of activity in professional societies, especially in the Society for Range Management and the Utah Native Plant Society, and in various other formal and informal outreach activities.

The Future

Currently, the Shrub Sciences Laboratory houses the Rocky Mountain Research Station Shrubland Biology and Restoration Research Work Unit. The unit's mission is to "develop knowledge, plant materials, and technology for successful long-term restoration of diverse shrubland plant communities to meet resource needs and values." Three research problems are identified and approved to accomplish this mission:

1. Develop basic knowledge about the genetic makeup, population dynamics, and biology of selected shrubland species deemed important for ecologically sound restoration efforts.
2. Develop and establish appropriate seed sources and effective techniques for establishing high diversity shrubland communities from seed.
3. Develop a better understanding of community-level consequences of past and present management practices and provide recommendations consistent with ecosystem management policies.

The unit accomplishes these goals, in part, with tight working relationships with Brigham Young University, where its scientists have adjunct faculty status, and with other universities and agencies. Especially close working relationships are in place with units of the National Forest System, the Bureau of Land Management, and the Utah Division of Wildlife Resources. Two units of the UDWR are close cooperators: the Range Trend Analysis Unit is collocated at the Shrub Sciences Laboratory, and UDWR Wildlife Habitat Improvement Unit in Ephraim, Utah, is collocated with the RMRS Great Basin Experimental Range.

As research work at the Shrub Sciences Laboratory moves into its second quarter century, the team of researchers anticipates that the research activities will build on the foundation of established research by continuing emphasis in plant materials research, restoring and rehabilitating damaged ecosystems, and documenting, capitalizing, and manipulating genetic variation. The team will be proactive in seeking new research opportunities and partnerships within the scope of its research mission and especially, in the near term, will give added emphasis to work in fire susceptible ecosystems, on invasive weed control and biology, and on the ecology and restoration of ecosystems on the urban interface.

Acknowledgments

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See appendix A for Shrub Sciences Laboratory references, 1975–2000.

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Appendix A: Publications of the Shrub Sciences Laboratory, 1975 to 2000

Publications included here are those of Shrub Sciences Laboratory personnel, work funded or otherwise substantially furthered by Shrub Sciences Laboratory resources, including work performed at the attached experimental ranges (Benmore, Desert, and Great Basin) and personnel working at those units.

1975

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1976

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1978

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Appendix B: Reports

These are unpublished reports on file at the Shrub Sciences Laboratory documenting extramural research agreements. These documents are not included in the table 2 totals.

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Monsen, S. B.; Kitchen, S. G. 1993. Annual report 1993: summary report of progress related to Interagency Agreement Number ID910 between USDI, Bureau of Land Management and USDA, Forest Service, Intermountain Research Station: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Shrub Sciences Laboratory, Provo, UT. Submitted to U.S. Department of the Interior, Bureau of Land Management, Idaho State Office, Boise, ID. 41 p.

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Pendleton, R. L.; Pendleton, B. K. 1995. Final report: MIPR W2V5AA51113582 microphytic crust biology. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Shrub Sciences Laboratory. Submitted to Construction Engineering Laboratory, U.S. Army Corp of Engineers, Champaign-Urbana, IL. 32 p.

Pendleton, R. L.; Pendleton, B. K. 1996. Final report: MIPR W52EU260390969 benefit of microphytic crust inoculation and arbuscular mycorrhizal fungi on productivity of VAM-dependent forbs. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Shrub Sciences Laboratory. Submitted to Construction Engineering Laboratory, U.S. Army Corp of Engineers, Champaign-Urbana, IL. 67 p.

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A Century of Genetics

Daniel J. Fairbanks

Abstract—In 1866, Gregor Mendel published his experiments on heredity in the garden pea (*Pisum sativum*). The fundamental principles of inheritance derived from his work apply to nearly all eukaryotic species and are now known as Mendelian principles. Since 1900, Mendel has been recognized as the founder of genetics. In 1900, three botanists, Carl Correns, Hugo De Vries, and Erich Tschermack von Seysenegg, had independently completed experiments that were similar to Mendel's, although much less extensive. When searching the literature, all three encountered Mendel's paper and realized that he had described the principles of inheritance and the experimental data to confirm them 34 years earlier. With their rediscovery, the science of genetics was born in 1900 along with the 20th century. William Bateson coined the term "genetics" and was the person most responsible for establishing the new science in the first decade of the 20th century. Thomas Hunt Morgan and his students established the chromosomal basis of heredity beginning in 1910. During the 1920s and 1930s, classical genetics was established, and eugenics became very popular among the more educated and wealthy members of society. Laws mandating sterilization of perceived unfit people were passed and carried out. By the late 1930s, Nicolai Vavilov had published his theory of centers of origin for cultivated plants and established a gene bank for his collections in Leningrad. During the siege of Leningrad in 1941–1942, nine of his coworkers chose to die of starvation rather than sacrifice the seeds and tubers that Vavilov had collected. In the meantime, Vavilov was imprisoned for his opposition to Lysenkoism. He soon died in prison of maltreatment. In the mid-1940s, George Beadle and Edward Tatum discovered the relationship between genes and enzymes, and Oswald Avery and his coworkers discovered that DNA is the genetic material of a bacterial species. In the early 1950s, Alfred Hershey and Martha Chase discovered that DNA is the genetic material of a bacteriophage. Shortly after this time, in 1953, James Watson and Francis Crick determined the structure of DNA based on evidence collected in several laboratories. Cracking the genetic code became one of the next priorities, a task that was completed in the 1960s. During the 1970s, recombinant DNA was made, an event that led to molecular applications in genetics and genetic engineering. The first genetically engineered pharmaceuticals soon followed. The 1970s and 1980s saw the development of efficient methods for DNA sequencing, which ultimately led to whole genome sequencing. The first bacterial genome was sequenced in 1995, the Brewer's yeast genome in 1996, and the *Drosophila*, *Arabidopsis*, and human genomes in 2000. Fittingly, the sequencing of the human genome, one of the greatest accomplishments in genetics, came at the 100th birthday of the science of genetics.

In the year 2000, the science of genetics celebrated its 100th anniversary. In the spring and early summer of 1900, three botanists, Hugo de Vries, Carl Correns, and Erich von Tschermack, reported their simultaneous and independent rediscovery of Mendel's principle of segregation, an event that sparked the rapid establishment of genetics as a new and important science. This paper highlights just a few of the major events that have made genetics one of the most powerful and rapidly progressing sciences.

Although genetics entered mainstream science rather suddenly in 1900, it traces its origin to the mid-1800s with the experiments of Gregor Mendel. In 1843, Mendel entered the St. Thomas monastery in the city of Brno, now in the Czech Republic, and was soon appointed as a seventh-grade science teacher. He failed his teacher certification examination, an event that prompted the abbot of the monastery to send him to the University of Vienna. While at the University, Mendel was enamored with the teachings of his botany professor, Dr. Franz Unger, who, even though Darwin's *Origin of Species* had not yet been published, focused his teachings on the evolution of species over long periods of geological time. During the time that Mendel was a student, Unger wrote an article in which he wrote this remarkable passage that foreshadowed Mendel's work: "Who can deny that new combinations arise out of this permutation of vegetation, always reducible to certain law-combinations, which emancipate themselves from the preceding characteristics of the species and appear as a new species" (Orel 1996).

Unger's teachings infuriated the local clergy who attempted to have him dismissed. Among the most vocal was Dr. Sebastian Brunner who wrote of Unger as "a man who openly denied the Creation and the Creator" and as one of the "professors at so-called Catholic Universities [who] deliver lectures on really beastly theories for years on end" (Olby 1985). Ironically Mendel was a devout member of the clergy, but he appears to have sided with Unger. Mendel wrote of his own work as "the only right way by which we can finally reach the solution of a question the importance of which cannot be overestimated in connection with the history of the evolution of organic forms" (Stern and Sherwood 1966).

In 1852, Mendel began experiments with pea hybrids that would last for 8 years. From the scientific literature that he had read extensively he already knew of the concept of dominance in peas for four of the seven traits he studied. His contribution was his development of a mathematical model to explain heredity. He discovered regular 3:1 ratios in the F_2 generations in all seven of his monohybrid experiments, and developed the now familiar mathematical model to explain the 3:1 ratio, which he expressed in the following equation:

$$\frac{A}{A}+\frac{A}{a}+\frac{a}{A}+\frac{a}{a}$$

where the letters in the numerator represent the alleles contributed by the male parent and those in the denominator

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In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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as the alleles contributed by the female parent. Because the large *A* is dominant, three of the four combinations produce the dominant phenotype and one the recessive. He tested this model by allowing the F_2 plants to self fertilize to produce F_3 offspring. He found that ⅓ of the F_2 plants with the dominant phenotype produced offspring with only the dominant phenotype, and that ⅔ produced offspring with both dominant and recessive phenotypes, precisely as his model predicted.

He then turned his attention to dihybrid and trihybrid experiments to ascertain whether the inheritance of one trait influences the inheritance of another. He discovered that all seven traits in various combinations of twos and threes were inherited independently of one another. On these two discoveries, the mathematical segregation of differing elements and the independent inheritance of traits, are based the two laws of inheritance attributed to Mendel: the law of segregation and the law of independent assortment.

Mendel presented his paper in 1865 and had it published the following year (Mendel 1866). For the next 34 years, no one, including Mendel, recognized that the laws he discovered applied almost universally to plants, animals, and humans. His paper was not completely forgotten; it was cited at least 15 times before 1900. However, it is clear from these citations that no one recognized its most important points. Mendel sent reprints with cover letters to several botanists, including Franz Unger, his former professor, but the only one to respond was Karl von Nägeli, who carried on correspondence with Mendel over a period of 7 years. Mendel had initiated studies with the hawkweed, and Nägeli encouraged Mendel to continue with these species. Neither Mendel nor Nägeli knew that hawkweed was an apomict, and thus it did not display the patterns of inheritance that Mendel had observed in peas, and by now in several other species.

Mendel died in 1884, unaware that he would become known as the founder of genetics. Sixteen years later, in 1900, DeVries working with several plant species, Correns with peas and maize, and Tschermak with peas, rediscovered Mendel's principle of segregation and the science of genetics was born. Two of the three rediscoverers, Correns and Tschermak, became strong advocates of Mendelism. De Vries, on the other hand, dismissed Mendelian inheritance within less than a year of his paper on it. The person most responsible for the establishment of Mendelism was the British naturalist William Bateson. Bateson read Mendel's paper while on a train in 1901 and soon thereafter embraced Mendelism with the passion of religious zealot. Bateson was so passionately supportive of Mendelism that De Vries warned him in a 1902 letter, "I prayed you last time, please don't stop at Mendel. I am now writing the second part of my book which treats crossing, and it becomes more and more clear to me that Mendelism is an exception to the general rule of crossing. In no way is it *the* rule!" (Olby 1985). The opposition to Mendelism only encouraged Bateson, who, together with Reginald Punnett and Edith Saunders, found Mendelian inheritance in many different species. It is to Bateson that we owe much of our current genetic terminology (including the word "genetics") and the establishment of Mendelian genetics as a credible science in the first decade of the 20th century.

Thomas Hunt Morgan was an American zoologist at Columbia University who at first rejected both the Mendelian theory of inheritance espoused by Bateson and the chromosomal theory of inheritance promoted by Edmund Wilson, also at Columbia. He opted instead for de Vries' mutation theory (which differs substantially from our current understanding of mutation). Complaining of the intellectual climate at Columbia, Morgan wrote in 1905 that it was "an atmosphere saturated with chromosomic acid" (Allen 1978). He completely reversed his views, however, within 5 years as he brought Mendelian and chromosomal theories of inheritance together as a single theory. In 1910 he observed a white-eyed fruit fly that was to change the direction of his career and the science of genetics. He discovered that the white-eye phenotype was associated with inheritance of the X chromosome.

At first, he was reluctant to conclude that the genes were actually a part of the chromosome. However, two discoveries by his students, Alfred Sturtevant and Calvin Bridges, made it clear that their so-called sex-linked genes must be a physical part of the X chromosome. Sturtevant, as an undergraduate student in 1911, had a flash of genius when he realized that genes might be located in a linear fashion on the chromosome. He gathered up the notebooks with the data from several of their experiments, and, in his words, "I went home and spent most of the night (to the neglect of my undergraduate homework) in producing the first chromosome map" (Sturtevant 1965). He placed five genes on a linear map and calculated the distances between them based on the frequencies of crossing over. Bridges discovered in 1913 that unusual cases of inheritance of mutant sex-linked alleles were associated with nondisjunction of chromosomes. The collective data strongly indicated that genes were organized in a linear fashion as part of the chromosome. Morgan and three of his students, Sturtevant, Muller, and Bridges, published in 1915 a landmark book entitled the *Mechanism of Mendelian Heredity* (Morgan and others 1915) in which they summarized all of their evidence that Mendelian and chromosomal theories of inheritance were one and the same. Bateson rejected the idea, but respected their work so much that he aptly wrote "not even the most skeptical of readers can go through the *Drosophila* work unmoved by a sense of admiration for the zeal and penetration with which it has been conducted, and for the great extension of genetic knowledge to which it has led—greater far than has been made in any one line of work since Mendel's own experiments" (Sturtevant 1965).

The students who coauthored this work with Morgan, Sturtevant, Bridges, and Muller, were to become three of the most influential geneticists in later years. Another laboratory was also soon to produce a similar group of prominent geneticists. At Cornell University, Rollins Emerson had taken on George Beadle, Marcus Rhoads, Charles Burnham, and Barbara McClintock as students to work with him on maize. McClintock had hoped to study plant breeding, but the Department of Plant Breeding at Cornell did not admit women at the time, so Emerson invited her to work with him in maize genetics. McClintock's enthusiasm for her knowledge is well illustrated in the following story, given in her words:

> I couldn't wait to take [the final exam for geology]. I loved the subject so much that I knew they wouldn't ask me anything I couldn't answer. I just knew the course. So I couldn't wait to get into the final exam. They gave out these blue books, to write in and on the front page you put down your

> own name. Well, I couldn't be bothered with putting my name down; I wanted to see those questions. I started writing right away—I was delighted, I just enjoyed it immensely. Everything was fine, but when I got to write my name down, I couldn't remember it. I couldn't remember to save me, and I waited there. I was much too embarrassed to ask anybody what my name was, because I knew they would think I was a screwball. I got more and more nervous, until finally (it took about twenty minutes) my name came to me.
>
> —Keller (1983)

Although McClintock is best known for her later discovery of transposable elements in maize, among her most significant publications was her demonstration that chromosomes were the physical carriers of genes. The work of Morgan and his students had shown the association of genes and chromosomes, which led them to conclude that genes were on chromosomes. However, McClintock and her coworker Harriet Creighton had observed cytological evidence of crossing over that was clearly associated with the recombination of linked genes in maize. Morgan gave a lecture at Cornell in 1931, and then took a tour of the labs. Creighton and McClintock showed Morgan their data, which they felt were rather meager. They had intended to grow their maize plants another year to collect more data before publishing the results. Morgan knew of similar work in Drosophila being conducted by Curt Stern, but did not tell them of it. He insisted that Creighton and McClintock publish their results immediately. He asked for a pen and paper and in their presence wrote a letter to the editor of the *Proceedings of the National Academy of Sciences* telling him that he would receive within 2 weeks a significant article from Creighton and McClintock that should be immediately published. The article beat Stern's by several months. Explaining his actions, Morgan simply said, "I thought it was about time that corn got a chance to beat *Drosophila*" (Keller 1983).

Like most other sciences, genetics was not immune to political influences. The eugenic movement gained momentum in the period from turn of the century to the 1930s. Based on incorrect assumptions about the inheritance of such traits as feeblemindedness, imbecility, and criminality, antimiscegenation and mandatory sterilization laws were passed in many states and in several European countries. Before such laws were rescinded, over 60,000 people suffered involuntary sterilization in the United States. Although many geneticists favored eugenics to some degree, some of them pointed out the theoretical flaws implicit in these laws. Morgan in particular renounced his membership in a society that promoted eugenics, and later in his Nobel acceptance speech, given in 1935, he stated, "The claims of a few enthusiasts that the human race can be entirely purified or renovated at this later date, by proper breeding, have I think been greatly exaggerated. Rather must we look to medical research to discover remedial measures to insure better health and more happiness for mankind" (Morgan 1935). Eugenics reached its most tragic point with the genocide of millions by the Nazi regime before and during World War II. Unfortunately, eugenic measures are still with us. Reports of genocide and ethnic cleansing are still an atrocious part of our modern world.

Some of the most tragic effects of politics and war on genetics were in Russia in the 1930s and 1940s. Nicolai Vavilov was a brilliant Russian plant geneticist who recognized the need to preserve genetic diversity in plants. His worldwide studies identified the centers of origin and diversity for the major food crops of the world. Vavilov and his associates collected seeds and tubers of those crops and created one of the world's first gene banks in Leningrad. In the winter of 1941–1942, Hitler's army laid siege to Leningrad and food soon ran out. Tens of thousands of the city's residents died of starvation. The scientists in the institute Vavilov had directed were surrounded by stores of rice, wheat, corn, peanuts, potatoes, and peas that contained the genetic diversity collected by Vavilov and his associates. Recognizing the need to preserve that diversity, they made a pact among themselves that none of them would eat the seeds and tubers. Nine of the scientists died of starvation while at their posts in the Institute rather than sacrifice the genetic diversity that was stored there.

A few years earlier, Vavilov was the most prominent geneticist in Russia. However, in the 1930s, Trofim Lysenko began to promote his Lamarckian ideas that the environment could direct specific changes in hereditary elements, and referred in distaste to Vavilov and his colleagues as "the dogmatic followers of Mendel and Morgan" (Medvedev 1969). Vavilov publicly resisted Lysenko, but in the end, Stalin declared Lysenko's views as state policy. In 1939, at one of his last attempts to challenge Lysenko, Vavilov stated his resolve, "We shall go to the pyre, we shall burn, but we shall not retreat from our convictions" (Medvedev 1969). Shortly thereafter, in 1940, Vavilov and several other Soviet geneticists were arrested and imprisoned for their refusal to follow Lysenko. As Hitler's army advanced during 1941, Vavilov as a prisoner was evacuated from St. Petersburg to Saratov prison and placed in a windowless underground cell called a death cell. There he died in January 1943, a year after the deaths of his colleagues in the institute. Numerous Soviet geneticists were imprisoned and killed because of their refusal to accept Lysenkoism. Lysenko reigned over Soviet genetics for nearly 3 decades until 1964 when Khrushchev, who had firmly supported Lysenko, was forced to resign.

We now return to the United States. In the early 1940s, George Beadle, one of Emerson's former students, and Edward Tatum discovered that genes were related to enzymes. In a sense, they had simply clarified the same concept that Archibald Garrod and William Bateson had proposed in 1902, but with much more evidence and in much more detail. The association between genes and proteins was evident, but their real relationship was yet to be revealed.

Although DNA was discovered by Friedrich Miescher shortly after Mendel did his work, the connection between DNA and heredity began to surface about the same time that Beadle and Tatum demonstrated the association of genes and proteins. In 1944, Oswald Avery, Colin McLeod, and Maclyn McCarty found that the hereditary substance of the bacterium *Streptococcus pneumoniae* was DNA. In 1952, Alfred Hershey and Martha Chase demonstrated that the hereditary material of the bacteriophage T2 was also DNA. However, even in light of these results, most scientists still refused to accept DNA as the hereditary substance. According to James Watson, "Al Hershey had sent me a long letter...summarizing the recently completed experiments by which he and Martha Chase established that a key feature of the infection of a bacterium by a phage was injection of DNA....Their experiment was...a powerful new proof that DNA is the primary genetic material....Nonetheless, almost no one in the audience of over four hundred microbiologists seemed interested as I read long sections of Hershey's letter" (Watson 1969).

The disinterest didn't last long. In 1953, Watson and Francis Crick, using data gathered entirely from the experiments of others, deduced the structure of DNA. One of the chief requirements of the hereditary material was the ability to self-replicate. At the conclusion of their classic paper, they penned this now-classic line, "It has not escaped our notice that the specific pairing we have postulated immediately suggests a possible copying mechanism for the genetic material" (Watson and Crick 1953).

About this same time, it was clear that DNA somehow encoded the composition of proteins, and that RNA was an intermediate between DNA and protein. The relationship between nucleotide sequence and amino acid sequence was yet to be established. Through brilliant mathematical analysis by Syndey Brenner, and through analysis of the effect of mutations on amino acid sequence, geneticists realized that the genetic code must be nonoverlapping and that three nucleotides must encode each amino acid. These realizations led Marshall Nirenberg, Heinrich Matthaei, Severo Ochoa, Philip Leder, Francis Crick, and others to decipher the genetic code. By 1965, they had identified the amino acids for 50 of the 64 codons. Then in 1966, the final gaps were bridged, and the genetic code was revealed.

The genetic code turned out to be nearly universal, an observation that had profound implications. Because of a universal code, a gene transferred from one species to another should encode the same protein in the recipient species as in the original species. This opened up great possibilities of genetic engineering, especially with bacteria. In the late 1970s, Goeddel and others (1979) successfully introduced a cDNA from the human growth hormone gene into *Escherichia coli*, and with a little genetic engineering of the promoter and initiation codon regions, achieved expression of pure human growth hormone in bacteria. This initiated the age of genetic pharmacology, which now produces such important human proteins as insulin, interferon, and clotting factors in bacteria for medicinal use. So valuable is this industry that the University of California and Eli Lilly & Co. spent over 30 million dollars in legal fees fighting each other over the patent for genetically engineered insulin. Lilly won the dispute.

For the most part, the molecular revolution and traditional genetics and breeding remained almost separate fields. Then in the 1980s came the convergence of the two with the use of DNA markers to address questions of inheritance and to improve the efficiency of both medical and agricultural genetics. The 1980s marked the beginning of genomics. Genetic maps, which before had taken years to develop, now could be completed sometimes in a period of weeks. DNA markers overcame the obstacles that had prevented efficient genetic analysis in humans, and the first saturated human genetic map was completed in 1994.

The ultimate genetic map, however, was the entire nucleotide sequence of a genome. Frederick Sanger, who developed the basic process that is now used in automated sequencers, reported with colleagues in 1977 the first entire nucleotide sequence of a genome, that of the phage phi X-174 which consists of 5,386 nucleotide pairs (Sanger and others 1977). It was a huge step from those days to the sequence of the genome from a cellular organism. Long before the first bacterial genome was sequenced, the human genome project, one of the most ambitious undertakings in the history of science, was begun. To sequence the 3 billion nucleotides of the human genome, scientists required substantial improvements in laboratory automation and vast cooperation among many different laboratories. The projected cost of the project was enormous and it drew significant criticism because many perceived it as drawing research funding away from other projects. However, the benefits that came from it, automated DNA sequencing in particular, have benefited genetic research in many areas, including much of the research presented in these proceedings.

In 1995, Craig Venter and his colleagues at the Institute for Genomic Research published the first genomic sequence of a cellular organism, that of the bacterium *Haemophilus influenzae* with 1,830,137 nucleotide pairs in its genome (Fleischmann and others 1995). Goffeau and others (1996) published the first sequence of a eukaryotic genome, that of *Saccharomyces cerevisiae*, Brewers yeast, whose genome contains about 13 million nucleotide pairs and 6,000 genes. The sequences of numerous bacterial species and that of the nematode worm *Caenorhabditis elegans* were also completed. In March 2000, the genomic sequence of *Drosophila melanogaster* was published, with 120 million nucleotide pairs in the euchromatic regions and about 13,600 genes (Adams and others 2000). *Arabidopsis thaliana* was the first plant species to be sequenced (The *Arabidopsis* Genome Initiative 2000). Fittingly, at the conclusion of one century of genetics, the first draft of the human genome was announced, 5 years ahead of schedule.

We have come a long way from Mendel's garden to the sequence of the human genome. I'll resist the temptation to speculate about what the future holds. One of the delights of studying the history of genetics is to see how wrong many authors were when they wrote decades ago about genetics in our day. This much I feel confident in predicting, however, that the future of genetics is very bright.

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Development and Use of Plant Resources for Western Wildlands

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Abstract—Concern for declines in big game habitat throughout the West and the pioneering work of revegetation researchers in the mid twentieth century led to increased use of native shrubs, grasses, and forbs for revegetation, and the 1975 establishment of the U.S. Department of Agriculture, Forest Service, Shrub Sciences Laboratory in Provo, Utah. During this period revegetation objectives shifted from an emphasis on production of commodities to conservation of biodiversity and ecosystem functions. Plant resource development altered from an agronomic approach focusing on plant improvement to one that incorporates ecological, genetic, and practical considerations. Although many problems remain, research, technological advances, efforts to stabilize the native seed industry, and improved seed testing and certification procedures are increasing our options for revegetating disturbed lands.

At the 1975 dedication of the Shrub Sciences Laboratory, the senior author and Donald R. Christensen, then of the Utah Division of Wildlife Resources, presented a paper "Woody Plants for Rehabilitating Rangelands in the Intermountain Region" (Monsen and Christensen 1976). This paper summarized contemporary and anticipated research needs for the selection and use of native shrubs on disturbed wildlands, particularly big game ranges. Efforts to improve habitat for expanding mule deer populations in the Western States began in the 1940s (McArthur 1992; Plummer and others 1968). Degradation resulting from abusive livestock grazing, agricultural development, and urbanization contributed to loss of shrublands that provided important winter and spring/fall ranges for big game (Plummer 1972; USDA Forest Service 1936). The objective of maintaining healthy deer herds led to plant materials research that emphasized the use of shrubs to provide browse and cover. This effort was led by Federal and university researchers and western Game and Fish Departments working in cooperation with land management agencies (Plummer and others 1957; Roundy 1966).

Concern over deteriorating big game ranges in Utah led to the 1954 initiation of a cooperative program between the Utah Department of Fish and Game and the U.S. Department of Agriculture, Forest Service, Intermountain Research Station (now the Rocky Mountain Research Station) that has endured to the present (Blaisdell 1972; McArthur 1992; Roundy and others 1997). Research resulting from this and similar efforts across the West enabled managers to begin seeding and planting a variety of shrubs as well as native and exotic herbaceous understory species to stabilize disturbances, restore wildlife habitat, and protect watersheds and other rangeland resources (Holmgren and Basile 1959; Hubbard 1962; Hubbard and others 1959; Plummer 1977; Plummer and others 1955, 1968). This research highlighted the importance of recognizing ecotypic variation in native species and matching plant materials to planting site conditions and management objectives. Much of the early work in Utah was summarized in the 1968 publication "Restoring Big Game Ranges in Utah" (Plummer and others 1968). Progress in Utah led to a greater recognition of shrubland resources and values (McKell and others 1972) and the 1975 establishment of the U.S. Department of Agriculture, Forest Service, Shrub Sciences Laboratory in Provo (Blaisdell 1972; McArthur 1992; Stutz 1975).

Plant Material Development and Use, 1912 to 1975

Shrub revegetation research developed from ongoing efforts to stabilize and restore Western wildlands. Livestock grazing excesses in the late nineteenth and early twentieth century negatively impacted vegetation and watershed stability (USDA Forest Service 1936). Massive erosion and major flood events led to the instigation of research and management programs to understand the causes of watershed deterioration and implement grazing management and rehabilitation programs to combat the problem (Forsling and Dayton 1931; Meeuwig 1960). Initial work begun in 1912 centered on disturbances at upper elevations (Monsen and McArthur 1995). In the 1920s a research program was implemented across the Intermountain Region to evaluate the adaptability and performance of a number of grass, forb, and shrub species and accessions (Forsling and Dayton 1931; Monsen and McArthur 1995; Plummer and Stewart 1944). Although native species were included in research studies and field trials from the beginning, exotic grasses were generally more effective in meeting the criteria of ease of planting, reliable establishment, rapid production of ground cover, good palatability and productivity, grazing tolerance, competitiveness with weeds, good seed quality, and low seed cost (Monsen and McArthur 1995). A number of introduced grasses including smooth brome (*Bromus inermis* Ley.), intermediate wheatgrass (*Elytrigia intermedia* [Host] Nevski), and orchardgrass (*Dactylis glomerata* L.) were widely used at mid and upper elevations. Revegetation of degraded sagebrush rangelands in low precipitation areas centered on the use of introduced wheatgrasses (*Agropyron*

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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Gaert. spp.). These were seeded on extensive tracts in the Great Basin and northern shrub steppe during the mid 1900s to improve forage availability for livestock and to control the spread of halogeton (*Halogeton glomeratus* [Bieb.] C.A. Mey.) (Johnson 1986; Mathews 1986; Young and Evans 1986).

Thus, for watershed and livestock plantings, a number of exotic grasses gained widespread use, while initial poor showings limited further research with natives (Roundy and Call 1988). In spite of their apparent effectiveness, problems posed by exotic grasses eventually became widely recognized. These included the disruption of soil structure and loss of remnant native species during site preparation for seeding, lack of diversity and vegetative structure in mature stands, and susceptibility to insects, disease, and drought (Box 1986; Pyke 1996). Importantly, exotic grasses often precluded recovery of natives, and in some cases they were subject to invasion by weedy species (Elliot and White 1987; Powell and others 1994; Walker and others 1995). These limitations, advances in shrub research, and a growing public concern for conserving ecological values of rangelands gradually led to increased emphasis on the inclusion of natives and a greater diversity of species in revegetation prescriptions. In addition to improvement of big game range, shrubs and other native species were being recognized as valuable for low maintenance landscaping, recreation areas, roadside disturbances, mined lands, and other severely disturbed sites (Blaisdell 1972; Plummer 1972).

For selection of revegetation plant materials, particularly woody species, researchers emphasized a combination of approaches used in forest tree seed improvement and techniques utilized in developing agronomic plant varieties (Plummer 1972). By this time, the wide genetic variability in terms of ecotypes, biotypes, and chromosome races present in many intermountain species as a result of past climatic change and plant migrations was widely recognized (for example, see Beetle 1960; Stebbins 1950; Stutz and Thomas 1964). Important natural shrub stands were identified for seed collection, and in some cases, seed orchards from selected populations of important species were established (Plummer 1972). Plummer advocated development of geographic ecotypes, selections adapted to specific areas and exhibiting desirable characteristics. These selections might represent particular ecotypes or specific plants from an ecotype, referred to as biotypes or races, that exhibited desirable characteristics (Plummer 1972). These characteristics were generally related to plant establishment or browse production and included germinability, seedling vigor, growth rate, palatability, winter leafiness, and tolerance of browsing (Monsen 1975; Plummer and others 1968).

Many accessions selected for study represented extensive shrub populations that were regularly harvested by commercial collectors and planted throughout the Intermountain area. Seeds from these stands and collections from additional populations of interest were widely field tested for adaptability and performance within and beyond the current range of the individual populations and species (for example, see Davis 1983; Edgerton and others 1983; Shaw and Monsen 1983 for antelope bitterbrush [*Purshia tridentata* {Pursh} DC.] and related species). This research ultimately resulted in the use of a large number of primarily native shrub species and accessions as well as a variety of native and exotic grasses and forbs. At the first major wildland shrub symposium in the Intermountain area, held in Logan, Utah, in 1971, Blaisdell (1972) reported that extensive screening and testing of shrubs by the Intermountain Research Station, the Utah Division of Wildlife Resources, and the Idaho Department of Fish and Game had resulted in the listing of approximately 75 woody species as promising for restoration of big game habitats (Plummer and others 1968). Of this group, about a dozen were most widely planted in large restoration projects. Four shrubs were considered the primary species to be investigated and promoted. These were basin big sagebrush (*Artemisia tridentata* [Nutt.] ssp. *tridentata*), fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.), antelope bitterbrush, and rubber rabbitbrush (*Chrysothamnus nauseosus* [Pallas] Britt).

Revegetation research fueled further studies of shrubland ecology and management (for example, see Giunta and others 1978; Nord 1965; Stevens and others 1977) and contributed to the expansion of the native seed industry. Observed variability in intermountain species led to studies of the genetic and physiological basis for these differences and contributed to our understanding of the evolution of the intermountain flora (Blauer and others 1975, 1976; Drobnick and Plummer 1966; McArthur, this proceedings; McArthur and others 1979; Stutz and others 1975; Stutz and Thomas 1964). Several seed companies began business in central Utah and near other centers of revegetation research and application within the region. Most companies handled both exotic and native species. Steep slopes and unstable sites where rapid establishment was critical were often transplanted rather than seeded, providing researchers and Federal, State, and private nurseries the impetus to develop propagation technology for requested species (Ferguson and Monsen 1974; Heit 1967, 1968, 1971; Schopmeyer 1974).

Early recognition of the cycle of excessive grazing, creation of openings in plant communities, invasion by annual weeds, changes in fire frequency and behavior, and alteration of secondary succession guided research on the establishment of wildland plantings (Plummer 1972). Germination, seedling establishment, and growth data from field trials were used to develop appropriate planting technologies and prescribe management and use of young plantings (Basile and Holmgren 1955, 1957; Plummer and others 1968). Existing agricultural equipment was adapted for harvesting, cleaning, and seeding the highly varied types of fruits and seeds planted. The Equipment Development Committee, comprised primarily of agency and commercial members, was established in 1942 to address the development of a disk and drill seeder for rangeland conditions (Larson 1982). Development of the Hansen seed dribbler, interseeders, aerial seeding devices, the anchor chain, and the rangeland drill enabled land managers to plant mixtures of potentially competitive species on rugged terrain (Larson 1982; Vallentine 1989).

Plant Materials Use and Development, 1975 to 2000

Federal Land Revegetation Policy

Changes in Federal land management policy during the twentieth century reflected trends in public concern for the condition and sustainability of public land resources and have directly or indirectly dictated approaches to the selection and use of plant materials. Over this period, policy shifted from an emphasis on commodity production to facilitation of multiple uses to conservation of biodiversity and ecosystem management (Davis 1997; Loomis 1993; Richards and others 1998; Tzoumis 1998). Current guidance for revegetation of Federal lands has evolved over the last 40 years and generally encourages the use of native species when feasible or practical (table 1). Additional direction is available for specific agencies and categories of land disturbances (see below). Land managers planning revegetation efforts are now attempting to address the scale-associated problems of reestablishing vegetation not only on site-specific projects but within the context of management at the landscape level (Bell and others 1997; Ehrenfeld and Toth 1997; Jelinski 1997; Whisenant 1999). Local revegetation policies and guidelines evolve and are updated more or less continuously (for example, USDA Forest Service 2000a; USDI Bureau of Land Management 1996). Concerns and conflicts revolve around genetic considerations, social acceptance of site preparation practices such as herbicide use or chaining, the use of exotics to control weeds or to reduce the spread of wildfires, protection of threatened and endangered plant and animal species, and preservation of local gene pools.

Drastically Disturbed Lands

Early efforts to reclaim mine disturbances on public lands emphasized the use of exotic grasses and forbs to provide rapid site stabilization and forage for livestock and wildlife. Sharply increasing public awareness and concern for environmental issues in the 1960s and the greater private funding available to meet compliance for bond release for revegetation of mined lands effected a gradual shift to the inclusion of greater numbers of native species in seeding mixes (Redente and Keammerer 1999). The Surface Environment and Mining Program (SEAM), chartered by the Forest Service in 1973, sponsored technology

Table 1—Selected Federal legislation and Executive Orders and Memoranda impacting the selection and use of plant materials, 1960 to present.

Document	Year	Direction
Multiple Use Sustained Yield Act (P.L. 86-517; U.S.C. 528-531)[a]	1960	Agencies directed to manage reserved Federal lands for recreation, watershed values, grazing, timber, fish, and wildlife, thus increasing the emphasis on noncommercial resources.
Classification and Multiple Use Act (P.L. 88-607; 43 U.S.C. 1411-1418)[a]	1964	Agencies directed to manage reserved Federal lands for recreation, watershed values, grazing, timber, fish, and wildlife, thus increasing the emphasis on noncommercial resources.
Wilderness Act (P.L. 88-577; 16 U.S.C. 1131-1136)[a]	1964	Provided for designation of wilderness areas to be “preserved and protected in their natural condition.”
National Environmental Policy Act (P.L. 91-190; 42 U.S.C. 4321 et. seq)[a]	1969	Federal agencies directed to analyze impacts of proposed disturbances in environmental assessments and include public participation in decisionmaking.
Forest and Rangeland Renewable Resources Planning Act (P.L. 93-378; 16 U.S.C. 1610-1616)[a]	1974	Federal agencies required to assess use and availability of natural resources on Federal lands and develop management direction for National Forests.
National Forest Management Act (P.L. 94-588; 16 U.S.C. 1600-1616)[a]	1976	Directed National Forests to submit management plans every 5 years.
Federal Land Policy and Management Act (P.L. 94-579; 43 U.S.C. 1701 et. seq.)[a]	1976	Prescribed BLM response to the Resources Planning Act. Required planning to protect biodiversity, designate wilderness study areas, and control extraction of locatable minerals.
Endangered Species Act (P.L. 93-205; U.S.C. 1531-43)[a]	1973	Responsibility for managing endangered species and their habitat transferred from the States to the U.S. Department of the Interior, Fish and Wildlife Service.
Executive Order 11987—Exotic Organisms (Carter 1977a)	1977	Federal agencies directed to restrict the introduction of exotic species into natural ecosystems.
Executive Memorandum on Environmentally and Economically Beneficial Practices on Federal Landscaped Grounds (Clinton 1994)	1994	Prescribed use of regionally native plants for landscaping Federal grounds, Federal projects, and Federally funded projects using low input landscaping practices.
Executive Order 13112—Invasive Species (Clinton 1999)	1999	Directed agencies to provide for restoration of native species and habitat conditions in ecosystems invaded by exotic species.

[a] For text see: Cornell Law School, Legal Information Institute (2000).

transfer programs and encouraged research that contributed substantially to plant material development, revegetation technology, and further growth of the native seed and plant industry (for example, see USDA Forest Service SEAM n.d.; USDA Forest Service 1979). The Surface Mining Control and Reclamation Act of 1977 (SMCRA; P.L. 95-87; 30 U.S.C. 1201 et seq.) (Cornell Law School, Legal Information Institute 2000) reinforced these efforts, mandating "a diverse, effective, and permanent vegetative cover of species native to the disturbed land or species that will support the planned post-mining uses of the land."

The SEAM Program and the SMCRA contributed to major advances in technology and plant materials development for revegetation of other disturbed lands. Plant materials selected primarily for mined land revegetation by universities and USDA NRCS Plant Materials Centers, Agricultural Research Service and Forest Service received widespread use. Development of seed and seeding technology, revegetation equipment, and plant propagation protocols facilitated use of an increased number of species. Research related to plant succession, weed invasions, and competitive interactions in mixed plantings on mined sites increased knowledge of native flora and led to overall advances in wildland revegetation.

DePuit and Redente (1988) examined long-term results obtained from seedings of native and introduced species on mined lands. They determined that introduced species might be more appropriate for rapid control of erosion. However, they found a stronger relationship between mature community structure and composition of the seed mix when native rather than exotic species were seeded. Although cost and establishment of native species were problematic, they concluded that reestablishment of native communities offered a number of advantages compared to exotic seedings. These included greater sustainability, lower management inputs, ease of integrating management of reestablished communities and surrounding native communities, and better quality of wildlife habitat produced.

Big Game Ranges

A wide assembly of ecotypes of shrub species considered important for big game ranges in Utah were collected for field trials prior to 1970. These plantings, coupled with seed germination and establishment studies, provided data required to support the release of a number of widely adapted woody and herbaceous cultivars by the USDA Forest Service, Utah Division of Wildlife Resources, and cooperators (McArthur, this proceedings). Some of these cultivars and an increasing number of other species were brought into cultivation for production of seeds for restoring big game ranges while seeds of others continued to be collected from wildland stands.

Establishment and maintenance of a seed warehouse by the Utah Division of Wildlife Resources aided in improving the availability of native and exotic species and ecotypes (table 2). This agency established procedures for purchasing a constant supply of seed each year, stabilizing the market and assuring sufficient sales to promote collection and marketing a number of species. It defined seed quality standards, delineated geographical regions or collection zones, and developed procedures to clean seeds of many native species. Other agencies and users benefited from this effort, as more species became increasingly available to a growing number of buyers. As seeds of additional species, particularly shrubs, began to be marketed regularly, it became possible to revegetate more shrub-dominated communities.

Table 2—Number of native and introduced species seeded by the Utah Division of Wildlife Resources during selected years from 1959 to 1999[a].

Origin	Life form	1959	1969	1979	1989	1999
Native						
	Grasses	0	4	6	9	19
	Forbs	0	6	8	8	9
	Shrubs	8	16	22	20	12
Introduced						
	Grasses	9	9	11	15	11
	Forbs	3	4	7	14	8
	Shrubs	1	0	1	1	1

[a] Walker 2000.

A number of seed companies specializing in the sale of native plants were established by the mid 1970s and provided a more constant supply of seed, particularly species required for game habitat improvement. The Utah Division of Wildlife Resources continued to support seed production studies for species grown under cultivation. Commercial growers who used information obtained from these studies were able to rapidly expand seed production.

Two rather important changes in revegetation priorities altered the emphasis on species selection for plantings. Prior to about 1980, considerable emphasis was given to planting key winter browse species such as antelope bitterbrush, fourwing saltbush, Stansbury cliffrose (*Cowania mexicana* D. Don var. *stansburiana* [Torr.] Welsh), and mountain mahoganies (*Cercocarpus* H. B. K. spp.) (Giunta and others 1978; Stevens and others 1977; Tiedemann and Johnson 1983; Tiedemann and others 1984). These and other species were commonly planted on sites where they did not naturally occur. Attempts to establish and maintain the shrubs in "offsite" growing conditions, particularly degraded sagebrush rangelands, were eventually recognized as being ecologically unsound. Seeding mixes were reevaluated to include species that were site adapted regardless of their forage traits. In addition, sagebrush and rabbitbrush, once the focus of agency weed eradication programs, gradually gained acceptance as appropriate revegetation species. This contributed to a major shift in seed demands (Rosentreter and Jorgensen 1986). Species of sagebrush and rabbitbrush are now among the most widely seeded.

Recent declines in stands of some native species and populations have impacted revegetation priorities. Cheatgrass expansion and increased wildfire frequency have resulted in the loss of extensive stands of antelope bitterbrush, Stansbury cliffrose, mountain mahogany, and Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young). In many cases the loss of these stands has severely limited the use of ecotypes that once dominated large areas.

Wetlands and Riparian Areas

Improvement of degraded riparian systems became a major management concern in the Western United States in the late 1970s and early 1980s (Swanson 1988). Damage to streams and associated riparian areas resulting from livestock grazing practices and other human activities impaired watershed function, decreased biological diversity, and adversely impacted economic and recreational activities both locally and downstream. Growing public recognition of the magnitude of these problems led to efforts to improve stream functioning and riparian condition through improved management or, when necessary, through active restoration (Kauffman and Krueger 1984; Skovlin 1984; Thomas and others 1979).

Concern over the condition of wetland and riparian areas also led to formulation of Federal policy to preserve and restore these habitats. Direction was provided by such documents as the Clean Water Act of 1972 (P.L. 92-500; 33 U.S.C. 1251 et seq.) (Cornell Law School, Legal Information Institute 2000) and amendments directing pollution control of streams, lakes, and estuaries; Executive Order 11988—Floodplain Management (Carter 1977b); and Executive Order 11990—Protection of Wetlands (Carter 1977c). Additional legislation and programs including the "Swampbuster" Provisions of the Food Security Act of 1985 (P.L. 99-198; 7 U.S.C. 1281 et seq.) and the Conservation Reserve Program authorized by this Act, the North American Wetlands Conservation Act of 1989 (P.L. 101-233; 16 U.S.C. 4401 et seq.), and the Wetlands Reserve Program authorized by the Food, Agriculture, and Conservation and Trade Act of 1990 (P.L. 101-624; 16 U.S.C. 3801 et seq.) support restoration and management of degraded wetlands, primarily on private lands (Cornell Law School, Legal Information Institute 2000; Mitsch and Gosselink 1993; Tzoumis 1998; White and others 1992). Both the Conservation Reserve Program and the Wetlands Reserve Program are administered by the USDA NRCS.

Restoration of disturbed wetland and riparian areas requires that affecting factors first be identified and controlled at the watershed level to restore proper hydrologic and biologic functioning. In many cases, adjustments in management permit natural recovery of riparian vegetation in these systems (Goodwin and others 1997; Hawkins and others 1997; Landers 1997). Seeds or vegetative material may be planted when active restoration is dictated by loss of seed or plant sources, drastic declines in the water table, or other factors. Wetland and riparian plantings have centered on the use of native species, and where possible, local populations (Borman 1996; Carlson 1992; Hughes 1996; Lambert 1995; Willard and Reed 1986). Vegetation in wetland and riparian areas exhibits high species diversity. Thus, revegetation of these areas has generated a demand for seed and planting stock of numerous species receiving little use in the past, but which are now often included on the availability lists of many nurseries and seed dealers.

Many wetland species are distributed across wide geographic and elevational ranges. Local accessions are generally selected for planting as little is known about genetic variation or the range of adaptation of individual populations within these species. Numerous riparian species spread vegetatively; plugs, wildings, rhizome sections and cuttings of these species are easily propagated and planted. Container seedlings, larger plants, cuttings, or poles are used on unstable sites prone to flooding and in areas where the water table declines substantially in summer. Results of recent research on seed germination requirements, the relative ease of storing and handling seeds, and concern for disturbances created by collection of vegetative material are contributing to increased use of seed for propagating riparian species.

The USDA NRCS Plant Materials Program has played a key leadership role in the selection and use of plant materials for riparian and wetland areas. Research conducted by Plant Material Centers provides much of the available data on variability within wetland and riparian species (Flessner and others 1992) as well as guidelines for their propagation and planting (Hoag 1995). Guides developed by the USDA NRCS aid in selection of native species that can be used successfully for revegetation within Major Land Resource Areas (Lambert 1999) or larger geographic areas (Bentrup and Hoag 1998; Lambert 1995; Ogle and others 2000). In addition, the agency has released a series of source-identified wetland and riparian plant materials for use when local sources of seed or vegetative material are not available (Englert and others 1999).

Wildfires and Weed Invasions

Throughout the twentieth century, the invasion of cheatgrass (*Bromus tectorum* L.) and other annual weeds onto rangelands degraded by excessive livestock grazing and other disturbances contributed to lengthened fire seasons and increased fire frequencies (Whisenant 1990; Young and others 1987). The annual grass/fire cycle enhances the spread of annual and perennial weeds, destroys native communities, and reduces ecosystem resilience (Entwistle and others 2000; McArthur and others 1990; Monsen and Kitchen 1994). By 1992 about 1.3 million ha of USDI BLM lands were dominated by annual grasses, and 30.8 million ha of public rangelands were weed infested or susceptible to invasion (Pellant and Hall 1994). From 1991 to 2000 an average of 645,113 ha of USDI BLM lands burned each year (USDI BLM 2000a). Post-fire rehabilitation efforts to reduce the spread of weeds, fuel buildup, and ecosystem simplification are conducted on a landscape scale and have provided a major impetus to growth of the wildland seed industry (table 3). The USDI BLM Emergency Fire Rehabilitation Handbook provides guidance for these projects and prescribes the use of native materials when available (USDI BLM 1998). Executive Order 13112—Invasive Species prescribes use of native materials to restore areas invaded by weeds (Clinton 1999). Introduced species received extensive use in the past due to their availability, low price, and ability to establish in low precipitation areas with high potential for weed invasion. Recent developments in site preparation techniques at the research and application levels offer promise of aiding the establishment of native species (Meyer and others 2000; Pellant and others 1999; Shaw and Monsen 2000). The increasing availability and use of native grass seed cultivars, particularly of native wheatgrasses including thickspike wheatgrass (*Elymus lanceolatus* Scribn. & J. G. Smith), Snake River wheatgrass (*Elymus wawaiensis* J. Carlson), and western wheatgrass (*Pascopyrum smithii* [Rydb.]) as

Table 3—Seeds purchased by the USDI Bureau of Land Management, Denver Federal Center, in three 2001 buys[a].

		Certified site-identified or certified variety			BLM specified origin or noncertified variety		Origin not specified or noncertified, variety not specified	
Origin	Life form	Species	Varieties	Pounds	Species	Pounds	Species	Pounds
Native								
	Grasses	16	23	1,448,300	13	246,600	6	52,950
	Forbs	0	0	0	2	2,100	4	28,650
	Shrubs	5	3	180,710	9	559,060	6	32,945
	Total	21	26	1,629,010	24	807,760	16	114,545
Introduced								
	Grasses	11	15	664,100	7	527,300	1	1,000
	Forbs	6	6	290,350	4	133,900	3	24,400
	Shrubs	1	1	5,300	1	157,800	0	0
	Total	18	22	959,750	12	819,000	4	25,400

[a] USDI Bureau of Land Management (2001).

well as wildland harvested Wyoming big sagebrush caused the balance of USDI BLM purchased seed to shift to regionally native species (Pellant and Monsen 1993) (table 3). However, the need to further diversify seedings in terms of species and populations and associated challenges are recognized.

Although many problems remain, efforts to restore native communities on rangelands over the last 2 decades have led to major advances in development of equipment for site preparation and seeding of mixtures and trashy seeds at appropriate rates and depths. Innovative methods are being implemented to insure seed availability and origin. Seed warehousing by the USDI Bureau of Land Management in Boise, Idaho, has added a measure of stability to the seed industry, improved the availability of seed supplies, and provided cold storage facilities for short-lived seeds.

National Forests have traditionally seeded introduced annual and perennial grass and forb cultivars and available native grass cultivars to provide soil stabilization following forest fires. However, concerns exist that the seeded grasses fail to provide adequate protection during the first season post-fire, and that the introductions may be highly persistent, sometimes invasive, and preclude recovery of native vegetation (Clark and McLean 1979; Powell and others 1994; Robichaud and others 2000). A recent update of the USDA Forest Service Burned Area Emergency Rehabilitation Handbook prescribes use of genetically local sources of native plants when possible or nonpersistent, noninvasive species if local material is not available (USDA Forest Service 2000d). Some National Forests are promoting the collection of local seed sources and seed increase of selected grasses and forbs. Seed transfer guidelines for the most commonly used shrubs are being developed for the Intermountain area (Mahalovich 2001a,b).

The magnitude of the wildfire and weed issues has contributed to the establishment of government programs and initiatives for plant materials development and use. The USDI BLM Green Stripping Program (Pellant 1990) was established in 1984 to develop technology for establishing fuel barriers to protect existing shrublands and plant materials for restoring native communities. Executive Order 13112—Invasive Species prescribed restoration of native species and habitats, where possible, on areas invaded by alien species (Clinton 1999). The extreme fire seasons of the last decade (1991 to 2000) contributed to development of the Great Basin Initiative, a proposal that provides a blueprint for planning and implementing a restoration program for Great Basin Ecosystems (USDI BLM 2000b).

Other Land Disturbances

Native and introduced plant materials are used for revegetating or mitigating an array of disturbances on public and private lands. The USDA NRCS and USDI National Park Service have collaborated since 1989 on a program to develop plant materials for revegetating roadway disturbances in National Parks (Haas 2001; Link 1993). To date, plant materials of more than 800 accessions of native species have been tested and increased, and 9,000 kg of seed and 520,000 seedlings have been produced through this agreement (Haas 2001). The U.S. Department of Transportation, Federal Highway Administration, provides policy guidance for revegetation conducted by State Departments of Transportation. Several Western States have native wildflower programs; current challenges are to combat invasive weeds and reestablish native species and communities where practical (Harper-Lore 1999, 2001). The Federal Native Plant Conservation Memorandum of Understanding, originally signed by 10 Federal agencies in 1994, established a committee to identify conservation needs for native plants, including the restoration of native species on public lands and promotion of similar activities on private lands. To date, 174 public and private organizations have signed on as cooperators with the committee (Plant Conservation Alliance 2001). This organization has the lead within Department of the Interior agencies to increase the availability of native plants (Office of Management and Budget 2001).

The Conservation Reserve Program (CRP), managed by the USDA NRCS, compensates landowners for retiring highly erodible land for 10 years (USDA Farm Service Agency 2001a). Providing the seed required for plantings on these lands has created a challenge for the conservation and wildland seed industry. From 1987 to 2001 nearly 4.4 million ha of CRP lands in the 11 Western States were planted with introduced grasses to improve soil stability, while another 6.9 million ha were planted with regionally native grasses (USDA Farm Service Agency 2001b). Plantings to improve wildlife habitat were installed on about 250,000 ha. During many years, insufficient seed of requested species, cultivars, or specific populations has been available for both CRP plantings and post-fire seedings on public lands. The result is that prices escalate and alternatives to the desired species mix are often purchased and seeded.

Genetic Considerations in Selecting and Using Plant Materials

Research during the past quarter century has considerably increased our knowledge of genetic diversity in western wildland species (for example, see McArthur, this proceedings). However, much remains to be learned regarding variability within individual species. Seed collectors, seed growers, nurserymen, agency personnel, revegetation practitioners, and researchers recognize that genetic considerations must play a role in selecting planting materials for revegetating disturbances. Controversy has arisen over the use of native versus exotic species, definitions of "native," and specifications for selection of native plant materials in order to preserve local populations (Belnap 1995; Gutknecht 1992; Millar and Libby 1989; Pyke 1996; Rice 1996). At issue is the question of whether gene flow between the seeded and local populations of cross-pollinated species will impede natural selection in the local populations and "swamp" or "pollute" their gene pool, or whether local populations might be outcompeted if nonlocal sources are planted, regardless of the plant's breeding system (Jones 1997b; Linhart 1995; Millar and Libby 1989; Rice 1996). At the same time, introgression can be an important evolutionary force, creating new gene complexes and potentially greater adaptability (Jones and Johnson 1998).

Researchers have attempted to provide frameworks for making appropriate plant material selections. Monsen and McArthur (1995), for example, proposed classifying sites into two categories:

> Type 1—Sites that are badly degraded or otherwise changed by loss or change of topsoil or by radical change of topography, hydrology, or fire cycles, or that have a high priority use such as watershed protection. These sites should be treated with the most appropriate plant materials available, indigenous or non-indigenous, for meeting critical objectives such as site stabilization, weed control, or protection of watershed values.
> Type 2—Sites with good potential for restoration to natural conditions. These sites should be treated and managed to return them to near predisturbance conditions.

Jones and Johnson (1998) recommend first assessing the site potential and desired landscape for the disturbance, determining seeding objectives, and considering the genetic integrity of materials to be used. The latter includes selection of material genetically similar to that occurring on the site and insuring that genetic shifts are minimized throughout the propagation cycle. Practical considerations or feasibility factors then enter into the process. These include seral status of the disturbance, examination of the presence or potential for weed invasions, and economic constraints. Within this framework the species list is reassessed and finalized. Appropriate genetic material for each species must then be selected. Scale of the disturbance, time and economic limitations, and seeding objectives often dictate the degree to which specific gene pools can be selected. Local seed sources are much more likely to be available for small-scale plantings than for portions of the sagebrush steppe heavily impacted by large fires.

Selection of appropriate plant materials is hindered by our limited knowledge of the reproductive biology and genetics of individual wildland species. For introduced species, selection generally involves identification of the cultivar most suited to the planting site. For natives, the problem is more complex. Ecotypes, biotypes, and chromosome races occur within many species and may be selected for specific site conditions (Borman 1996; Jones 1997b; Jones and Johnson 1998). For more extensive disturbances, collections of a single taxa gathered from sites throughout the area may be combined to form multiple component plant materials. These provide broad genetic diversity and adaptation to the range of conditions encountered within the disturbance (Jones 1997b; Millar and Libby 1989; Munda and Smith 1995; Stutz 1983). Materials released through the variety or pre-varietal release program may be options when local seed sources are unavailable. Plant breeding techniques may be utilized to overcome specific problems such as seed dormancy that prevent the use of a species for revegetation (Jones 1997b). Plant breeding approaches such as the use of multiple component materials and modified convergent-divergent selection processes are used to breed plant materials with increased rather than narrowed genetic diversity for potential use on extensive disturbances (Munda and Smith 1995).

Seed Certification

Early revegetation plantings generally utilized seed harvested from noncertified stands of introduced or native grasses or from wildland stands of natives. Selection trials for improved plant materials suitable for revegetation work, generally grasses, were conducted using agricultural plant selection and breeding methods and materials were released to commercial growers as cultivars through State Crop Improvement Associations. The International Crop Improvement Association, organized in 1919 with members in the United States and Canada and renamed the Association of Official Seed Certifying Agencies in 1968, fostered development of improved crop varieties, uniform naming of cultivars, and a certification system for regulating the propagation, multiplication, and dissemination of improved seed (Copeland and McDonald 1985). The four generation system adopted led to production of "blue tag" or certified seed, which provides growers with assurance of genetic purity and acceptable quality. Field isolation requirements, checks for weeds and off-types, and inspection of seed conditioning, quality, and identity are some of the services provided through the certification system (Copeland and McDonald 1985). Limitations on numbers and lengths of generations that cross-pollinated varieties may be grown outside the area of use are applied when necessary to reduce the risk of genetic drift.

Some of the earliest cultivars used on wildlands were released in the 1940s. Examples include the introductions

'Manchar' smooth brome released in 1943 and 'Greenar' intermediate wheatgrass released in 1946 (Englert and others 1999), and the natives 'Bromar' mountain brome (*Bromus carinatus* H. & A.) and 'Primar' slender wheatgrass (*Elymus trachycaulus* [Link] Gould ex Shinners) released in 1946. The USDA Natural Resources Conservation Service, Agricultural Research Service, and Forest Service; land grant universities; and other public and private entities continue important programs to test individual species for range of adaptation and specific desirable traits and to develop widely adapted releases for wildland seedings (Alderson and Sharp 1994; Englert and others 1999; McArthur, this proceedings). Physiological tests including measurements of respiration and temperature have been developed in an attempt to provide a more rapid assessment of adaptability than the normal series of field trials (Jones and others 1999; McArthur and others 1998; Monaco and others 1996; Smith and others 1996).

The formal release system generally functions well for introduced grasses and legumes and for some native species that can be reliably produced in seed fields or seed orchards. However, the highly ecotypic nature of many wildland species, low seed production, and problems encountered in producing some species under agricultural conditions due to difficulties encountered in harvesting, conditioning, planting, and stand establishment hindered cultivar development for other important native species. Erratic or limited market conditions and storage problems associated with some species further frustrated these efforts. Most woody species require several years of growth before producing seed, thus slowing testing and establishment of shrub seed orchards and reducing the opportunity for economically viable production. In light of these and other problems and the numerous species, ecotypes, and local populations potentially required for revegetation efforts, seed collectors and growers have employed a variety of methods in addition to the formal release process for providing plant materials for revegetation. Grass and forb seeds are collected from wildland stands where they can be mechanically harvested or easily hand harvested. Shrub seeds are collected from major wildland stands or from areas producing good seed crops in a given year. Some easily grown, nonselected populations are planted in seed fields or orchards and harvested. Agencies and other entities purchasing seeds have adapted approaches for obtaining seeds from desired species and locations. The Utah Division of Wildlife Resources purchases and warehouses seeds from specified areas to meet anticipated needs. The USDI Bureau of Land Management may specify specific stands for collection with agency overview (Fritz 2001). In British Columbia, the Ministry of Forests has published a general transfer guideline for nontree species and recommended that the use of the same seed planning zones developed for trees be applied to these species (Bakker 1999).

Buyers, however, have continually faced difficulties in obtaining adequate quantities of seeds of known origin to insure that the seed source will be adapted to planting conditions. In an attempt to deal with this problem, The Association of Official Seed Certification Agencies has developed a Source Identified seed program for revegetation species by modifying the long-established Source Identified program utilized for tree seed (Currans and others 1997; Young 1995, 1996; Young and others 1995). This program applies to both wildland-collected and field-grown seed or vegetative material of indigenous or nonindigenous species. Verification of identity for field-grown seed is conducted as for the traditional release system. Due to limitations of personnel and funding, however, onsite inspections of wildland collections often occur for only a fraction of the applications (Currans and others 1997).

The alternative "Source-Identified" or "Pre-variety Germplasm Certification" Program is considered a "fast track" approach for making available genetically manipulated or nongenetically manipulated (natural track) plant materials of known origin when there is an immediate need for the material, alternative sources are not available, or market limitations preclude the development of the germplasm to the cultivar status (AOSCA 1997). Germplasms are designated "Source-Identified" when the geographic origin is known, but no comparisons have been made with other germplasms of the species. "Selected Class" germplasm demonstrates promise of superior or unique traits when grown in common gardens with other germplasms of the same species, while "Tested" germplasm maintains these traits through progeny testing. "Tested" germplasms may be released as named cultivars if they are found to be widely adapted and market conditions warrant the release (Young 1995, 1996; Young and others 1995). Most material released through this program falls into the nongenetically manipulated "Natural" category. Within each category, plant materials are further identified by the number of generations they are removed from their origin. As with the traditional certification program, the number of generations permitted for seed production and the restrictions on the number of years seed may be collected from a perennial seed field or orchard vary among species (AOSCA 1997). Although not adopted until 1993, the Pre-variety Germplasm Certification program is seeing widespread use. More than 50 percent of USDA NRCS releases during the 1990s were released through this program (table 4). In Utah, 95,262 kg of wildland collected seed were Source-Identified in 1999 (Young 2001). About 23 percent of USDI Bureau of Land Management native shrub seed purchases based on weight of pure live seed were Source-Identified in 2000 (table 3) (USDI BLM 2000c).

Seed Quality

The last 25 years have seen major advances in the development of procedures for testing the seed quality of native and introduced species used for revegetation. Difficulties are encountered due to the large number of species, subspecies, and varieties being used and the extreme variability in morphology, dormancy, and germination requirements encountered among taxa, populations, and years of collection. Reliable measurements of seed quality are critical for setting and comparing seed prices and for calculating seeding rates. Numerous studies of the seed ecology and biology of revegetation species have been conducted over the last quarter century (see references in McArthur, this proceedings, for contributions of the Shrubland Biology and Restoration Project and cooperators alone). However, resources expended for the study of even common species are extremely limited compared to research funding for individual

Table 4—U.S. Department of Agriculture, Natural Resources Conservation Service plant releases by decade, 1950 to 1999[a].

		1950–1959		1960–1969		1970–1979		1980–1989		1990–1999	
Origin	Life form	Pre-varietal releases	Cultivars	Pre-varietal releases	Cultivars	Pre-varietal releases	Cultivars	Pre-varietal releases	Cultivars	Pre-varietal releases	Cultivars
Native											
	Grass	0	5	3	11	0	24	0	27	39	24
	Forbs	1	0	2	0	0	7	0	9	21	4
	Shrubs	0	0	0	1	0	9	0	24	8	13
	Trees	0	0	0	0	0	1	0	9	6	7
Introduced											
	Grasses	10	15	1	13	1	13	0	15	2	10
	Forbs	4	3	4	7	1	6	0	10	0	7
	Shrubs	0	0	0	1	0	8	0	4	0	1
	Trees	0	0	0	0	0	4	0	2	1	6

[a]Englert and others 1999.

agricultural crop species. The seed biology of many native genera and species remains essentially unknown.

Seed laws in most States require that a licensed laboratory test the seed lots before or at the time of sale (Currans and others 1997). Problems have occurred throughout the history of revegetation efforts in the Western United States because tests were not always completed and seed of very low quality was sometimes sold. Some laboratories do not accept seed lots of species for which there are no rules. Others accept seed lots and apply tests developed in-house with procedures and results varying from laboratory to laboratory. The Association of Official Seed Analysts (AOSA) and other organizations have attempted to address problems associated with testing native seeds. A user's guide to the procedures, values, and interpretation of seed tests and results was developed by the Western Forest and Range Seed Council in 1986 (Stein and others 1986). In 1998 the AOSA organized a symposium that addressed problems and progress in native seed testing (AOSA 2001).

Tests most commonly conducted include purity, seed weight, and germination or viability. Problems encountered in purity testing result largely from inadequate or nonrandom sampling. For some species, further problems are introduced by differences in interpretation of the seed unit (Kitchen 2000). Purity testing is particularly problematic for species such as winterfat (*Ceratoides lanata* [Pursh] J. T. Howell) or prostrate kochia (*Kochia prostrata* [L.] Schrader) that typically produce many small or empty fruits and for sagebrush, rabbitbrush, and other species that are often sold at low purities. In addition, purity tests for such seed lots can be extremely time consuming and costly. Recommendations for sampling and quantities of seed required for testing, refined definitions of the seed unit for problematic species, and training sessions for users as well as seed analysts are included among approaches for improving estimates of purity and their interpretation (AOSA 2000; Currans and others 1997; Stein and others 1986).

Although the average numbers of seeds per kilogram have been published for many species (AOSA 2000; Redente and others 1982; Schopmeyer 1974; Stevens and others 1996; Vories 1980), these can differ immensely among populations and collection years. The number of seeds per kilogram is also dependent upon the extent to which various structures surrounding the fruit or seed are removed during cleaning (Kitchen 2000). Thus, in many cases tests of individual seed lots are necessary for completing seeding rate calculations.

Assessments of seed germinability and viability are critical to determination of seed quality. New AOSA rules for testing germination of additional wildland species are being developed, refereed, and adopted each year (AOSA 2000). Cooperative agreements (1985 to 1989 and 1997 to present) between the Utah Department of Agriculture (now Utah Department of Agriculture and Food), the Utah Division of Wildlife Resources, and the Shrub Sciences Laboratory have contributed to the adoption of 37 rules for widely used revegetation species (Kitchen 2000; McArthur, this proceedings). Difficulties arise when species without rules must be used. Currans and others (1997) reported that 67 percent of the species sold by two Utah seed companies, including many commonly sold species with named cultivars, did not have rules. Additional problems arise as native and exotic revegetation species often exhibit extreme dormancy, and variability in dormancy and germination requirements often occur among and within seedlots of individual taxa. Development of additional rules and innovative approaches for testing germination of species exhibiting variability in germination requirements within or among populations are needed to reduce these problems (Kitchen 2001).

Viability testing using tetrazolium chloride staining is often used as an alternative to germination testing when a rule is not available or when lengthy time periods are required for germination (Peters 2000). A revised handbook on tetrazolium testing prepared through collaboration by the AOSA and the Society of Commercial Seed Technologists (Peters 2000) updates the original handbook that emphasized agricultural species, primarily grasses (Grabe 1970). The new volume provides procedures for 103 families and 375 genera. Difficulties continue due to differences in interpretations of embryo staining, inadequate analyst experience and training, and a need for additional guidelines. Limitations result from the inability of viability tests to detect dormancy, minor seed damage, disease, fungal infections, or chemical or fungicide damage (Vankus 1997). Additional research on viability testing and opportunities for analysts to work with individual wildland species are needed to further improve the value of viability tests (Currans and others 1997).

Site Preparation and Planting

Development of effective site preparation and planting practices and equipment have been major goals of revegetation research in the Intermountain area from the beginning (Holmgren 1956; Jordan n.d.; Plummer and others 1957). Reducing competition on rangelands infested with annual grasses and rapidly spreading perennial weeds (Sheley and Petroff 1999) and planting mixtures of species with diverse seeds across extensive and irregular terrain present complex problems. As a greater array of native species are now being planted together to reestablish more complete communities, seedbed preparation and planting methodologies must become more complex. Seeds of individual species require specific seeedbed conditions and emerging seedlings differ widely in resource requirements and growth rates. Seeds of different species often must be planted at different depths and seeded at different rates to attain desired densities. Through the efforts of the Revegetation Technology and Equipment Committee (originally the Equipment Development Committee, later renamed the Vegetative Rehabilitation and Equipment Workshop), commercial enterprises, agency personnel, and others, major advances in revegetation equipment development have occurred over the last two decades. However, modification of agricultural equipment and the design and fabrication of equipment for the relatively small rangeland market continue to pose a challenge for commercial enterprises.

Disturbed rangelands generally support competitive weeds that must be controlled if new plantings are to survive and establish. Mechanical tillage, burning, and herbicides treatments are frequently employed to reduce competition. A major challenge has recently arisen in the restoration of rangelands where retention of residual species is desired. Remnant native broadleaf herbs, grasses, and shrubs often persist in low numbers in degraded communities. These plants may provide critical seed sources ultimately needed to repopulate the site. Selective treatment to reduce competition and establish desired species is accomplished by interseeding strips or patches within the area to initiate or hasten natural recovery. Improved approaches for interseeding would find widespread application.

Literature and Databases

Numerous efforts have been made over the last 25 years to summarize research data on the use of native and introduced species for revegetation and to make it more readily available to users. The U.S. Department of Agriculture, Agriculture Handbook 450, Seeds of Woody Plants in the United States, originally published in 1948 and expanded in 1974 (Schopmeyer 1974), summarized data of use to nurserymen and seed dealers for propagation of trees and woody shrubs. The book was again revised by Young and Young (1992), and is currently undergoing a major revision and expansion by the USDA Forest Service (USDA Forest Service 2000e). Numerous other publications summarize information on germination of wildland grasses, forbs, shrubs and trees. Some also include ecological information, propagation techniques, and planting and seeding recommendations (for example, Bentrup and Hoag 1998; Carlson and McArthur 1985; Fulbright and others 1982; Landis and Simonich 1982; Link 1993; McArthur and others 1978; Monsen and Shaw 1983; Monsen and Stevens, in review; Redente and others 1982; Rose and others 1998; Smith and Smith n.d.; Stevens and others 1996; Vories 1980; Wark and others 1995; Wasser 1982; Young and Young 1986). Similar information is becoming more available on the Internet. Examples include the Plants Database, a source of information on plants of the United States, including their use as plant materials (USDA NRCS 2000); Vegspec, a web-based decision support system for planning revegetation programs (USDA NRCS and others 2000); the Plant Materials Program, which describes USDA NRCS Plant Materials and their availability (USDA NRCS 2000); the Native Plants Network with protocols for propagation of native plants (University of Idaho 2000); the National Tree Seed Laboratory (USDA Forest Service 2000b); Grass Varieties in the United States (Alderson and Sharp 1994); and the State and Private Forestry Reforestation, Nurseries and Genetic Resources Program with information on nursery management and propagation of forest and conservation seedlings (USDA Forest Service 2000c). The Native Plants Journal, first published by the USDA Forest Service and the University of Idaho in January 2000 (University of Idaho 2000) features papers on plant propagation and use of native plants.

Conclusions

Monsen and Christensen's 1976 paper listed five areas for future plant materials research emphasis: (1) further study of the range of adaptability of species and ecotypes being used; (2) selection and development of additional species and ecotypes for revegetation uses; (3) development of a dependable supply of high-quality seeds and transplanting stock; (4) improvements in site preparation and planting procedures for the establishment of shrubs on rangelands; and (5) reduction of plant losses to insects and diseases. All of these themes remain important today. The last 25 years have seen important advances in all phases of revegetation science and applications. Rather than focusing on specific uses, the aim of revegetation now is to restore functional plant communities dominated by adapted native species where practical. Additional work is needed to provide the research data and verification procedures to ensure selection of adapted seed sources and maintain their identity. To accomplish true restorations, there is a need to develop revegetation technology for additional species. Seed production guides are generally provided with cultivar releases, but seed production and propagation techniques are needed to provide adequate seed and plant supplies of numerous other species (Jones 1997a; McArthur and Young 1999). Germination and viability procedures must be developed for more species, and new approaches taken to reduce inconsistencies in laboratory test results (Kitchen 2001). Adequate storage facilities are needed to permit accumulation of seeds in good production years, improve availability of commonly used species and sources, and stabilize the seed industry. Additional site preparation and seeding technology and equipment are required to provide weed control and permit seeding of diverse seed mixtures. Understanding of establishment requirements and species interactions is needed to successfully reestablish diverse plant communities.

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Scientific Challenges in Shrubland Ecosystems

William T. Sommers

Abstract—A primary goal in land management is to sustain the health, diversity, and productivity of the country's rangelands and shrublands for future generations. This type of sustainable management is to assure the availability and appropriate use of scientific information for decisionmaking. Some of most challenging scientific problems of shrubland ecosystem management are nonnative invasive species, probable effects of global climate change, detrimental effects due to land use change, restoration of degraded environments, and maintaining the quality and quantity of water.

Introduction

One of the primary goals of land managers and landowners in the Western United States is to sustain the health, diversity, and productivity of our Nation's rangelands and shrublands to meet the needs of present and future generations. Effectively meeting this goal requires current information about the land and its resources, an understanding of the public's wishes, and actions that support the environment, the economy, and the local community. Key to attaining this goal is the availability of scientific information and the appropriate use of that information in informing decisionmaking. Sustainable management provides research the context and purpose to address some of our most difficult scientific challenges in shrubland ecosystems. These challenges include the: (1) biological invasion by nonnative invasive species, (2) probable effects of global climate change, (3) detrimental effects due to land use change, (4) restoration of degraded environments, and (5) maintaining the quality and quantity of water.

Nonnative Invasive Species

These species are one of the greatest threats to rangeland health, even though they might be considered both a cause and consequence of ecosystem degradation. Invasive species can compromise an ecosystem's ability to maintain its structure or function and can dramatically increase fire frequency and intensity, reduce property values, and increase management costs. In the future, it is likely that these impacts will be exacerbated by global climate change because scenarios suggest more favorable conditions for the introduction and spread of invasive species.

Scientific information is critically needed to prevent and mitigate the extensive invasive species damage on our rangelands. It is crucial that more emphasis be placed on pathway analyses, risk assessments, and predictive models. Further research and development is also needed on the biology and ecology of invasive species, their host-site relationships, and monitoring protocols.

Probable Effects of Global Climate Change

Our current natural ecosystems are threatened by the probable effects of global climate change. Future scenarios suggest that the rate of global climate change will increase and the magnitude and frequency of ecological processes will likely be greater in the next 100 years. This means there may be many scientific uncertainties. Science and technology opportunities need to focus on reducing the risks of climate change and adapting to the inevitable changes. Additional efforts are needed in assessing potential thresholds and breakpoints, improving long-term data sets and baseline indicators to measure environmental conditions, assessing the impacts of multiple stresses, and focusing on future changes in severe weather and extreme events.

Detrimental Effects Due to Land Use Changes

Shrublands play a key role in sequestration and greenhouse gas emissions. However, their location, composition, and health are noticeably changing because of land use changes. These land use changes have the potential to alter the balance between emissions and absorption and negatively impact ecological conditions. We need to understand the physical, biological, and social interactions within a fragmented landscape. Land use change research should include remote sensing, modeling techniques, and spatial analysis products to improve this understanding.

Many of our Nation's watersheds are deteriorating at alarming rates. Degraded, poorly functioning ecosystems limit our management options and increase the expense and frequency of our management activities. This degradation and disturbance can include a loss of ecosystem resilience and productivity, accelerated erosion and impaired soil development; accumulations of nutrients and chemicals, alterations in the biogeochemical cycles and hydrologic pathways, artificial and simplified structure and composition, modification of interactions and dynamics, reductions in biological diversity; and deterioration of water quality.

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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Restoration of Degraded Environments

Whether the cause is an influx of invasive species or harmful environmental effects due to land use change, there are an increasing number of acres needing restoration, an increasing number of conflicts over treatment options, and rising restoration costs. These trends indicate that lagging ecological restoration represents a major impediment to sustainable management of ecosystems at individual sites and at landscape scales. Clearly, there is a major need for additional investments in restoration science. Additional efforts are needed to study economic costs, benefits, risks, and efficacy of restoration options, prioritization methods for restoration actions, postrestoration prediction models, and performance monitoring. Areas for restoration emphasis should include ecosystems impacted by nonnative invasive species, degraded high-priority watersheds, and fire damaged lands.

The urgency of the restoration challenge facing resource managers and users is increasing. The demands of expanding human populations and development are making it progressively more difficult to conserve native flora and fauna, and to sustain the delivery of ecosystem goods and services from increasingly degraded public lands and waters. Degraded, poorly functioning ecosystems significantly limit management options. Nevertheless, public land and resource management agencies are mandated to protect and restore the health and productivity of the ecosystems entrusted to their stewardship. Unfortunately, management policies and practices are inadequate and in some cases inappropriate for restoring ecosystems to fully functioning condition. This management inadequacy is largely because the scientific basis for restoration based on understanding of the structure, composition, and function of ecosystems and their resilience to human and natural disturbance is inadequate.

Maintaining the Quality and Quantity of Water

Healthy watersheds play a vital role in maintaining the integrity of our water systems to supply people with drinking water, recreation, and commodities. Reducing erosion and contaminated runoff, maintaining soil quality and productivity, and safeguarding water quality and quantity will help maintain healthy watersheds. Research focusing on stream corridors and riparian areas, abandoned minelands, and headwaters is needed to perpetuate healthy watersheds. Basic and applied research on the effects of land management on the functioning of watershed and riparian landscape features and long-term process studies on fire and grazing continue to be of important in providing a scientific basis for restoring sensitive watersheds.

Our research can provide insight into long-term trends in the health and productivity and provide critical data to identify or predict potential changes caused by these scientific challenges.

In closing I would like to stress the importance of accountability. We need to do a better job documenting the impact of these scientific challenges and highlighting the value of the shrubland resource. This documentation requires consistent, comprehensive information. The Montreal Process Criteria and Indicator framework (figure 1) is an operational framework that provides reliable and accurate resource condition information about the extent, condition, and trend of sustainability across the landscape. This common language can communicate to a wide array of audiences across multiple scales, climatic zones, regions, agencies, and ownership boundaries while the consistent methodology provides a foundation for effectiveness and warning of critical issues. The Montreal Process, as it pertains to rangelands, is described in a special issue (volume 7 number 2) of "The International Journal of Sustainable Development and World Ecology" (Flather and Sieg 2000; Joyce 2000; Joyce and others 2000; McArthur and others 2000; Mitchell and Joyce 2000; Neary and others 2000).

Thank you for the invitation to give this presentation. I look forward to hearing more about the exiting new knowledge and technologies that are developing to help us sustain the health, productivity, and diversity of our private and public shrublands.

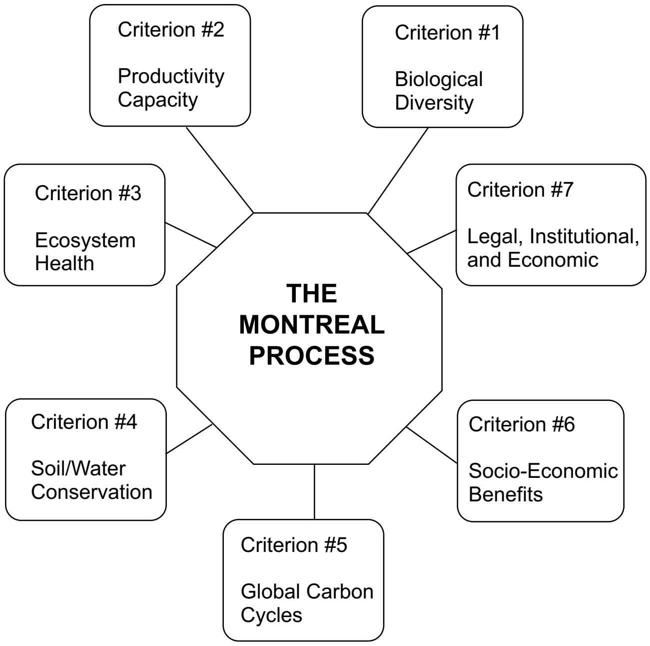

Figure 1—Seven criteria (shown here) and 67 criteria make up the Montreal Process.

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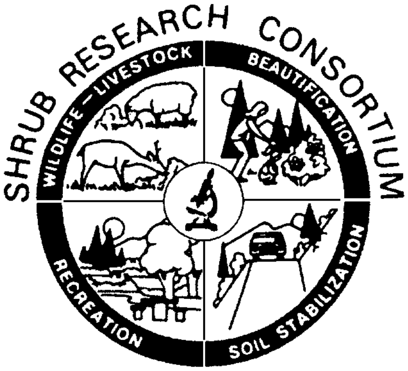

Genetics and Biodiversity

Artemisia Systematics and Phylogeny: Cytogenetic and Molecular Insights

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Abstract—The genus *Artemisia* (Asteraceae, Anthemideae, Artemisiinae) is a large genus, one of the largest genera in its family. It is comprised of about 500 taxa at the specific or subspecific level, distributed in 5 sections or subgenera. Most species are perennial and many are landscape dominants of arid or semiarid regions. *Artemisia* is widely distributed in the Northern Hemisphere but poorly represented in the Southern Hemisphere. It is more richly represented in Eurasia than it is in North America. A number of *Artemisia* species have a high economic value for food, medicine, forage, ornamentals, and other uses. Some taxa are invasive weeds, which can adversely affect harvests. Even though some features (carpological and palynological ones) are quite constant and characteristic of the genus, a high degree of morphological variation exists. *Artemisia* has two basic chromosome numbers, with ploidy levels ranging from diploid to dodecaploid for x = 9 and from diploid to hexaploid for x = 8. Polyploidy and dysploidy are two very relevant evolutionary mechanisms in the genus, particularly the first one, which is present in all its major groups. The classical systematics of *Artemisia* have been refined by molecular methods, for example, internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA, chloroplast DNA restriction site (cpDNA) data, and randomly amplified polymorphic DNA (RAPD) analysis but in the main hold well. This presentation provides a general introduction and characterization of *Artemisia* with particular emphasis on its systematics and evolution as illuminated by cytogenetic and molecular data.

Introduction

Artemisia, one of the larger genera in the family Asteraceae and the largest genus in the tribe Anthemideae, comprises from 200 to more than 500 taxa at the specific or subspecific level (depending on the authors, for example, Bremer and Humphries 1993; Ling 1991a,b, 1995a,b; Mabberley 1990; McArthur 1979), which are distributed in 5 sections or subgenera (Torrell and others 1999b). Many *Artemisia* species have a high economic value in several fields. Some examples are as food plants (absinth–*A. absinthium*–and other taxa, such as *A. genipi*, used in preparation of liquors); as spices (tarragon or estragon–*A. dracunculus*); in medicine, as an antihelminthic (*A. santonicum* and related taxa) and a new promising source of anti-malaria biochemicals (*A. annua*); as forage (*A. herba-alba* and related species in African and Asian steppes and semideserts and *A. tridentata* and its allies in North American shrublands); as ornamentals (*A. absinthium*, *A. caucasica*, and *A. stelleriana* among many others); and as soil stabilizing agents in badly disturbed habitats, for example, highways, railroads, and mines (*A. ludoviciana* and *A. vulgaris*)—see Bailey Hortorium Staff (1976) and Turner and Wassen (1999) for general reference. On the other hand, some taxa, such as *A. verlotiorum*, are invasive weeds, which can adversely affect harvests. Some others may be toxic (*A. absinthium*, for instance) or causative of pollen-induced allergies (the Iberian endemic *A. barrelieri* among others; Giner and others 1999). Marco and Barberá (1990) give a conspectus of the chemical composition of *Artemisia*, and revisions of applied aspects of the genus can be found in Pareto (1985) and Tan and others (1998). The high number of taxa, the dominance of some of them in landscapes, and the usefulness of many of them have attracted the interest of the researchers, who have produced a considerable amount of literature concerning *Artemisia* in many disparate fields of study (systematics in all its approaches, ecology, chemistry, pharmacology, and so forth). This paper provides a general review of different systematic and evolutionary aspects of the genus, with special emphasis on cytogenetic and molecular data.

Life Form and Morphology

Artemisia species are most commonly shrubs, rarely perennial herbs and more rarely annual or biennial herbs. Thus, perennial plants largely dominate the genus; only 5 percent of the taxa (approximately 10 species) are annual or biennial species. Leaves are alternate or sparse, usually more or less divided (exceptionally entire, such as in *A. dracunculus* and *A. cana*), with extremely variable shapes and dimensions. Flower heads are small, basically ovoid, cylindrical or hemispheric in shape, constituted by a rather small number (4–40) of flosculose florets (lacking ligulate ones), and grouped in racemose or paniculate synflorescences. Fruits are pappus-lacking achenes or cypselas, characteristic of the genus (Korobkov 1981; Ouyahya and Viano 1985, 1990; Persson 1974; Vallès and Seoane 1992). Palynological characters are useful markers for the genus *Artemisia*. The weak (verrucose) exine ornamentation contrasts with the higher (spinulose) one of the other members of the tribe Anthemideae, as already pointed out by Wodehouse (1926) and confirmed by later authors (Dimon 1971; Vallès and others 1987). Some of the morphological traits of *Artemisia* (non-opposite leaves, absence of radial florets, non-paleate head receptacle, many capitula with few florets in each

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synflorescence, achenes without pappus) are considered phylogenetically derived characters, within the phylogenetically advanced family Asteraceae (Cronquist 1977).

Phenology and Reproductive Biology

Phenology is a good distinctive trait for *Artemisia* in respect to the remaining Anthemideae or Asteraceae genera. Most *Artemisia* species flower in autumn; however, a few taxa start flowering in summer and others flower in the winter. In the Northern Hemisphere, the flowering period ranges from June to January and fruiting period from August to March. Pollination is basically anemogamous; *Artemisia* and closely related genera are the only tribe Anthemideae genera that have this kind of pollination (Heywood and Humphries 1977; Leppick 1970), evidently related to the pollen ornamentation; nevertheless, frequent insect visits have been reported in different species of the genus, which makes it reasonable to think that a certain percentage of entomogamous pollination occurs (Garnock-Jones 1986; Vallès 1989). Even though they lack the pappus (except for the distinctive *A. papposa*), the achenes of *Artemisia* are at least partly anemochorous due to their very small dimensions and low weight. Zoochory and hydrochory also have significance in the genus. *Artemisia* shows a relatively low capability of fruit dispersion far from mother plants and a relatively high seedling mortality index. These dispersal disadvantages are compensated for and plants are efficiently propagated due to high fruit productivity, germination rates, and general plant vigor (Bostock and Benton 1979; Oliva and others 1997; Vallès 1989; Walton and others 1986).

Ecology and Geographical Distribution

Artemisia species are found in many ecosystems: from desert communities (*A. santolina* in Uzbekistanian and Iranian deserts, for instance) to humid environments (*A. molinieri*, an endemic species to southeastern France and *A. cana* ssp. *bolanderi*, endemic to the Oregon area of the United States, the only taxa in the genus to live in temporarily inundated soils); from near sea level (*A. caerulescens* from European marine salt marshes) to the top of high mountains, at almost 4,000 m (the Iranian *A. melanolepis* and the North American *A. pattersonii* and *A. scopulorum*); some species are ruderal (as *A. vulgaris*). The genus is widely distributed in the Northern Hemisphere but uncommon in the Southern Hemisphere (only about 10 species). Most *Artemisia* species grow sparsely or form small populations, but several taxa form large, expansive populations and characterize landscapes. Different steppe and semidesert shrubby communities are dominated by species belonging to the subgenera *Seriphidium* (Mediterranean region, Central Asia) or *Tridentatae* (North America).

Classification

In such a large genus, it is to be expected that many attempts have been made to establish an infrageneric classification. The main proposals are compared in Table 1, where we can see that some large infrageneric groups are more or less present in all *Artemisia* classifications. Besser (1829, 1832, 1834, 1835) and Candolle (1837) established these groups as sections. They follow and are based on a few morphological characters:

Artemisia (originally named *Abrotanum* Besser). Heterogamous capitula with outer florets female and central florets hermaphrodite, and fertile and glabrous receptacle.

Absinthium DC. Heterogamous capitula with outer florets female and central florets hermaphrodite and fertile and hairy receptacle. Some authors merge this section into the precedent one.

Dracunculus Besser. Heterogamous capitula with outer florets female and central florets hermaphrodite but female-sterile and glabrous receptacle. Cassini (1817) transferred the species of this section to a new genus, *Oligosporus* Cass.

Seriphidium Besser. Homogamous capitula with all florets hermaphrodite and fertile and glabrous receptacle.

Table 1—Comparison among different infrageneric classifications of *Artemisia*.

Category	Infrageneric taxa					Reference
Genera	*Absinthium*	*Abrotanum*	*Artemisia*			Tournefort (1700)
Genus	*Artemisia*					Linné (1735)
Genera	*Artemisia*				*Oligosporus*	Cassini (1817); Lessing (1832)
Sections	*Absinthium*	*Abrotanum*	*Seriphidium*		*Dracunculus*	Besser (1829, 1832, 1834, 1835); De Candolle (1837)
Subgenera	*Euartemisia*		*Seriphidium*		*Euartemisia*	Rouy (1903)
Subgenera	*Absinthium*	*Abrotanum*	*Seriphidium*		*Dracunculus*	Rydberg (1916)
Sections			*Seriphidium*	*Tridentatae*		
Subgenera	*Artemisia*		*Seriphidium*		*Dracunculus*	Polyakov (1961b)
Subgenera	*Absinthium*	*Artemisia*	*Seriphidium*		*Dracunculus*	Persson (1974)
Sections	*Artemisia*				*Dracunculus*	Tutin and others (1976)
Subgenera	*Artemisia*		*Seriphidium*	*Tridentatae*	*Dracunculus*	McArthur and others (1981)
Subgenera	*Artemisia*		*Seriphidium*		*Dracunculus*	Podlech (1986)
Genera	*Artemisia*		*Seriphidium*		*Artemisia*	Ling (1991a,b)
Subgenera	*Artemisia*		*Seriphidium*		*Dracunculus*	

Rydberg (1916) created the new section *Tridentatae* Rydb. to include the main part of North American *Seriphidium*, which he treated as a subgenus. McArthur (McArthur and others 1981) elevated this section to the subgeneric level. Ling (1982, 1991a,b, 1995a,b) proposed separation of one of the main *Artemisia* sections (or subgenera) as a large (almost 150 species) independent genus, *Seriphidium* (Besser ex Hook.) Fourr. (table 1). Bremer and Humphries (1993) and Bremer (1994) have accepted this segregation in their cladistic revisions of the tribe Anthemideae and the family Asteraceae, respectively.

Some small (even monotypic) genera have also been removed from *Artemisia*, such as *Filifolium* Kitam., *Kaschgaria* Poljakov, *Neopallasia* Poljakov, *Turaniphytum* Poljakov, *Elachanthemum* Y. Ling & Y.R. Ling, *Artemisiella* A. Ghafoor, *Artemisiastrum* Rydb., *Mausolea* Poljakov and *Picrothamnus* Nutt. (Bremer and Humphries 1993; Ghafoor 1992; Ling and Ling 1978; Poljakov 1961a; Rydberg 1916). However, many current treatments retain these proposed segregates within *Artemisia*. Most of the genera included in the subtribe Artemisiinae contain some species previously described as members of *Artemisia*.

Cytogenetics

Artemisia chromosomes are rather small (2–8 μm). Karyotypes tend to be symmetric, considering both the interchromosomal and the intrachromosomal asymmetry (McArthur and Plummer 1978; McArthur and Pope 1979; McArthur and others 1981; Mendelak and Schweizer 1986; Oliva and Vallès 1994; Schweizer and Ehrendorfer 1983; Vallès and Siljak-Yakovlev 1997); they fit into 2A and 2B classes (Stebbins 1971). The use of Giemsa C-banding and chromomycin and bisbenzimide fluorochrome banding (Mendelak and Schweizer 1986; Oliva and Vallès 1994; Schweizer and Ehrendorfer 1983; Vallès and Siljak-Yakovlev 1997; Torrell and Vallès, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona) provide the opportunity to use heterochromatic chromosome segments banding patterns—called banding style by Schweizer and Ehrendorfer (1983)—for systematic study. There is a predominance of telomeric bands over intercalary and centromeric bands. Chromomycin-positive (GC-rich) bands appear often linked to the nucleolus organizing regions in satellited chromosomes. Preliminary studies using fluorescent *in situ* hybridization (FISH) show that 18S rDNA tends to be located in the chromomycin-positive regions (Torrell and others, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona). The general pattern basically characterized by telomeric bands is also found in other genera of the tribe Anthemideae (Schweizer and Ehrendorfer 1983). B chromosomes have been reported in different numbers (1–5) in some species and populations of the genus (McArthur and others 1981; McArthur and Sanderson 1999a; Torrell and others 1999a, 2000; Vallès and Siljak-Yakovlev 1997; Torrell and Vallès, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona).

The genus has two basic chromosome numbers, the largely predominating x = 9 and the less extended x = 8. X = 9 is not only the most common basic number in the genus *Artemisia*, but in the tribe Anthemideae and the family Asteraceae as well (McArthur and Sanderson 1999; Oliva and Vallès 1994; Schweizer and Ehrendorfer 1983; Solbrig 1977; Vallès and Siljak-Yakovlev 1997). A single species has been reported at x = 7 (*Artemisia pattersonii*—Wiens and Richter 1966). We do not believe this isolated circumstance warrants consideration as a basic chromosome number for the genus; rather, we believe this must have been an aneuploid reduction. Two phenomena have been basic in the chromosome evolution in the genus: polyploidy and dysploidy.

Polyploidy

Apart from being a common evolutionary mechanism in plants, it has been widely recognized as particularly active in *Artemisia* (Ehrendorfer 1964, 1980; Estes 1969; Koul 1965; McArthur and Pope 1979; McArthur and others 1981; McArthur and Sanderson 1999; Oliva and Vallès 1994; Persson 1974; Torrell and others 1999b, 2000; Vallès 1987a, 1987b; Vallès and Siljak-Yakovlev 1997). A high percentage of *Artemisia* species are polyploid. This phenomenon is present in all the major groups into which the genus is divided. Both basic chromosome numbers show polyploidy, with levels up to 12x for x = 9 and 6x for x = 8. The circumboreal, but largely Eurasian, *Artemisia dracunculus*, for which the chromosome numbers 2n = 18, 36, 54, 72 and 90 have been reported (Kawatani and Ohno 1964; Rousi 1969) constitutes a good example of a complete series from diploid to decaploid levels, based on x = 9. The large, western North American subgenus *Tridentatae* (= sagebrush), also based on x = 9, provides another robust example of polyploidy from diploid (2n = 18) to octoploid (2n = 72) levels (McArthur and Sanderson 1999). The dodecaploid level has been reported to now only for one species, *A. macrantha* (Malakhova 1990). For x = 8, the *Artemisia vulgaris* group shows a series from diploid to hexaploid levels (Vallès 1987a; Vallès and Torrell, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona). Recent studies (Torrell and Vallès 2001) show that nuclear DNA content (ranging approximately from 3 to 27 pg) is well correlated with ploidy level, and that evolutionary trends in genome size in the genus comprise both decreases and increases in DNA content, as it has been reported to happen in other groups belonging to the family Asteraceae (Cerbah and others 1999; Price and Bachmann 1975).

Dysploidy

The existence of two basic numbers shows *Artemisia* as a dysploid genus. Dysploidy is present in three of the main groups in the genus (*Artemisia*, *Absinthium* and *Dracunculus*); *Seriphidium* and *Tridentatae* display only one basic number, x = 9. Kawatani and Ohno (1964) inferred that x = 9 was the original basic number from the fact that it is the most common one in the genus. Vallès and Siljak-Yakovlev (1997) found evidence for a chromosomal fusion in *A. vulgaris*, which experimentally supported the hypothesis that descending dysploidy in the genus is derived. This 2n = 16 species has a chromosome pair much longer than the remaining 7 pairs. This long pair of chromosomes is almost perfectly metacentric and includes a centromeric heterochromatic region. In addition to that, this chromosome pair shows a high centromeric fragility, so that both arms of every chromosome often appear distinctly separated after squashing. These traits are evidence of a chromosomal fusion. This can explain the appearance of a number of x = 8 based species, as well as the existence of some erroneous x = 9 based counts for some of these taxa. Subsequent research has confirmed the same fusion syndrome in other species, such as *A. judaica*, *A. lucentica,* and *A. reptans* (Torrell and Vallès, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona), and *A. incana* and *A. splendens* (Torrell and others 2000), representing different groups in which dysploid processes have occurred. Polyploid x = 8 taxa (for example, *A. splendens*, 2n = 32) have two larger metacentric chromosome pairs, confirming the likelihood of a fusion event prior to polyploidization (Torrell and others 2000). The idea of descending dysploidy as an evolutionary trend is consistent with what is known in different genera in the family Asteraceae (Siljak-Yakovlev 1996; Solbrig 1977). Other examples of dysploid processes are known in the tribe Anthemideae (Heywood and Humphries 1977), even though this is not a common mechanism in the tribe (Mitsuoka and Ehrendorfer 1972; Schweizer and Ehrendorfer 1983).

Chromosome Number Evolution

Figure 1 presents a scheme of the putative chromosome number evolution in *Artemisia*. The examples described above illustrate almost all changes in chromosome number and ploidy level. There is only one point left: the appearance of 2n = 34 populations or taxa. This chromosome number may be reached from 2n = 18 through 2n = 36 or from 2n = 16 through 2n = 32. In the first case we cite the example of *A. umbelliformis*, with one 2n = 18 subspecies (ssp. *eriantha*) and another one (ssp. *umbelliformis*) for which 2n = 36 and 2n = 34 have been reported (Oliva and Vallès 1994). Chromosome morphology suggests an allotetraploid origin for *A. umbelliformis* ssp. *umbelliformis*, with ssp. *eriantha* as one of the ancestors (Ehrendorfer 1980; Gutermann 1979; Oliva and Vallès 1994); 2n = 34 populations seem stabilized enough to discard a simple case of aneuploidy and to consider a dysploid-polyploid origin of a new secondary basic number, x = 17. Some populations of the *A. vulgaris* complex may also have reached this number from 2n = 16 by means of polyploidy and duplication of one chromosome pair (Vallès and Torrell, unpublished data on file at Laboratori de Botànica, Facultat de Farmàcia, Universitat de Barcelona).

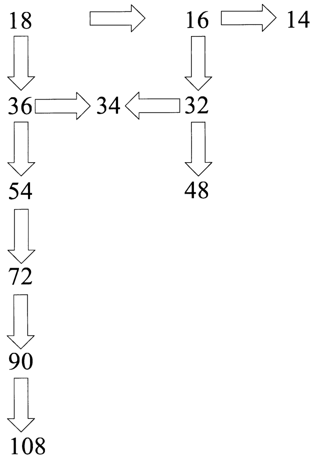

Figure 1—Chromosome number evolution in the genus *Artemisia*.

Molecular Biology

Working on *Artemisia* it is easy to be convinced that, as Persson (1974) stated, the currently accepted main groups within the genus do not represent natural groups. So, different attempts have been made in recent years to refine or redefine the systematics of the genus to the light of molecular data (Kornkven and others 1998, 1999; McArthur and others 1998a,b; Torrell and others 1999b). Two main questions (generic delimitation and infrageneric classification) concerning classification may be addressed by molecular studies.

Generic Delimitation

As stated above (see Classification section), different authors proposed to segregate some of the main infrageneric groups in *Artemisia*, namely *Oligosporus* (Cassini 1817) and *Seriphidium* (Bremer 1994; Bremer and Humphries 1993; Ling, 1982, 1991a,b, 1995a,b), as independent genera. Phylogeny based on the nuclear ribosomal DNA internal transcribed spacers (ITS-1 and ITS-2) sequences does not support these segregations and shows a monophyletic genus in its broad, classical sense (Torrell and others 1999b). Molecular data support morphological ones. Only minor morphological-physiological traits (receptacle indumentum and sex of peripheral florets) separate *Dracunculus* (the basis for the genus *Oligosporus*) and *Seriphidium* from other main groups in the genus, whereas major characters, such as pollen and cypsela morphology, clearly define them as members of the genus *Artemisia*.

Infrageneric Classification

ITS sequencing data define five major clades within *Artemisia*, which are similar, but not identical, to the five main groups discussed in the Classification section (above) (table 1). Figure 2 shows these clades, which have the following links with the classically recognized groups:

> *Tridentatae* and *Dracunculus* are delimited as traditionally conceived. *Absinthium* and *Seriphidium* are resolved in clades with the addition of some species up to now included in *Artemisia*, a completely fragmented group in the ITS phylogeny (which agrees with the extraordinary morphological variation within the group).
>
> Finally, a clade is constituted by the taxa of the group of *A. vulgaris*, the type species of the genus.

The analysis of molecular data shows the monophyly of subgenus *Tridentatae* (RAPD: McArthur and others 1998a;

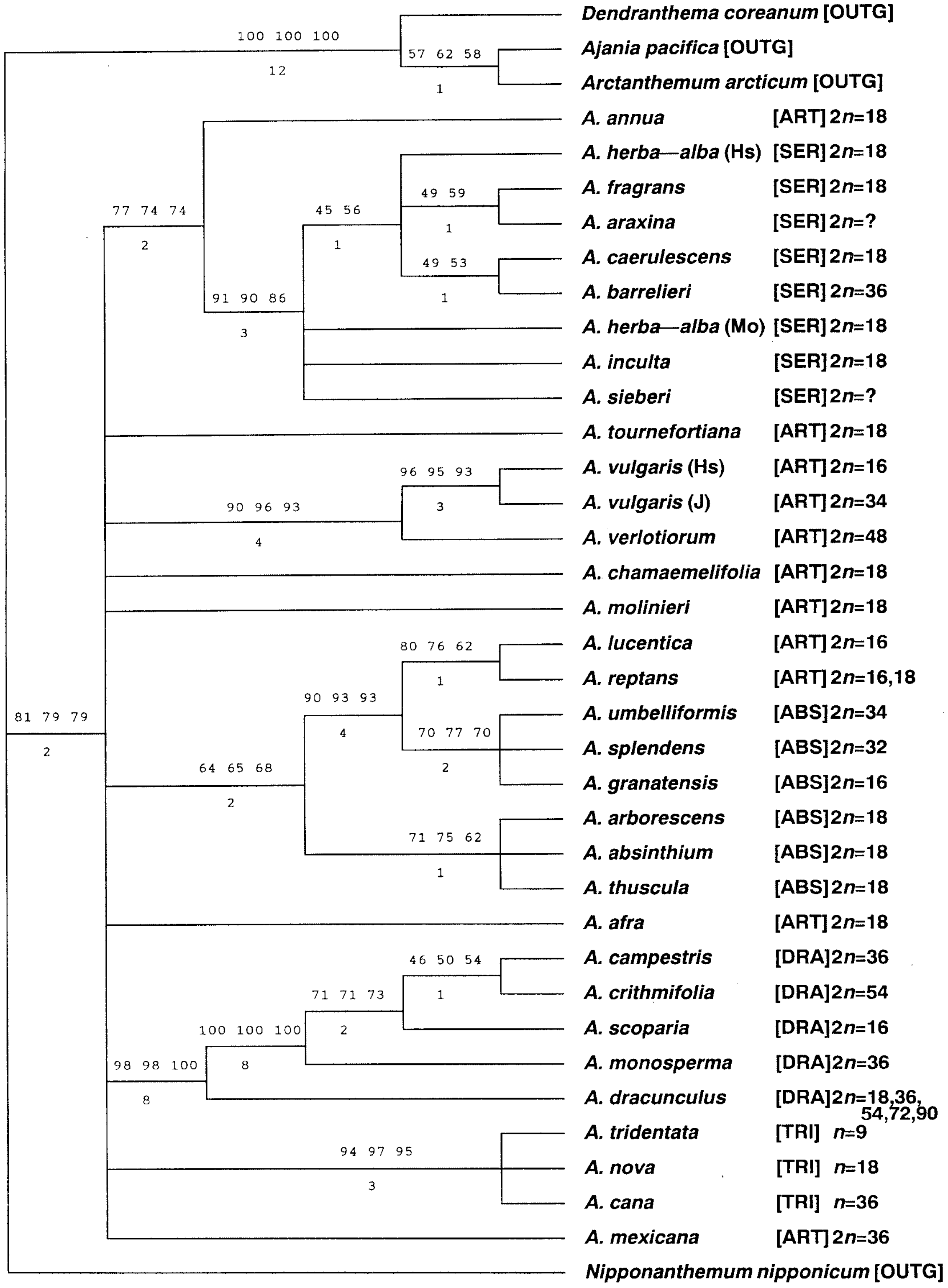

Figure 2—Cladogram showing the hypothetical ITS phylogeny of *Artemisia* (adapted from Torrell and others, 1999b). Consistency index excluding uninformative characters (CI) = 0.471; retention index (RI) = 0.740. Numbers above branches are bootstrap percentages and parsimony jackknife results: first, Lidén and others (1997) bootstrap method; second, Plunkett and others (1996) bootstrap method; third, parsimony jackknife values. Numbers below branches are decay indices. ART = Section/Subgenus *Artemisia*, SER = Section/Subgenus *Seriphidium*, ABS = Section/Subgenus *Absinthium*, DRA = Section/Subgenus *Dracunculus*, TRI = Section/Subgenus *Tridentatae*, OUTG = Outgroup.

ITS sequencing: Kornkven and others 1998; Torrell and others 1999b; chloroplast DNA: Kornkven and others 1999) and clearly supports the independence of this North American endemic group from *Seriphidium* (Torrell and others 1999b). Bremer and Humphries (1993) and Ling (1995b) included the members of *Tridentatae* in the genus *Seriphidium*, even though different authors had suggested, on the basis of morphological, karyological or chemical characters, the independence and the convergent evolution of both subgenera or even a closer relationship between *Tridentatae* and *Artemisia* than between *Tridentatae* and *Seriphidium* (Jeffrey 1995; McArthur 1979; McArthur and others 1981, 1998a,b; McArthur and Plummer 1978; Seaman 1982; Shultz 1986).

Perspectives in the Study of *Artemisia*

The present article has summarized a significant part of the considerable amount of research carried out in different fields about the genus *Artemisia*. We can conclude that it is a rather well-studied genus, but some of its systematic and phylogenetic aspects remain unsolved as, for example, the placement of *A. filifolia, A. palmeri,* and *A. californica*, see Hall and Clements (1923) and McArthur and Sanderson (1999), or the infrageneric classification (Torrell and others 1999b). Apart from research about applied aspects that are very relevant in this genus, even though they are not the main object of this paper, many biosystematic studies—in morphology, population biology, cytogenetics, and molecular biology, among others—are suitable in order to obtain a better knowledge of the genus. We believe that karyological (from chromosome counts to molecular cytogenetics) and molecular (combining different techniques in as many taxa as possible) studies in *Artemisia* and the subtribe to which it belongs (Artemisiinae) will be effective tools in better systematic definition.

These further studies may support or contradict the present evidences and nuances. They may demonstrate that a new revision of the genus is necessary or contrariwise they may confirm our present understanding in regard to both the infrageneric classification and the relationships between *Artemisia* and its closely related genera (subtribe Artemisiinae). However, we believe that it is certain that multidisciplinary systematic and phylogenetic studies will continue on this interesting and important group of plants.

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Chromosome Races of Fourwing Saltbush (*Atriplex canescens*), Chenopodiaceae

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Abstract—*Atriplex canescens* (Pursh.) Nutt. is the most widespread species of perennial *Atriplex* in North America, distributed from southern San Luis Potosi, Mexico, to southern Alberta and Saskatchewan, Canada, and from the Pacific Coast of California and Baja California to Texas, Oklahoma, Nebraska, Kansas, and the Dakotas. Throughout its distributional range, *A. canescens* shows considerable between-population variation. Some of this variation may be due to phenotypic plasticity, but most of it appears to be genetic. Mutations, polyploidy, introgressive hybridization, and segregation from interspecific hybrids all appear to have contributed to its extensive heritable variation. Polyploidy is unusually common with numerous chromosome races (2x, 4x, 6x, 8x, 10x, 12x, 14x, 20x).

Proper identification is important to the utilization of fourwing saltbush in reclamation. While many of the races have been named as varieties, others have not. Even though differentiated by ploidy, chemical constituents, geographic distribution, and morphological characters, they may lack sufficient diagnostic differences to allow facile identification, at least in the herbarium. Rather than combining unnamed races under those that do have a taxonomic name, it seems better at present not to use the formal infraspecific categories in treating the fourwing saltbushes, but to consider them all as races. One new variety, ***Atriplex canescens* var. *obtusifolia* var. nov.,** is described, and the combination ***Atriplex canescens* var. *prosopidium* (I. M. Johnston) comb. nov.** is made.

Introduction

Atriplex canescens forms a polyploid complex based on x = 9, with chromosome numbers of 2x, 4x, 6x, 8x, 10x, 12x, 14x, and 20x (Sanderson and Stutz 1994; Stutz and Sanderson 1979). The most widespread and economically important of these are the 4x (tetraploid) and 6x (hexaploid), while diploids and higher polyploids are less widespread or local endemics.

Atriplex belongs to the order Caryophyllales, in which many of the taxa differ from other dicots in having perisperm as a nutritive tissue, rather than endosperm. It seems likely that lack of endosperm (Cronquist 1988; Cronquist and Thorne 1994), and therefore of endosperm-based barriers against polyploidization (Ramsey and Schemske 1998), may be a factor in the abundance of polyploidy within these taxa (Sanderson and others 1999). Another somewhat distinguishing factor of *Atriplex* may be the ability for multisomic segregation in polyploids with little meiotic irregularity, probably both for genic reasons (Jackson and Casey 1979) as well as small chromosome size (Ruas and others 1998; Stebbins 1971). An apparent intolerance of taxa in the Chenopodiaceae to aneuploidy is worth noting. Practically the entire family has a base number of x = 9 (exceptions are *Spinacia* and *Camphorosma*, x = 12, and a few species with x = 8 and 7 in *Chenopodium*) (McArthur and Sanderson 1984), and it can also be inferred that the frequency of chromosomal reorganization is low. Because of these and possibly other characteristics, the cytogenetic behavior of chenopods is somewhat different than that of dicots in general. Examination of meiotic behavior in numerous species hybrids in *Atriplex* suggests that little chromosomal differentiation exists between North American perennial species (Stutz and Sanderson, unpublished data on file at Brigham Young University). As a result, hybrids tend to be fertile and meiotic behavior in polyploids is, therefore, probably of an autoploid type, even when hybridization between species is involved.

This paper presents a key and descriptions for fourwing saltbush chromosomal races, along with commentary upon their nature and possible origins.

Methods and Materials

Chromosome counts were made by acetocarmine squash methods (Sanderson and Stutz 1994). More than 1,800 individuals from 800 populations were counted over a number of years. Flavonoids were identified as aglycones by paper chromatography using aluminum chloride as a color reagent (Sanderson and Stutz 1994), and more than 1,200 determinations for fourwing saltbush taxa were made (table 1). Populations were examined in the field, and representative specimens deposited at BRY and other herbaria.

Results and Discussion

Establishment of Polyploidy

Because of different probabilities of cytological events at successive ploidy levels, distinct pathways of polyploidization appear to predominate at the diploid, tetraploid, and hexaploid levels in North American *Atriplex*. At the diploid level,

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Table 1—Discriminative flavonoid characters of fourwing saltbush. All taxa also produce the common flavonols kaempferol, quercetin, and isorhamnetin (not listed). Besides the universally present unsubstituted flavonols, derivatives modified at the 3 or 6 positions may be observed, as shown below, and tricin, a flavone, is also present in certain taxa.

	Number of samples examined	6-methoxy-substituted flavonols	3-0-methyl-substituted flavonols	Tricin
2x				
Angustifolia (Mexico)	15	–	+	–
Angustifolia (USA)	60	–	–	–
Brevis	48	–	+	–
Garrettii	21	–	+	–
Gigantea	31	–	–	–
Linearis	61	+/–(very weak)	–	+
Piochensis	12	–	–	–
Stewartii	2	–	–	–
4x				
Angustifolia–4x	24	+	–	–
Aptera	42	+	–	–
Bonnevillensis	44	+	–	–
Canescens	17	+	–	–
Cunescens	6	+	–	–
Mexicana	8	–	+	–
Navajoensis	41	+/–(polymorphic)	–	–
Occidentalis	330	+	–	–
6x				
Diegensis	10	+	–	–
Nana	65	+/–(polymorphic)	–	+
Nevadensis	119	–	–	+
Occidentalis–6x	28	+	–	–
Prostrata	9	–	+	–
Rachelensis–6x	17	+	–	–
Tooelensis	6	+	–	–
Vallis	69	+	–	–
8x				
Cuyamaensis (Laciniata–8x)	9	–	–	+
Obtusifolia	24	+	–	–
Prosopidium–8x	2	–	–	+
Rachelensis	11	+	–	–
10x				
Prosopidium	5	–	–	+
12x				
Laciniata	51	–	–	+
Macilenta	28	–	–	+
14x				
Laciniata–14x	24	–	–	+
20x				
Grandidentatum	33	–[a]	–	+

[a] Traces are occasionally seen, apparently due to hybridization with *Atriplex polycarpa*.

an interesting type of chromosome number increase seems to prevail, which we term polyploidization by introgression. When it happens that a diploid population comes into sympatry with a tetraploid, possibly genetically dissimilar or even a separate species, unidirectional introgression from the diploid into the tetraploid may result (Lowe and Abbott 2000; Petit and others 1999; Qu and others 1998; Stebbins 1971; Zohary and Nur 1959). If this occurs, and providing that the diploid enjoys sufficient numerical dominance, the tetraploid may be significantly altered by the introgression, eventually to the point that its original racial or taxonomic identity may no longer be obvious. At that point, if the population were examined, it would of necessity be categorized as belonging to the race or species of the diploid, although having a tetraploid chromosomal level.

Unidirectional introgression may be the result of either of the two more probable cytological mechanisms in this situation, the formation of triploid hybrids, followed by fertilization of their unreduced 3x gametes with x gametes ($x + 2x = 3x$, $3x + x = 4x$), or more directly, the combination of unreduced gametes from the diploid with normal gametes from the tetraploid (2x + 2x = 4x) (Lowe and Abbott 2000; Zohary and Nur 1959). However, since observed introgression between diploids and tetraploids seems exclusively unidirectional (Stutz and Sanderson, unpublished data on file at Brigham Young University), a third pathway involving generation of progeny out of the segregation of euploid gametes in triploids, which might result in bi-directional introgression, does not appear common.

The relative frequencies of polyploidization by unidirectional introgression versus that for within-population autoploidy, besides depending on ease of hybridization, would in addition depend on the relative opportunities for establishment of the polyploidized products from each pathway (both mechanisms are dependent upon the formation of unreduced gametes). Establishment of within-population autoploidy would require a relatively unlikely isolation of the tetraploid products, which could otherwise be swamped by pollen flow from the diploid parent, leading to sterile products. In contrast, an established population already exists by definition for tetraploids in the introgressive pathway, once introgression has begun, enabling the polyploidization process to proceed smoothly and rapidly and to succeed more frequently. Also, as a practical matter, diploids are weak competitors and easily limited to special habitats or isolated locations (Sanderson and Stutz, unpublished data on file at Brigham Young University; this paper), with tetraploids expanding and eventually taking over. Because of adaptive characteristics that appear to commonly be passed from older tetraploids to the newly formed ones, fertility and vigor of tetraploid introgressants tend to be high. One trace of the founding original tetraploid's genetic influence that seems to persist in introgressed populations is the enzymatic capacity for flavonol 6-oxygenation, a trait that is generally absent from diploid perennials (Sanderson and Stutz 1984) but present in most tetraploid North American *Atriplex*. Because of this distribution, flavonol 6-oxygenation is often a useful marker in documenting the introgressive process.

From the tetraploid level, further polyploidization differs somewhat from polyploidization out of the diploid level. Because numerical combinations with unreduced gametes produced by tetraploids do not readily yield a match for gametes produced by hexaploids (2x + 3x = 5x; 4x + 3x = 7x; 2x + 6x = 8x; 4x + 6x = 10x), hybridization between tetraploid and hexaploid populations would not serve directly as a route for unidirectional introgression. However, an even-ploid product can be formed directly from unreduced gametes in tetraploids (2x + 4x = 6x, as opposed to x + 2x = 3x in diploids) to yield hexaploid offspring. Unreduced gametes can be inferred to be relatively common at the tetraploid and higher ploidy levels (Stutz and Sanderson, unpublished data on file at Brigham Young University). The probability of spontaneous within-population polyploidization to a higher level, observed to be rare at the diploid level, might, therefore, be expected to be higher within tetraploid populations. In fact, hexaploid individuals are observed occasionally in populations of tetraploid *Atriplex canescens* (Stutz and Sanderson, unpublished data on file at Brigham Young University). These individuals might either become isolated to begin a hexaploid population, or could hybridize with existing hexaploid taxa to bring about, indirectly, introgression from tetraploids into hexaploids. Such introgression seems to be much less widespread, however. While hybridization appears a factor in formation and development of *Atriplex* hexaploids, it does not reach the level of importance inferred for the origin of tetraploidy.

At higher ploidy levels, there are an increasing number of possible pathways involving unreduced gametes, hybridization, or backcrossing for producing even-ploid offspring at various ploidy levels. However, these tend to conflict with each other to prevent easy resolution. The chromosome number progressions that are observed in the two higher polyploid series in *Atriplex canescens,* from the Chihuahuan and the Sonoran Deserts (Sanderson and Stutz 1994; this paper), seem to suggest chance isolation of relatively rare products.

Identification of the Races

Our studies (Sanderson and Stutz 1994; Stutz and Sanderson 1979, this paper) and those of Dunford (1984, 1985) show that the chromosomal races of *Atriplex canescens* are usually identifiable on morphological grounds, as well as by cytological and geographical criteria. The most generally useful characters in distinguishing fourwing saltbush races are the leaf dimensions, notwithstanding the tremendous seasonal variations exhibited by leaves. Seasonal variation exists because larger leaves are produced during times of vigorous growth, while clustered smaller leaves appear in leaf axils during slower growth on unelongated or partially elongated shoots. As explained in an earlier report (Sanderson and Stutz 1994), in seasons of aridity, first the larger and then successively smaller leaves are shed to reduce water loss. Some races also produce distinctive winter leaves that are small, involute, and curled against the stem. As has been noted in previous studies (Dunford 1985; Sanderson and Stutz 1994; Stutz and Sanderson 1979), with the exception of race Garrettii (Garrettii and Stewartii may be considered separate species from *A. canescens* proper—see below for racial description and discussion), diploids have leaf length-to-width ratios generally above 10:1. This ratio decreases from diploid to tetraploid chromosome levels, and also somewhat more from tetraploid to hexaploid levels. Foliage color is generally more yellowish in diploids, apparently because of reabsorption of a portion of the chlorophyll during arid, relatively dormant seasons (Munné-Bosch and Alegre 2000), a response that is absent or less noticeable in polyploids. While leaves of all *Atriplex* species have a covering of bladder hairs, the Diegensis (6x) race is greener and less pubescent, while the Rachelensis (8x) race is more gray-canescent than most species. Prosopidium (8x, 10x), Grandidentatum, and others have very abundant hairs, giving the foliage a whitish or bluish appearance.

Races sometimes also differ in chemical constituents, for instance, in presence or absence of 6-methoxylated flavonols, as already mentioned. While fourwing saltbushes as a group produce abundant, bitter triterpene saponins, these are usually reduced in quantity in races Vallis and Diegensis. The key to races in this report is somewhat a work in progress, and it seems likely that with further observation, characteristics will be identified (for example, winter leaves, or anther size) that can strengthen racial descriptions.

Use of Racial and Taxonomic Designations

As sometimes suggested by molecular phylogenetic studies (Bolger and Simpson 1995; Hardig and others 2000; Setoguchi and others 1998), and as seen in the evolutionary behavior of island taxa (Ganders and others 2000; Soltis and others 1996), speciation may frequently proceed in bursts, yielding groups of taxa with approximately equal relationships to a common ancestor. Where this type of situation exists, it would be phylogenetically misleading to lump arbitrary subsets of the related taxa. Burst-type of speciation has been suggested for North American *Atriplex* (Stutz 1978) generally, and may be suggested in the present study by the surprising number of fourwing saltbush races in lower ploidy levels. Because in fourwing saltbush many of the races recognized here have not been designated as varieties or subspecies, it would seem inappropriate to apply the existing infraspecific categories because the taxonomically unnamed races would then have to be combined with some of the named taxa. This situation requires that all of the evolutionary units of fourwing saltbush be granted taxonomic status, or that formal infraspecific categories be ignored in favor of racial designations, which is what we have chosen to do here. It is our opinion, however, that for utilitarian reasons every evolutionary unit that can be proven to exist ought to be able to have a taxonomic name, although it might not then be desirable to include all infraspecific taxa in a flora designed, for example, for field use. This is an issue that will eventually be dealt with by the plant taxonomic community, as the number of known instances of cryptic speciation is multiplied and as more and more plants are studied in detail. Like some other taxonomic problems, it appears to arise because of fundamental differences in speciation and evolutionary behavior between plants and animals (Cronquist 1988; Grant 1971), especially regarding their propensities for hybridization and polyploidization, and the resulting hazard for systematists of applying inappropriate zoological constructs to plants.

Description of Fourwing Saltbush Races

Fourwing saltbush races are listed alphabetically within ploidy levels, and their taxonomic designations, if any, are listed.

Race Angustifolia (2x)

Taxonomic nomenclature: *Atriplex canescens* var. *angustifolia* (Torrey) S. Watson, Proceedings of the American Academy of Arts, Sciences and Letters 9: 121. 1874.

Type: Valley of the Rio Grande from El Paso to 40 miles below San Elceario, *Wright 1742* (lectotype NY).

Robust shrub 1–3 m in height, leaves narrowly linear, well developed leaves during drier parts of the summer only 1–2 (3) mm wide in most populations, flat or slightly folded. Some growing season leaves usually retained during winter, often with dwarf, down-curved leaves present on short shoots. Fruiting wings usually large, 1–2 cm in width, 6-methoxy flavonols absent.

Angustifolia occurs in New Mexico, westernmost Texas, some localities in Arizona, and in the Mexican States of Chihuahua, Coahuila, and southern Nuevo Leon, often on sand. During warm arid periods, the foliage becomes somewhat yellowish-green, in contrast to the relatively gray-green foliage of Occidentalis (4x) and most other polyploids of *A. canescens*. Mexican plants differ from those in the United States by the production (abundant) of flavonol 3-methyl ethers (table 1). A form of Angustifolia with more robust summer and winter leaves occurs in the vicinity of San Ysidro and Zia Pueblo in New Mexico, and possibly elsewhere.

In spite of an earlier start of anthesis and only partial flowering overlap with Occidentalis, Angustifolia gives rise to numerous intermediate populations at the tetraploid level that may be called "Angustifolia-4x" (see racial description below). These probably arise through production by diploid plants of unreduced gametes that unite with the 2x gametes of tetraploids (2x + 2x = 4x), resulting in rapid one-way introgression, believed to be a common phenomenon in *Atriplex* (see above in Results and Discussion). Although affected tetraploids more or less resemble Angustifolia, conversion of flavonoid pattern has not been observed, the synthetic ability for 6-methoxy flavonols being consistently retained. Leaf length-width ratio and other characters are seldom also precisely those of diploids. Most tetraploids are strongly competitive, and have probably replaced diploids over wide areas.

Race Brevis (2x)

Taxonomic name: none.

Small shrubs to about 0.5 (1) m, growing season leaves small, narrowly linear. Early growing season leaves reaching about 5 mm in width, dry season leaves only 1–2 (3) mm in width. Winter foliage of small, folded, down-curved leaves on short shoots, more or less appressed against the stem, the summer foliage leaves being shed (sometimes even in the greenhouse). Fruit including wings usually less than 1 cm in width, 6-methoxy flavonols absent.

Race Brevis is endemic to the west side of the Rio Grande Gorge, in northern Taos County, New Mexico, and southernmost Conejos County, Colorado, on basaltic substrates. It looks like a miniature Angustifolia, short in stature, with small leaves and relatively small fruits. It is distinguished at most seasons from Occidentalis and from introgressed tetraploids in the same area by somewhat narrower leaves and a more yellowish foliage color. Foliage color has been observed to be especially useful at a time in the spring when 4x introgressants are actively growing, but Brevis is still in dormancy. Both of them flower at approximately the same time.

Like Angustifolia, Brevis appears to cause modification of adjacent tetraploid populations by one-way introgression, and numerous dwarf tetraploids are found in northern Taos County and in San Luis Valley, Colorado. More study is needed on individual and seasonal variation occurring in zones of introgression to better distinguish tetraploid variations from diploids at all times of year.

Brevis differs markedly from Angustifolia in climatic tolerance. San Luis Valley, the habitat of Brevis, is altitudinally high, about 2,100 to 2,400 m (7,000–8,000 ft) and, therefore, exceptionally cold in the winter. Brevis has distinctive winter foliage, while Angustifolia usually does not seem to, although more years of observation are needed. Angustifolia is sufficiently cold sensitive that plants from several sources all winter killed at Provo, Utah, at an elevation of less than 1,500 m (5,000 ft).

Race Garrettii (2x)

Taxonomic names: *Atriplex garrettii* Rydberg, Bulletin of the Torrey Botany Club 39: 312. 1912. *Atriplex canescens* ssp. *garrettii* (Rydb.) Hall & Clements, Carnegie Institute of Washington, Publ. 326: 344. 1923. *Atriplex canescens* var. *garrettii* (Rydb.) Benson, American Journal of Botany 30: 326. 1943.

Type: USA, Utah, Grand County: vicinity of Moab, *Rydberg & Garrett 8465* (holotype NY, isotypes US, UT, photograph POM).

Small bushes, usually about 0.3 m or less in height, leaves oval to obovate, fruiting wings well developed, 6-methoxy flavonols absent.

Race Garrettii is found on slopes on saline shale and mixed sandstone-shale, stratigraphically below the Navajo Sandstone, in canyons of the Colorado River drainage in southeastern Utah. After the spring growing season, the foliage normally becomes a rather bright yellowish-green. Garrettii is closely related to the tetraploid race Navajoensis (*A. garrettii* var. *navajoensis*), of similar foliage color, but taller and with longer and slightly narrower leaves, evidently a derivative of hybridization and one-way introgression involving races Garrettii (2x) and Occidentalis (4x).

Race Gigantea (2x)

Taxonomic name: *Atriplex canescens* var. *gigantea* Welsh & Stutz, Great Basin Naturalist 44: 189. 1984.

Type: Utah, Juab County: Lynndyl sand dunes T35S R4W, *Welsh & Moore 5126* (holotype BRY).

Large bushes, length-width ratio of summer leaves greater than 10:1, leaf width occasionally reaching 1 cm. Some smaller leaves of the summer foliage retained in winter (although more observation is needed), with small short-shoot leaves of winter morphology also present. Fruits large, to about 2 cm in width including wings, 6-methoxy flavonols absent.

Endemic to the Little Sahara Dunes, Juab County, Utah. Tetraploid plants of race Occidentalis grow on shallower, more stabilized sand at this location, with plants of Gigantea occurring only on the active dunes (Stutz and others 1975). The yellowish-green cast often seen in diploids is weaker but still slightly visible, outside of the spring season of active growth. Little or no hybridization occurs between Gigantea and Occidentalis because of a disjunction in flowering time, Gigantea flowering much later than sympatric Occidentalis.

Race Linearis (2x)

Taxonomic names: *Atriplex linearis* S. Watson, Proceedings of the American Academy of Arts, Sciences and Letters 24: 72. 1889. *Atriplex canescens* ssp. *linearis* (S. Watson) Hall & Clements, Carnegie Institute of Washington, publ. 326: 344. 1923. *Atriplex canescens* var. *linearis* (S. Watson) Munz, Manual of Southern California Botany 141: 598. 1935.

Type: Mexico, Sonora: in alkaline soil about Guaymas, *Palmer 235* (lectotype GH).

Bushes low except in unusually favorable sites, commonly about 0.3 m in height, foliage slightly bluish compared to other *Atriplex* (fruits and foliage sometimes blackish in dried specimens), leaves linear, mostly 3 (7) mm wide or less. Fruiting wings deeply toothed or lobed, very small and reduced to wing-ridges, or larger and irregular. Fruit body sometimes hardened and swollen. Fruits, including wings usually 5–7 (10) mm wide or less, mostly sessile but varying within a plant from sessile to short pedicellate, or rarely long pedicellate. Fruiting beaks more or less prominent (the end of the paired fruiting bracts that extend beyond the winged part of the fruit), entire, or occasionally 3-toothed, 6-methoxy flavonols weak or absent.

Plants of this race grow in alkaline or low-lying areas of the Sonoran Desert of California, Baja California, Arizona, and Sonora. Linearis bears a strong superficial resemblance to the 12x race Macilenta (they are combined in Brown 1956), but can be distinguished by foliage color, and the short or absent fruiting pedicels, and relatively prominent beak of Linearis. The sometimes spongiform fruit body may suggest a phylogenetic connection of Linearis to *Atriplex acanthocarpa* of the Chihuahuan Desert.

Race Piochensis (2x)

Taxonomic name: none.

Moderate sized shrub, 1 to 1.5 m high, and as in Race Angustifolia, leaves during the drier growing season narrowly linear. Leaves of winter foliage on short shoots, small, often folded, but mostly not reflexed, 6-methoxy flavonols absent.

Piochensis occurs in southern Lake Valley in eastern Lincoln County, Nevada, at elevations of 1,500 m (5,000 ft) or greater, with Wyoming big sagebrush or pinyon-juniper. It shows little of the yellowish color often seen in diploids. Introgressed tetraploids are widely distributed in the same area.

Tetraploids with very long and narrow leaves are found at Overton and Valley of Fire State Park, Clark County, Nevada, 195 km to the south, and may be evidence of a wider distribution for Piochensis in the past. In addition, a small population of diploids fairly similar to Piochensis in leaf color and winter foliage have been found on a sandy reclamation site near Tuba City, northern Arizona (Glenn and others 1998). Although the seed sources (which included *A. canescens*) for the reclamation are unknown, morphological variation suggestive of fairly widespread introgression into Occidentalis in the area indicates that the Piochensis-like plants are native and not just a recent introduction.

Tetraploid populations or individuals having longer and narrower leaves are also occasionally encountered in northwestern New Mexico. However, Angustifolia occurs along roadsides in that region, and so either it or Piochensis could be responsible. In any case, it seems possible there are other populations of Piochensis not discovered yet. Their location might be revealed by the occurrence of Piochensis-like variation among plants of Occidentalis in the locality.

Race Stewartii (2x)

Taxonomic names: *Atriplex stewartii* I.M. Johnston, Journal of the Arnold Arboretum 22: 110. 1940. *Atriplex acanthocarpa* ssp. *stewartii* (I.M. Johnston) Henrickson, Southwestern Naturalist 33: 457. 1988.

Type: Coahuila, Llano de Guaje: margin of playa at base of Lomas del Aparejo, abundant, erect globose bush 10–16 in. tall, August 28, 1940, *Johnston & Muller 777* (holotype GH).

Suffrutescent plant, leaves narrowly linear to oblong, margins of larger leaves often broadly and shallowly toothed and wavy. Fruit four-winged, wings well developed, 6-methoxy flavonols absent.

Stewartii occurs in el Bolson de Mapimí (Mapimi Basin) in western Coahuila, Mexico. Vegetatively this plant resembles *Atriplex acanthocarpa,* but the four-winged fruits suggest relationship to *A. canescens*. Winged fruits might have come about either by hybridization of *A. acanthocarpa* and *A. canescens*, giving rise to Stewartii as a hybrid derivative, or alternatively, four wings may have been a plesiomorphic character within ancestors of a group consisting of *A. canescens* and most of the North American suffrutescent species, for example *A. acanthocarpa*, *A. gardneri*, and *A. falcata*. Observation of breakdown of the four-winged character in *A. canescens* hybrids suggests that the winged character is multigenic, with individual loci producing wing fragments or tubercles by themselves. Tubercles on fruiting bracts are common in all of the suffrutescent members of this group, although they are unusually elongated and spine-like when present in *A. acanthocarpa*.

Race Angustifolia-4x (4x)

Taxonomic names: none.

Plants more or less resembling Angustifolia (2x), at least at some times of year, but also somewhat intermediate between that and Occidentalis (4x), 6-methoxy flavonols present.

Angustifolia-4x is common in New Mexico, apparently because of active or previously occurring 2x–4x hybridization. Plants referable to this race are also found in the Sonoran Desert and occasionally in northern Arizona and southern Nevada, suggesting a wider distribution of Angustifolia (2x) or the closely related Piochensis (2x) in former times. However, they seem to be rare or absent in Mexican portions of the Chihuahuan Desert, apparently the ancestral home for Angustifolia (2x).

Race Aptera (4x)

Taxonomic names: *Atriplex aptera* Nelson, Botanical Gazette 34:356. 1902. *Atriplex canescens* ssp. *aptera* (Nelson) Hall & Clements, Carnegie Inst. of Washington, publication 326: 343, pl. 58. 1923. *Atriplex canescens* var. *aptera* (Nelson) C. L. Hitchcock, Vascular Plants of the Pacific Northwest 2: 186. 1964.

Type: Wyoming: Laramie, September, 1901, *Elias Nelson 738* (holotype PH).

Plants mostly low growing, leaves shorter and wider than in races Occidentalis or Canescens. Fruits usually small, 5–7 (10) mm in width, fruiting wings lacerate or lobed, wings often irregular in the sense that some of the wings may be only partial, and that wing fragments may sometimes grow between normal wing positions, 6-methoxy flavonols present.

Aptera occurs in Alberta, Saskatchewan, Montana, the Dakotas, eastern Wyoming, and northwestern Nebraska of the western Great Plains. The frequently irregular wings of Aptera are similar to those seen in the hybrids of wingless species with fourwing saltbush, both as observed in nature and as produced synthetically. Aptera is believed to have the parentage of race Occidentalis x *Atriplex gardneri*. There is a more or less clinal variation from robust in the south to slender in the north in Aptera that seems to reflect a series of separate origins or hybridizations, involving in the south *A. gardneri* var. *gardneri*, and in the north (mostly Canada) *A. nuttallii* in the sense of Bassett and others (1983). The latter might best also be considered a variety of *A. gardneri*.

Race Bonnevillensis (4x)

Taxonomic names: *Atriplex bonnevillensis* C. A. Hanson, Studies in Systematic Botany 1:1. 1962. *Atriplex canescens* var. *bonnevillensis* (C. A. Hanson) Welsh, Great Basin Naturalist 44: 190. 1984.

Type: Utah: Millard County, Desert Range Experiment Station, dry lake bed 1.5 miles northeast of headquarters, *Hanson 356* (holotype BRY, isotypes K, GH, POM, UC, US).

Plants low growing, fruiting wings lobed or laciniate, often irregular. Fruits small, usually about 5–7 mm or less in width, highly variable within and between plants, occasionally wingless, then often resembling those of *Atriplex tridentata*, with the paired fruiting bracts having three or more teeth*,* 6-methoxy flavonols present.

Bonnevillensis is found in a few isolated locations in the eastern Great Basin desert. The known populations are in bottomlands or near populations of *Atriplex tridentata*. It is of evident hybrid origin, by race Occidentalis crossing with a suffrutescent species. Hanson (1962), the descriptor, suggested *A. falcata* (2x except for one known 4x population in central Nevada), a relatively uncommon taxon of valley bottoms and slopes with fruiting bracts fusiform and untoothed, but usually tuberculate, as the second parent. However, as is the case with some other diploid suffrutescent species that rarely hybridize, natural hybrids involving diploid *A. falcata* are seldom observed. A species more often hybridizing, and more acceptable on the basis of bract dentition, is *A. tridentata* (mostly 6x), a bottomland species with bracts having side teeth or at least “shoulders.” Origin from the latter would most likely have required the difficult derivation of tetraploid individuals by segregation of euploid gametes (2x) from 5-ploid hybrids (2x + 3x = 5x), while euploid gametes (3x) appropriate for derivation of hexaploid individuals should be equally frequent, as confirmed by Stutz and others (1979). Furthermore, since the presence of occasional hexaploid individuals in tetraploid Occidentalis, as commonly observed, should allow facile introgression at the hexaploid level, a hexaploid overall outcome should be strongly favored for hybridization and introgression between race Occidentalis and *A. tridentata*. The tetraploid chromosome number of Bonnevillensis is, therefore, surprising. Perhaps, however, the circumstance of an overwhelming preponderance of plants of Occidentalis compared to those of *A. tridentata* would be sufficient to tip the balance towards tetraploidy in spite of these factors. A possible scenario is as follows: given a small population of *A. tridentata* (6x) receiving intense pollen rain of race Occidentalis (4x), much of the reproductive capacity of the hexaploids would be taken up with production of sterile pentaploid hybrids, so that they would seldom reproduce. The pentaploids would produce occasional 2x and 3x euploid gametes, and so, under the pollen rain from tetraploids, their relatively rare offspring would be mostly tetraploid and pentaploid (2x + 2x = 4x; 3x + 2x = 5x). After the original hexaploid plants had reached the end of their lifespans, only pentaploid and tetraploid plants would remain. The newly formed tetraploid offspring should reproduce more abundantly, in comparison with the meager reproductive ability of the mostly sterile pentaploids. When the pentaploids in turn had dwindled and died out, the population would then consist entirely of introgressants at the tetraploid level. These would continue to receive genetic influence from the Occidentalis pollen rain as long as the population of Occidentalis continued to exist nearby, which continues to be the case at most of the Bonnevillensis sites. Another much simpler alternative for the origin of Bonnevillensis could have been by hybridization of Occidentalis with the less common tetraploid race of *A. tridentata*.

Race Canescens (4x)

Taxonomic names: *Calligonum canescens* Pursh, Flora Americae Septentrionalis 370. 1814. *Atriplex canescens* (Pursh) Nutt., Genera of North American Plants 1:197. 1818.

Type collection: South Dakota: Lyman County, Big Bend of the Missouri, *Lewis on Sept. 21, 1804* (holotype PH).

Low shrubs or suffrutescent, spreading through root sprouting, sometimes to 20 x 20 m. Single-sex clones visible where plants are sufficiently far apart, otherwise sexes intermingling. Leaves somewhat longer and narrower than those of race Aptera, with which there may be some intergradation, 6-methoxy flavonols present.

Found on badlands and shale, mostly along the Missouri River. Both race Aptera and race Canescens occur as localized, widely separated populations, and may have gained their present distributions at a time of greater aridity, when competition from grasses was less.

Race Cunescens (4x)

Taxonomic names: none.

Low shrubs, about 1–2 dm in height, resembling Occidentalis, but with fruits having reduced or missing wings fairly common, 6-methoxy flavonols present.

Found in Carbon and Emery Counties, Utah. Cunescens may have arisen as a segregant from the hybridization Occidentalis x *Atriplex cuneata,* the latter a common species in the Colorado Plateau, and hence the name “Cunescens.”

Race Mexicana (4x)

Taxonomic names: none.

Bush size and leaf form are variable between populations, although generally resembling race Occidentalis, 6-methoxy flavonols absent.

The presence of Mexicana has been documented by flavonoid and chromosome number samples, from Entronque San Roberto in southern Nuevo Leon, to at least as far as the city of San Luis Potosi, but its distribution needs further study. There appears to be wide morphological variation between presently known locations, suggesting that it contains more than one phylogentic unit. Shorter forms may have given rise to the hexaploid race Prostrata of southern Nuevo Leon. Unlike the more northerly tetraploid Occidentalis, it exhibits a 6-methoxy flavonol negative flavonoid pattern, like the Sonoran and Chihuahuan Desert higher polyploids (table 1). It would, therefore, be a likely candidate as their ancestor at the tetraploid level. Probably, tetraploids of this flavonoid type were once somewhat more widespread, but have been overwhelmed genetically by introgression from Occidentalis.

Race Navajoensis (4x)

Taxonomic names: *Atriplex navajoensis* C. A. Hanson, Studies in Systematic Botany 1: 3. 1962. *Atriplex garrettii* var. *navajoensis* (C. A. Hanson) Welsh & Crompton, Great Basin Naturalist 55: 326. 1995.

Type: Arizona: Coconino County, east side of Navajo Bridge (abundant), *C. A. Hanson 388* (holotype BRY, isotypes K, GH, POM, UC, US).

Low shrub to 0.5 m in height, usually 1–2 dm in height exclusive of the inflorescence. Leaves to about 1 cm wide, obovate to obcuneate, 6-methoxy flavonols variably present.

Found on the Vermillion cliffs of Coconino County, Arizona, for a few miles in each direction from Lee’s Ferry. As suggested by the describer, this entity appears to have had the hybrid origin Occidentalis x Garrettii. As would be expected, there is a strong resemblance between Garrettii and Navajoensis, and there is variation in the direction of Garretti in Navajoensis populations near the Colorado River at Lee’s Ferry (Stutz and Sanderson, unpublished data on file at Brigham Young University). Hybridization with Occidentalis continues at the present time at Lee’s Ferry.

Race Occidentalis (4x)

Taxonomic names: *Pterochiton occidentale* Torr. & Frem., Rep. exped. Rocky Mts. 318. 1845. *Atriplex canescens* var. *occidentalis* (Torr. & Frem.) Welsh & Stutz, Great Basin Naturalist 44: 188. 1984.

Type: Utah: “probably from the borders of the Great Salt Lake,” *Fremont in 1843* (holotype NY).

Woody shrub 0.75–1.5 (2) m in height, leaves linear oblanceolate or linear ovate, the smaller often folded, apices acute or obtuse. Distinctive winter foliage of small, reflexed-appressed leaves occurring in many populations. Fruiting beak small or absent, fruiting wings entire or somewhat dentate, usually variable within a population, fruit usually 0.7–1.0 cm wide, 6-methoxy flavonols present.

This race is vigorous and widespread, occurring in the Western United States and Northern Mexico. It tolerates a variety of substrates, although sometimes demonstrating a preference for sand. It has been reported that spreading by root sprouts occurs in occasional plants in some New Mexican populations (Barrow 1997). Occidentalis plants are erect, woody shrubs, in contrast to those of race Canescens on the Missouri River. Plants of most populations of Occidentalis resprout from the roots when cut off or burned, but have not been otherwise observed to reproduce by rootsprouting.

Race Diegensis (6x)

Taxonomic name: none.

Moderate to large shrubs, leafy. Foliage color greenish, usually rather dark, pubescence relatively thin, 6-methoxy flavonol positive.

All our chromosome counts for the Pacific Coast from Los Angeles to the border between Baja California Norte and Baja California Sur have been hexaploid, and flavonoid samples have shown the plants to be 6-methoxy flavonol positive. Flavonoid pattern and morphological similarity would suggest a relationship of hexaploid Diegensis with the widespread tetraploid race Occidentalis, or perhaps with Angustifolia-4x or Vallis 6x. More study is needed regarding distribution and characteristics of this race.

Race Nana (6x)

Taxonomic names: none.

Low shrubs, most often 2 dm tall or less, although sometimes taller, depending on genotype and moisture availability. Fruits small, 5–7 mm wide including wings, highly variable within and between plants. Fruiting wings laciniate and often irregular with some of the wings incomplete or with wing fragments growing in the areas between the normal four wings, or wings in some individuals reduced to small ridges on the fruit, or else absent, 6-methoxy flavonols are produced in a minority of plants.

Nana occurs in southern Eureka and northern Nye Counties in Little Smokey Valley and in the Black Rock volcanic area. Its enormous variability and its intermediacy between *Atriplex canescens* and the suffrutescent species indicate it is of hybrid origin. In comparing Nana to the two *A canescens* races present in the area that might have participated in its origin, failure to detect 6-methoxy flavonols in most plants suggests Race Nevadensis (6x) as the fourwing saltbush parent rather than Occidentalis (4x). The suffrutescent parent of Nana might have been *Atriplex falcata* (2x, 4x) or *A. tridentata* (4x, 6x). Wingless fruit variants mostly have fruiting bracts that are toothed or have "shoulders," ordinarily indicative of *A. tridentata* influence. However, there is a widespread entity of apparent falcata-tridentata parentage in eastern Nevada (*A. anomala*, 6x) that may be a more likely suffrutescent ancestor.

As noted in the key there is a population of plants similar to some variants of Nana in Buena Vista Valley below Unionville, Pershing County, that may be derived from the hybridization Nevadensis x *A. tridentata*. DNA analysis would be desirable to definitively determine origins of the various hybrid taxa, including Bonnevillensis (4x), Nana (6x), and *A. nuttallii* according to Stutz (6x).

The latter is not treated here because its fruits have only irregular wing segments and tubercles, not four definite wings. Flavonoids (consistently 6-methy flavonol positive) would favor Occidentalis rather than Nevadensis as the fourwing saltbush ancestor of *A. nuttallii*, while instances of sympatry and intergradation by *Atriplex tridentata* would suggest that species as another major contributor.

Race Nevadensis (6x)

Taxonomic name: none.

Shrub slightly smaller than Occidentalis, usually 3–6 dm in height, fruiting wings usually more deeply toothed than those of Occidentalis, primary (not clustered) leaves of the male inflorescence usually 5–7 mm wide or more, in contrast to those of Occidentalis in Nevada, which are more often less than 5 mm in width, 6-methoxy flavonol negative.

Found in the borders of the Mojave Desert in western and central Nevada. Occidentalis is found both to the north and to the south of the zone occupied by Nevadensis. The flavonoid constitution of race Nevadensis suggests derivation from the tetraploid race Mexicana, currently limited to central Mexico, rather than from Occidentalis, the widespread tetraploid of northern Mexico and the Western United States.

Race Occidentalis-6x (6x)

Taxonomic name: none.

Similar to Occidentalis (4x), but leaves wider.

Several isolated hexaploid populations are known from southern Arizona and other areas. Since populations of tetraploid Occidentalis frequently contain a few hexaploid individuals, the formation of hexaploid populations from these should take place readily. The relatively southern distribution of hexaploid populations suggests they may be inherently less cold tolerant than tetraploids. More study is needed to compare Occidentalis-6x, Diegensis, and Vallis, which in view of their 6-methoxy flavonol-positive flavonoid patterns, are all related to Occidentalis (4x).

Race Prostrata (6x)

Taxonomic names: none.

Low plants hedged by heavy grazing, most only 1–2 cm in height, but doubtlessly capable of growing somewhat taller under more favorable circumstances, 6-methoxy flavonol negative.

Found in the valley of Entronque San Roberto and La Paz, about 50 miles southbound from Saltillo on Mexico Federal Highway 57. Prostrata usually grows with grasses, also very close cropped. A similar to much taller tetraploid found in the same valley and in other areas to the south is designated "Mexicana."

Race Rachelensis-6x (6x)

Taxonomic names: none.

Shrub, commonly 0.5 m in height or less. Primary inflorescence leaves do not seem to be retained into summer and autumn as in Nevadensis, larger foliage leaves wider than those of Occidentalis. Winter leaves also seem to be slightly wider than those of Nevadensis when they are viewed side by side, 6-methoxy flavonol positive.

Found on lower slopes in Sand Springs Valley, Lincoln County, Nevada, where the town of Rachel is located (upper slopes sometimes have Occidentalis). A possible origin for this entity might be Rachelensis (8x) x Occidentalis (4x + 2x = 6x). Rachelensis-6x closely resembles the octoploid except that it is less gray-canescent. It grows a little above the octoploid in the valley and is more abundant.

Race Tooelensis (6x)

Taxonomic names: none.

Shrubs to 0.5 m in height, leaves averaging wider than those of tetraploid Occidentalis, 6-methoxy flavonol positive.

Found on both sides of Utah Highway 112 in a restricted area between the towns of Tooele and Grantsville, Utah, it is threatened by agriculture and urbanization. This is an area of silt dunes that were active in producing dust storms during the 1930s due to drought and overgrazing. The area was rehabilitated by the CCC and planted with seeds of *Atriplex canescens,* said to have come from a warehouse in Colorado. It is possible that the seeds may have been mostly those of race Vallis (6x). Tooelensis differs from Vallis in flowering until late in the summer, and probably in its climatic tolerances. It is observed to hybridize with *Atriplex tridentata* (6x), which may, therefore, have contributed genetically to its origin. A somewhat different possibility is that Tooelensis was formed more anciently by hybridization of Occidentalis and *A tridentata*. Presence of spontaneous hexaploid individuals within Occidentalis could have allowed introgression of fourwing saltbush traits into an *A. tridentata* population, which in an unusually favorable situation (namely, a very small population of *A. tridentata* surrounded by abundant Occidentalis) could have driven introgression far in the direction of fourwing saltbush. The formation of mostly sterile pentaploid hybrids (2x + 3x = 5x), from which occasional euploid derivatives at the hexaploid or tetraploid levels might be expected (Stutz and others 1979), could have also contributed. Because the area of occurrence was observed to be devoid of vegetation in the 1930s, origin from race Vallis seems more likely.

Race Vallis (6x)

Taxonomic names: none.

Shrubs, usually shorter than those of race Occidentalis, often less than 0.5 m in height, flowering later than other races in the same area, forming large stands. Leaves averaging wider than those of Occidentalis (4x), foliage appearing slightly darker gray, 6-methoxy flavonol positive.

Found in bottomlands along the Rio Puerco, the Rio Grande as far south as west Texas, and at the south of White Sands and Alamogordo. There are also populations appearing to be Vallis between Las Cruces, New Mexico, and southeastern Arizona, but their chromosome number in most cases has not been determined.

Vallis can easily be distinguished from other fourwing saltbushes in central and southern New Mexico because of its distinctively later flowering time (June rather than May). Flavonoid composition would suggest a derivation from Occidentalis.

Race Cuyamaensis (8x)

Taxonomic names: none.

Shrubs 1–2 m in height, leaves averaging larger than those of Occidentalis, fruiting wings with large toothlike lobes, 6-methoxy flavonol negative.

Found in lowlands near the river in Cuyama Valley, Kern County, California. Occidentalis (4x) is also locally present but seems to prefer slopes. Flavonoids suggest that Cuyamaensis is not affiliated with Occidentalis, but with Mexicana (4x), Nevadensis (6x), and the Mexican higher polyploids.

Race Obtusifolia (8x)

Taxonomic names: *Atriplex canescens* var. *obtusifolia* Sanderson & Stutz, **var. nov.**

Type: Mexico: Coahuila, 5 miles south of Cuatro Cienegas. 28 May 1980, *Stutz 8573* (holotype BRY).

Atriplex prosopidium Johnston affinis sed statura minori, foliis flavo-viride-pallidis non caeruleo-viridi-pallidis.

Shrubs 1–5 dm in height, leaves yellowish-green pallid rather than bluish-green pallid as in Prosopidium, widely oblanceolate to oblong, apically rounded to retuse, fruiting wings crenate to irregularly lobed, sometimes with partial wings, or with wing fragments appearing between normal wing positions, 6-methoxy flavonol positive.

Obtusifolia resembles race Prosopidium (*Atriplex prosopidium*) to a considerable degree in leaf shape, but differs from it in having a shorter stature, a greener, not bluish foliage color, and in producing 6-methoxy flavonols. Prosopidium from its type locality is 10x, but Prosopidium plants from the valley of Monclova are 8x, like Obtusifolia. The sometimes irregular fruits suggest hybridization, perhaps with the suffrutescent species *A. obovata* (6x, 6-methoxy flavonol negative), but since A. obovata is 6-methoxy flavonol negative, 6-methoxy flavonoid production by Obtusifolia would not be expected if those were the only parents. Obtusifolia is found in bottomlands in the valley of Cuatro Cienegas, Coahuila, where it forms a major element of the vegetation.

Race Prosopidium-8x (8x)

Taxonomic names: see Prosopidium (10x).

Shrubs 5–12 dm in height, leaves small, relatively short and broad, the larger usually 15–20 mm in length, apices obtuse to retuse, foliage bluish-pallid, 6-methoxy flavonol negative.

Found in the valley of Monclova. According to the descriptor, it is found mostly north of the city, growing in gypsiferous soils with *Prosopis glandulosa*. The occurrence of Prosopidium-8x may have been reduced by urbanization and agriculture.

A small and isolated 8x population was observed on the west side of the valley that appeared intermediate with Occidentalis. A cross between Occidentalis and 8x

Prosopidium might initially produce a hexaploid that, by way of an unreduced gamete, could backcross to Occidentalis to produce occasional progeny at the octoploid level, probably along with a lot of mostly sterile odd-ploids. The origin of 8x Prosopidium might have been by the hybrid combination Mexicana x *Atriplex obovata*, the latter a 6-methoxy flavonol negative suffrutescent species.

Race Rachelensis (8x)

Taxonomic names: none.

Shrubs 0.2–1 m in height, foliage heavily gray-furfuraceous, 6-methoxy flavonols present.

Found near the playa (dry lake bottom) in Sand Springs Valley near Rachel. A very similar hexaploid is also present at slightly greater elevations around the valley that is not as gray. Both 6x and 8x Rachelensis have 6-methoxy flavonols, suggesting the parentage of race Occidentalis. A possible scenario is that the octoploid originated through hybridization between Nevadensis (6x) and Occidentalis (4x), both found nearby, with an unreduced gamete from Nevadensis (6x + 2x = 8x). Rachelensis-6x in turn might have been generated from hybrids between Rachelensis (8x) and Occidentalis (4x), by the combination of normal gametes from each (4x + 2x = 6x).

Race Prosopidium (10x)

Taxonomic names: *Atriplex canescens* var. *prosopidium* (Johnston) Sanderson & Stutz **comb. nov.** *Atriplex prosopidium* Johnston, Journal of the Arnold Arboretum 24: 227. 1943.

Type: Mexico, Coahuila: south of El Oso, rounded bush 2–3 ft tall, *Johnston 8877* (holotype GH).

Shrubs 0.5–1.2 m in height, leaves oblanceolate to widely oblanceolate or oblong-ovate, fruiting wings prominently paucidentate.

Found in the southern part of the Valle las Calaveras, which begins about 17 km North of the town of Cuatro Cienegas, and also near the town of Sacramento, between Cuatro Cienegas and Monclova. More study is desirable to look for possible differences in morphology between 8x and 10x Prosopidium. Both were examined by the descriptor (Johnston 1943). A possible origin for 10x Prosopidium could have been the combination of a reduced with an unreduced gamete within 8x Prosopidium to produce a 12-ploid, followed by backcross to the 8x (4x + 8x = 12x; 6x + 4x = 10x). Any further crossing would expectedly lead to sterile products, but if isolated, 10x plants could cross among themselves.

Race Laciniata (12x)

Taxonomic names: *Atriplex canescens* var. *laciniata* Parish, Flora of California 1: 442. 1914.

Type: California, Riverside County: Caleb (a town at the southern end of the Salton Sea), *Parish 8256* (holotype CAS, isotype GH, photograph POM).

Large shrubs, 1–2 m in height, leaves usually up to 25 (30) mm in length, the apex commonly rounded. Fruits, including wings up to 1.5 (2) cm wide, usually pedicellate, the wings fimbriately or laciniately cleft or lobed, lobe tips often appearing slightly swollen, fruiting beak with "shoulders" to 3-toothed, relatively inconspicuous, 6-methoxy flavonols absent.

Found in California in the Sonoran and the western Mojave Deserts and in northeastern Baja California Norte, often on sand. Macilenta (12x) is similar, but with smaller fruits. The dissected fruiting wings of Laciniata are suggestive of an origin by hybridization. The most apparent candidate would be *Atriplex polycarpa* (4x, 8x), except that it has the wrong flavonoid composition (6-methoxy flavonol positive). Some other species might be possible but most of them are diploid. The flavonoids of Laciniata (6-methoxy flavonol negative) would suggest race Cuyamaensis (8x), Nevadensis (6x), or Mexicana (4x) as the fourwing saltbush parent, rather than Occidentalis.

Race Macilenta (12x)

Taxonomic names: *Atriplex canescens* var. *macilenta* Jepson, Flora of California 1: 442. 1914.

Type: California, Imperial County: Bluffs of the Alamo, Calexico, *Parish 8258* (lectotype GH).

Medium shrubs, usually 0.5–1 m in height, leaves usually up to 25 mm in length, the apex commonly rounded. Fruits small, often like a laciniata fruit in miniature, width including wings about 5–7 mm, fruiting bracts fimbriately to laciniately lobed, fruiting beak with "shoulders" to 3-toothed, inconspicuous in comparison to the projections of the wings, 6-methoxy flavonols absent.

Found in the Sonoran Desert of California. Fruit and shrub size vary from one place to another and intergrade with Laciniata. Small fruit size and variability are suggestive of hybridization, but leaf shape does not suggest a parent with leaves greatly different than those of Laciniata. Two acceptable candidates might therefore be *Atriplex polycarpa* (4x, 8x), which has *A. canescens*-like leaves in wetter seasons, and race Linearis (2x). *Atriplex polycarpa* 8x might have formed a 12-ploid via an unreduced gamete, and the 12-ploid might then have hybridized readily with Laciniata. In the case of Linearis, a mostly sterile 13-ploid could be produced by union of an unreduced Laciniata gamete plus a normal linearis gamete (12x + x = 13x), and euploid gametes (6x) should then occasionally be produced by segregation. Neither origin seems clearly satisfactory. On the one hand, 6-methoxy flavonols are present in *Atriplex polycarpa,* but not in Macilenta (nor Laciniata). On the other, a very slight genetic contribution from Linearis would hardly seem enough to change the fruit characteristics to the extent seen in Macilenta, unless there was a gene of strong effect involved or the introgression was long recurrent. If Linearis was indeed involved, however, it might explain the sometimes confusing similarity between Linearis and Macilenta.

Race Laciniata-14x (14x)

Taxonomic names: see Laciniata (12x).

Large shrubs, fruits fimbriate to laciniate or coarsely dentate, 6-methoxy flavonols absent.

Known from a few miles east of the Colorado River mouth in westernmost Sonora to the resort town of Golfo de Santa Clara, and perhaps further eastward. Because we did not travel extensively in the Gran Desierto, distributions of Laciniata-14x and Grandidentatum are incompletely known.

Race Grandidentatum (20x)

Taxonomic names: *Atriplex canescens* var. *grandidentatum* Sanderson & Stutz, American Journal of Botany 81: 1045-1053. 1994.

Type: Mexico, Sonora: 25 km east of Puerto Peñasco, *Sanderson 93047*(holotype BRY, isotype MEXU).

Large shrubs, larger leaves usually 15–60 mm in length, slightly to moderately blue-green pallid, 5–10 mm in width, apically obtuse to acute or occasionally emarginated, fruits about 1–2 cm in width, including wings, large-toothed or laciniate, 6-methoxy flavonols mainly absent.

Found along the upper Sonoran coast in the Desierto de Altar and at least the western side of the Gran Desierto, mostly on sand.

As noted in a previous publication (Sanderson and Stutz 1994), Grandidentatum has been observed to hybridize with *Atriplex polycarpa* 8x. This may be the reason for small amounts of 6-methoxy flavonols that can be occasionally detected in Grandidentatum samples.

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Preliminary Key to Fourwing Saltbush Races

1. Plants suffrutescent, stems dieing at the end of the season. Leaves linear to oblong or lanceolate, oblanceolate, the larger often with several teeth along the margin and the margins wavy. El Bolson de Mapimi (Mapimi Basin), Coahuila, Mexico . . . . **Race Stewartii** (2x, 6-methoxy flavonol negative)
1. Plants usually shrubby. Leaf margin teeth very rare, or if more common, leaves roundish and often 1 cm or more wide
 2. Leaves less than 5 times as long as broad, the larger usually 1 cm wide or more. Plants a bright yellowish green during much of the year but green or gray-green during growth, less than 0.5 m in height, growing within a few miles of the Colorado River in Utah or Arizona
  3. Leaves ovate or obovate, mostly less than 3 times as long as broad. Found in drainages above Glenn Canyon Dam in Utah and Arizona . . . . **Race Garrettii** (2x, 6-methoxy flavonol negative)
  3. Leaves obovate to obcuneate, 2 to 4 times as long as broad and about 1 cm wide. Vermillion Cliffs near Lee's Ferry, Arizona . . . . **Race Navajoensis** (4x, 6-methoxy flavonol negative or positive)
 2. Leaves narrower or smaller, plants usually larger. *Atriplex canescens* in the narrower sense, keyed by geographic area, as follows:

Plants of the Pacific Northwest (4x only) . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

Plants of the western Great Plains (4x only)
1. Aboveground stems short lived, plants usually 0.5 m or less in height. Strongly rootsprouting, individual clones often covering many square meters. Found in South Dakota, especially along the Missouri River, on badland soils . . . . **Race Canescens** (4x, 6-methoxy flavonol positive)
1. Aboveground stems woody, persistent, most plants not spreading clonally
 2. Fruit wings small, usually lobed, laciniate or irregular. Fruits including wings, 5–7 (10) mm wide or less. Low plants with wide leaves. Alberta, Saskatchewan, Montana, North and South Dakota, Wyoming . . . . **Race Aptera** (4x, 6-methoxy flavonol positive)
 2. Fruit wings normal in form and size, the margins entire to toothed. Fruits including wings about 7–10 mm wide. Mostly Nebraska southward . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

Plants of Nevada or northern Arizona (2x, 4x, 6x, 8x)
1. Plants of Sand Springs Valley (near the town of Rachel), Lincoln County, Nevada
 2. Larger leaves in the fall usually 5 mm or less in width. Plants of higher elevations around the valley edges, especially along the highway approaching Rachael from the east . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)
 2. Larger leaves in the fall usually more than 5 mm in width. Lower elevations
  3. Gray-canescent plants of low elevations known from the area between the highway and the dry lake bed (playya) . . . . **Race Rachelensis** (8x, 6-methoxy flavonol positive)
  3. Plants of similar appearance but not as gray, growing above the previous on lower valley slopes. Large populations in some areas, especially north of the playa . . . . **Race Rachelensis 6x** (6x, 6-methoxy flavonol positive)
1. Plants of other areas
 4. Length-width ratio of larger leaves about 10:1 or greater during most of the year
  5. Plants growing at elevations of 1,500 m (5,000 ft) or greater in Lake Valley at Pioche, Lincoln County, also known from the vicinity of Tuba City, Arizona . . . . **Race Piochensis** (2x, 6-methoxy flavonol negative)
  5. Plants at lower elevations or other locations. Known from Valley of Fire and Overton, Nevada, and scattered plants in northern Arizona and northwestern New Mexico, intergrading with Occidentalis . . . . **Angustifolia 4x** (4x, 6-methoxy flavonol positive)
 4. Length-width ratio of larger leaves usually below 10:1
  6. Fruiting wings small, fruits to about 5 (7) mm in width including wings, deeply lobed, often irregular in size and sometimes in position. Fruits strongly variable within and between plants, usually including some plants of a population with a few wingless fruits. Found in southern Eureka, and northern Nye Counties. Plants growing in the bottom of northern Buena Vista Valley, below Unionville, Pershing County, may have larger fruits but could perhaps also be classified here. (Not included in the key, because it cannot be said to have four wings, but only wing fragments, is the putative hybrid derivative *Atriplex nuttallii,* in the sense of Stutz (Stutz and Sanderson 1998), of the Humboldt River valley and other locations in the Battle Mountain area) . . . . **Race Nana** (6x, mostly 6-methoxy flavonol negative, with occasional plants positive)
  6. Fruiting wings normal in size, sometimes strongly dentate but extending the length of the fruit and growing in only the four ordinary positions, fruits usually 7–10 mm in width
   7. Larger leaves of the male inflorescence, when under 25 mm in length, 7 mm or more in width in the majority of plants of a population. Anthers mostly 0.75 to 1.00 mm in length. Borders of the Mojave Desert in western and central Nevada . . . . **Race Nevadensis** (6x, 6-methoxy flavonol negative)
   7. Larger leaves of the male inflorescence usually less than 7 mm in width. Anthers usually 0.50 mm in length or less. More generally distributed than Nevadensis (above), both to the north and south . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

Plants of Utah or western Colorado (2x, 4x, 6x)

1. Length-width ratio of larger summer leaves 10:1 or greater. Plants of the Little Sahara Dunes, Juab County, Utah . . . . **Race Gigantea** (2x, 6-methoxy flavonol negative)

Length-width ratio of larger summer leaves less than 10:1

  3. Fruiting wings small and irregular or occasionally absent, fruits, including wings usually 5 (7) mm or less in width. Known from Juab and Millard Counties of western Utah . . . . **Race Bonnevillensis** (4x, 6-methoxy flavonol positive)
  3. Fruiting wings sometimes small or more often normal in size, usually entire to moderately toothed. Fruits, including wings usually 7–10 mm wide
    4. Plants of Tooele County, Utah, between the towns of Tooele and Grantsville on the north and south sides of Utah Highway 112, about 2 miles east of Grantsville. Grayish, shorter plants with wider leaves, flowering until late summer (plants closer to Grantsville are race Occidentalis) . . **Race Tooelensis** (6x, 6-methoxy flavonol positive)
    4. Plants widespread or of other areas
      5. Plants mostly about 2 dm in height or less, of Carbon or Emery County, Utah . . . . **Race Cunescens** (4x, 6-methoxy flavonol positive)
      5. Plants averaging well over 2 dm in height. Widespread . . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

Plants of New Mexico, or San Luis Valley, southern Colorado (2x, 4x, 6x)

1. Plants of San Luis Valley, Colorado, or Taos County, New Mexico
  2. Plants generally over 0.5 m in height . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)
  2. Plants mostly about 0.5 m or less in height
    3. Width of largest summer leaves 2–3 mm during seasons of drought, foliage usually yellowish. Occurring west of the Rio Grande in Taos County, New Mexico, and south of Antonito in Conejos County, Colorado . . . . **Race Brevis** (2x, 6-methoxy flavonol negative)
    3. Width of larger leaves usually about 5 mm or greater except in winter, foliage more greenish. More widespread than the previous . . . . **Occidentalis x Brevis introgressants** (4x, 6-methxy flavonol positive)

1. Plants not of San Luis Valley or Taos County, New Mexico
  4. Length-width ratio of larger leaves about 10 or greater
    5. Larger leaves at some seasons only 2–3 mm in width in most populations, foliage with a pronounced yellowish color in dry hot seasons. Typically growing on sand dunes or mesquite hummocks, usually on uplands above tetraploids and hexaploids; however, mixed 2x-4x populations are rather common in the Rio Grande Valley . . . . **Race Angustifolia** (2x, 6-methoxy flavonol negative)
    5. Larger leaves usually wider than 2–3 mm at all seasons, foliage color not as yellow. Leaf length-width ratio not much exceeding 10:1, usually less at some seasons. Occurring on a variety of substrates . . . . **Race Angustifolia-4x** (4x, 6-methoxy flavonol positive)
  4. Leaf length width ratio less than 10, larger leaves wider than 2–3 mm during all seasons. Foliage more consistently grayish during all seasons
    6. Plants with new flowers appearing only in June, if not of northern New Mexico. Low bottomland plants of a slightly darkish foliage color . . . . **Race Vallis** (6x, 6-methoxy flavonol positive)
    6. Plants with new flowers appearing in May, except at higher elevations in the north. Larger plants, often occurring on slopes, with a somewhat more yellowish dry-season foliage color than the previous . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

Plants of California, southern Arizona, Baja California, or Sonora (2x, 4x, 6x, 8x, 12x, 14x, 20x)

1. Length-width ratio of larger leaves about 10:1 or greater
  2. Fruits with small or irregular wings, width, including wings usually 5 (10) mm or less. Bottomland plants, the foliage usually with a slight bluish cast. Fruits usually not pedicellate, but prominently beaked . . . . **Race Linearis** (2x, 6-methoxy flavonol negative)
  2. Fruit with well developed wings, width including wings usually 7–10 mm or more. Plants usually of well-drained sites, fruits pedicellate, fruiting beaks usually obscure or absent
    3. Plants of Imperial Valley, California, and the western Sonoran and Mojave Deserts . . . . **Race Angustifolia-4x** (4x, 6-methoxy flavonol positive)
    3. Plants of the Arizona portion of the Sonoran Desert, especially south of Tucson . . . . **Race Angustifolia** (2x, 6-methoxy flavonol negative)

1. Length-width ratio of larger leaves mostly less than 10:1
  4. Fruit wings usually entire to moderately toothed
    5. Plants of the Pacific Coast of Baja California Norte and California, below Los Angeles . . . . **Race Diegensis** (6x, 6-methoxy flavonol positive)
    5. Plants of other areas
      6. Leaves narrower at a given season. Plants widespread . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)
      6. Leaves wider by comparison. Isolated populations . . . . . . **Race Occidentalis-6x** (6x, 6-methoxy flavonol positive)
  4. Fruiting wings of all or most plants having large teeth, or prominently lobed or incised

6. Plants of Cuyama valley, California, mostly in bottomlands. Fruiting wings with large irregular teeth. (Occidentalis present in the general locality also, on slopes) . . . . **Race Cuyamaensis** (8x, 6-methoxy flavonol negative)

6. Plants of the southern Mojave or Sonoran Deserts

7. Southern California and Baja California Norte

8. Plants usually 1 m in height or more, fruiting bracts normal to large in size, fruits about 7–15 (20) mm in width including wings . . . . **Race Laciniata** (12x, 6-methoxy flavonol negative)

8. Plants usually less than 1 m in height, fruiting bracts small, fruit usually 5–7 (10) mm or less in width, including wings

9. Plants normally 0.5 m in height or less, fruits mostly sessile, foliage with a bluish cast in the field (a few populations with wider leaves will key out here) . . . . **Race Linearis** (2x, 6-methoxy flavonol negative)

9. Plants mostly greater than 0.5 m in height, fruits mostly pedicellate, foliage often pale, but greenish. Apparently intergrading with Laciniata . . . . **Race Macilenta** (12x, 6-methoxy flavonol negative)

7. Coastal northern Sonora

10. West of Gran Desierto . . . . **Race Laciniata 14x** (14x, 6-methoxy flavonol negative)

10. Gran Desierto(?) and Desierto de Altar . . . . **Race Grandidentatum** (20x, 6-methoxy flavonol negative)

Plants of the Chihuahuan Desert of Mexico (2x, 4x, 6x, 8x, 10x)

1. Length-width ratio of larger leaves 10:1 or more, larger leaves during dry seasons usually 2–3 mm in width or less, dry season foliage color markedly yellowish. . . . . **Race Angustifolia** (2x, 6-methoxy flavonol negative)

1. Length-width ratio of larger leaves usually less than 10:1, larger leaves, even during drier seasons, usually over 2–3 mm in width. Foliage color not as strongly yellowish

2. Foliage bluish-green pallid, leaf apices usually rounded, leaves short and fairly wide

3. Plants of Coahuila

4. Plants of Valle Las Calaveras, between the towns of Ocampo and Cuatro Cienegas, or at Sacramento, Coahuila. Pure large stands (where not extirpated by agriculture) or growing with Race Occidentalis . . . . **Race Prosopidium** (10x, 6-methoxy flavonol negative)

4. Plants of the valley of Monclova, Coahuila . . . . **Race Prosopidium-8x** (8x, 6-methoxy flavonol negative)

3. Plants of Chihuahua . . . . Prosopidium? (6x, 6-methoxy flavonol status unknown)

2. Foliage grayish-green or yellowish-green pallid, leaf apices rounded or not

5. Plants of the valley of Cuatro Cienegas, Coahuila. Leaf apices rounded, leaves relatively short and wide, plants usually below 0.5 m in height, forming large uniform stands. Differing from races of Prosopidium by shorter stature and non-bluish foliage color . . . . **Race Obtusifolia** (8x, 6-methoxy flavonol positive)

5. Plants widespread or of other localities, leaves not particularly short and wide

6. Plants of southern Nuevo Leon or San Luis Potosi

7. Plants 2 or 3 dm in height or less, most often only a few cm, growing in the valley bottom from Ent. San Roberto for about 20 km northward . . . . **Race Prostrata** (6x, 6-methoxy flavonol negative)

7. Plants of various populations ranging in stature from very low like Prostrata to much taller, growing from La Paz southward to about 20 km north of Ent. San Roberto, and from San Roberto to at least as far as the city of San Luis Potosi. . . . . **Race Mexicana** (4x, 6-methoxy flavonol negative)

6. Plants more northern . . . . **Race Occidentalis** (4x, 6-methoxy flavonol positive)

A Molecular Phylogeny for *Cercocarpus* H.B.K. (Rosaceae) Using the External Transcribed Spacer of the Nuclear Ribosomal Repeat

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Abstract—*Cercocarpus* H.B.K. (Rosaceae) taxa are important members of the plant communities of the western states and Mexico, yet the systematics of this genus are unknown primarily from lack of clear morphological delimitations between taxa. In recent years, molecular data have proven useful for resolving relationships among species and the diversity within species that have otherwise remained elusive. We will report here preliminary data on the phylogenetic utility of two noncoding regions within the nuclear ribosomal DNA (nrDNA) for *Cercocarpus*; the internal transcribed spacer (ITS) region and the external transcribed spacer (ETS) region. The ITS and ETS were amplified and sequenced in five individuals representing four *Cercocarpus* taxa. Maximum parsimony and maximum likelihood phylogenies were created from the two aligned data sets and compared. We found that the ETS has considerably more phylogenetically informative sequence variation than the ITS, which had almost no signal. Further sampling of ETS sequences in *Cercocarpus* taxa produced four main ETS types. The four ETS types were alignable only in the extreme 5' and 3' regions of the ETS sequence. Large regions of the ETS sequences were unalignable between different ETS types. Phylogenetic analysis of a reduced data set including just the regions in common between ETS types suggest that the different ETS types in *Cercocarpus* diverged prior to the origin of the genus, making them paralogous. This deep coalescence requires that a single ETS type be used for reconstruction.

Introduction

Cercocarpus H.B.K. (Rosaceae) is a New World genus composed of montane xerophytic shrubs and trees, found in deserts, chaparral, and mountainous regions of western North America with a center of diversity in northern Mexico. Botanists have paid attention to the ecology and management of *Cercocarpus* in the United States because the evergreen leaves found on most members of the genus have high levels of protein and are an important winter forage for wildlife and livestock in western states (Blauer and others 1975; Davis and Brotherson 1991).

The systematics of *Cercocarpus* are largely unknown; the genus lacks a consensus classification or phylogeny. Since it was first described, *Cercocarpus* has undergone three revisions (Schneider 1905; Rydberg 1913; Martin 1950), each varying widely in the ranks assigned to taxa and the number of species. Much of the current taxonomy of *Cercocarpus* is based on quantitative characteristics involving leaf morphology (Schneider 1905; Rydberg 1913; Martin 1950). Confusion about the number and circumscription of species within *Cercocarpus* arises primarily from the lack of clear morphological delimitations between taxa. Variations in leaf morphology show a continuum within and between taxa, making it difficult to define boundaries among species (Brayton and Mooney 1966; Mortenson 1973). A phylogeny based on leaf characters is poorly supported due to severe homoplasy.

In recent years, molecular data have proved useful for resolving relationships among morphologically similar species and for understanding the diversity within species (Soltis and Soltis 1998 and references therein). A phylogeny and a clear definition of taxa using molecular markers within *Cercocarpus* is critical to an understanding of the evolution and systematics of *Cercocarpus.* Knowledge of the systematics of *Cerocarpus* may enhance its breeding and help prevent undesirable hybridization of species and ecotypes planted in reclaimed areas using bulk seed.

We report here preliminary results on the phylogenetic utility of two noncoding regions within the 18S-26S nuclear ribosomal DNA (nrDNA) repeat for *Cercocarpus*: the internal transcribed spacer (ITS) region and the external transcribed spacer (ETS) region (fig. 1). Both the ITS region and

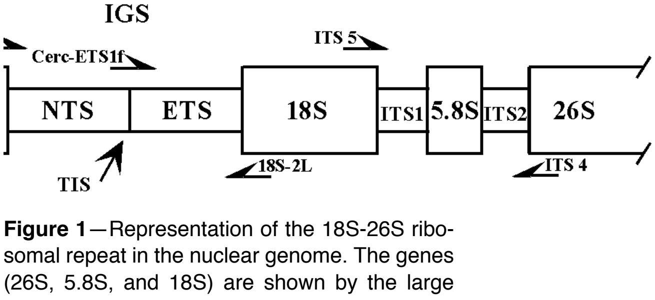

Figure 1—Representation of the 18S-26S ribosomal repeat in the nuclear genome. The genes (26S, 5.8S, and 18S) are shown by the large boxes. Transcription begins at the TIS. Both the ETS and both ITS regions are removed after transcription. The general location and direction of the primers used in this study are shown by arrows and italized text.

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the ETS region have been used with success in phylogenetic reconstruction at the generic and specific level in other plant groups (for example, Baldwin 1995; Bena 1998; Baldwin and Markos 1998; Linder and others 2000). Recently, the ETS has been shown to contain informative variation in groups where ITS does not (Bena 1998; Baldwin and Markos 1998; Linder and others 2000).

Materials and Methods

Taxon Sampling

For this report, we follow the taxonomy of Martin (1950) with the exception of the Mexican taxa, for which we turned to an unpublished treatment by J. Henrickson (personal communication). Twenty-six taxa were sampled (table 1). In six cases more than a single individual represented a taxon. For each sample, DNA was extracted from the collections using a modified CTAB procedure (Doyle and Doyle 1987). Genomic DNA extractions were cleaned using the Elu-quik DNA purification kit (Schleicher and Schuell) prior to PCR amplification.

Amplification, Sequencing, and Analysis of the ITS Region

To test the phylogenetic utility of the ITS region in *Cercocarpus*, we selected five individuals representing four exemplar taxa of *Cercocarpus* (table 1). This sampling strategy was designed to compare the amount of variation observed between very closely related individuals (two individuals of *C. montanus* var. *montanus*) and more distantly related taxa, as determined by recent work on the leaf architecture of *Cercocarpus* by Lis (1992). The ITS region was amplified using the primers *ITS 5* and *ITS 4* (Innis and others 1990). A negative control was also used that lacked template DNA. Fifty microliter PCRs were performed using 30mM Tricine, pH 8.4, 2mM MgCl2, 50 mM KCl, 5 percent acetamide, 100 uM of each dNTP, 1.0 unit of Taq polymerase, and 30 nM of each amplification primer. Twenty ng of template DNA was added and the reactions were overlaid with mineral oil and run on an MJ Research Thermal Cycler programmed for a hot start (95 °C, 5 min; 74 °C, 7 min) and 30 cycles of 94 °C for 30 sec, 50 °C for 45 sec, and 72 °C for 1 min. A final extension of 72 °C for 7 min was also included.

Table 1—Collection and ETS type data for the 26 populations of *Cercocarpus* and *Purshia* analyzed. Collectors: JH-James Henrickson, BVH-Brian Vanden Heuvel, BC-Bonnie Crozier. Vouchers are housed at the University of Texas (TEX).

Taxon	Population no.	Collection location and number	ETS type(s)
C. montanus var. *montanus*	5[a]	Douglas Co., CO BVH 5	1
	8	Platte Co., WY BVH 8	1
	10[a]	Custer Co., SD BVH 10	1
C. montanus var. *glaber*	12	Brewster Co., TX JH 20663	1
	14	Brewster Co., TX JH 20665	1
	15	Brewster Co., TX JH 20666	1
	16	Brewster Co., TX JH 20667	1
	17[a]	Coahuila, MX JH 20439b	1
C. montanus var. *paucidentatus*	1	Tamaulipas, MX JH 19218	1
	27C	Eddy Co., NM BVH 27	1
C. montanus var. *blancheae*	19	Los Angeles Co., CA BVH 123a	2
	20	Los Angeles Co., CA BVH 123b	2
	21	Los Angeles Co., CA BVH 123c	2
	62D	Tulare Co., CA BVH 127a	1
	65C	Tulare Co., CA BVH 127b	2
	65D	Tulare Co., CA BVH 127c	1
C. montanus var. *traskiae*	52B	Los Angelas Co., CA JH 22312	2
C. montanus var. *minutiflorus*	57	San Diego Co., CA JH 22311	1, 2
C. fothergilloides var. *mojadensis*	18[a]	Coahuila, MX JH 13156	2
	66	Coahuila, MX BVH and JH 11824	3
C. fothergilloides var. *medranoanus*	82	Tamaulipas, MX BVH and JH 22444	1, 3
C. macrophyllus	26	Coahuila, MX BC 1034	1, 2
C. rzedowskii	78	Tamaulipas, MX BVH and JH 22446	1
	81	Tamaulipas, MX BVH and JH 22460	4
C. ledifolius var. *intermontanus*	45	Box Elder Co., UT BVH 45	1
C. ledifolius var. *ledifolius*	41	Emery Co., UT BVH 41	1
C. ledifolius var. *intricatus*	25[a]	Garfield Co., UT BVH 45	1
Purshia tridentata	34	La Plata Co., CO BVH 34	

[a] Individuals for which the ITS and ETS were compared.

Three uL of the reaction mixture was run on a 1.5 percent agarose gel in a 0.5X TBE buffer. PCR products were visualized with ethidium bromide under UV light. PCR products were purified (QIAquick PCR purification kit, QIAGEN) and sequenced on an ABI Prism 377 automated sequencer using standard reagents at the Core Facility of the Molecular Biology Institute at the University of Texas. Sequences were proofread and then aligned using Clustal W in MegAlign (DNAstar, 1998), followed by adjustment by eye. Aligned ITS sequence data was used to generate phylogenetic trees in PAUP 4.0.0d64 (kindly provided by David Swofford). Gaps were treated as missing data. Trees were constructed using maximum likelihood and maximum parsimony algorithms with the exhaustive search option. The specific parameters for the ML analysis were unequal transition-transversion rates and empirically determined nucleotide frequencies. Support for the monophyly of groups was evaluated using bootstraping (Felsenstein 1985).

Developing the ETS in *Cercocarpus*

To develop the ETS region for phylogenetic reconstruction in *Cercocarpus*, we amplified the entire intragenic spacer (IGS) of *C. montanus* (collection #5) and *C. intricatus* (collection #25) (table 1) using the primers *1M* and *18S-2L* ((Linder and others 2000)) present in conserved regions of the 26S and 18S genes, respectively (fig. 1), and following the same PCR parameters listed above except an extension time of 2 min. per cycle. We sequenced from the 3' end of the amplified product in both taxa following the same procedures as for the ITS regions. Because the ETS region was too long to sequence with a single primer, we developed internal primers to sequence through the transcription initiation site (TIS). We identified the TIS based on similarity with the TISs in other plant groups. As a result of its role in transcription of the rDNA repeat, the TIS is under strong selection to stay conserved, making it a good choice for priming throughout *Cercocarpus*. We designed *Cerc-ETS1f* (5'-tataaaggggaggcctcatt-3') to include the TIS and have high sequence similarity to both taxa (fig. 1). Using this primer in combination with *18S-2L*, we amplified the ETS reliably for all *Cercocarpus* taxa from which DNA was extracted from fresh material.

The ETS sequence for *Purshia tridentata*, used as the outgroup for this study, was obtained by amplifying the whole IGS as described above for *Cercocarpus*. We then sequenced from the 3' end of the amplified product until we identified the TIS.

For each *Cercocarpus* taxon, one of two strategies was conducted for sequencing the ETS. If the ETS amplification produced a single PCR product, the product was sequenced directly as outlined in the above section. If the ETS amplification produced multiple-length PCR products, we cloned the PCR products using the TOPO-TA cloning kit (Invitrogen). At least 10 colonies were screed for the ETS insert by direct PCR amplification using the same PCR parameters except a 10 min. hot start at 95 °C to lyse the cells. At least two of these amplifications were sequenced for each individual for each ETS length variant.

Comparison of the Phylogenetic Utility of the ITS and the ETS in *Cercocarpus*

The ETS sequences from the same five *Cercocarpus* individuals sampled to test the phylogenetic utility of the ITS were proofread and aligned using Clustal W in MegAlign (DNAstar 1998), followed by adjustment by eye. The five ETS sequences consisted of four ETS type 1 sequences and one ETS type 2 sequence (table 1, fig. 2). Only the 5' and 3' common regions of the ETS sequences (see Reults) were included in the analyses (fig. 2). Maximum parsimony and maximum likelihood analyses were carried out in PAUP 4.0.0d64 as described for ITS.

Alignment and Phylogenetic Analysis of the ETS Types

All ETS sequences, regardless of type, were aligned using Clustal W followed by adjustment by eye. Only regions of the ETS sequences that were alignable between different ETS types were included in the analyses (fig. 2). For ETS type 3 sequences, only the 5' common region was included in the aligned sequence matrix. Only the 3' common region of the ETS sequence of *P. tridentata* was included to serve as the outgroup (fig. 2). Therefore, ETS type 3 sequences placement in the phylogeny is based only on its relationship to the

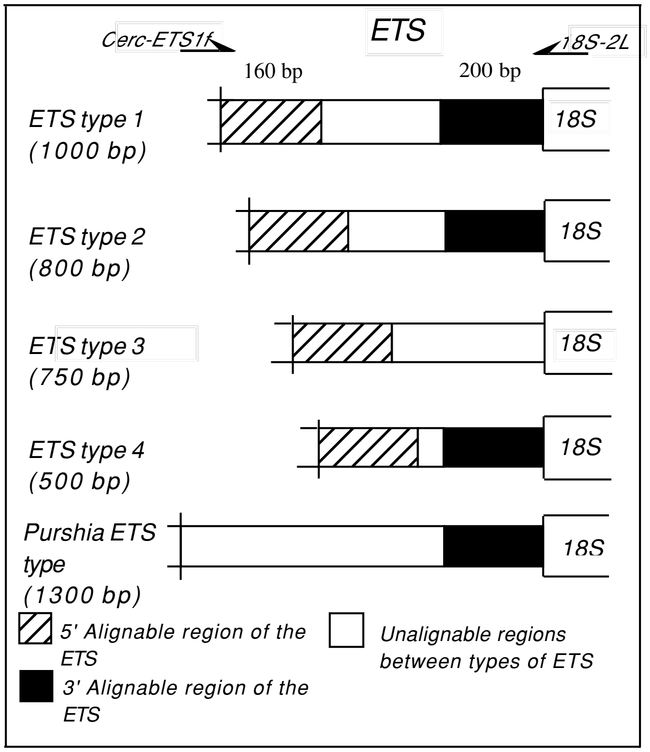

Figure 2—Representation of all four ETS types found in *Cercocarpus* to date and the ETS found in *Purshia tridentata*. Representations begin at the transcription initiation site (TIS) and go to the 18S gene. The hatched boxes indicate the 5' region that is alignable among ETS types. The black boxes show the location of the 3' region that is alignable among ETS types.

other ETS types and not on a direct comparison to the outgroup. The resulting sequence matrix totaled 300 aligned base pairs. Maximum parsimony and maximum likelihood analyses were carried out in PAUP 4.0.0d64 as described for ITS.

Results

Identification of Four ETS Types in *Cercocarpus*

Amplification and sequencing of the ETS region using the primers *Cerc-ETS1f* and *18S-2L* resulted in the identification of four distinct ETSs (table 1, fig. 2). The different ETS types ranged from 1,000 bp to 500 bp in *Cercocarpus* and was 1,300 bp in the outgroup *Purshia*. Three *Cercocarpus* individuals were found to contain multiple ETS types, 16 individuals had ETS type 1 only, four individuals had ETS type 2 only, one individual had ETS type 3 only, and one individual had ETS type 4 only (table 1).

Comparison of the ITS and the ETS Regions

The ITS tree was based on an alignment of 700 bp, which included the ITS1, ITS2, and 5.8S gene (fig. 1). ML and MP analyses produced the same tree topology. Only the MP results are presented here (fig. 3). The MP ITS tree had a length of 2 and very weak bootstrap support for internal branches due to lack of phylogenetically informative variation in the ITS region for the five individuals sampled.

The ETS tree for the same five individuals was based on 360 bp of aligned sequence data in the 5' and 3' common regions (fig. 3). ML and MP resulted in the same tree topology so only the MP results are presented (fig. 3). The ETS tree had a length of 20 steps and considerably higher bootstrap support for internal branches.

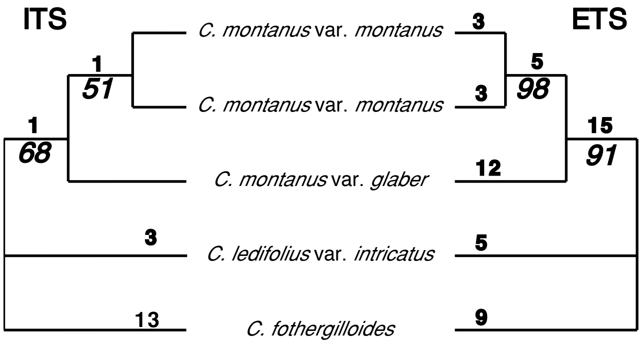

Figure 3—A comparison of MP phylogenies produced from 700 bp of aligned ITS sequences and 360 bp of aligned ETS sequence data. Numbers above branches are the numbers of steps, numbers below are bootstrap values.

Phylogenetic Analysis Using the ETS

The MP analysis of 5' and 3' common regions (360 bp) of 26 individuals of *Cercocarpus* and one individual of *Purshia tridentata* resulted in over 10,000 equally parsimonious trees of length 176. Figure 4 is a 50 percent majority rule consensus tree based upon those trees. Each ETS type formed its own clade, indicating the evolution of the types prior to the origin of the genus. Further, each of the multiple ETS types in *C. montanus* var. *minutiflorus* (pop. 57), *C. fothergilloides* var. *medranoanus* (pop. 82), and *C. macrophyllus* (pop. 26) belonged to their respective "type" clade (fig. 4). ETS type 1 sequences form a well supported clade, which is

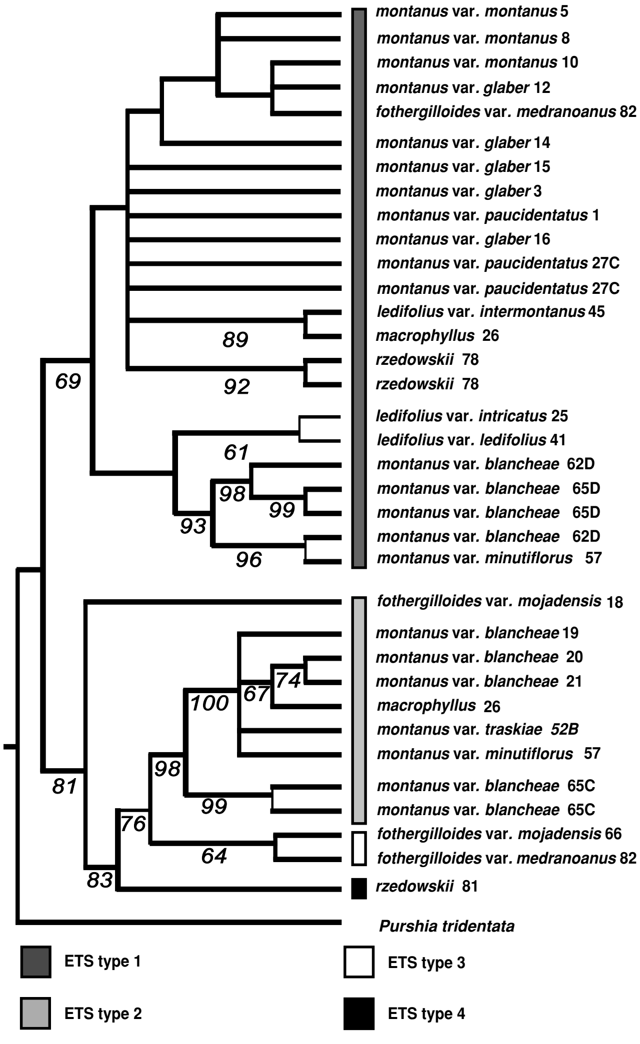

Figure 4—Fifty percent majority rule maximum parsimony consensus tree produced from the 360 bp alignment of the common regions between ETS types. The dark grey box indicates the monophyly of the ETS type 1 sequences, the light grey box indicates ETS sequences of type 2, the white box indicates the monophyly of ETS type 3 sequences, and the black box indicates the placement of the ETS type 4 sequence. Numbers below the branches indicate bootstrap support.

sister to a clade containing ETS types 2, 3, and 4. Because ETS type 3 sequences lack a 3' common region and the outgroup (*P. tridentata*) sequence lacks 5' common region, placement of ETS type 3 sequences in the phylogeny is based on comparison to the other *Cercocarpus* ETS sequences and not to direct comparison to the outgroup (fig. 2). ETS type 1 sequences form a well supported clade, which is sister to a clade containing ETS type 2, 3, and 4 sequences.

Discussion

Comparison of the ITS and the ETS Regions in *Cercocarpus*

The ITS region has been very attractive for phylogenetic reconstruction in plants because it evolves rapidly, it is subject to concerted evolution, and it is easily amplified using universal primers in the flanking genes (Baldwin and others 1995). However, in some studies of recently evolved plant lineages, the ITS region lacks enough phylogenetically informative variation to resolve relationships (Bain and Jansen 1995; Baldwin and others 1995; Francisco-Ortega and others 1997; Schilling and others 1998; Soltis and Kuzoff 1993). This lack of variation in the ITS in some plant groups (Fabaceae and Asteraceae) has led some researchers to look at the ETS for more variation (Bena 1998; Baldwin and Markos 1998; Linder and others 2000). Our results indicate that the ETS is also more phylogenetically informative than the ITS in *Cercocarpus* (Rosaceae). The length of the MP tree increased tenfold from 2 steps for the ITS tree to 20 steps for the ETS tree, even though the aligned ETS sequence data had only half the number of aligned base pairs as the ITS (fig. 3). Also, the bootstrap support for internal nodes increased dramatically in the ETS tree. Our results add to those of others (Bena and others 1998; Baldwin and Markos 1998; Linder and others 2000) that indicate that the ETS can be more phylogenetically useful for resolving the relationships of recently evolved taxa.

So little informative variation in the ITS for *Cercocarpus* adds weight to claims that *Cercocarpus* is a recently evolved group (Martin 1950), because there hasn't been enough time for variation to accumulate in the ITS. Recent origin of *Cercocarpus* would explain why there has been such disagreement in the taxonomy and circumscription of taxa (Schneider 1905; Rydberg 1913; Martin 1950).

Multiple ETS Types and Phylogenetic Analysis Using the ETS in *Cercocarpus*

Multiple ETS types have been found in other plant groups, including three genera in the Asteraceae: *Asteriscus*, *Calycadenia*, and *Helianthus* (Baldwin and Markos 1998; Linder and others 2000). However, the multiple ETS types found in these genera only differed in numbers of sub-repeats and did not show such large scale structural differences. The large structural differences found among the ETS types in *Cercocarpus* may be the result of past DNA mispairing events during replication due to secondary structure. We are currently cloning the ETS from genomic DNA obtained from different *Cercocarpus* individuals with known ETS types to further explore the molecular evolution of the ETS in *Cercocarpus*.

In an earlier study where multiple ETS types were found in individuals (Linder and others 2000), the types were all found to have originated within a species. There was no evidence for deep coalescence of the types. In *Cercocarpus*, we have found evidence for ETS types that have coalescence times earlier than the origination of the genus. ETS types 1, 3, and 4 are monophyletic groups, and ETS type 2 is a very closely related paraphyletic group. This is surprising because concerted evolution of the 18S-26S nrDNA repeat has commonly been invoked to reduce or eliminate the effects of deep coalescence on phylogenetic reconstruction (Moritz and Hillis 1996; Zimmer and others 1980). Within *Cercocarpus*, lack of concerted evolution or lineage sorting followed by hybridization has produced patterns of relationship that do not fit the usual pattern. We do not have enough data to tell which of these scenarios is more likely. In either case, the data suggest that the ETS types are paralogous with an ancient coalescence time. Different *Cercocarpus* ETS types, therefore, should not be used together for phylogenetic analysis. No problem should arise if a single ETS type is used for phylogenetic reconstruction. We believe that, with more sampling, a phylogeny using ETS type 1 will produce a usable nuclear phylogeny for *Cercocarpus*. ETS type 1 was found in all *Cercocarpus* taxa except *C. montanus* var. *traskiae* and *C. fothergilloides* var. *mojadensis* (table 1). Continued sampling of these two taxa may discover usable ETS type 1 sequences to include in the phylogenetic reconstruction.

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Microsatellite Markers and Polymorphism in Cheatgrass (*Bromus tectorum* L.)

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Abstract—Cheatgrass (*Bromus tectorum*) individuals were genetically characterized using polymorphic microsatellite markers. Through analysis of alleles of five polymorphic loci, genotypes were constructed of individuals from four populations in Utah and Nevada. There were 15 different genotypes: Whiterocks, UT, had nine genotypes, Hobble Creek, UT, had seven genotypes, Strawberry, UT, had four genotypes and Potosi Pass, NV, had one genotype that was unique among all areas studied. These results are similar to what has been found in previous germination phenology and head smut resistance tests. Further analysis of cheatgrass populations using these markers will assist in the analysis of cheatgrass head smut host/pathogen dynamics and in the development of a biological control agent for cheatgrass.

Introduction

Cheatgrass is an introduced annual grass that often spreads into disturbed areas, rapidly establishing itself as the dominant species. It inhibits reestablishment of native plants (Melgoza and others 1990) and, because cheatgrass dies early in the summer, sites with high cover of cheatgrass are prone to frequent fires. In the arid shrubland of the Great Basin, fires stimulated by the increase of cheatgrass heighten mortality of important shrubs such as *Artemesia tridentata* in addition to causing extensive economic damage (Young and Evans 1978).

Through analysis of cheatgrass germination phenology, Meyer and Allen (1999) showed that populations of cheatgrass exhibit adaptive genetic variation corresponding with habitat. This genetic variation is presumably the result of habitat-specific selection pressure acting on introduced genotypes. Because cheatgrass is an obligate inbreeder, populations are made up of an assortment of inbred lines, each with potentially unique genotypes (Novak and others 1991). Each unique genotype may be the result of a separate introduction of cheatgrass into a population (Novak and others 1991). Because genetic variation in traits such as germination phenology or head smut resistance exists among the inbred lines, different lines in a population are variously susceptible to environmental controlling factors such as frost, drought, or disease. Meyer and others (2001) showed that resistance of cheatgrass to *Ustilago bullata* head smut is often genotype specific. This resistance polymorphism is one example of habitat-specific selection pressure. Characterization of the inbred line composition of a population will lead to a greater understanding of the processes leading to extensive colonization of an area by cheatgrass.

Isozyme studies have detected some among-population genetic polymorphism in cheatgrass, but isozyme techniques are not sensitive enough to detect inbred lines (Novak and others 1991). Microsatellite loci (loci with di- or tri-nucleotide repeats) have recently become popular in forensics and other studies where detailed genetic information is needed (Graham and others 2000). We have developed genetic markers using microsatellites, and they are variable enough to detect within-population variation in cheatgrass. Data generated from analysis of these markers will lead to an increased understanding of the invasion strategies of cheatgrass and may prove invaluable in developing biological control methods.

Materials and Methods

We designed oligonucleotide primer sets specific to microsatellite loci in cheatgrass by screening a cheatgrass λ-phage genomic library with dinucleotide repeat oligonucleotide probes, sequencing positive clones, and designing primers to flank sequences with tandem repeat areas. To construct the library, we extracted genomic DNA using a modified CTAB protocol (Bult and others 1992). We then digested the DNA with the restriction enzyme Sau3A and ligated the fragments into λ-phage using the ZAP Express Predigested Vector Kit (Stratagene: La Jolla, CA). The ligation yielded a genomic library of approximately 100,000 clones. We screened approximately 11,200 clones for short tandem repeats by lifting plaques onto nylon membranes and hybridizing the recombinant DNA with poly-CA and poly-CT oligonucleotide polymers labeled with DIG (Roche: Indianapolis, IN). Positive clones were detected by an antibody/color detection system (NBT/BCIP) and sequenced with a Perkin-Elmer ABI 377 automated DNA sequencer. We detected 23 positive clones through our screening process, and 10 of the sequences generated from these clones contained regions of six to 18 dinucleotide repeats. We

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Table 1—Population habitat and location information (Meyer and others 2000).

			Climate			Location	
Population	Elevation	Plant community type	Mean annual precipitation	Mean January temperature	Mean July temperature	County	State
	m		*mm*	- - - - - - - - - - *°C*	- - - - - - - - - - -		
Potosi Pass	1,850	Blackbrush-juniper (warm desert margin)	250	1.7	26.5	Clark	Nevada
Whiterocks	1,450	Shadscale (cold desert)	180	–2.3	25.8	Tooele	Utah
Hobble Creek	1,800	Sagebrush-gambel oak (foothills)	400	–2.1	24.8	Utah	Utah
Strawberry	2,400	Subalpine meadow	560	–7.8	16.1	Wasatch	Utah

designed primer sets to yield amplification products between 80bp and 300bp. We labeled one primer from each set with a fluorescent marker for analysis on the automated sequencer. Polymerase chain reaction (PCR) conditions were optimized using an Eppendorf Mastercycle Gradient thermocycler by varying temperature and magnesium concentration.

We ran PCR reactions in 15µl or 10µl total volume with 200µM dNTPs, 1.7 to 3.3 mM $MgCl_2$, 0.2µM each oligonucleotide of a primer pair, 0.008U/µl Taq DNA Polymerase (Promega), and 1X PCR buffer (2mM Tris-HCl (pH 8.0), 10mM KCL, 10µM EDTA, 100µM DTT, 5 percent glycerol, 0.05 percent Tween 20, and 0.05 percent Ninidet-P40, supplied by Promega). We performed cycling regimes on a Perkin-Elmer 9600 thermocycler with an initial 96 °C denaturing step for 3 min and a final extension step of 5 min at 72 °C. During the initial screening of the loci, we varied optimum annealing temperatures for the primers. After the initial screening, we switched polymerases to HotStarTaq (Qiagen). After switching to HotStarTaq, all polymorphic loci amplified well with an annealing temperature of 60 °C. Polymorphic loci included Bt03, Bt05, Bt26, Bt30, and Bt33.

Results and Discussion

We analyzed plants from Whiterocks (cold desert, UT), Strawberry (montane, UT), Potosi Pass (warm desert, NV), and Hobble Creek (foothills, UT) (table 1). These areas of study were chosen because studies by Meyer and others (2001) focus on these areas. The first 10 plants from each population used in our study are from the same lines used by Meyer and Allen (1999) and Meyer and others (2001). Further research will analyze the correlation among different studies.

In a preliminary screen of 166 individuals from these populations, five loci were polymorphic, amplifying between two and seven different alleles (tables 2 and 3). We are in the process of developing more loci, and will use them to form a more complete picture of the cheatgrass populations. This paper offers a brief overview of the genotypes amplified by the current loci, but is not intended to be a thorough study of the cheatgrass populations. A complete analysis of the populations will be made at a later date when a representative number of loci and individuals have been sampled.

Of the 50 samples from Whiterocks, we identified nine different genotypes, with one genotype (B) representing half of the samples (table 4). The B genotype was found in only two of the 39 samples analyzed in Hobble Creek. The most abundant genotypes at Hobble Creek were E and I, both present in small numbers at Whiterocks. Five samples from Strawberry shared a genotype present in both Hobble Creek and Whiterocks. One Strawberry sample also shared a genotype present only at Hobble Creek and not Whiterocks. However, the most abundant genotype present in Strawberry was not found in either Hobble Creek or Whiterocks. Unlike the other three collection sites, Potosi Pass shared no genotypes with any other populations. Three of the five loci used to construct the genotypes amplified unique

Table 2—Summary of loci and alleles.

Locus	Core repeat	Size range	No. of alleles	Primer sequences
Bt03	$(CA)_7$	112–114	2	Forward: GCATGTCCACCTCCATGGCCACGCC Reverse: CTGTCTTCCTCCCTCCCTCACTTGTGTTCC
Bt05	$(CT)_9$	165–178	8	Forward: GGGAAAGCAAGCCGTTTCCGCGTTG Reverse: CGGTGGACGACGGGAAAGCGGAGCA
Bt26	$(CT)_{18}$	152–156	2	Forward: ATCCGTCCCTCTTTCTTTGCGCTGC Reverse: GGAGGAAGAAGAATGACCGAGAGAG
Bt30	$(GT)_8$	112–118	4	Forward: GCCACTTTTTTTCCGAACAGACACC Reverse: CAAAAGCAGAGTGCAGATGTAAATGAAATT
Bt33	$(AG)_3(AG)_7(AGG)_5$	221–223	2	Forward: CTGCTATATCATGAGGCCATTGGGA Reverse: AGTTTGTACAGCAGCCTGAGGCATG

Table 3—Genotypes: each number represents an allele of Bt03, Bt05, Bt26, Bt30, and Bt33, respectively.

Genotype	ID
11111	A
12111	B
12141	C
12211	D
14111	E
14121	F
15111	G
15211	H
16111	I
12121	K
13111	L
23232	M
16121	N
17111	O
17121	P
Total	15

Table 4—Genotypes (A-P, not J) of individuals in Whiterocks (WR), Hobble Creek (HC), Potosi Pass (PP), and Strawberry (ST).

Population	Genotype															
n	A	B	C	D	E	F	G	H	I	K	L	M	N	O	P	Total
WR	1	25	8	4	1	1	1	5	4							50
HC	1	2			17	2			12	1	1		3			39
PP												52				52
ST		5								1				6	13	25
Total	2	32	8	4	18	3	1	5	16	2	1	52	3	6	13	166

alleles in Potosi Pass samples. Because both genotype composition and environmental conditions among the populations vary, the most successful genotypes in each population may be environmentally selected.

Potosi Pass is a recently invaded warm desert site with environmental conditions different than the other populations studied. Analysis of 52 samples from Potosi Pass showed that they were all the same genotype (M), which was not found in any other population studied. In Meyer and others (2001), the individuals from Potosi Pass were not susceptible to head smut collected from any of the other populations, but were 100 percent susceptible to head smut from Potosi Pass. Polymorphism among populations was also found by Meyer and Allen (1999) in their germination studies: Potosi Pass samples exhibited different germination patterns than Whiterocks, Hobble Creek, or Strawberry. Meyer and Allen also found that Potosi Pass individuals had no vernalization requirement, whereas all other populations require vernalization to flower (Meyer, unpublished data). The data from these previous studies and the data presented in this paper all suggest that the Potosi Pass population is composed of one inbred line that was introduced separately from the other lines we identified and is unique to Potosi Pass.

If loci had mutated rapidly since the invasion of each site, we would expect to see a completely random assortment of alleles in each population due to mutation, with 256 possible genotypes. However, we have only observed 15 genotypes, indicating that observed alleles are presumably the same as ancestral types.

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Biodiversity, Ecology, and Microelement Composition of Kyzylkum Desert Shrubs (Uzbekistan)

Lyuba A. Kapustina

Abstract—Geobotanic research and large-scale mapping with the help of Geographical Information System (GIS) permit us to find out the present state of Kyzylkum Desert shrublands, regularities of plant communities distribution, and chemical composition of the main dominant shrubs. Zonal vegetation types were formed on the basis of Old Xerophilous and Old Mediterranean floras in the Paleogene and Neogene periods. Composition of plant associations and their anthropogenic modification largely depends on physical and chemical properties of the soils. Climax associations of *Artemisia diffusa, Astragalus villosissimus, Convolvulus hamadae,* and *Ceratoides latens* are connected with almost saline-free soils. Communities of *Artemisia turanica, Salsola arbuscula,* and *S. arbusculiformis* are found on soils with the lowest salt content, and *Haloxylon aphyllum, Nanophyton erinaceum,* and *Salsola orientalis* communities prefer average and very saline soils. Microelement concentration of the shrubs depends on chemical composition of their habitats.

Introduction

The region of our investigation belongs to the Turanian Province of the Irano-Turanian subdistrict of the Sahara-Gobi Desert zone (Lavrenko 1962). Mean annual temperature is +14 °C. Rainfall in the region amounts to less than 150 millimeters per year. The annual sunshine period is about 3,000 hours.

Gypsum Desert and Saline Desert

All these types are located from 100 m to 300 m above sea level under rather similar climatic conditions. The desert ecosystems, by virtue of natural peculiarities, are distinguished by a rich variety of flora and fauna. There are more than 5,000 species of vascular plants in Uzbekistan (Red data book 1999). Among these many are rare, endemic and relict plants, which need protection by efficient measures. The flora of the Kyzylkum Desert contains about 937 vascular plants, and the fauna consists of over 500 species and sub-species of vertebrates and about 950 species of non-vertebrates. The following main categories of desert ecosystems can be found in Uzbekistan: Sand Desert; Clay (or Gypsum) Desert and Saline Desert. All these types are located from 100 to 300 m above sea level under similar climatic conditions. The desert ecosystems, by virtue of natural peculiarities, are distinguished by a rich variety of flora and fauna.

The development of industrial enterprises and agriculture are the main reasons for changes of ecological conditions, for impoverishment of biodiversity, and for genetic resources. Grazing has multiple effects on natural ecosystems. Animals defoliate vegetation and, consequently, affect plant growth, vigor, reproduction, species composition, plant cover, and biomass. At the same time animals trample the soil thus reducing bulk density and infiltration rates and increasing overland flow. On the other hand, as they move around the grazing land they redistribute nutrients in the ecosystem. All these effects, however, are minor and therefore reversible if grazing intensity is light to moderate. On the contrary, they become severe and irreversible by heavy grazing. Grazing intensity, therefore, is a crucial factor affecting the Kyzylkum Desert ecosystems. Intensive pastoralism combined with overhunting has reduced wildlife and has influenced the number and diversity of rare animal species such as *Gazella subgutturosa, Ovis polii severtzovi, Felix margarita*, *Felix manul*, *Felix ocreata caudata*, *Falco cherrug coasti*, *Otis undulata macqueenii,* and so forth.

Material and Methods

Results of long-term paleobotanical, floristic and ecological researches are used in this work (Popov 1927; Iljin 1946; Kamelin 1979; Kapustina and others 1996). Investigation of the present state of vegetation was carried out according to the traditional geobotanical and GIS methods (Aleksandrova 1964; Hill and others 1996). Modifications of the vegetation are compared with relief changes, salinization and mechanical composition of the soils. The vegetation has been classified according to Kamelin (1979). During the geobotanical investigations in the field, ecological profiles were plotted crossing mountain slopes and plains. Plant and soil samples were taken along these profiles. The chemical compositions of plants and soils were determined by spectral analysis. Degree and type of the most saline soils were classified according to Kovda and Egorova (Pankov 1974; Alekcandrova and Naidenov 1976).

Results and Discussion

Arid territories are present in Uzbekistan since the beginning of the Jurassic. Similar xerophytic flora with representatives of *Rutaceae, Capparidaceae, Geraniaceae,*

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Frankeniaceae, and *Chenopodiaceae* emerged in the Southern Hemisphere in the Upper Cretaceous and Tertiary. The formation of saline and sandy deserts began in the Paleogene. At that time savanna vegetation types were dominant. The main savanna types were destroyed by the arctic climate in the Pliocene. An exchange of xerophytic flora (Popov 1927; Iljin 1946; Bobrov 1965) was distributed on the Old lands of the Northern species between the West and East of the Old Mediterranean region at the end of the Neogene. Many of the Old Mediterranean genera were formed at the same time and are the basis of the modern composition of the xerophytic desert vegetation (Iljin 1946; Kamelin 1979). In recent times two types, extremely arid and semiarid, of the Temperate Floracenotype can be distinguished in the desert vegetation of Uzbekistan (Kamelin 1979). The first group of extremely arid types includes: Turanian Shrub-Desert type, Turanian Psammophyton type, Irano-Turanian Psammosavanna type, Halophyton Turanicum type and Desert Forest on humid soils. Shrubs are a very important part of the vegetation in the arid zone.

Types of Habitats in the Kyzylkum Desert

Gypsum Desert occupies about 29 percent of Uzbekistan and is represented by Turanian Shrub Desert type on gray-brown soils. This type was formed on the bases of Old Mediterranean and Old Xerophilous floras in the Neogene period. Groups of oligothermal and mesothermal euxerophilous shrubs are prevailing (Kamelin 1979). Gray-brown soils flora consists of more than 400 species and includes species that occur on shallow soils of residual mountains and mixed rock; 25 percent are endemics of Middle Asia, and 3.5 percent are endemics of the Kyzylkum Desert. Forty one species depend on soil gypsum horizons for water and mineral nutrition. Forty-seven species are shrubs. Climax associations are formed by *Artemisia diffusa, A. turanica, Salsola orientalis, S. arbuscula* with *Carex pachystylis* and *Poa bulbosa* (grasses of the semisavanna group). Xeric semishrubland on loam gray-brown soils (*Artemisia diffusa* communities including *Artemisia turanica, Salsola orientalis, S. arbuscula* and *Aellenia subaphylla*) and xeric pelitic semishrubland on clay gray-brown soils (*Artemisia turanica* communities with *Salsola orientalis, S. arbuscula, Artemisia diffusa, Carex pachystylis* and *Poa bulbosa*) are predominant on the Southern mountain plains. Xeric psammophytic semishrubland on sandiest gray-brown soils (*Artemisia diffusa* communities with *Salsola arbuscula, Ferula foetida, Calligonum leucocladum, Ceratoides latens, Haloxylon aphyllum*) and xeric shrubland on the loam gray-brown soils (*Salsola arbuscula* communities with *Artemisia diffusa, A. turanica, Carex pachystylis* and *Salsola orietalis*) are spread on the Northern and Western mountain plains. *Artemisia diffusa* and *Salsola arbusculiformis* communities with *Artemisia terrae-albae, Rhamnus sintenisii, Convolvulus fruticosus* and *Atraphaxis spinosa* are predominant on the calcareous low desert mountain slopes. *Salsola orientalis* communities with *Anabasis brachiata, A. truncata, Nanophyton erinaceum* and *Artemisia turanica* are spread on the saline soils of the mountain plains and rocks (table 1).

Formations of *Anabasis salsa, A. brachiata, A. eriopoda, A. truncata* and *Artrophytum lehmannianum* can be considered as Old Euxerophilous Paleofloracenotype in the Turanian desert flora, and *Atraphaxis spinosa* and *Calligonum junceum* as Old Mediterranean species emerging in the Paleogene. At present these are spread on paleogenic slopes of low desert mountains.

Sandy Desert is formed on sandy desert soils and loose sands. The area of the sandy desert in Uzbekistan makes up 27 percent of the Republic. Within the sandy desert there are about 320 vascular plants from 31 families and 134 genera. Of these 53 percent are endemics of Middle Asia; the rest is represented by Irano-Turanian, Turanian-Caucasian and Turanian-European elements. Between them are 62 endemic shrubs on sandy desert soils: representatives are *Calligonum* spp., *Ammodendron conollyi, A. karelinii, Salsola paletzkiana, Eremosparton flaccidum, Smirnovia turkestana, Dendrostella arenaria, Tamarix androssovii, Astragalus* from sections, *Ammodendron* and *Eremophysa, Convolvulus divaricatus, C. erinaceus, Acanthophyllum borszczowii, A. korolkovii, Ammothamnus lehmanii,* and *Artemisia diffusa* (Melnikova 1973). Real psammophytes comprise 174 species; of these, 40 species are also common in the gypsum desert and 60 in the mountain foothills. The

Table 1—Biodiversity of the shrubland in the Kyzylkum Desert.

Shrubland	Area (km^2)
Haloxylon persicum	58,714
H. aphyllum	6,720
Ammodendron conollyi	17,678
Salsola richteri and *S. paletskiana*	392
Salsola arbuscula	2,339
Low desert mountain shrubland (*Rhamnus sintenisii, Convolvulus fruticosus* and *Atraphaxis spinosa*)	1,650
Nanophyton erinaceum	1,224
Anabasis salsa, A. eriopoda and *A. brachiata*	267
Astragallus villosissimus	223
Convolvulus hamadae	70
Ceratoides latens	1,064
Artemisia diffusa and *A. turanica*	22,229
Salsola gemmascens	22
Salsola orientalis	1,629

ecological and biological peculiarities of sandy habitats cause the occurrence of diverse forms. Trees and shrubs form a characteristic part of the "psammophyte vegetation" and make up to 30 percent of the flora composition. Twenty shrub species are edificators and subedificators of plant communities. Climax and subclimax stages are presented by communities of the Turanian Psammophytic type that was formed on the basis of the Old Mediterranean flora in the Neogene. There are groups of oligothermal, and not so often mesothermal euxerophilous psammophilous trees and shrubs (Kamelin 1979). *Salsola arbuscula, Calligonum microcarpum*, *C. leucocladum, C. setosum, Haloxylon aphyllum* and *Haloxylon persicum* form climax and serial associations on the sandiest gray-brown and sandy desert soils. Syngenetic stages are presented by sparse communities of Psammodendron Irano-Turanian type on loosely fixed sandy soils. Eroded xeric and psammophytic vegetation is wide spread in the region of study. This type was formed from the Old Xerophilous flora in the Paleogene and Neogene. Later on, some communities became relict and were enriched by Turanian Psammophytic species. There are groups of mesothermal xerophilous and psammophilous trees, shrubs and herbs (Kamelin 1979) on eroded sandy desert soils. In places with strong desertification on less hardened, furrowed sands and dunes as well as on sand plains are communities of *Ammodendron conollyi*, *Convolvulus korolkovii, Salsola richteri*, *Calligonum setosum, Acanthophyllum borszczowii,* and *Salsola richteri*. The perennials *Peganum harmala* and *Stipagrostis pennata* are dominant.

Saline Desert occupies about 3 percent of Uzbekistan. It developed on the saltiest plains and closed depressions (such as Mingbulak, Auminzatay, and Karakata). Characteristic features of saline areas are constant humidity of superficial soil horizons and occurrence of temporary reservoirs. There are 304 species on these soil types; 30 percent of the species are the real halophytes. Fifty two species are shrubs; some of these form the communities of the Halophyton Turanicum type that are widely spread on the saltiest habitats. This type was formed on the basis of Old Xerophilous and Old Mediterranean floras in the Paleogene and Neogene. There are groups of mesothermal euxerophilous halophilous trees, shrubs, perennials and rare succulent shrubs (Kamelin 1979). *Haloxylon aphyllum* communities with *Girgensohnia oppositiflora, Salsola praecox, Artemisia diffusa, Calligonum erinaceum* are spread on saline sandy desert soils. Salty pelitic shrubland communities of *Anabasis salsa, A. aphylla, Halocnemum strobilaceum, Halostachys caspica, Limonium suffruticosum, Kalidium caspicum, Frankenia bucharica, Atriplex cana* and *Suaeda microphylla* are spread on saline gray-brown soils and solonchaks.

Desert Forest on humid soils covers about 3 percent of the territory and was formed on the basis of Old Xerophilous and Arctic Tertiary Floras in the Pliocene (Kamelin 1979). The area of this type has been reduced in the Pleistocene and Anthropogene. There are mesothermal or rarely oligothermal hydrophilous trees and shrubs. *Tamarix ramosissima, T. elongata, T. hispida, T.laxa, T. florida, Ulmus pumila, Populus diversifolia, Halimodendron halodendron, Lycium turcomanicum* and *L. ruthenicum* form communities on humid soils near the Amudaria and Syrdarya rivers, artificial lakes and canals. *Nitraria schoberi* shrub communities are a relict part of this florocenotype. The flora consists of 285 species; about 190 species are typical for these habitats only. Of these, 28 species are endemic in Middle Asia and four in Uzbekistan. Thirty-five species are widely distributed in the river valleys of Central Asia, Dsungaria and Iran; some of them (*Populus* spp., *Tamarix* spp. and *Salix songarica*) are edificators of this vegetation.

Xerophilous Shrubs of the **Semiarid Type** formed the main zonal type of the Turanian up to the Ice Age. At present the shrub formations of this type (*Artemisia juncea, Astragalus scleroxylon, Convolvulus fruticosus, Salsola arbusculiformis*, and *Nanophyton erinaceun*) are found only on the paleogene slopes of the low desert mountains (such as, Kuldzuktay, Bukantay, Tamdutay, and Kokchatay).

Ecological Types of Desert Shrubs and Their Adaptive Strategy

Desert shrubs can be divided into three groups according to their biological structures and ecological peculiarities (Butnik 1991; Alimuchamedova 1979; Rachimova 1991): hyper-xerophytes, eu-xerophytes and meso-xerophytes (table 2).

Hyper-xerophytes have succulent assimilative organs and are microphyllous or aphyllous. Their above ground organs develop slowly, but root development is quick. Stability of water balance and photosynthesis, sclerotization of axial organs and a vegetative period from spring up to late autumn characterize this group. They have two types of adaptive strategy. The first one, aphylly, is the strategy of substitution and reduction of leaves by an assimilating shoot cortex as a result of cell-division change in the growing point. The second one, sclerophylly, consists of deep embedded stomatas, thick and complicated structure of outer epidermis walls and fiber-cell sheath bundles to prevent loss of water through evaporation (Butnik,1991). Transpiration rate varies from 123 to 660 mm^3 of O_2—fresh weight per hour (Nigmatov and Alekseeva 1998); osmotic pressure is 5–10 atm in spring and 44 atm in autumn. Growth occurs in the very hot summer time, when temperatures are about 60–63 °C and have a low index of potential photosynthesis: 21–31 mg CO_2/g^2 per hour (Zakharianc 1971). The greater part of the representatives of this group belong to the *Chenopodiaceae* family (*Haloxylon aphyllum, Halothamnus subaphyllus, Salsola orientalis, Nanophyton erinaceum, Anabasis eriopoda, Salsola arbuscula, S. arbusculiformis* and *S. paletzkiana*).

Eu-xerophytes solve the problem of evaporation decrease in the xerothermic period by dropping 70 percent of their leaves, and have more xeromorphous than succulent structure. Additional adaptive strategies to desert conditions without high specialization are pubescence, thickening of outer epidermis walls and sclereids (Butnik 1991). The vegetative growth period of this group of plants continues from spring to late autumn. Intensity of transpiration varies from 1,170 mm^3 of O_2 of fresh weight per hour (spring) up to 180 (summer); osmotic pressure is 6–9 atmospheres in spring and 67 in summer (Rachimova 1991); index of potential photosynthesis is higher than in the first group

Table 2—Ecological types of desert shrubs.

Type of desert shrubs	Species	Adaptive strategy	Intensity of transpiration (mm^3 of 02 for the gram of fresh weight per hour)	Osmotic pressure (atm)	Index of potential photosynthesis (mg CO_2/g^2 per hour)	Vegetative growth period
Hyper-xerophytes	*Haloxylon aphyllum,* *Halothamnus subaphyllus,* *Salsola orientalis,* *Nanophyton erinaceum* and *Anabasis eriopoda,* *Salsola arbuscula,* *S. arbusculiformis* and *S. paletzkiana*	Aphylly and sclerophylly	123–660	5–44	21–31	From spring up to late autumn
Eu-xerophytes	*Ceratoides latens,* *Ammodendron conollyi,* *Astragalus villosissimus* and *Kochia prostrata*	Defoliation (70 percent), pubescence, thicknening of epidermis walls	1,170–180	16–9–67	31–50	From spring time to late autumn
Meso–xerophytes	*Artemisia diffusa,* *A. turanica* and *A. ferganensis*	Defoliation (100 percent), thin leaves, pubescence, biological rest in summer time	1,704–30 (80)–410	12–32	44–55	Three vegetative phases

–31 to 50 mg CO_2/g^2 per hour. Eu-xerophytes can stand +59 °C; their root systems go 4 to 5 m deep. Desert shrubs *Ceratoides latens, Ammodendron conollyi, Astragalus villosissimus,* and *Kochia prostrata* belong to this group.

Meso-xerophytes drop 80 to 100 percent of their leaves in the hottest period of summer. They are not as adapted to the xerothermic period like hyper-xerophytes and eu-xerophytes and have some elements of xeric structure: thin leaves, covered with hairs, biological repose in summer time and the possibility to use essential oils in the hot time for protecting the plant from excessive heating due to very high temperatures. *Artemisia* shrubs of the subgenus *Seriphidium* belong to this group. Species of this subgenus have three vegetative phases: first is mesothermic (in the spring)—for growing and development, second is xerothermic (in the summer) for biological rest, and third is microthermic (in the autumn and winter) for seed production and dying of the inflorescences. The root system of these shrubs goes about 2 to 2.5 m deep. Intensity of transpiration of this group varies from 1,704 to a maximum of 2,388 mm^3 O_2 for 1 g of fresh weight per hour (spring) up to 30–80 (summer) and 410 (autumn); osmotic pressure is 12 atm in spring time, 28 in summer and 32 in autumn; index of potential photosynthesis is 44 to 55 mg CO_2/g^2 per hour (Rachimova 1991).

Adaptation to Saline Soils

The distribution of vegetation in the Uzbekistan Desert zone depends on the adaptation to the moist saline soils. Analysis of the desert shrub communities distribution and chemical composition of soils have shown that three edaphotypes (Bikov 1981; Freitag 1991; Akjigitova 1996) can be distinguished in the Kyzylkum Desert: euhalophytes, hemihalophytes and halo-glycophytes.

Euhalophytes have a wide tolerance range and are very well adapted to the average and high saline soils containing magnesium-calcium sulphate. Dry residue of the complete water extract from these soils is about 1.8 to 2.5 percent (table 3). Due to their adaptation they belong to salt accumulating- and salt-excreting halophytes. *Haloxylon aphyllum,*

Table 3—Chemical composition of soils in the zone of maximum root distribution of dominant shrubs (percent).

Species	Dry residue	HCO3	Cl	SO4	NO3	Ca	Mg	K	Na
Haloxylon aphyllum	2.58	0.6	2.45	32.9	0.16	27.4	1.6	0.08	6.81
Salsola orientalis	2.39	0.6	2.4	32.1	0.65	29.0	3.3	0.08	3.45
Salsola arbusculiformis	0.37	0.6	0.1	4.46	0.02	4.2	0.75	0.36	0.16
Salsola arbuscula	0.1	0.9	0.1	0.6	0.03	0.5	0.2	0.2	0.73
Artemisia diffusa	0.08	0.8	0.1	0.5	0.03	0.5	0.55	0.18	0.13
Artemisia turanica	0.13	0.8	0.05	1.1	0.03	1.25	0.2	0.34	0.19

Salsola orientalis, S. gemmascens, Anabasis salsa, A. brachiata and *Nanophyton erinaceum* are Chenopodiace shrubs and they are predominant in this group.

Hemihalophytes are shrubs of average saline soils containing magnesium-calcium sulphate. Dry residum of the complete water extract from these soils varies from 0.9 to 1.7 percent (table 3). Species of this group are *Salsola arbuscula, Arthrophytum lehmannianum, Nitraria schoberi, Artemisia turanica, A. ferganensis,* and *A. santolina;* they are sometimes spread on lower or high saline soils, too, but do not form communities in this habitat.

Haloglycophytes are shrubs with weak tolerance to very saline soils. Dry residue of the complete water extract from these soils is not more than 0.3 percent (table 3). *Artemisia diffusa, Astragalus villosissimus, Convolvulus hamadae, S. arbusculiformis* and *Ceratoides latens* belong to this group. Sometimes communities of these species are found on almost saline-free soils (the dry residue of the complete water extract from these soils is about 0.08 percent).

The chemical composition of plants growing in the same habitats, but belonging to different life-forms, is various and depends on physiological and ecological factors (Biogeochemical and Geobotanical Investigations 1972). According to chemical composition of desert shrubs in the Kyzylkum Desert we could establish that the following species accumulate elements most actively: *Artemisia diffusa* and *A. turanica*—Cu, W, V, Cr, Pb, Zn, Ni, Mo, Co, Bi,P and Sn*;* *Artemisia sogdiana*—U, Pb, Cd, Zn and Mo; *Astragalus villosissimus*—Ni, Ag, Pb, Sr, Zn, P and Cu; *Salsola arbuscula*—Mn, Sr, Ba, Pb, U and Ni; *Salsola orientalis*—Sr, Ba; *Calligonum microcarpum*—P, Pb and Ni; *Ceratoides latens*—Mo, Zn, Cu; and *Nanophyton erinaceun*—Ag,Cu and Pb (fig. 1). Pb was best accumulated *Artemisia diffusa* and *Calligonum microcarpum*; Zn and Cu—*Artemisia diffusa* and *Halocnemum strobilaceum*; V and Cr—*Artemisia diffusa.*

Conclusion

Shrublands are predominant in the Kyzylkumm Desert. Three ecological types of desert shrubs widely spread on different soils. The greater part of the representatives of hyper-xerophytes are adapted to average and very saline soils and belong to euhalophytes. Chemical compositions of desert shrubs (*Artemisia diffusa, Calligonum microcarpum, Ceratoides latens and Salsola arbuscula*) can be used us indicators of the polluted zones and deposits.

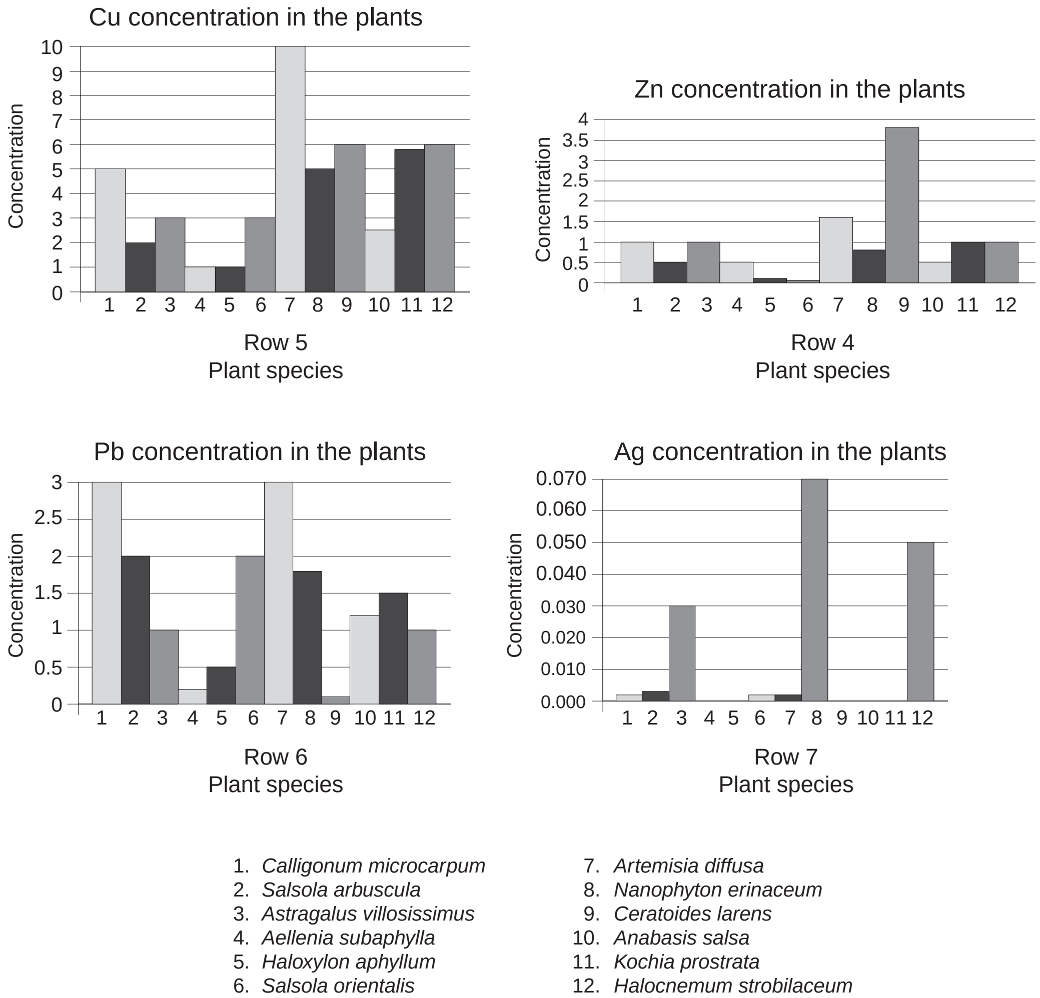

Figure 1—Microelement composition of shrubs in the Kyzylkum Desert (percent concentration: n x 0.001).

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Artemisia Communities in Arid Zones of Uzbekistan (Central Asia)

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Montserrat Torrell
Joan Vallès

Abstract—Central Asia, and particularly the former Soviet Middle Asian countries, with more than 180 taxa (45 endemics), is one of the centers of origin and speciation of the genus *Artemisia* L. (Asteraceae, Anthemideae). Several species of this genus, mainly belonging to subgenus *Seriphidium* (Besser) Rouy, are shrubs that dominate the landscape and form large communities in arid (desertic, semidesertic, steppic, and other) zones of this region. Arid lands constitute approximately 90 percent of the territory of Uzbekistan, and there are approximately 40 *Artemisia* species. In this paper we present a characterization of some of these species (including six Central Asian endemics) and communities, with ecological, chorological (with a distribution map), biogeographical, cytogenetic, and chemical data. We also include some references to plant use and management in these areas.

Introduction

The region of our investigation belongs to the Turanian (or Aralo-Caspian) and Turkestanian Provinces of the Irano-Turanian region in the Tethyan (Ancient Mediterranean) floristic subkingdom (Takhtajan 1986). The Middle Asiatic Desert includes the Irano-Turanian Desert region that occupies the southern portion of the Aralo-Caspian Desert and the southern part of Kazakhstan, including Dsungaria. The Central Asiatic Desert comprises a part of Dsungaria, the Gobi Desert, the western part of Ordos on the great bend of the Hwan-Ho, Ala-Schan, Bei-Schan, and the Tarim basin (Kaschgaria), together with the Takla-Makan Desert and the more elevated Tsaidan basin (Walter 1979).

One hundred and eighty *Artemisia* species are present in Middle Asia, 45 of which are endemic to this zone (Poljakov 1961b). From these taxa, 36 grow in Uzbekistan, some of them in desert or semidesert zones, and others in mountain zones. The existence of 19 Middle Asian endemic species of the genus (Vvedenskii 1962) is remarkable in Uzbekistan.

Investigations of the *Artemisia* species and their distribution were carried out using basic ecogeographical and mapping methods. In addition to the location of *Artemisia* species and communities in Uzbekistan (fig. 1), we present some data on general distribution, ecology, chemical composition, chromosome numbers, and uses of the main taxa of the genus (table 1).

The species belonging to the subgenus *Seriphidium*, which includes most of the Central Asian taxa of *Artemisia* that are relevant in the landscape, have some elements of xeric structure: tomentose leaves, biological repose in summer, and the possibility to expel essential oils in hot weather for plant protection from excessive heating due to very high temperatures. Species of this subgenus have three vegetation phases: (1) mesothermic (in spring) for growing and development, (2) xerothermic (in summer) for biological repose, and (3) microthermic (in autumn and winter) for seed production and death of the inflorescences. The structure of *A. ferganensis, A. porrecta,* and *A. serotina* is simpler, because they have only a very small woody perennial stem (Mailun 1976). Most of the species in this subgenus are predominant in vegetation and good forage plants for livestock. Dry mass content of the forage plants of desert shrubland with predominating *Artemisia* species varies from 1.3 to 2.6 centner per hectare. Forage plant dry mass protein content varies from 0.15 to 0.09 centner per hectare. Some species are used for other purposes, such as *A. juncea* (medicine and perfumery) and *A. serotina* (soap-boiling) (Larin 1937; Goryaev and others 1962).

Essential oil content of *Artemisia* species predominating in vegetation in different zones of Uzbekistan varies from 0.32 to 3.1 percent, the highest concentrators being *A. dracunculus* (up to 3.1 percent), *A. ferganensis* (up to 2.1 percent), and *A. porrecta* (up to 1.5 percent) (Goryaev and others 1962). Camphor is present in the essential oils of *A. leucodes* (93 percent), *A. ferganensis* (85 percent), and *A. porrecta* (37 percent); cinneol in *A. serotina* (78 percent), *A. porrecta* (47 percent), and *A. leucodes* (35 percent); and thujone in *A. baldshuanica* (60 percent) (Goryaev and others 1962). Flavonoids are present in *A. leucodes, A. dracunculus,* and *A. serotina*; sesquiterpene lactones in *A. tenuisecta, A. santolina, A. serotina, A. juncea,* and *A. leucodes*; coumarins in *A. porrecta, A. diffusa,* and *A. dracunculus*; acetylenes in *A. turanica* and *A. dracunculus* (Marco and Barberá 1990). Essential oil concentration in weed species varies from 0.34 percent *(A. tournefortiana* and *A. annua)* to 1 percent (*A. vulgaris, A. scoparia,* and *A. absinthium*—up to 2 percent) (Goryaev and others 1962). Most of these weed species also contain acetylenes, coumarins, flavonoids and sesquiterpene lactones (Marco and Barberá 1990).

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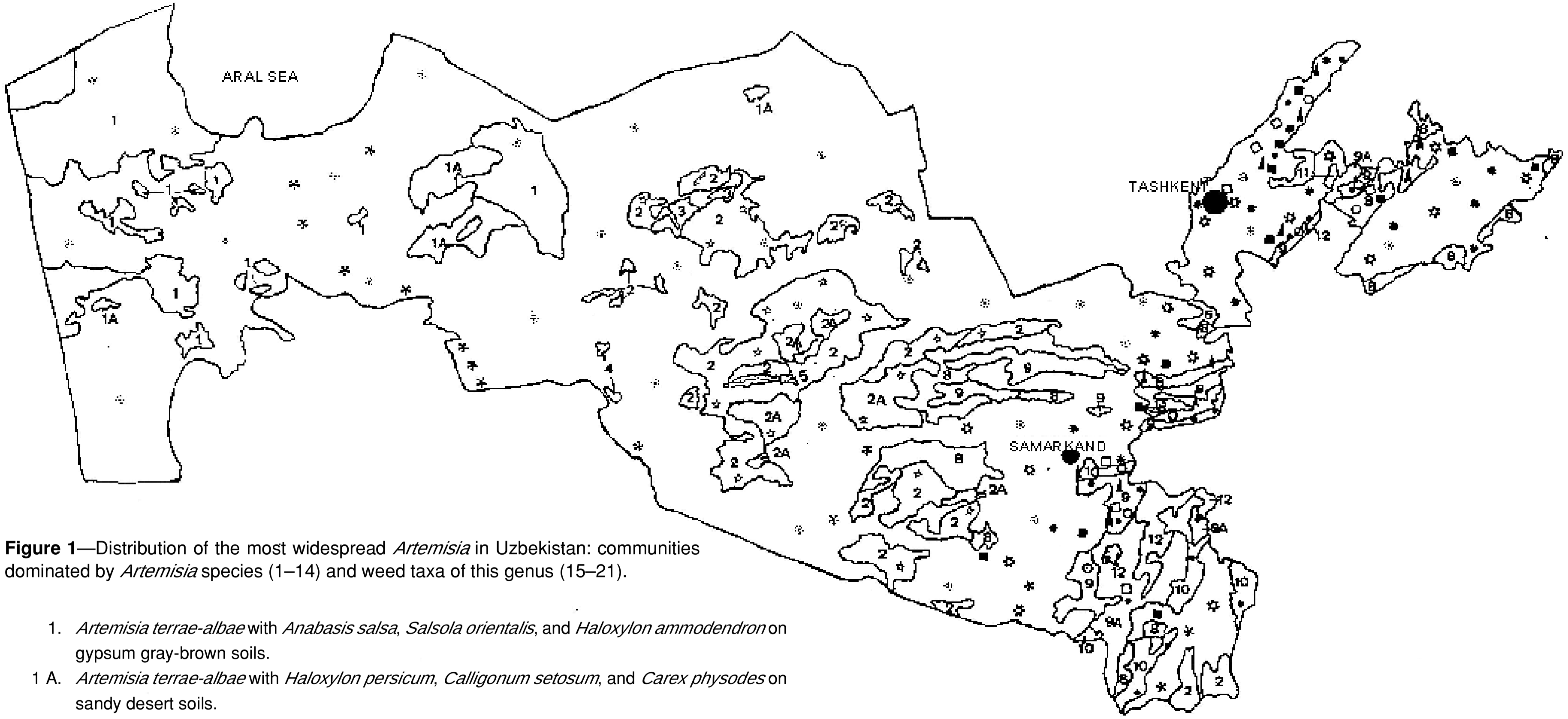

Figure 1—Distribution of the most widespread *Artemisia* in Uzbekistan: communities dominated by *Artemisia* species (1–14) and weed taxa of this genus (15–21).

1. *Artemisia terrae-albae* with *Anabasis salsa*, *Salsola orientalis*, and *Haloxylon ammodendron* on gypsum gray-brown soils.
1 A. *Artemisia terrae-albae* with *Haloxylon persicum*, *Calligonum setosum*, and *Carex physodes* on sandy desert soils.
2. *Artemisia diffusa* with *Calligonum leucocladum*, *Astragalus villosissimus*, and *Carex physodes* on sandy desert and sandy gray-brown soils.
2A. *Artemisia diffusa* with *Salsola orientalis*, *Carex pachystylis*, *Salsola arbuscula*, and *Ferula foetida* on gray- brown soils.
☆ 3. *Artemisia turanica* with *A. diffusa*, *Carex pachystylis*, *Poa bulbosa*, *Salsola arbuscula*, and *S. orientalis* on gray-brown soils.
4. *Artemisia santolina* with *Carex physodes* and *Mausolea eriocarpa* on sandy desert soils.
5. *Artemisia juncea* with *A. diffusa*, *Ceratoides latens*, *Convolvulus fruticosus*, *Astragalus scleroxylon*, *Zygophyllum atriplicoides*, and *Salsola arbusculiformis* on gray-brown soils of the low mountain slopes.
6. *Artemisia ferganensis* with *A. diffusa*, *Halocharis hispida*, and *Climacoptera longistylosa*, on saltiest light serozem soils.
7. *Artemisia leucodes* with *A. diffusa*, *Convolvulus hamadae*, and *Astragalus villosissimus*.
8. *Artemisia sogdiana* with *Carex pachystylis*, *Poa bulbosa*, *Bromus danthoniae*, *Ceratocarpus utriculosus*, and *Vulpia myuros* on typical serozem soils.
9. *Artemisia tenuisecta* with *Elytrigia trichophora*, *Prangos pabularia*, *Inula grandis*, and *Amygdalus spinosissima* on typical and dark serozem soils.
9A. *Artemisia tenuisecta* with *Juniperus seravschanica*, *J. semiglobosa*, and *Elytrigia trichophora* on typical brown soils.
10. *Artemisia baldshuanica* with *Carex pachystylis*, *Amygdalus bucharica*, *Otostegia bucharica*, and *Pistacia vera* on dark serozem soils.
11. *Artemisia lehmanniana* with *Festuca sulcata* on light-brown soils.
12. *Artemisia dracunculus* with *Cousinia allolepis*, *C. macilenta*, *Acanthophyllum alatavicum*, *Festuca sulcata*, and *Prangos pabularia* on light-brown soils.
○ 13. *Artemisia porrecta* with *Carex pachystylis*, *Salsola sclerantha*, *Phlomis thapsoides*, and *Eremostachys eriocalyx* on serozem soils, sometimes slightly salty.
● 14. *Artemisia persica* with *Cerasus verrucosa*, *Dactylus glomerata*, *Poa nemoralis*, *Agropyron trichophorum*, and *Origanum tyttanthum* on chernozem soils.
□ 15. *Artemisia sieversiana.*
⁘ 16. *Artemisia scoparia.*
✱ 17. *Artemisia tournefortiana.*
✿ 18. *Artemisia annua.*
n 19. *Artemisia absinthium.*
✳ 20. *Artemisia vulgaris.*
▲ 21. *Artemisia serotina.*

Table 1—Systematic, chorological, ecological, chemical, and karyological data on Uzbek *Artemisia* species, and main uses of these taxa (information drawn from references and our personal knowledge).

Subgenus	Species (and life form)	Distribution area	Ecology	Chemical composition	Utilization	Chromosome number (2n)
Artemisia	*A. vulgaris* L. (perennial)	Central Asia, Siberia China, Afghanistan, Japan, India, Caucasus, North America, Mediterranean region, Mongolia, West Europe, European part of the former Soviet Union	Weed species, from plain up to the middle zone of mountains, river beaches, gardens, and meadows	Essential oil containing cinneol, thujone, paraffin, and borneol. Acetylenes, coumarins, flavonoids, and sesquiterpene lactones. Root contains inulin, tannic substances, and resin. Leaves contain vitamins A and C.	Food for livestock, rabbit, beaver, gopher, marmot. Used for medical purposes by local people. Leaves and stems are used as a condiment for meat dishes.	16
	A. persica Boiss. (perennial)	Central Asia (Tian-Shan, Pamir-Alai), Iran, Tibet, Afghanistan	Road metal slopes from foot up to middle zones of the mountains	Essential oil containing pinene, camphorene, camphor, borneol, and bornilacetate. Leaves and steams contain alkaloids, acetylenes, and coumarins.	Mountain specimens of this species can be used to obtain camphor.	18
	A. tournefortiana Reichenb. (annual or biennial)	Central Asia, Caucasus, Tibet, Afghanistan, Iran	River valleys from plain up to the middle zone of mountains, forests near rivers, and weed species in gardens	Essential oil containing aldehydes, phenols, alkaloids, acetylenes, and sesquiterpene lactones.		18
	A. annua L. (annual)	Central Asia, Siberia, Europe, Iran, China, Afghanistan, Japan, North India, North Africa, North America, Far East, Caucasus	Weed, ruderal in gardens, fields, villages, and towns	Essential oil containing pinene, camphene, cinneol, artemisiactene, and artemisiactane. Alkaloids, acetylenes, coumarins, flavonoids, and sesquiterpene lactones.	Perfumery. Condiment. Root extract used for wool and leather dyeing in lemon-yellow color.	18
Absinthium	*A. absinthium* L. (perennial)	Central Asia, Siberia, Western Europe, Iran, Afghanistan, North India, North America, Caucasus, Mediterranean, European part of former Soviet Union	From plain up to the middle zone of mountains, river beaches, forests near rivers	Essential oil containing absinthol, thuyone, felandrene, pinene, cadinene, terpenes, and absinthin. Acetylenes, coumarins, flavonoids, and sesquiterpene lactones. Leaves contain vitamin C and carotene.	Food for rabbits. Essential oil is used for pharmaceutical and vodka industries. Leaves are used as spice. Plant is used for medical purposes from ancient time.	18
	A. sieversiana Willd. (annual or biennial)	Central Asia, Siberia, China, Japan, Mongolia, east of the European part of former Soviet Union	Road metal slopes from foot up to middle zones of mountains, river and canal beaches, weed species in gardens and fields	Essential oil. Alkaloids in leaves, stems, and flowers. Acetylenes, coumarins, flavonoids, and sesquiterpene lactones.	This plant can be used for siloing.	18
Dracunculus	*A. scoparia* Waldst. et Kit. (annual or biennial)	Central Asia, Siberia, Western Europe, China, Afghanistan, Japan, North India, Caucasus, European part of former Soviet Union	Weed species widely spread on plains, foothills, and gardens	Essential oil containing α- and β-pinene, and myrcene. Acetylenes, coumarins, flavonoids.	Food for camel, horse, sheep, and rabbit.	16

(con.)

Table 1—Con.

Subgenus	Species (and life form)	Distribution area	Ecology	Chemical composition	Utilization	Chromosome number (2n)
	A. dracunculus L. (perennial)	Central Asia, Siberia, south of the European part of former Soviet Union, Minor Asia Afghanistan, North America, Mongolia	Subalpine and alpine meadows from 2,800 to 3,700 m on fulvous type soils	Essential oil containing sabinene and myrcene.	Perfumery, used by local people. Food plant.	18, 36, 72, 90
Seriphidium	*A. tenuisecta* Nevski (perennial)	Central Asia	Communities widespread on the slopes of the lower and middle zones of Tian-Shan and Pamir-Alai Mountains	Essential oil. Alkaloids, organic acids, and ethers. Sesquiterpene lactones.	Food for livestock.	18
Section *Seriphidium*	*A. ferganensis* Krasch. ex Poljak. (perennial)	Central Asia	Communities on loam, loam-road metal and sandy loam salty soils of river valleys, from foothills up to middle mountain zones	Essential oil containing camphor, α-thujone, carvone, cinneol. Sesquiterpene alcohols. Green shoots and leaves contain alkaloids.	Food for livestock.	36
	A. porrecta Krasch. ex Poljak. (perennial)	Central Asia	On loam, road metal and stony slopes from foothills up to middle mountain zones	Essential oil containing camphor, cinneol, aldehydes, phenols, and azulene sesquiterpenes. Coumarins.	Food for livestock.	18
	A. serotina Bunge (perennial)	Central Asia	On the loam and loam-road metal, sometimes slightly salty soils of plains, foothills, and lower zones of the mountains	Essential oil containing cinneol, camphor, acids, and carotene. Stem and leaves contain alkaloids and flavonoids.	Food for livestock. Used for soap-boiling.	18
	A. turanica Krasch. (perennial)	Central Asia, Iran, Afghanistan	Sandy, loam, gray-brown and gray-brown road metal soils of the desert plains and foothills	Essential oil. Tannin. Resin. Acetylenes.	Food for livestock.	18
	A. diffusa Krasch. ex Poljak. (perennial)	Central Asia	Sandy and gray-brown desert soils, serozem of the foothills	Essential oil. Coumarins.	Food for livestock. Used to make hay stocks by local people.	36
	A. sogdiana Bunge (perennial)	Central Asia, Afghanistan	Loam-road metal soils (sometimes slightly salty) and stony slopes from foothills up to middle mountain zones	Essential oil.		36
	A. baldshuanica Krasch. et Zapr. (perennial)	Central Asia (South Pamir-Alai)	Loam-road metal and stony slopes of the North Exposition from foothills up to middle mountain zones	Essential oil containing α- and β-thujone, thujone alcohol, isothujvalerianate, and aldehydes.		36
	A. lehmanniana Bunge (perennial)	Central Asia	Subalpine and alpine meadows from 2,800 to 3,700 m on fulvous type soils	Essential oils. Phenols, cetones, sesquiterpenes.		Unknown

(con.)

Table 1—Con.

Subgenus	Species (and life form)	Distribution area	Ecology	Chemical composition	Utilization	Chromosome number (2n)
	A. santolina Schrenk. (perennial)	Central Asia, Iran, China	Sandy, sometimes slightly salty, desert soils	Sesquiterpene lactones.	Food for livestock.	18
	A. terrae-albae Krasch. (perennial)	Central Asia, Mongolia, Western China	Gypsum gray-brown soil of plateau and sandy desert soils, northern part of the desert zone	Essential oil containing cuminaldehyde, cinneol, borneol, camphor, and artemisiacetone.	Food for livestock.	Unknown
Section *Junceum*	*A. juncea* Kar. et Kir. (perennial)	Central Asia, China	Alluvial road metal-sandy-loam soils of the plain, loam-road metal and stony slopes from foothills up to lower mountain zones	Essential oil. Tannic substances. Resin. Sesquiterpene lactones.		18
	A. leucodes Schrenk. (annual or biennial)	Central Asia	Sandy desert soils of the plains, loam and road metal-loam soils of the foothills and lower mountains	Essential oil containing camphor, cinneol, cis-pinocampheol, borneol ether, isovalerianic acid, azulene sesquiterpenes, and azulenes. Santonin. Flavonoids and sesquiterpene lactones.	Used for medicinal purposes and perfumery.	18

Artemisia Communities in Uzbekistan

The Uzbek Desert zone is included in the Turanian Province. The mean annual temperature is 14 °C, and the mean annual precipitation is 130 mm per year. The annual duration of the sun radiance is about 3,000 hours. Climax communities of the Turanian Desert type are dominated by *A. diffusa* Krasch., *A. turanica* Krasch., and *A. terrae-albae* Krasch. Figure 1 shows the distribution of the most widespread *Artemisia* species in Uzbekistan, not only those that are dominating in different communities, but the weed taxa of the genus as well.

Artemisia diffusa (fig. 2A) is a South Turanian species endemic of Middle Asia. It is a very ramified shrub, about 20 to 50 cm tall, with dense white indumentum. This plant is more widespread and predominant in different soil types of the desert zone in Uzbekistan. About 50 *A. diffusa* associations have been described in Uzbekistan, which contain 140 vascular plant species: 34 shrubs, 28 perennial herbs, and 77 annual species (Granitov 1964; Melnikova 1973; Momotov 1973; Zakirov 1973).

Artemisia turanica (fig. 2A) is distributed in Middle Asia, Iran, and Afghanistan (Vvedenskii 1962). It is a shrub about 20 to 40 cm tall, with violet-brown (or black) stems. It is often codominant in the *A. diffusa* communities and sometimes predominante in salty loam gray-brown soils of the pre-mountain plains. Desert *Artemisia* (*A. diffusa, A. turanica*) are very polymorphic, and in their communities there are often plants that have been considered by several authors as hybrids between both species, even though they are closer to *A. turanica* in habit (Poljakov 1958, 1961a; Momotov 1973). Anatomical characteristics of those species are variable in the different types of the soils of Kyzylkum Desert. In the drier conditions of loam soils, leaves are flatter, with denser nervation; water-carrier facing cells are larger and thick-walled mesophylle; sprouts are more lignified. *Artemisia turanica* is more adapted to strict conditions and has a higher stomata density than *A. diffusa* (Alimuchamedova 1983; Padunina and Momotov 1983). Twenty *A. turanica* associations were described in Uzbekistan. Floral composition varies from 25 to 57 (5 shrubs, 16 perennial herbs, and 36 annual) species (Granitov 1964; Melnikova 1973; Momotov 1973; Zakirov 1973). Xeric pelitic shrubland of *A. diffusa* and *A. turanica* communities with *Salsola orientalis, S. arbuscula*, *Carex pahystylis,* and *Poa bulbosa* predominate on loam and clay gray-brown soils of the mountain plains. Xeric psammophytic communities of *A. diffusa* with *Calligonum leucocladum, Astragalus villosissimus, Carex physodes, Convolvulus hamadae, Salsola arbuscula,* and *Ferula foetida* predominate on sandy gray-brown soils and sandy desert soils. Xeric petrophytic shrubland of *A. diffusa* and A. *turanica* with *Salsola arbusculiformis*, *Convolvulus fruticosus, Stipa aktauensi, Astragalus scleroxylon,* and *Atrophaxis spinosa* is spread on the calcareous slopes of low desert mountains. Salty shrubland of these species with *Climacoptera lanata*, *Gamanthus gamocarpus,* and *Girgensohnia oppositiflora* is distributed on saline gray-brown soils and solonchaks.

Artemisia terrae-albae (fig. 2B), a North Turanian species, is one of the most important plants in the plant cover of

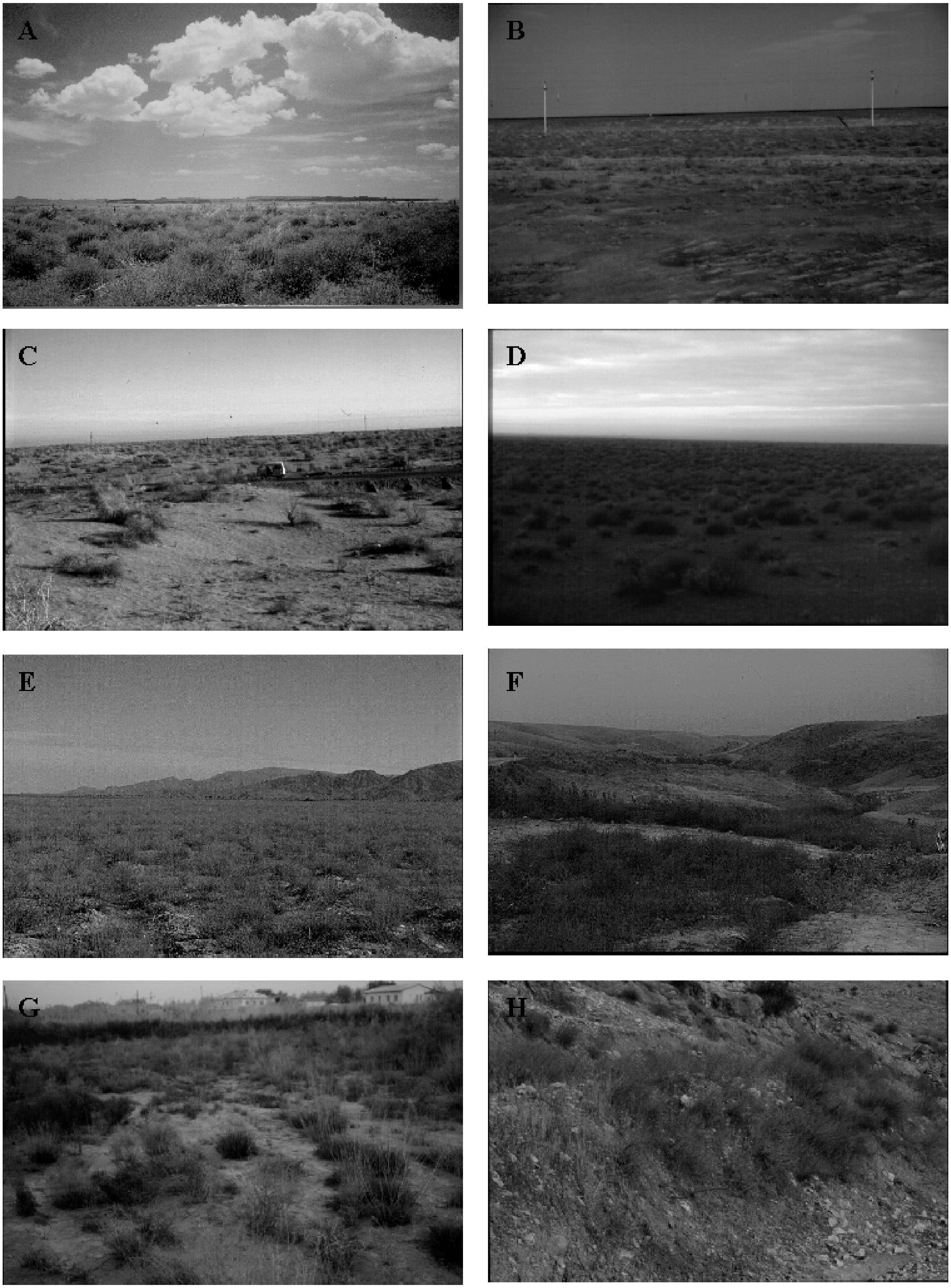

Figure 2—Communities dominated by different *Artemisia* species in Uzbekistan. (A) *A. diffusa* and *A. turanica*. (B) *A. terrae-albae*. (C) *A. santolina*. (D) *Mausolea eriocarpa* (*Artemisia eriocarpa*). (E) *A. sogdiana*. (F) *A. serotina*. (G) *A. ferganensis*. (H) *A.baldshuanica*.

Kazakhstan and the Central Asian Desert zone (Musaev 1968; Safronona 1998), including the Uzbekistan Northern Desert part. It is a shrub about 25 cm tall. The leaves have an epidermis of small cells with a thick cuticle layer and are densely tomentose (Zakrzevski and Korovin 1935). Epidermic cells contain tannic substances. The distribution area of this species includes Middle Asia and Mongolia (Vvedenskii 1962). *Artemisia terrae-albae* communities (with *Anabasis salsa, Salsola orientalis*, and *Haloxylon ammodendron*) are widespread on gypsum gray-brown soils of the Usturt Plateau, and occur in a small territory (with *Haloxylon persicum, Calligonum setosum,* and *Carex physodes*) in the desert sandy soils, and sandy gray-brown soils in the North Desert zone. There are 10 *A. terrae-albae* associations in Uzbekistan. Their floral composition varies from seven species on gypsum soils to 48 species (22 percent shrubs, 27 percent perennial herbs, and 51 percent annuals) on sandy gray-brown soils (Momotov 1973).

Artemisia santolina (fig. 2C) is a desert white tomentose shrub about 40 to 60 cm tall. This species spreads in Middle Asia, Iran, and China, but very seldom predominates in the vegetation cover of Uzbekistan. Small spots of *A. santolina* communities with *Mausolea eriocarpa* (*Artemisia eriocarpa*) (fig. 2D) and *Carex physodes* occur in sandy desert soils of the southwest part of the desert zone near the Amu-Daria River. Their floral composition is about 12 species.

Shrublands with *A. sogdiana, A. serotina, A. ferganensis, A. porrecta, A. baldshuanica,* and *A. tenuisecta* communities predominate in the semidesert and low mountain zones of Uzbekistan (Mailun 1976). Soils are represented by serozems with gypsum or detritus in some places. Average annual temperature is 12 to 15 °C. Average annual precipitation is 250 to 400 mm. The width of the mountain semidesert belt is 30 to 50 km and makes up two-thirds (more than 64,000 km^2) of the mountain territories of the Republic.

Artemisia sogdiana (fig. 2E) is a shrub about 40 cm tall, with 10 to 15 cm that is woody perennial part. Leaves are slightly tomentose. The epidermis is thicker than that of other *Artemisia* species. A*rtemisia sogdiana* stomata size and distribution are similar to those of *A. turanica*. Epidermal cell walls have a winding structure. These are mesomorphic indications (Alimuchamedova 1983). Distribution area of *A. sogdiana* expands in Middle Asia and Afghanistan (Vvedenskii 1962). Communities are widespread from premountain plains up to low mountain zones (500 to 800 m). There are 28 *A. sogdiana* associations in Uzbekistan. Their floristic composition is approximately 150 species (Mailun 1976). Most typical species in *A. sogdiana* communities are *Carex pachystylis, Poa bulbosa*, *Bromus danthoniae, Ceratocarpus utriculosus, Vulpia myuros, Cousinia resinosa, Phlomis thapsoides, Eremostachys eriocalyx,* and *Psoralea drupacea*.

Artemisia serotina (fig. 2F), endemic to Middle Asia, has a short perennial part and numerous herbaceous stems about 40 to 80 cm tall, very tomentose in the beginning of the vegetation period and almost glabrous to the end. This plant grows on different types of soils from plains to lower parts of mountain zones (Vvedenskii 1962) and is very often codominant in *A. sogdiana* and *A. serotina* communities, with *Phlomis thapsoides, Cousinia resinosa, Haplophyllum perforatum, Solenanthus turkestanicus, Poa bulbosa, Carex pachystylis, Garhadiolus angulosus, Lens orientalis,* and *Medicago rigidula*. These communities are secondary and occupy very small places in Uzbekistan.

Artemisia ferganensis (fig. 2G) is an endemic shrub to Central Asia, with its perennial part about 10 cm and only a few tomentose offshoots about 60 to 100 cm tall. This plant grows in different type of soils and sometimes on very salty places like a halophyte. According to anatomical and morphological indications, *A. ferganensis* has less xeromorphic structure (bigger leaves, stomata, and main rib; dense leaf nervation) than *A. turanica*, *A. diffusa,* and *A. sogdiana* (Alimuchamedova 1983). Communities dominated by *Artemisia ferganensis*, with *Camphorosma monspeliaca, Salsola orientalis, Kalidium caspicum, Climacoptera intricata, C. longistylosa, Suaeda arcuata,* and *Halocharis hispida,* occupy small salty places near Aidar Lake and in the Fergana Valley. Sometimes *A. ferganensis* predominates on loam soils of the low mountains with *Taeniatherum crinitum, Aegilops truncialis, Bromus danthoniae, Poa bulbosa, Hordeum bulbosum, Phleum paniculatum, Alyssum marginatum, Srigosella trichocarpa, Psoralea drupacea,* and *Eremurus sogdianus*. *Artemsiia ferganensis* has been planted in the Aral Sea region for arid land regeneration and pasture-improving purposes.

Artemisia porrecta is an endemic shrub to Middle Asia, with erect herbaceous stems about 75 cm tall. Its morphological structure is very close to that of *A. ferganensis,* but they differ by inflorescence form. There are three associations of *A. porrecta*, with *Carex pachystylis*, *Phlomis thapsoides, Eremostachys eriocalyx, Salsola sclerantha, Girgensohia oppositiflora, Hordeum leporinum,* and *Aegilops squarrosa* on salty soils along the rivers from lower to middle mountain zones in Uzbekistan (Mailun 1976).

Artemisia baldshuanica (fig. 2H) is an endemic species to Middle Asia, with a very limited distribution area in the South Pamir-Alai Mountain system. This shrub has erect stems about 60 to 100 cm tall with a woody part 20 to 40 cm (Vvedenskii 1962). *Artemisia baldshuanica* communities are spread on northern slopes, sometimes with crushed stones, from foothills up to the middle part of the mountains. There are three associations with this species in Uzbekistan, with *Dactylis glomerata, Agropyron trichophorum, Calamagrostis epigeios, Origanum tyttanthum, Phlomis bucharica, Ziziphora brevicalyx, Muretia fragrantissima, Agropyron trichophorum, Carex pachystylis, Poa bulbosa, Gentiana olivieri, Gagea stipitata,* and *Ixiolirion tataricum*. *Artemisia baldshuanica* is codominant in *Amygdalus bucharica, Pistacia vera, Otostegia bucharica,* and *Juniperus seravschanica* communities on stony slopes (Mailun 1976).

Artemisia tenuisecta is an endemic shrub to Middle Asia (West Tian-Shan and Pamir-Alai), about 35 to 75 cm tall, with woody and rather thick stems, and very tomentose in the beginning of the vegetation period (Vvedenskii 1962). This species needs highly humid and warm weather. There are 16 associations with this species in Uzbekistan. Their floristic composition comprises about 136 species (Mailun 1976). *Artemisia tenuisecta* is codominant with *Elytrigia trichophora, Amygdalus spinosissima, Atrophaxis pyrifolia, Rosa maracandica, Caragana alaica, Spiraea hypricifolia, Hammada leptoclada, Prangos pabularia, Inula grandis, Poa bulbosa,* and *Carex pachystylis* on typical sierozems of foothills and lower mountains (600 to 1,500 m above sea level), and with *Juniperus seravschanica* and *J. semiglobosa* on typical brown soils. *Artemisia tenuisecta* communities with *Agropyron trichophorum, A. intermedium, A. setuliferum, Festuca valesiaca, Althaea nudiflora, Elytrigia trichophora, Prangos pabularia, Inula grandis,* and *Amygdalus spinosissima* occupy areas of mountain steppes at heights up to 2,000 to 2,600 m above sea level. Dark sierozems are the main soils, although pale-gray and brown mountain-steppe soils occur in under parts. Average annual temperature is 11 to 14 °C.

Artemisia lehmanniana, A. dracunculus, and *A. persica* form shrublands on the slopes and tops of the mountains higher than 2,000 m (Akjigitova and Mailun 1984). *Artemisia lehmanniana* is an endemic shrub to Middle Asia, about 15 to 45 cm tall, with short, perennial, woody,very ramified stems. *Artemisia dracunculus* has erect herbaceous stems about 40 to 80 cm tall and very characteristic—very rare in the genus—entire leaves. It occurs in Middle Asia, Siberia, the southern part of the former Soviet Union, Minor Asia, Afghanistan, North America, and Mongolia. *Artemisia persica* is a gray-green shrub with stout woody stems. Its distribution area comprises Middle Asia, Iran, Afghanistan, and Tibet. Those three species are codominant in *Juniperus seravschanica* and *J. semiglobosa* communities, accompanied by *Lonicera altmannii, Rosa hissarica, R. maracandica, Malus sieversii, Acer semenovii, Adonis turkestanica, Arenaria griffithii, Phlomis olgae,* and *Acantholimon erythraeum. Artemisia lehmanniana* and *A. persica* predominate in higher steppe mountain zones, and subalpine and alpine meadows located between 2,800 and 3,700 m and characterized by a significant rate of humidity (precipitation rate up to 800 mm) and a temperately cold climate with average annual temperature of 8 °C. Soils belong to the mountain-meadow-steppe fulvous type and, less often, to the chernozem-like subalpine type. Associations of *A. lehmanniana* and *A. persica* with *Festuca valesiaca, Cerasus verrucosa, Dactylis glomerata, Poa nemoralis, Cousinia verticillaris, Koeleria gracilis, Bromus inermis,* and *Arenaria griffithii* are typical in the steppe zone, and those with *Prangos pabularia, Ligularia thomsonii, Polygonum coriarium, Ferula tenuisecta, Cicer maracanthum,* and *Phlomis severtzovii* are found in subalpine and alpine meadows.

Karyology and Distribution

Sixteen *Artemisia* species form shrubland communities in the desert and mountain zones of Uzbekistan. Most widespread communities are dominated by species belonging to the subgenus *Seriphidium*: *A. diffusa* in the desert zone; *A. sogdiana* on premountain plains and the low mountain zone; *A. tenuisecta* and *A. baldshuanica* from foothills up to the middle part of the mountains; and *A. lehmanniana* in the higher mountain zone. These species are endemic to Middle Asia. From a karyological viewpoint, it is worth noting that widespread species in the desert and semidesert zones (*A. diffusa, A. sogdiana*) are polyploid (2n = 36), whereas more chorologically restricted species—adapted to xerophilous conditions in the desert (*A. turanica, A. santolina, A. leucodes*) or to more humid conditions in the mountains (*A. tenuisecta, A. juncea, A. serotina, A. porrecta*)—are diploid (2n = 18). This fact, noted by Vallès and others (2001), agrees with the rather general assumption that polyploids usually cover larger territories than related diploids (Ehrendorfer 1980), even though many exceptions to this rule can be found (Bretagnolle and others 1998).

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Kochia prostrata Germplasm Collection Expedition to Kazakhstan

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Abstract—The low stature of 'Immigrant' forage kochia (*Kochia prostrata*) limits its use as winter forage and habitat for livestock and wildlife. In October 1999, a germplasm collection trip was undertaken to obtain forage kochia ecotypes that have potential to improve fall and winter forage. The collection area was north of the Aral Sea in the Clay and Sand Desert Steppes of Kazakhstan. Seed samples brought back to the U.S. included 192 forage kochia ecotypes. The desert shrub ecosystems had major components of chenopods. In general, the area was classified as Brown Desert Steppe, Light Chestnut Steppe, Solonetz, or Degraded Solonetz. Most soils in the Clay Desert Steppes had a clay to clay loam subsoil and were generally saline and alkaline. Elevation ranged from 250 to 1,000 feet above sea level. Average annual precipitation was 6 to 9 inches. Average annual air and soil surface temperatures were 41 and 44 degrees Fahrenheit, respectively. On average, forage kochia made up 6 percent of the plant composition on sites in the native steppe where it was present, ranging from 1 to 20 percent. Forage kochia was more prevalent when present on disturbed areas such as abandon fields, homesteads, and roadways, where it comprised 15 to 60 percent of the plant composition. Flow cytometry analysis revealed that 2x, 4x, and 6x ploidy levels of forage kochia were collected.

Introduction

Forage kochia (*Kochia prostrata*) is a valuable semi-shrub for rangeland rehabilitation. Some of its uses include soil stabilization in saline/alkaline semi-arid sites, green stripping to help control wildfires, wildlife and livestock forage and cover, and to suppress invasion of annual weeds such as cheatgrass (*Bromus tectorum*) and halogeton (*Hologeton glomeratus*) (Harrison and others 2000). A 3-year study investigating the adaptability and potential for 'weedy' invasiveness of forage kochia was conducted by the United States Department of Agriculture, Agriculture Research Service (USDA-ARS), Forage and Range Research Laboratory (FRRL) in Logan, UT. Harrison and others (2000) reported that forage kochia was widely adapted to the semi-arid and arid ecosystems of the Great Basin Intermountain Region, but was not an aggressive or weedy invader of perennial or closed plant communities.

A forage kochia breeding and genetics program was initiated in 1998 at the USDA-ARS-FRRL in response to increasing interest in forage kochia for fall/winter livestock grazing on privately owned land. With only one cultivar (Immigrant) in the U.S.A. there was a lack of available germplasm to start a breeding program. Part of the interest in new cultivars included development of taller statured plants for improved winter grazing and better game bird and small mammal habitat. Because little variation had been observed in Immigrant for stature and height, scientists at the USDA-ARS-FRRL attempted to obtain seed of Kazakhstan germplasm from the N.I. Vavilov of Plant Industry. As part of a cooperative program between the U.S.A. and Russia, the USDA-ARS International Programs helped fund a forage kochia collection trip to Russia and Kazakhstan.

Collection Expedition Team and Itinerary

The collection team consisted of the six authors of this paper and represented the USDA-ARS, N.I. Vavilov Research Institute of Plant Industry (VIR) (in Russia), and the National Academic Center for Agricultural Research of the Ministry of Science and Higher Education of the Republic of Kazakhstan.

Leg 1 of the expedition consisted of a collection trip to the South of Chelkar, Kazakhstan and East of the Aral Sea prior to the arrival of the U.S. participants. The collection route for leg 2, which included the U.S. participants, was to the Kazakhstan steppe north of Chelkar, Kazakhstan. Leg 3 of the expedition occurred after the departure of the U.S. participants and went southwest of Chelkar (northwest of the Aral Sea). With the exception of a listing of the species collected and sent to the U.S. from leg 1 and 3, all other

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details in this paper pertain to leg 2 in which the U.S. participants were present.

The purpose of the collection trip was clearly defined in the beginning as:

1. To expand the U.S. germplasm base of forage kochia.
2. To make a collection of forage kochia ecotypes which would have the potential to be used in the development of a valuable summer, fall and winter forage.
3. To continue to develop contacts and to expand upon interactions for germplasm exchange and related agricultural research with scientists and administrators associated with the N.I. Vavilov Institute of Plant Industry at St. Petersburg, Russia and the Aral Sea Experiment Station for Plant Genetic Resources at Chelkar, Kazakhstan.

While forage kochia was the primary species of interest, additional species were collected that might fit into the same niche as forage kochia.

Itinerary for the Second Leg of Germplasm Collection Expedition

The collection trip occurred in the fall of 1999 with travel dates for the U.S. participants being October 2 to October 28, 1999. Because of logistics only 11 of those days were spent collecting plant materials. The rest of the time was spent in travel, visiting institutions, and preparing the seed for export to the U.S. as outlined below.

Itinerary:

Travel Logan, UT to Moscow, Russia…Oct. 2-3
Travel Moscow, Russia to Chelkar, Kazakhstan…Oct 4-6
Collection-Chelkar, Kazakhstan northward to Karabutak, Kazakhstan; Karabutak southeast to Irghiz, Kazakhstan; Irghiz southwest to Chelkar, Kazakhstan…Oct 7-17
Collection-Sandy desert south of Chelkar…Oct 19
Travel Chelkar, Kazakhstan to St. Petersburg, Russia…Oct 20-23
St. Petersburg, Russia (N.I. Vavilov Research Institute)…Oct 24-27
Travel St. Petersburg, Russia to Logan, UT…Oct 28

Institutions Visited:

Aral Sea Experiment Station for Plant Genetic Resources, 27 Biyekenov Street, Aktyubinsk Region, Chelkar Town, Republic of Kazakhstan, 464760.
N.I. Vavilov Institute of Plant Industry, 42 Bolshaya Morskaya Street, 190000, St. Petersburg, Russia.

Collection Trip Results and Summary

The expedition was very successful and 246 accessions representing 11 species were collected (table 1). The majority of the accessions, 192, were forage kochia (*Kochia prostrata*). An additional, 88 forage kochia accessions were collected during legs 1 and 3.

Those leading the expedition told us that we were the third U.S. collection team to visit the Aral Sea Experiment Station for Plant Genetic Resources in Chelkar, Kazakhstan. The two previous teams were the Westover-Enlow expedition in 1934 (N.I. Vavilov personally accompanied this expedition) and the Asay-Johnson expedition in 1992 (Asay and others 1992). According to the Kazakhstan and Russian scientists, our expedition route did not overlap with Asay and Johnson's, but unfortunately it was too late in the year to make a broad collection of the grass species in the area. We were also told that we were the first Americans to target forage kochia for germplasm collection.

As experienced by Asay and Johnson in 1992, the Foreign Relations Department (Sergey Alexanian and Sergey Shuvalov) and other staff at VIR in St. Petersburg were extremely cooperative, and did an excellent job of facilitating the expedition. Dr. Nicolai Dzyubenko (Vice director of Science and Head of Forage Crops) and Sergey Shuvalov were primarily responsible for organizing our expedition and accompanying us throughout the trip. Dr. Dzyubenko had been director of the Aral Sea Experiment Station for nine years and was familiar with the collection routes and native vegetation. Mr. Shuvalov was fluent in English and acted as interpreter as well as biologist on the collection expedition. Excellent support was also provided through the Aral Sea Experiment Station of Plant Genetic Resources in Chelkar, which provided facilities and arranged for hiring

Table 1—Species collected during leg 1 of expedition to Kazakhstan in 1999[a].

Species	Number of collections	Species	Number of collections
Kochia prostrata	192	*Leymus* [*Elymus*] *giganta*	2
Krascheninnikovia [*Ceratoides*] *papposa*	13	*Elymus angustifolius*	7
Atriplex cana	8	*Agropyron fragile*	7
Camphorosma lessingii	10	*Agropyron desertorum*	2
Anabasis salsa	1	*Stipa sareptana*	1
Medicago falcata	3		

[a] In additon, 88 collections of *Kochia prostrata* from the first and third leg of the expedition were brought to the United States. Additional species collected on the first tnd third legs were: *Haloxylon ammondendron*—98 collections, *Camphorosma lessingii*—49 collections, and *Salsola orientalis*—92 collections.

vehicles and drivers for the expedition. This experiment station was previously under the direction of VIR, but is now administered through the National Academic Center for Agricultural Research of the Ministry of Science and Higher Education of the Republic of Kazakhstan (NACAR). However, close cooperation between VIR and the experiment station is evident. Auskhan Khusainov, director of the Aral Sea Experiment Station for Genetic Resources, provided excellent planning and organizational assistance for the trip. He was directly responsible for the logistics of our travel in Kazakhstan and accompanied us in the field, providing taxonomic expertise on the vegetation.

Asay and Johnson noted severe budget restraints at both VIR and the Aral Sea Experiment Station during their visit in 1992. Funding for these institutes was even less in 1999. The staff at the Aral Sea Experiment Station had been reduced to the Director, Mr. Khusainov, and a few maintenance employees. There were no evaluated experimental plots still in existence. The Vavilov Institute also was operating under severe budget restraints, but fortunately appeared to have stabilized and hopefully can rebuild its staff and research activities during the next decade. A recent grant from USAID had allowed them to modernize their long-term seed storage. With the current budget restraints they were mainly focused on germplasm collection and preservation, and had greatly reduced their germplasm evaluation programs. We visited staff and toured projects at the VIR headquarters in St. Petersburg, Russia. Staff visited included Prof. Victor A. Dragavtsev, Director General of the Institute; Dr. Sergey Alexanian, Head of Foreign Relations; Dr. Alexandr Afonin, Climatology; Dr. Vadim Molodkin, Head of Plant Genetic Resources Long-Term Storage Laboratory; Dr. Tamara Smekalova, Herbarium; Andrew Omelchenko, Chief of Computer-Aided Information Systems; Leonid Malyshev, Senior Scientific Researcher of the Fodder Crops Dept.; and Antone Krylov from the Foreign Relations office.

Environmental and Collection Details for Leg 2

Leg 2 of the collection expedition was conducted to the north of Chelkar. The route went as far north as Karabutak, Kazakhstan (a few miles south of the Russian border) and east to Irghiz, Kazakhstan. To our knowledge, we (Waldron and Harrison) were the first Americans to make plant collections in this area. The area had experienced a drought and many plants appeared to be stunted. Livestock numbers were reported to be 1⁄10 those of a decade ago, nevertheless, we found grazing everywhere we went, with concentrated animal numbers around villages.

Forage kochia germplasm was collected at 64 sites. These sites were in the Clay and Sand Deserts which included the Brown Desert Steppe, Light Chestnut Steppe, Degraded Solonetz, and Solonetz (Atlas of Agriculture of the USSR 1960). According to scientists from the N.I. Vavilov Institute of Plant Industry these areas have the highest concentration of forage kochia in the former Soviet Union. Plant associations included: *Agropyron–Stipa– Artemisia; Artemisia terrae-albae; Artemisia terrae-albae–Krascheninnikovia (Ceratoides);Artemisia–Salsola–Kochia;Atriplex–Anabasis–Artemisia; Artemisia–Anabasis; and Anabasis*. Soil surface textures included sands, fine sands, sandy loam, sandy clay loam, silt loam, clay loam, clay, and gravelly and cobbley. Most soils in the Clay Desert had a clay loam or clay subsoil and were saline and alkaline. The Solonetz sites had extremely high concentrations of alkali and salt. The subsoil in the Sandy Desert was mainly sand to fine sand. Elevations ranged from 250 feet near the city of Irghiz to 1000 feet above sea level north of Karabutak. Annual precipitation, averaged over 14 to 43 years, listed Chelkar at 6 to 9 inches, Irghiz at 6 to 8 inches, and Karabutak at 10 to 12 inches (Climate of the U.S.S.R. 1968; Agricultural management in the Aktyubinsk region 1958). Average air and soil surface temperatures at Chelkar are 41.9 °F and 46.4 °F, respectively; at Irghiz 41.5 °F and 44.6 °F, respectively; and at Karabutak 37.3 °F and 41.0 °F, respectively (Climate of the U.S.S.R. 1968).

We made 246 germplasm collections of which 192 were forage kochia. Collections are listed by species in table 1. Species associated with forage kochia included:

Forbs—Yarrow (*Achillea micrantha*), annual chenopod, annual kochia (*Kochia laniflora* and *Kochia scoparia*), knapweed (*Centaurea picris* and other spp.), knotweed (*Polygonum* spp.), buckwheat (*Eriogonum* sp.), fisheye (*Ceratocarpus arenarius*), Russian thistle (*Salsola iberica*), locoweed (*Astragalus* sp.), and yellow flower alfalfa (*Medicago falcata*);

Shrubs—*Artemisia austriaca*, *Artemisia arenaria*, *Artemisia terrae-albae*, *Salsola orientalis*, winterfat (*Krascheninnikovia* [*Ceratoides*] *ewersmanniana* and *Krascheninnikovia* [*Ceratoides*] *papposa*), saltbush (*Atriplex cana*), camphorosma (*Camphorosma lessingii*), Anabasis (*Anabasis salsa*), *Ephreda* spp., and *Haloxylon aphyllum*;

Grasses—Siberian wheatgrass (*Agropyron fragile*), crested wheatgrass (*Agropyron desertorum*), needlegrass (*Stipa sareptana*), giant wildrye (*Leymus* [*Elymus*] *giganta*), spreading wildrye (*Elymus angustifolius*), *Bromus inermis*, *Poa* spp., *Festuca ovina* and other *Festuca* spp., *Stipa capillata*, reedgrass (*Calamagrostis* sp.), redtop (*Agrostis* sp.), orchardgrass (*Dactylis glomerata*), saltgrass (*Distichlis* sp.), tall wheatgrass (*Thinopyrum ponticum*), *Elymus* spp., *Leymus* spp., quackgrass (*Elytrigia repens*), foxtail (*Hordeum* sp.), and junegrass (*Koeleria* sp.).

Forage kochia on average made up 6 percent, ranging from 1 to 20 percent, of the perennial plant composition on native steppe sites where it was present. Percentage composition depended on the site and associated species. For example lower percentages of forage kochia were found on the *Agropyron–Stipa–Artemisia, Artemisia terrae–albae*, and *Artemisia–Krascheninnikovia (Ceratoides)* sites while higher percentages were found in the *Artemisia–Salsola–Kochia*, and *Atriplex–Anabasis–Artemisia* sites. Overall, *Artemisia terrae–albae* was the dominant species throughout the native steppe area. When it was present, forage kochia made up a higher percentage of the plant composition in disturbed areas, such as along road sides, in abandoned fields, and on farmsteads where a high percent of annuals were present. On these sites forage kochia ranged from 15 to 60 percent, and averaged 32 percent of the plant composition.

As indicated above forage kochia made up a small percentage of the perennial plant communities. Nowhere on the Kazakhstan steppes did we observe forage kochia to be dominant in communities comprised of sagebrush, winterfat, saltbush, *Anabasis*, crested and siberian wheatgrass, and needlegrass. Instead, forage kochia complimented the biodiversity of such communities. In addition, we did not observe forage kochia invading from disturbed sites into the surrounding perennial plant communities.

The forage kochia germplasm collected was mainly the glabrous and red-green stem forage kochia (*Kochia prostrata* ssp. *virescens*), however, some of the forms were gray with heavy pubescence on the leaves and stems and were classified as ssp. *grisea*. Other forms were in-between the red-green stem and the gray stem subspecies which indicated that the two subspecies may hybridize. This was confirmed by Dr. Dzyubenko and Mr. Khusainov whose combined experience with forage kochia expands over 20 years. Seed was collected by bulking seed from plants with similar morphological characteristics found at the same site. The morphological characteristics included: Height—one to three feet; Seeds—small and large, and few to numerous; Branches or tillers—few to numerous, and basal or high on the stem; Leaves—mostly basal or throughout the stems and branches; stem diameters—fine (about 1⁄16 inch) or thick stems (about 1⁄4 inch); stem color—red, yellowish-green, or gray; leaves, branches and stem—glabrous or pubescent.

Dr. Dzyubenko and Mr. Khusainov were not aware of any current forage kochia genetics or breeding programs in Russia or Kazakhstan. Earlier cytogenetics work in the former U.S.S.R. had documented diploid, tetraploid, hexaploid, and octoploid forage kochia types, and naturally occurring aneuploids resulting from hybridization between ploidy levels. In addition, these scientists suggested that the two subspecies of *virescens* and *grisea*, which are frequently recognized in North American literature, are not well defined and in their native habitat readily hybridize with each other resulting in morphological types intermediate between the subspecies. The possibility of inter-ploidy and inter-subspecies hybridization may partially explain the large amount of variation within forage kochia populations at many collection sites.

The use and value of forage kochia in Kazakhstan was discussed among trip participants throughout the trip. Obviously, forage kochia is an important part of the plant composition throughout the northern Kazakhstan steppe and had been heavily to moderately grazed in most of the collection sites. It was often selectively grazed indicating high palatability and/or high nutritional content. The number of grazing animals on the steppe has dropped to 1⁄10 the number present at the breakup of the Soviet Union. This greatly reduced grazing pressure and allowed us to collect seed even in grazed areas. The numbers of grazing/browsing animals in order of frequency were cattle, sheep and goats, horses, camels, and Saiga (antelope). We observed utilization of forage kochia by cattle, sheep and goats, and horses, and assumed that camels and Saiga were also grazing the forage kochia. We observed large areas of the native steppe that had been mowed and hayed for winter feed. Forage kochia comprised 1 to 20 percent of that feed with *Artemisia terrae-alba* being the major component and *Stipa* sp. and *Agropyron fragile* making up lesser components. Even though forage kochia made up a low percentage of the overall biomass in the hay, we assumed that its high nutritional value made it an important component in overwintering livestock. We did not observe solid stands of forage kochia or areas where it had been seeded, and in fact we only saw one attempt to improve the steppe by seeding of any improved forage species—a planting of crested wheatgrass. However, Dr. Dzyubenko and Mr. Khusainov told of 20,000 ha of forage kochia that had been planted in southern Kazakhstan. That area was used for grazing sheep in late fall and early spring to flush the ewes and increase the number of live births.

Evaluation of Collected Material

Most of the collected seed cleared quarantine and arrived at the FRRL in mid-December, 1999. Seedlings were started in the greenhouse in cones. Over 8,000 plants, representing most of the forage kochia collections and some of the Ceratoides collections were transplanted in late April (2000) at two semi-arid locations in central and northern Utah. Seed of 58 forage kochia entries that were sent by Dr. Dzyubenko from the 3rd leg of the collection trip arrived too late for the 2000 season and will be started and transplanted in 2001.

Ploidy Level of Collected Forage Kochia

Our observations and discussions in Kazakhstan concerning ploidy levels and natural subspecies hybridization prompted us to do a rapid test of ploidy level using flow cytometry. Leaf samples from five plants of each collection were bulked together and analyzed using Immigrant as a standard.

These tests confirmed that we had collected plants of three ploidy levels: 2x, 4x, and 6x. In some instances it appeared that seed from plants of different ploidy levels had been mixed together (for example, we rarely collected seed from only an individual plant). Most surprising was the number of collections sites where two or more ploidy levels were coexisting (table 2). Ecological genetics would suggest that over time one ploidy level should be most fit and eventually displace the other ploidy levels. During the successional phase the different ploidy levels may cross with each other

Table 2—Ploidy level of forage kochia at sites where more than one collection was made.

Number of sites	Ploidy level observed
4	2x only
7	4x only
10	6x only
2	2x and 4x
7	2x and 6x
4	4x and 6x
6	2x, 4x, and 6x

resulting in aneuploidy, however, we saw very little evidence from the flow cytometry analysis to suggest the presence of aneuploids. These results are being verified by the USDA Forest Service Shrub Lab in Provo, UT.

Summary

In summary, 280 collections of forage kochia were made during a collection expedition to the Kazakhstan steppe in October 1999. These collections greatly broaden the forage kochia germplasm available in the U.S. and include three ploidy levels, two subspecies, and diverse morphological types. The collections are being evaluated at the USDA-ARS Forage and Range Research Lab, in Logan, Utah and will be used to develop new forage kochia cultivars for use as fall/winter forage, greenstripping, and range reclamation.

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Narrow Hybrid Zone Between Two Subspecies of Big Sagebrush (*Artemisia tridentata*: Asteraceae): XI. Plant-Insect Interactions in Reciprocal Transplant Gardens

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Abstract—Basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*) hybridize in a narrow zone near Salt Creek, Utah. Reciprocal transplant experiments in this hybrid zone demonstrate that hybrids are more fit than either parental subspecies, but only in the hybrid zone. Do hybrids experience greater, or lesser, use by herbivorous insects, especially in the hybrid zone? And do certain species of herbivorous insects prefer one or the other parental subspecies of big sagebrush? We studied plant-insect interactions in three reciprocal transplant gardens that span the hybrid zone at Salt Creek. Gardens were in the basin and mountain big sagebrush zones and also in the hybrid zone. Transplanted seedlings came from two parental and three hybrid source populations. Densities of herbivorous insects varied among the gardens and source populations, but the interaction between garden and source population was statistically insignificant. Most of the variation in herbivore density was among gardens, rather than among source populations. Only grasshoppers and lepidopteran leaf miners showed significant preferences among the source populations; grasshoppers preferred mountain big sagebrush and leaf miners preferred near-basin hybrids. Coccids, *Clastoptera*, *Trirhabda*, coleophorid larvae, and lepidopteran leaf miners showed significant differences in density among the gardens. Finally, the hybrids were not a sink for herbivorous insects, nor did they have lower herbivore loads.

Introduction

Hybrid zones involving plants are natural laboratories for studying the mutual adaptations of herbivorous insects and their hosts (Strauss 1994; Fritz 1999). Thomas Whitham (1989), working on *Pemiphagus* aphid galls in a *Populus* hybrid zone, suggested that hybrids may often support much greater herbivore loads than parental taxa, and by attracting herbivorous insects may hinder adaptation to the parental taxa. He called this phenomenon the hybrid sink effect. But more recent work on a variety of plant hybrid zones has shown that the responses of insects to hybrids and parental taxa is not so simple, nor so general. Herbivorous insects may indeed prefer hybrids when coadaptation for suites of defensive chemicals has been disrupted in the hybrids, or when hybrids are stressed (Whitham 1989; Floate and others 1993; Morrow and others 1994; Whitham and others 1994; Christensen and others 1995; Kalischuk and others 1997). But insects may often show no preferences (Hanhimäki and others 1994; Graham and others 1995), or may prefer one or both parental taxa (Boecklen and Spellenberg 1990). In a single hybrid zone, Fritz and others (1994) found that some herbivores preferred hybrids, some preferred parentals, and some had no preferences.

To critically evaluate plant-herbivore interactions, reciprocal transplant experiments involving plant hybrid zones are needed (Fritz 1999). Indeed, one cannot state with certainty that a particular species of insect prefers to feed on a particular plant genotype unless both genotype and environment are controlled in a natural setting. In this paper, we show that insect use of big sagebrush hybrids and parental taxa in a reciprocal transplant experiment depends upon both genetic differences among the big sagebrush taxa and environmental differences across the hybrid zone. The environmental effects, however, are much stronger than the genetic effects.

Methods

Big Sagebrush Hybrid Zone

Big sagebrush (*Artemisia tridentata*) is the most widely distributed shrub in North America. Its environmental tolerance is extreme—from arid flats to subalpine meadows. As is true of many widely distributed species, clinal and subspecific variation is common. And different subspecies of big sagebrush hybridize, often in extremely narrow hybrid zones. For example, low elevational populations of basin big sagebrush (*A. tridentata* ssp. *tridentata*) hybridize with high elevational populations of mountain big sagebrush (*A. t.* ssp. *vaseyana*) wherever their distributions overlap. Introgression

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is bidirectional (McArthur and others 1988), and the hybrids consist of advanced generations and backcrosses.

Durant McArthur began studying sagebrush hybrids almost 25 years ago (McArthur and others 1979), and we (including Freeman's and McArthur's students and colleagues) have studied the hybrid zone between basin and mountain big sagebrush at Salt Creek, Utah, since 1989 (Freeman and others 1991). The parental taxa at Salt Creek differ in height, stem and leaf shape, and inflorescence structure (Freeman and others 1991), terpene and coumarin composition (Welch and McArthur 1981; McArthur and others 1988; Freeman and others 1991; Byrd and others 1999), and DNA markers (McArthur and others 1998b). We have also studied herbivory and reproduction (Graham and others 1995), developmental instability (Freeman and others 1995; Tracy and others, in preparation), and soil properties (Wang 1996; Wang and others 1998). In 1993, we began a reciprocal transplant experiment in the Salt Creek hybrid zone. This experiment was designed to critically test the predictions of three hybrid zone models: the dynamic equilibrium model, the mosaic hybrid zone model, and the bounded hybrid superiority model.

The big sagebrush hybrid zone at Salt Creek is best explained by the bounded hybrid superiority model (Wang and others 1997). This model suggests that hybrids have the highest reproductive fitness, but only in the hybrid zone (Moore 1977). The competing dynamic equilibrium model maintains that hybrid zones are stabilized by selection against hybrids, and by gene flow across the zone (Barton and Hewitt 1985); the hybrid zone is independent of the environment. And the mosaic hybrid zone model maintains that exogenous selection acts against hybrids, but that parental taxa are adapted to different environments (Harrison and Rand 1989; Arnold 1997).

Studies in the transplant gardens at Salt Creek have included reproductive fitness (Wang and others 1997; Freeman and others 1999), respiration and water potential (McArthur and others 1998a), nutrient uptake (Wang 1996; Wang and others 1999), and growth (Freeman and others 1999). These studies are summarized in Graham and others (1999). Current research involves taxon-specific soil mycorrhizal associations (Miglia and others, unpublished data) and developmental stability (Graham and others, unpublished data). Graham and others (1995) studied the distribution and use of big sagebrush by gall-formers, grasshoppers, aphids, and deer in the hybrid zone, but this research did not involve the transplant gardens. Messina and others (1996) looked at insects on hybrid and parental sagebrush grown in a single common garden, but the garden was not actually in a hybrid zone.

Study Site

The reciprocal transplant gardens span the big sagebrush hybrid zone at Salt Creek, near Nephi, Utah (Uinta National Forest, Juab Co., Fountain Green North Quadrangle). Basin big sagebrush occur along Salt Creek and its tributaries, to an elevation of about 1,790 m. Mountain big sagebrush occur from about 1,850 m to timberline on nearby Mt. Nebo. The hybrids occur from 1,790 to 1,830 m elevation, in a narrow band between the basin and mountain populations (Freeman and others 1991).

We studied five stands of big sagebrush at Salt Creek: the two parental subspecies and three classes of hybrids. We refer to *A. t.* ssp. *tridentata* as **basin**, *A. t.* ssp. *vaseyana* as **mountain**, the middle hybrid as **hybrid**, the hybrid between basin and middle hybrid as **near basin**, and the hybrid between mountain and middle hybrid as **near mountain**.

Reciprocal Transplant Gardens

We germinated seeds from the five source populations (basin, near basin, hybrid, near mountain, and mountain), grew the seedlings for one year in a greenhouse, and planted twelve seedlings from each source in each of three gardens (basin, hybrid, mountain) during May 1993. The gardens were enclosed with 2.5 m high fences, for protection from elk, deer, and cattle.

The basin garden is on a bench just above the flood plain of Salt Creek, at an elevation of 1776 m. The mountain garden is on the lower slope of Mt. Nebo, at an elevation of 1870 m. The hybrid garden is in a relatively flat meadow, at an elevation of 1800 m, and midway between the basin and mountain gardens. (See Wang and others [1997] for additional details.)

Census of Insects

We counted insects on big sagebrush in our three gardens during the week of June 21-27, 1997. Although this is a relatively brief sampling period, it occurs at a time of year when insect activity on sagebrush is at a peak. Respiration rates and water potential reach their seasonal peaks in early summer (McArthur and others 1998a), and temperatures are not yet warm enough to restrict insect activity. For grasshoppers, we counted both the insects and the physical evidence of their browsing. And because the ant *Formica dakotensis montigena* makes its nest below ground, at the base of sagebrush, we only recorded its presence or absence on a plant. Samples of all insects were preserved in 70 percent ethanol for later identification.

Plant size may influence numbers and diversity of insects. To estimate density of herbivores, we needed an estimate of relative plant volume. A measure of volume is $v = hc^2$, where h is height and c is crown diameter. This is a measure of the volume of the smallest square-ended box enclosing a plant.

Statistical Analysis

Plant size varied among gardens and taxa, so we expressed all counts as densities (i.e. number divided by v). We used MANOVA to compare insect densities of the most common insect species among gardens and source populations. We used a crossed design, with replication. Individual plants (the replicates) were nested within the garden by source population. Both garden and source were fixed variables in the MANOVA. A separate MANOVA was done for the three main guilds of insects: chewers, suckers, and gall-formers. (Data on the gall-formers is from Graham and others 2001). As an adjunct to the MANOVAs, we also performed univariate two-way ANOVAs for each variable. We used analysis of covariance (ANCOVA) to compare insect diversities among gardens and source populations.

Most of the insects on sagebrush had contagious (clumped) distributions. Southwood (1978) recommends a logarithmic transformation for highly contagious distributions. We found that a logarithmic transformation of the densities ($\log_{10}[x + 1]$) gave the best approximation to a normal distribution, and stabilized the variance.

Results

Herbivore Density and Distribution

Herbivorous insects on big sagebrush included several orthopterans, homopterans, lepidopterans, and coleopterans (table 1). Dipteran gall-formers, which were also present, are treated in a separate paper (Graham and others 2001). There were significant differences in densities of herbivores among the three gardens and five source populations (table 2). The effect of garden, however, was more highly significant than that of source population. Five herbivores (coccids, spittlebug larvae, *Trirhabda pilosa*, coleophorid larvae, and leaf miners) differed significantly among gardens, while only two species (grasshoppers and leafminers) differed significantly among source populations. Gardens by source population interactions were insignificant.

Herbivorous insects fall into three feeding guilds: leaf chewers and miners, phloem and xylem suckers, and gall-formers. Leaf chewers include the grasshoppers, chrysomelid beetles, and lepidopteran larvae. Grasshoppers (*Melanoplus* sp. and other species) were in low densities in all three gardens, but preferred mountain big sagebrush (fig. 1).

Both larval and adult chrysomelids fed on big sagebrush. *Trirhabda pilosa* has a metallic-green larva that can inflict significant damage on sagebrush. The larvae were only on a few plants in the hybrid garden. In contrast, the adults were only in the basin garden (fig. 2). The larva and adult *Exema conspersa* feed on leaves. Their densities did not vary among gardens or source populations (table 2 and fig. 2). Other coleoptera, such as weevils (*Sternechus* sp.) and scarabid beetles, (*Dichelonyx* sp.) were rare.

Larval lepidoptera included a pterophorid moth, a case-bearing coleophorid moth, and an unidentified leaf miner. All three species feed on leaves. While the pterophorids were uncommon, the more abundant coleophorids differed significantly among gardens (table 2), and were most abundant in the basin garden (fig. 3). Leaf miner densities varied among gardens and source populations (table 2). They were more abundant in the mountain garden, and preferred near-basin plants (fig. 3).

Phloem and xylem suckers include the aphids, coccids, spittlebugs, leafhoppers, cicadas, and true bugs. Two species of aphids were *Obtusicauda coweni* and *O. filifoliae*. Neither showed significant differences in density among gardens or source populations (table 2 and fig. 4). Coccids (scale insects) showed significant differences among gardens (table 2). They were most common in the basin garden, absent from the mountain garden, and of intermediate abundance in the hybrid garden (fig. 5). Spittlebugs (*Clastoptera* sp.) showed significant variation among gardens (table 2). They were also most abundant in the basin garden (fig. 5). Leafhoppers, cicadas, and true bugs (*Lygus* sp.) were rare.

Table 1—Insects found on big sagebrush in the reciprocal transplant gardens.

Scientific name	Family: Order	Description
Herbivorous Insects		
Melanoplus sp.	Acrididae: Orthoptera	Browsing on stem
Unknown grasshoppers	Acrididae: Orthoptera	Browsing on stem
Obtusicauda coweni	Aphididae: Homoptera	Black phloem-feeding aphid
Obtusicauda filifoliae	Aphididae: Homoptera	Green phloem-feeding aphid
Scale Insect	Coccidae: Homoptera	Phloem feeder
Clastoptera sp.	Cercopidae: Homoptera	Phloem-feeding nymph
Leafhopper	Cicadellidae: Homoptera	Phloem feeder
Cicada	Cicadidae: Homoptera	Phloem feeder
Lygus sp.	Miridae: Hemiptera	Phloem feeding larva and adult
Sternechus sp.	Curculionidae: Coleoptera	Leaf chewing adult
Trirhabda pilosa	Chrysomelidae: Coleoptera	Leaf chewing larva and adult
Exema conspersa	Chrysomelidae: Coleoptera	Case-bearing larva and leaf chewing adult
Octinodes sp.	Elateridae: Coleoptera	Non-feeding adult
Dichelonyx sp.	Scarabaeidae: Coleoptera	Leaf chewer
Lyctus sp.	Lyctidae: Coleptera	Wood borer
Moth larva	Pterophoridae: Lepidoptera	Leaf chewing caterpillar
Casebearing moth	Coleophoridae: Lepidoptera	Leaf chewing caterpillar
Unidentified moth larva	Lepidoptera	Leaf miner
Non-herbivorous Insects, and other Arthropods		
Hippodamia apicaulis	Coccinellidae: Coleoptera	Ladybird beetle
Formica dakotensis	Formicidae: Hymenoptera	Nest at base of plant
Monomorium minimum	Formicidae: Hymenoptera	Tending coccids
Wasp	Hymenoptera	
Spider	Aranae	

Table 2—Multivariate and univariate ANOVAs for the effects of garden, source, and garden by source interaction on density of herbivorous insects.

MANOVA

Source	Df	Wilks' λ	*F*	*P*
Garden	18, 240	0.28962	11.44244	<0.001
Source	36, 451	0.66124	1.46339	0.044
Garden x Source	72, 737	0.49543	1.25367	0.083

Univariate ANOVAs (*F* statistics)

Effect (degrees of freedom in parentheses)

Insect	Garden (2, 128)	Source (4, 128)	Garden x Source (8, 128)
Acrididae	2.564	2.495 *	1.275
Obtusicauda coweni	0.888	2.091	1.240
Obtusicauda filifoliae	1.718	0.638	0.733
Coccidae	10.239 ***	1.283	1.627
Clastoptera sp.	7.480 **	0.660	1.908
Exema conspersa	1.914	1.238	0.488
Trirhabda pilosa	6.266 **	2.327	1.561
Coleophoridae, larva	4.488 *	0.276	0.873
Leaf Miners	95.587 ***	3.393 *	1.976

* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

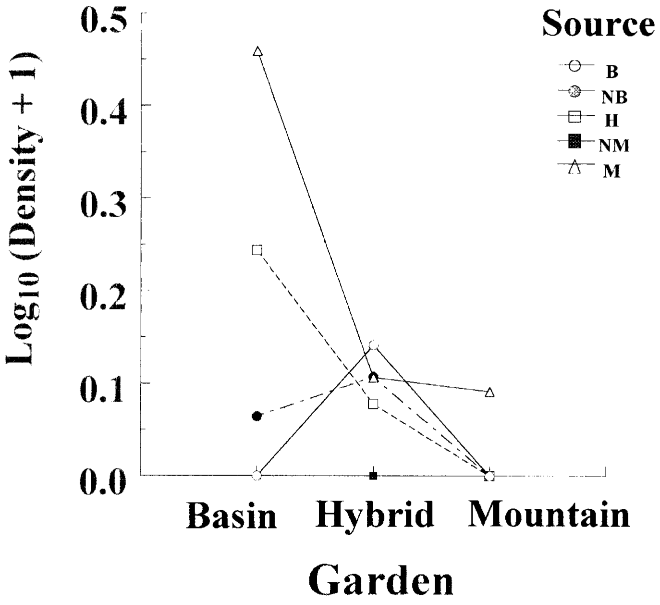

Figure 1—Interaction of garden and source population on density of hoppers and hopper browse. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

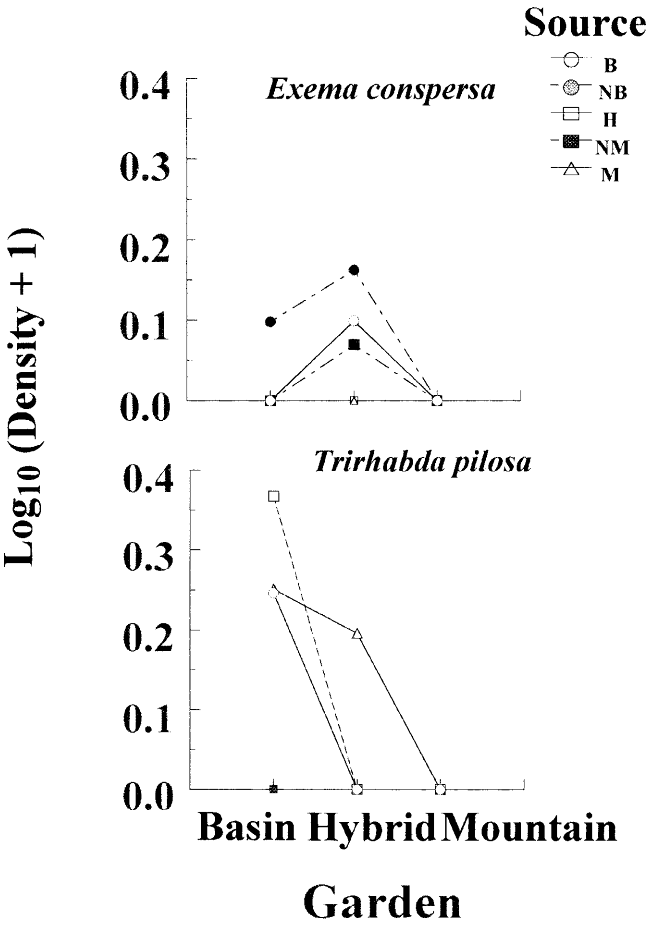

Figure 2—Interaction of garden and source population on density of coleopteran adults and larvae of *Exema conspersa* and *Trirhabda pilosa*. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

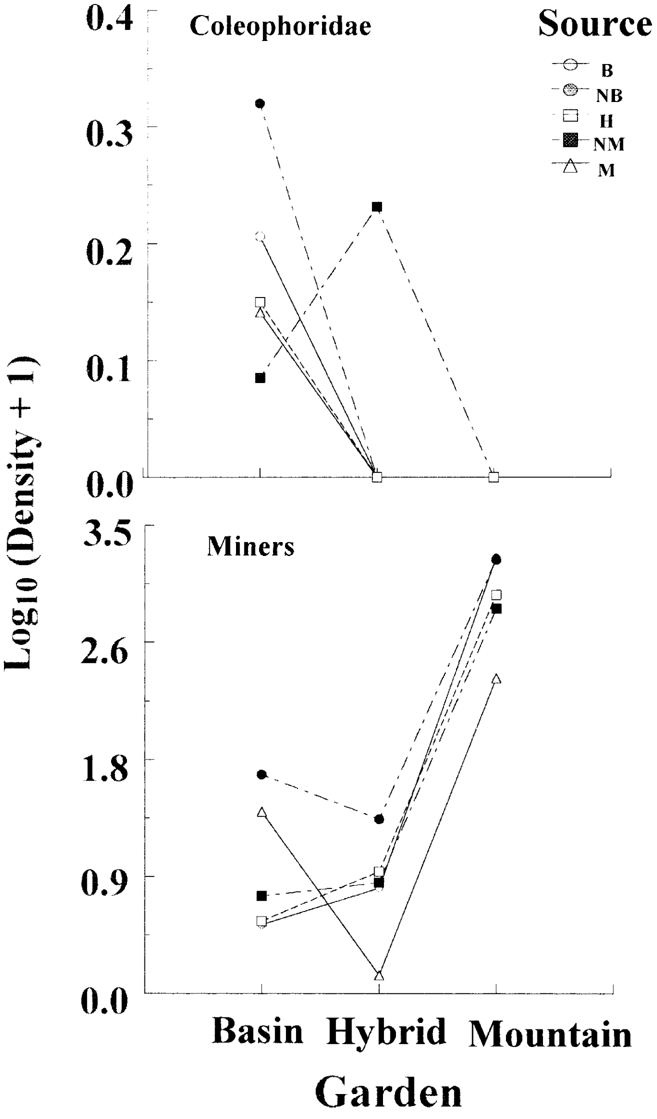

Figure 3—Interaction of garden and source population on density of coleophorid larvae and lepidopteran leaf miners. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

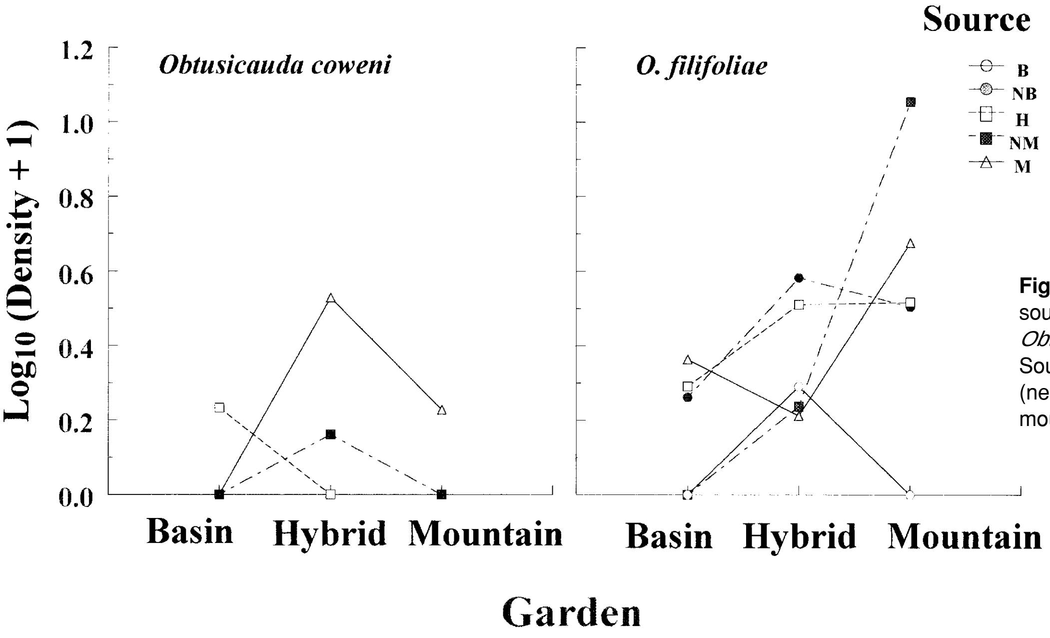

Figure 4—Interaction of garden and source population on density of aphids *Obtusicauda coweni* and *O. filifoliae*. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

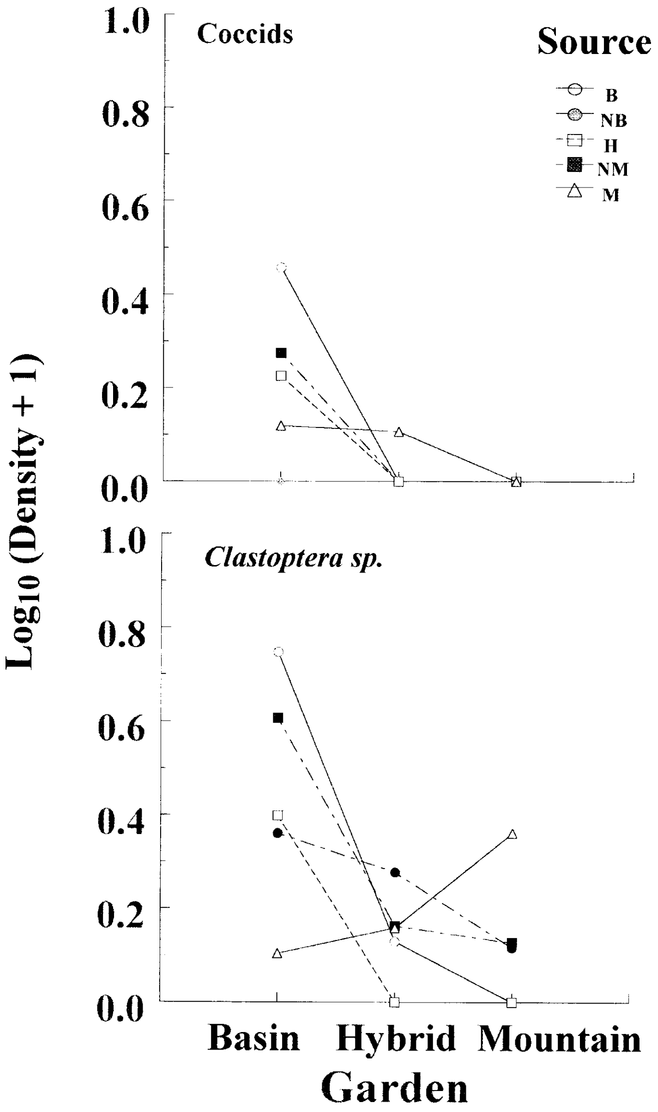

Figure 5—Interaction of garden and source population on density of coccids and spittlebug (*Clastoptera* sp.) larvae. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

The three guilds (leaf chewers and miners, phloem and xylem suckers, and gall-makers) showed significant differences in density among gardens and source populations (table 3). (Data on gall-formers is from Graham and others [2001]). There was also a significant garden by source population interaction (fig. 6). Gall-makers were the most abundant of the three guilds; phloem suckers were the least abundant. Densities of galls and leaf chewers and miners were highest in the mountain garden, but varied with source population (fig. 6). Phloem suckers did not differ significantly among gardens or source populations (table 3).

Herbivore Diversity

Do garden and source population have an effect on species diversity of herbivorous insects? Because the size of a plant may also influence the species diversity of insects, we used analysis of covariance to eliminate the effect of plant size. The effect of plant size ($\log_{10}[v + 1]$) on species diversity ($\log_{10}[S + 1]$), where S is the number of species, was both linear and homogeneous with respect to garden, source, and garden by source, for herbivores.

Table 3—Multivariate and univariate ANOVAs for the effects of garden, source, and garden by source interaction on density of three guilds. Data on galls is from Graham and others (2001).

MANOVA

Source	Df	Wilks' λ	*F*	*P*
Garden	6, 252	0.17658	57.95019	<0.001
Source	12, 334	0.71593	3.74334	<0.001
Garden x Source	24, 366	0.71834	1.84275	0.010

Univariate ANOVAs (*F* statistics)

Effect (degrees of freedom in parentheses)

Guild	Garden (2, 128)	Source (4, 128)	Garden x source (8, 128)
Chewers and miners	90.257 ***	4.268 **	2.488 *
Suckers	0.179	0.759	1.100
Gall-formers	128.935 ***	6.340 ***	2.202 *

* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

Diversity of herbivorous insects depends upon both shrub size and garden (table 4). The number of herbivorous species increased with increasing plant volume ($b = 1.4695$, $t = 2.661$, $P = 0.009$). And the hybrid garden had fewer species of herbivorous insects than either the basin or mountain gardens (fig. 7).

Incidental Nonherbivores

The nonherbivorous arthropods included two species of ants (*Formica dakotensis montigena* and *Monomorium minimum*). *Formica d. montigena* nested under leaf thatch below the canopy, and around the trunk, of individual plants. These large red and black ants vigorously defended their nests, and plants. *Formica dakotensis* was more common in the mountain garden, but showed no obvious preference for sagebrush from any of the five source populations. Presence of a *Formica* nest at the base of a plant had no effect on the diversity of herbivores and galls (MANCOVA, $F_{2,139} = 0.088$, $P = 0.916$) or on the density of leaf chewing insects and sucking insects (MANCOVA, $F_{2,137} = 0.802$, $P = 0.451$). The smaller black ant (*Monomorium minimum*), restricted to the basin garden, was usually associated with, and tending, coccids. Its density was correlated with coccid density ($r = 0.5339$, df = 142, $P < 0.001$), but not with aphid density ($r = 0.0338$, df = 142, $P > 0.50$).

Several predatory arthropods were present on the sagebrush. The ladybird beetle *Hippodamia apicaulis* was fairly common, as were several species of unidentified spiders. The click beetle (*Octinodes* sp.) and lyctid wood borer (*Lyctus* sp.) were rare. Occasional wasps were seen, but not collected.

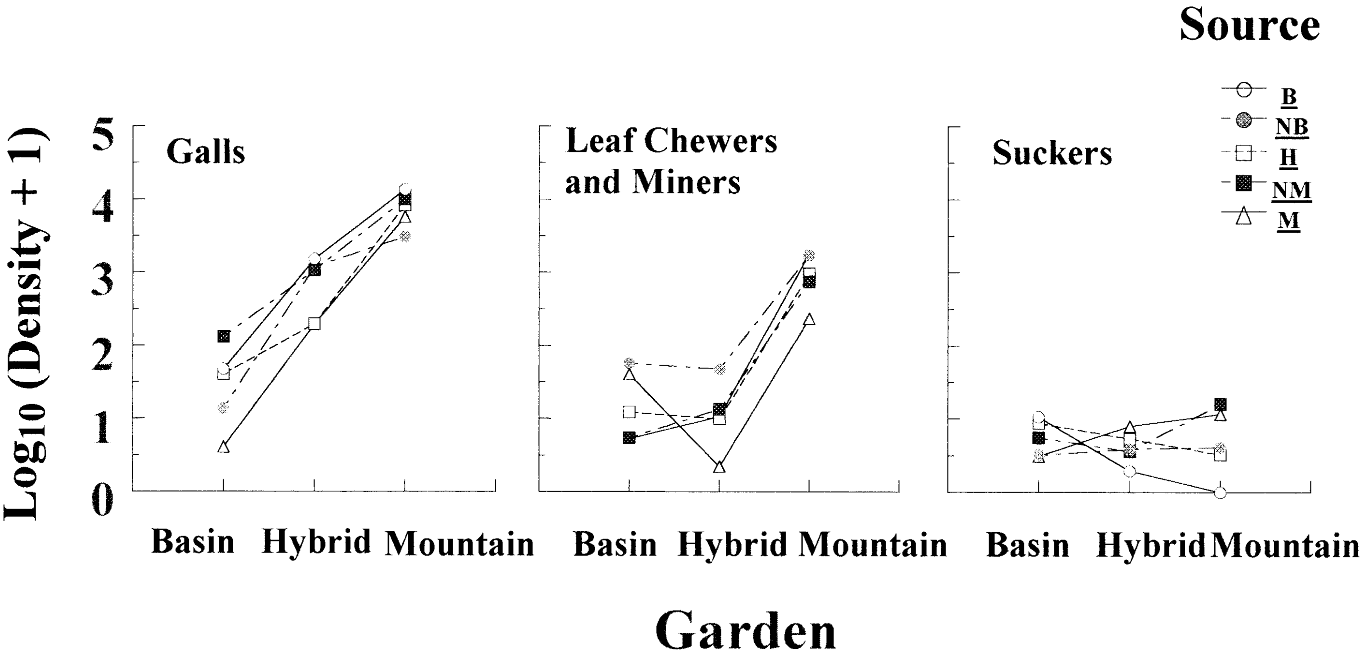

Figure 6—Summary of interactions of garden and source population on densities of leaf chewers and miners, and phloem suckers. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

Table 4—Analysis of covariance for the effects of garden and source population on diversity of herbivorous insects ($\log_{10}[S+1]$). Plant volume ($\log_{10}[V+1]$) is the covariate.

Source	Df	MS	*F*	*P*
Garden	2	0.23	8.09	<0.001
Source	4	0.01	0.49	0.743
Garden x Source	8	0.02	0.87	0.545
Size	1	0.20	7.08	0.009

Discussion

Densities of herbivorous insects on hybrid and parental big sagebrush vary with both genotype and environment. Messina and others (1996) found that herbivore use of hybrid and parental big sagebrush in a common garden in northern Utah depended upon plant genotype. Our experiment extends their results by examining hybrids and parentals in reciprocal transplant gardens that span an actual hybrid zone. Of the two main effects, environment (garden) had a greater effect on herbivore density than did genotype (source population). We found the same pattern for gall-formers (Graham and others 2001). Nevertheless, gall-formers showed significant genotype-environment interactions, while none of the individual species of chewers and suckers did.

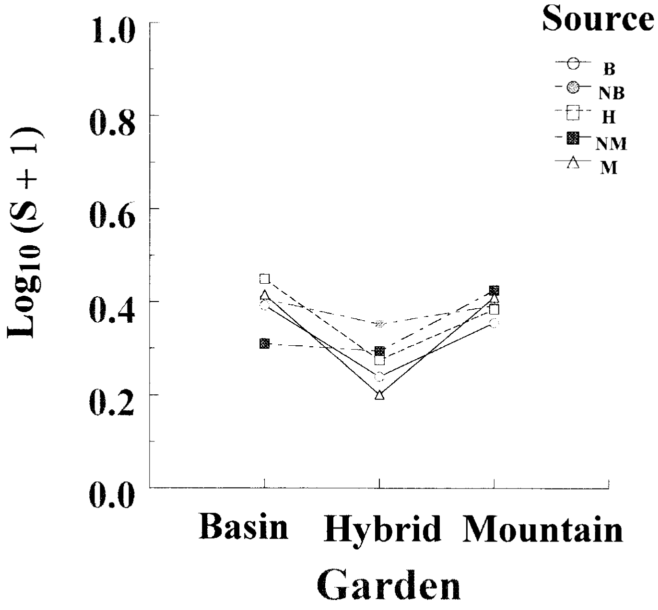

Figure 7—Interaction of garden and source population on diversity of herbivorous insects, after removing the effect of plant volume on diversity. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

Among the herbivorous insects, only the grasshoppers and leaf miners showed any evidence of host specificity. Grasshoppers were absent from near-mountain plants, but this may result from sampling bias, since their densities were low. Leaf miners clearly preferred near-basin plants, but they were present on all five populations.

Aphids of the genus *Obtusicauda* are *Artemisia* specialists (Robinson and Halbert 1989). Graham and others (1995) found more aphids on middle and near-mountain hybrids in 1989. Nevertheless, in 1997 we found no evidence of specialization on hybrids or parental subspecies by either *O. filifoliae* or *O. coweni*. *Obtusicauda coweni* and *O. filifoliae* were equally common in all three gardens, and showed no preferences among the five source populations. Greater densities of aphids on hybrids in 1989 may have been related to rainfall patterns in that year, and also to the time of year the aphids were censused (August). In July, water potential of sagebrush is still high in all three gardens, but by September, plants in the mountain garden are experiencing greater water stress than those in either the hybrid or basin gardens (McArthur and others 1998a). Low water potential can reduce sap intake by aphids, resulting in lower reproductive potential or movement to new plants (Kennedy and Stroyan 1959). Thus, in some years spatial and temporal variation in aphid density and distribution may result from environmental and temporal variation in water availability (Moran and Whitham 1988).

Herbivorous insects may severely affect the fitness of individual plants. The chrysomelid beetle *Trirhabda pilosa* can defoliate and kill entire populations of big sagebrush, especially at higher elevations (Pringle 1960). Both larvae and adults are leaf chewers. We found no evidence of such high population densities in our gardens. In the 10 years we have studied the hybrid zone at Salt Creek, we have not seen defoliation by *Trirhabda*. Only a small number of plants were infested with either larvae (in the hybrid garden) or adults (in the basin garden). The distribution of larvae and adults in the hybrid and basin gardens is probably related to timing of emergence. After reaching a length of about 10 mm, larvae drop off the host plant, pupate in the soil, and emerge as adults 1 to 2 weeks later (Pringle 1960). In August 1998, we observed many adults in the mountain garden, so we were probably sampling too early in 1997 to find larvae or adults in the mountain garden.

Incidental arthropods may have a significant influence on plant-herbivore interactions. Ants often interact with aphids, and in the process reduce herbivory by leaf-chewing insects (Pringle 1960; Floate and Whitham 1994). They also prey on ovipositing *Rhopalomyia* (Jones and others 1983). We did not, however, find a significant association of *Formica dakotensis* or *Monomorium minimum* with aphids, nor a negative association with either galls or leaf chewing insects. This is true despite the fact that *Formica* vigorously defended individual plants. *Formica dakotensis* is a temporary social parasite on the *F. fuscus* group (Wheeler and others 1994). *Formica obscuripes*, another member of the *rufa* group, also nests under sagebrush, and is known to kill and remove the plant from its nest (Cole 1932, as cited by Creighton 1950). According to Robinson and Halbert (1989), *Obtusicauda* aphids are not tended by ants. *Monomorium minimum* was found tending scales, rather than aphids.

Conclusion

Only grasshoppers and leafminers appear to distinguish among hybrid and parental genotypes. Coccids, *Clastoptera*, *Trirhabda pilosa*, coleophorid larvae, and lepidopteran leaf miners, on the other hand, all show more significant variation among environments. Most importantly, hybrids in the big sagebrush hybrid zone are not more heavily grazed than the parental taxa; the hybrid zone is not a sink for herbivores. Nor do they experience less grazing than the parental taxa in the hybrid zone. Insects vary along the elevational gradient, and a few also seem to target particular taxa.

Acknowledgments

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Use of Distance Measures to Assess Environmental and Genetic Variability Across Sagebrush Hybrid Zones

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Abstract—Reciprocal transplant studies in the big sagebrush hybrid zone at Salt Creek Canyon, Utah, showed that hybrids between basin (*Artemisia tridentata* ssp. *tridentata*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*) are more fit than either parental taxon, but only when raised in the hybrid zone. Hybrids are less fit than the native parent when raised in the parental environments. Why this is the case remains an open question. Our earlier work has shown that the hybrid zone occurs in an ecotone where the soil, vegetation, and herbivorous insect community all differ markedly from that found in the parental habitats. Moreover, the spatial variation in soil chemistry was greater in the hybrid zone than in either parental habitat. Does the enhanced genetic variation that results from hybridization allow hybrids to adapt to hyperspatial variability within the hybrid zone? Here we used Euclidean distance measures to examine this question for sagebrush hybrid zones found at Salt Creek and Clear Creek Canyons in Utah. Specifically, we examine the spatial variation in soil chemistry, vegetation, and insect communities. We also explore the interplant variability in the production of terpenes, ten elemental leaf concentrations, and the plants' biological absorption coefficients. While the hybrid zone is spatially more variable for soil chemistry, it is not more variable in terms of the vegetation nor herbivorous insects. Spatial variation for these features of the environment was greatest in the mountain zone, least in the basin zone and intermediate in the hybrid zone. In all three gardens overall, hybrid plants displayed greater variation than either parental taxon, in terms of their leaf elemental chemistry and biological absorption coefficients. However, the variability for all parental and hybrid plants increased when raised in alien gardens.

Introduction

The bounded hybrid superiority model postulates that the maintenance of stable hybrid zones is due to genotype-by-environment interactions. Accordingly, the parental taxa and hybrids each have superior fitness in their native habitats. Hybrids are presumed to be more fit within the hybrid zone, but less fit outside it, compared to either parental taxon. Reciprocal transplant experiments are required to test this model, as descriptive studies or single common-garden experiments confound genetic and environmental effects, thereby preventing assessment of genotype-by-environment interactions. Recently, a number of reciprocal transplant experiments have been conducted with plants (Young 1996; Wang and others 1997; Emms and Arnold 1997). These studies found that the fitness of hybrids was generally equal or superior to that of the parental taxa within the hybrid zone, but less fit than either parental type outside the hybrid zone. This was most evident when estimates were made using composite fitness parameters (Wang and others 1997).

Why should superiority of hybrid fitness be confined to within the margins of the hybrid zone? As Kettlewell (1956) demonstrated, fitness can be a function of both genotype and the environment, so the above question actually comprises three different questions: (1) what is special about the environment of the hybrid zone? (2) why should hybrids exhibit superior fitness in this unique environment compared to the parental taxa? and (3) why can't hybrids expand their range and thereby displace the parental taxa?

While considerable attention has been given to the genetic analysis of hybrid zones (see Arnold 1997 for an excellent review), ecological analyses have received much less attention. Most ecological work has focused on the influence of plant hybrid zones on herbivore distribution and abundance (Whitham and others 1999; Pilson 1999; Moula 1999; Fritz 1999, and references therein). These studies are fascinating, but they do not address the issues raised here because the environment is not examined from a plant's perspective.

We have adopted an ecological approach to our study of the big sagebrush hybrid zone. A number of features relevant to the performance of plants (in other words, soil mineral composition and the distribution and abundance of other

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In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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Table 1—Sources of data used in this paper.

Insect Community Composition	Graham and others, 2001; Graham and others, this proceedings
Plant Chemistry	Wang and others 1999
Plant Community Composition	Freeman and others 1999
Plant Developmental Instability	Freeman and others 1995
Plant Terpenes	Byrd and others 1999
Soil Chemistry	Wang and others 1998

plant species and herbivorous insects) have been investigated (table 1). Profiles of defensive chemicals produced by the plants have also been examined. Thus far, these studies have supplied partial answers to the above three questions.

We have shown that the hybrid zone occurs in an ecotone. Specifically: (1) soil chemistry differs radically between the parental sites and parental habitat soils differ markedly from that of the hybrid zone; (2) soils from the hybrid zone are not just intermediate blends of the parental habitat soils, but have their own unique properties; (3) plant species composition and vegetation (estimated as percent of ground cover) differ significantly between the parental sites and these sites also differ from the hybrid zone; and (4) vegetation in the hybrid zone community is not a simple blend of that in the parental communities, but rather includes some unique species. In short, both soil chemistry and vegetation have unique features in the hybrid zone, to which the hybrids have adapted. However, hybrids are maladapted to the environmental conditions existing in either parental zone (Wang and others 1997). Why hybrids, and not the parental taxa, are adapted to the unique features of the hybrid zone (question 2) remains open.

In an earlier paper (Wang and others 1998), Euclidean distance measures showed that the big sagebrush hybrid zone is spatially more variable in soil elemental composition than either parental site (fig. 1). This suggests that the enhanced genetic variation resulting from hybridization may be necessary to cope with the increased spatial variation of soil chemistry within the hybrid zone. The present study extends that analysis to examine the variability in vegetation, insect herbivore loads, and terpene profiles of leaves. Interplant variability is also examined for plants raised in common gardens, using elemental leaf concentrations and the ratio of elemental leaf to soil concentrations (in other words, the biological absorption coefficients, BACs). This latter analysis examines how the variability among plants changes when the plant is raised in a nonnative environment.

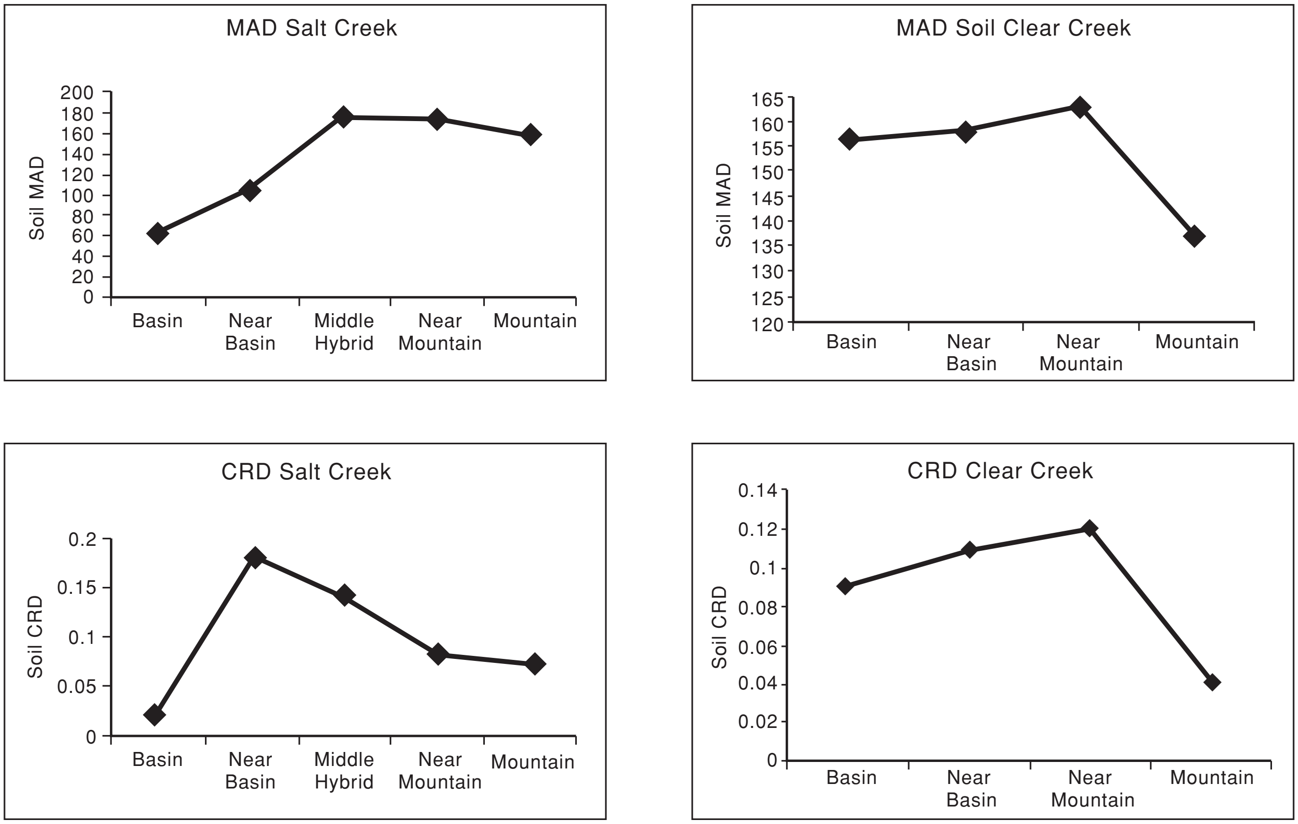

Figure 1—MAD and CRD distances based upon soil chemistry for both the Salt Creek and Clear Creek hybrid zones.

Methods

Methods for a specific data collection are given in the primary article dealing with that subject (table 1). We have primarily conducted our studies in Utah at both Salt Creek and Clear Creek Canyons. Salt Creek Canyon is located at the south end of the Wasatch Mountains near Nephi, whereas Clear Creek Canyon is located near Richfield and drains the east slope of the Pavant and Tushar Mountains. Sampling in both study areas occurred across the hybrid zone in native vegetation; however, data was also collected from three experimental gardens established in Salt Creek Canyon (one in each parental population and one in the middle of the hybrid zone—see Wang 1996). In the native vegetation at Salt Creek Canyon, five sampling sites were established (one in each parental population and three within the hybrid zone), while four were established at Clear Creek Canyon (one in each parental population and two within the hybrid zone). Soil chemistry was assessed at both sites, whereas vegetation was only assessed at Clear Creek Canyon because portions of Salt Creek Canyon have been seeded with alien grasses. Cattle grazing occurs at both locations. Terpene profiles and insect abundance were analyzed for transplant-garden plants at Salt Creek Canyon. Leaf chemistry was also addressed using plants indigenous to a site.

Euclidean distance was used to measure spatial environmental heterogeneity. Specifically, to examine differences due to magnitudes, the mean absolute Euclidean distance (MAD) was determined by applying the following equation (Freeman and others 1995):

$$\mathrm{MAD} = S\ X_{ij}\text{-}X_{ik}\ S$$

Using soil chemistry as an example, X_{ij} is the measure of the magnitude of the i^{th} element in sample j, X_{ik} represents the concentration of the same element in sample k, and S represents the number of elements included in the distance estimate. We measured the concentrations of 10 elements in the soil, so, in this case, S = 10. The concentration of each element forms an axis in the analysis, and the distance between the samples is a measure of their dissimilarity. This distance is summed for each axis and then divided by the number of elements to yield the MAD estimate. Chord distance (CRD) is similar, but examines proportions rather than absolute amounts:

$$\mathrm{CRD} = s\ 2(1\text{-}\mathrm{ccos}_{jk})$$

where

$$\mathrm{ccos}_{jk} = S\ (X_{ij}\ X_{ik})$$

$$sS\ X^2_{ij}SX^2_{ik}$$

In brief, the distance between samples is projected onto a unit circle and the chord that separates the two samples is a measure of the dissimilarity in the proportion of elements measured in the soils. Vegetation, terpenes and leaf chemistry were treated in a similar manner.

Data Analysis

When analyzing the distances for vegetation, terpenes, and herbivore loads, a Kruskal-Wallis test was used because the data did not conform to the assumptions of an ANOVA (Zar 1984). However, ANOVAs were used to analyze elemental leaf concentrations and their biological absorption coefficients.

Results

Soil Chemistry

Soil chemistry plays such an important role in the present study that we will summarize the results of Wang and others (1998). Both MAD and CRD distances differed significantly among the sites at Salt Creek Canyon ($\chi^2 > 40.0$ $P < 0.00001$ in both cases) (fig. 1). MAD distances at the basin site were significantly less than at the middle-hybrid site, but not at the near-basin or mountain sites. The near-basin and mountain sites did not differ significantly from the middle hybrid or near-mountain sites. CRD distances differed significantly between the basin and four other sites at Salt Creek Canyon. At Clear Creek Canyon, MADs did not differ among the sites, but CRDs did ($\chi^2 > 40.0$). The mean CRD at the mountain site was significantly less than at the other three sites, while the mean CRD at the near-mountain site was significantly greater than the means at either the basin or near-basin site. This indicates that at Salt Creek Canyon, both the concentrations and proportions of elements in the soils were spatially more variable in the hybrid zone than at the basin site. While the spatial variability was greater in the hybrid zone than at the mountain site, the difference was not significant. At Clear Creek Canyon, the spatial variation in the proportion of elements was greater in the hybrid zone than at the mountain site.

Vegetation

MADs differed significantly among the sites ($\chi^2 = 23.4$, $P < 0.000034$, table 2). Mean MAD at the basin site was significantly greater than at the other three sites, while these sites did not differ from one another. This indicates that quadrats in the basin site had greater disparity in the amount of vegetation than that occurring at the other sites. CRD distance also differed significantly among the sites ($\chi^2 = 135.0$, $P < 0.000001$). The mean CRD at the basin site was significantly less than that at the near-basin and mountain sites, but did not differ from that at the near-mountain

Table 2—Analysis of spatial heterogeneity of the vegetation using Euclidean distance measures at the Clear Creek Site. The MAD examines differences among quadrats in the amount of vegetation while the CRD examines differences in the proportion of vegetation contributed by each species. Means subscripted by the same letter do not differ significantly from one another at the 0.05 level.

	Basin	Near basin	Near mountain	Mountain	χ^2	P
MAD	2.21_a	1.75_b	1.88_b	1.85_b	23.37	0.000034
CRD	0.96_a	1.05_b	0.94_a	1.25_c	134.99	0.000001

Table 3—Analysis of spatial heterogeneity of the insect community using Euclidean distance measures at the Clear Creek Site. The MAD examines differences among plants in the number of insects while the CRD examines differences in the proportion of individuals contributed by each species. Means subscripted by the same letter do not differ significantly from one another at the 0.05 level.

Garden	Source	MAD	CRD
Basin	Basin	7.39_c	0.16_a
Basin	Near Basin	12.36_d	0.54_b
Basin	Middle Hybrid	12.41_d	0.25_a
Basin	Near Mountain	13.78_d	0.19_a
Basin	Mountain	15.05_d	0.35_a
Hybrid	Basin	6.31_c	0.30_a
Hybrid	Near Basin	7.10_c	0.55_b
Hybrid	Middle Hybrid	3.09_b	0.57_b
Hybrid	Near Mountain	5.52_b	0.25_a
Hybrid	Mountain	3.07_b	0.57_b
Mountain	Basin	0.67_a	1.04_c
Mountain	Near Basin	0.85_a	0.98_c
Mountain	Middle Hybrid	1.61_a	0.58_b
Mountain	Near Mountain	1.54_a	0.98_c
Mountain	Mountain	0.38_a	1.07_c

site. Mean CRD at the near-basin site was significantly greater than that at the near-mountain site, but significantly less than that at the mountain site. Mean CRD at the mountain site was significantly greater than that at the other three sites. Collectively, these results indicate that the proportion of vegetation contributed by a species was remarkably uniform at the basin site, but that the density of vegetation there varied greatly among the quadrats. While at the mountain site, the amount of vegetation was quite constant but the composition of the vegetation varied greatly among the quadrats. Thus, by either measure, the **parental sites are more variable** than either hybrid site.

Insects

MADs were examined for plants in the common gardens. The data were not normally distributed, so a Kruskal-Wallis test was used for this analysis. A single coding variable was also used to indicate both garden and source populations (table 3). As there are three gardens and five source populations, this coding variable had 15 states. MADs differed significantly among these 15 states ($\chi^2 = 571.9, P < 0.000001$). In general, two major trends are evident: (1) the site-indigenous population always had the smallest MAD and (2) hybrids had greater MADs than the parental taxa (this trend is more evident in the parental gardens, though the nonindigenous hybrids had higher MADs even in the hybrid garden). The mean CRDs also varied significantly among the 15 states of the coding variable ($\chi^2 = 214.4, P < 0.000001$). In general, the mean CRD was lowest in the basin garden and highest in the mountain garden, with basin plants having lower CRDs than mountain plants. One form of hybrid had the highest CRDs in the basin and hybrid gardens, but not in the mountain garden where mountain plants had the highest CRD. Thus, the total density of insects appears to be most variable on the nonsite indigenous and hybrid plants. Like the vegetation, the proportional contribution of an insect species to the total herbivore load was more uniform in the basin than mountain garden. In the basin and middle-hybrid gardens the proportions of insect species varied most among the hybrids, but in the mountain garden, native parental plants had greater variability.

Terpenes

MADs differed significantly among the five sampling locations at Salt Creek Canyon ($\chi^2 = 42.8$, $P < 0.000001$) (table 4). Mean MAD at the basin site was significantly less than that at the near-mountain and mountain sites. No other differences were significant. CRDs did not differ among the sites ($\chi^2 = 0.4$, P = n.s.).

Leaf Chemistry

Site Indigenous Plants—Leaf chemistry was examined for both site-indigenous and transplant-garden plants. For site-indigenous plants, MADs were significantly greater for the basin and middle-hybrid plants than for the mountain and near-basin plants. Near-mountain plants were intermediate (table 5). CRDs also differed significantly among the sites ($F_{4,135} = 4.19$ P, < 0.003, table 5 and fig. 2). CRDs were greatest for the middle-hybrid and basin plants and lowest for near-basin and mountain plants. MADs based on the biological absorption coefficient also differed significantly among the sites, ($F_{4,135} = 12.48$, $P < 0.001$, table 5), being significantly higher for basin plants than for any hybrid or mountain plants. Mountain plants had the lowest MAD distances. Similarly, CRDs varied among the sites ($F_{4,135} = 2.73$, $P < 0.03$, table 5) and were highest for the near-mountain plants and lowest for the middle-hybrid plants.

Transplant Gardens

Elemental Concentrations—MADs based upon elemental concentrations differed significantly among the gardens ($F_{2,.210} = 7.195$, $P < 0.001$). The mountain garden had the lowest MADs, which differed significantly from those in the

Table 4—Analysis of the spatial heterogeneity of terpenes produced by plants at Salt Creek Canyon. The MAD examines differences among plants in the quantities of terpenes produced while the CRD examines differences in the proportion of terpenes produced. Means subscripted by the same letter do not differ at the 0.05 level.

	Basin	Near basin	Middle hybrid	Near mountain	Mountain	χ^2	P
MAD	0.41a	0.45a	0.47a	0.87b	0.74b	42.8	0.000001
CRD	1.37	1.37	1.37	1.35	1.34	0.4	N. S.

Table 5—An analysis of the spatial heterogeneity among plants in concentrations of 10 elements in leaf tissue. The MAD distance examines the concentrations of the elements; the CRD distance examines the proportions of elements. Both site-indigenous and reciprocally transplanted individuals were examined. Means subscripted by the same letter do not differ at 0.05 level.

	Site-indigenous plants						
Elemental concentrations	**Basin**	**Near basin**	**Middle hybrid**	**Near mountain**	**Mountain**	**F(4,135)**	**P**
MAD	526.57_a	294.28_b	542.72_a	400.44_{ab}	312.68_b	6.14	0.001
CRD	0.15_{ab}	0.09_a	0.18_b	0.13_{ab}	0.1_a	4.19	0.003
Biological absorption coefficient							
MAD	10.14_a	6.37_b	6.95_b	5.71_b	3.2_c	12.48	0.001
CRD	0.09_{ab}	0.07_{ab}	0.06_a	0.10_b	0.09_{ab}	2.73	0.03

basin and hybrid gardens; the MADs for these latter two gardens did not differ from one another. MADs also differed significantly among source populations (F $_{4,210}$ =3.231, P < 0.013, table 6). The near-basin plants had the largest MADs, which differed from the MADs of the basin and near-mountain plants, but not the middle-hybrid or mountain plants. There was no difference among the gardens and the interaction term was not significant. CRDs differed significantly among the source populations (F $_{4,210}$ = 3.955 P < 0.004, table 6), but not among the gardens. The mean CRD distance was significantly greater among the mountain plants than among the basin, near-mountain and middle-hybrid plants. The mean CRD among near-basin plants was intermediate. The garden-by-source population interaction was marginally significant (F $_{8,210}$ = 1.93, P < 0.058, table 7).

Biological Absorption Coefficients

MADs distances among plants showed the following significant trend: basin garden > middle hybrid garden > mountain garden (F $_{2,210}$ = 27.003, P < 0.001). MADs also varied significantly among the source populations (F $_{4,210}$ = 4.001, P < 0.004, table 6). MADs were greatest among the middle hybrids, and least among near-mountain hybrids. The other source populations were intermediate and did not differ from each other, the middle-hybrid or near-mountain plants. The interaction among gardens and source populations was also significant, (F $_{8,210}$ = 4.563, P < 0.001, table 6 and fig. 2). As a general rule, site-indigenous plants had the lowest MADs, while nonindigenous parental plants and at least one type of hybrid had the greatest MADs.

CRDs showed the following significant trend: mountain garden > basin garden > middle-hybrid garden (F $_{2,210}$ = 48.070, P < 0.001). CRDs also varied significantly among the source population (F $_{4,210}$ = 9.210, P < 0.000, table 6 and fig. 2). CRDs were significantly greater for middle hybrid and basin plants than for mountain and near-mountain plants. Near-basin plants were intermediate. The interaction between garden and source population was also significant (F $_{8,210}$ = 3.420, P < 0.001, table 6). In general, CRDs were greatest for hybrid and basin plants and lowest for mountain plants; however, relative ranking among the different hybrid sources varied among the gardens.

Table 6—An analysis of the spatial heterogeneity in the concentrations of elements and the biological absorption coefficients among plants in the transplant gardens at Salt Creek Canyon. The MAD distance examines heterogeneity in the concentrations of elements while the CRD distance examines differences in the proportions of the elements.

		Source population				
Elemental concentration		**Basin**	**Near basin**	**Middle hybrid**	**Near mountain**	**Mountain**
Garden						
MAD	Basin	560.77_a	808.16_b	593.87_a	533.63_a	824.88_b
MAD	Hybrid	628.41	779.26	711.44	624.7	729.87
MAD	Mountain	509.6	629.93	590.22	463.27	426.23
CRD	Basin	0.16_{ab}	0.19_{ab}	0.12_{ab}	0.09_a	0.21_b
CRD	Hybrid	0.1_a	0.17_{ab}	0.11_a	0.18_{ab}	0.22_b
CRD	Mountain	0.14	0.14	0.16	0.13	0.16
Biological absorption coefficients						
MAD	Basin	75.42_a	100.85_{ab}	81.75_a	74_a	107_b
MAD	Hybrid	65.16	48.66	62.56	53.85	47.45
MAD	Mountain	59.66_a	63.5_a	84.71_a	25.11_b	27.03_b
CRD	Basin	0.19a	0.13ab	0.15ab	0.09b	0.12ab
CRD	Hybrid	0.09	0.07	0.1	0.07	0.05
CRD	Mountain	0.2ab	0.26bc	0.31c	0.15a	0.12a

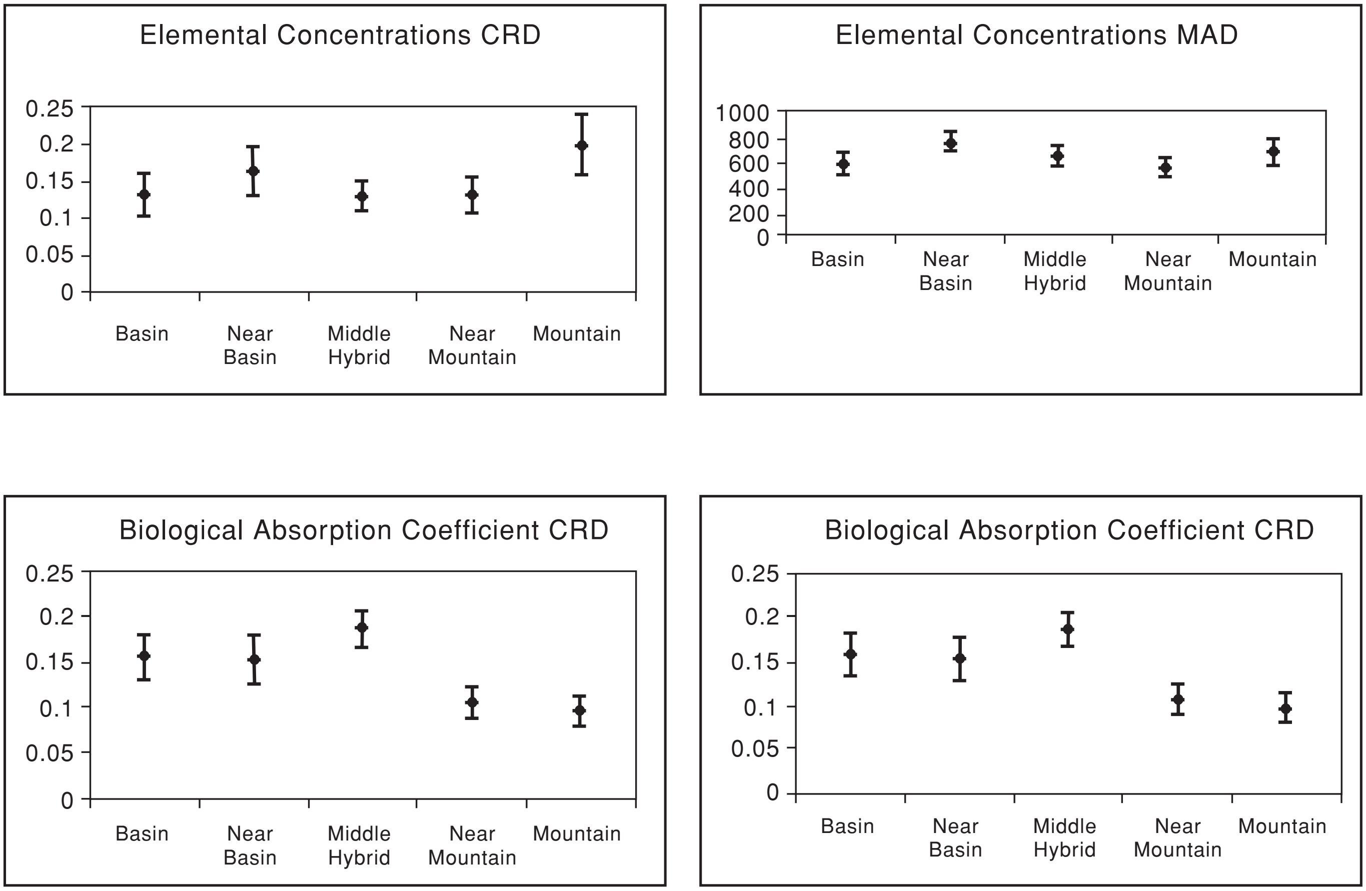

Figure 2—Comparison of MAD and CRD distances based upon plant chemistry among the five source populations.

Discussion

Here we examined the potential correlation between the spatial variability of key ecological parameters across two big sagebrush hybrid zones, as well as the enhanced genetic variation conferred by hybridization. Variability in parental and hybrid plant responses (in terms of secondary chemicals, leaf elemental composition and biological absorption coefficients) to these ecological gradients were also examined in reciprocal transplant gardens across one hybrid zone. The results, while complex, nonetheless demonstrate several important points. First, the hybrid zone occurs at an ecotone. Prior analysis of the soils demonstrated that soil chemistry changes abruptly across the hybrid zone and becomes spatially more variable, particularly in the proportions of elements, within the hybrid zone. The vegetation goes from a floristically poor community in the basin zone to a very diverse community in the mountain zone. While the amount of ground cover is quite variable in the basin community, species composition is remarkably uniform. The reverse is true in the mountain zone. Species composition changes markedly from quadrat to quadrat, but the amount of plant cover is relatively uniform. The product of these two measures shows that the hybrid zone is intermediate for both trends and is more uniform in both the amount of cover and species composition than either parental site. The insects found on sagebrush plants follow the same basic trends as the vegetation. The numbers of insects feeding on plants in the basin garden varied greatly among the plants, but the species composition of these insects was quite uniform. In the mountain garden (where there are considerably more species), the species composition of insects feeding on big sagebrush varied considerably from plant to plant, but insect density was quite uniform. The hybrid zone was intermediate just as it was with the vegetation. Thus it appears that the hybrid zone is found in a zone of sharp ecological transition.

The second major trend involves the reciprocal transplant gardens. Both insect and leaf chemistry data show variation among plants from the same source population to be greater for nonnative plants than those site-indigenous plants. This trend suggests that nonnative plants are more stressed than those indigenous to a particular site. This idea is not new; organisms under stress are known to display greater genetic variation (see Galaud and others 1993 for an excellent example). Similarly, insects are well known to prefer plants under stress (Whitham and others 1994; White 1976; Waring and Cobb 1992; Paige and Capman 1993). These results are, therefore, easy to understand in light of well-established patterns.

The third trend is that in the transplant gardens, overall, hybrids typically display greater plant-to-plant variation primarily in their biological absorption coefficients, but also in leaf chemistry. The source population term in the ANOVA model reflects at least a partial genetic contribution. Our findings that hybrids display greater variability is not surprising. Hybridization is well known to lead to increased phenotypic variability. This also corresponds well with our earlier results showing enhanced spatial variation in the proportions of elements in the soils (Wang and others 1998).

We have repeatedly shown that structuring of the big sagebrush hybrid zone is due to plant-by-soil interactions. Microbes are well known to mediate this type of interaction. A separate study (Miglia and others, in preparation) shows that the microbial community varies across the hybrid zone, and that growth of big sagebrush is contingent upon both the source population from which the plants originated and the microbial composition of the soils in which the plants were raised. This may partially explain the boundaries of the hybrid zone. Within each zone, indigenous plants should be under directional selection, thereby resulting in their adaptation to the indigenous microbial community. If this is true, then hybridization appears to provide the genetic variation needed to adapt to the more variable and unique edaphic properties (both biological and chemical) of the hybrid zone.

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Phenotypic Sex Ratios of *Atriplex canescens* Shrubs in Relation to Cattle Browsing

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Abstract—Previous studies conducted at our research site on the shortgrass steppe in Colorado showed that phenotypic sex ratios of tetraploid fourwing saltbush (*Atriplex canescens* Pursh [Nutt]) shrubs were less female biased in grazed pastures than in adjacent exclosures. The potential effects of cattle browsing on shrub sex ratios were studied both in the field and in a greenhouse. In the field study, winter or late summer grazing resulted in higher utilization of female shrubs relative to males. In early spring, when shrubs were browsed the least, utilization of male and female shrubs was not different. Release from cattle browsing (in temporary exclosures) was related to sexual phenotype shifts toward femaleness that occurred mostly in shrubs with monecious phenotypes. Such shifts, however, did not translate into detectable changes in overall phenotypic shrub sex ratios. In the greenhouse study, female clones of fourwing saltbush appeared to be more negatively affected by artificial defoliation than were male or monecious clones. Sex biased herbivory, and (to a lesser extent) shrub gender specific responses to defoliation may have promoted higher mortality among female shrubs possibly leading to shrub sex ratio alteration at this site. Browsing-induced sex shifts are probably not an important factor affecting shrub sex ratios at this site.

Introduction

Sex ratios of dioecious shrubs can change across the landscape or through time in response to environmental stress (Freeman and others 1976; McArthur and Freeman 1982; Freeman and others 1993; Allen and Antos 1993). Gender-specific responses, both to availability of key resources and to a number of biotic and abiotic stressors, are responsible for such variations (Freeman and others 1980; Freeman and others 1984). There are at least two basic processes that can lead to sex ratio alterations, namely: (a) differential mortality of females and males (Williams and others 1978); or (b) phenotypic sex shifting in individuals with sexually labile genotypes (Freeman and McArthur 1984; McArthur and others 1992). In stands of tetraploid fourwing saltbush (*Atriplex canescens*) on the shortgrass steppe in Colorado, Cibils and others (1997) found that female fourwing saltbush shrubs were more abundant inside exclosures than in adjacent grazed pastures.

Fourwing saltbush is fairly sensitive to defoliation (Buwai and Trlica 1977; Benjamin and others 1995). Seasonal rest periods are required to keep browsed populations viable (Pieper and Donart 1978; Price and others 1989). Gender-biased herbivory, that is common in a number of dioecious shrubs including some saltbushes (*Atriplex* sp.) (Watson 1995 and references therein; Maywald and others 1998; Maywald 1999), and/or gender-specific responses to browsing, could promote different mortality rates among male and female fourwing saltbush shrubs. Additionally, since close to 55 percent of tetraploid fourwing saltbush shrubs carry sexually labile genotypes and can shift toward maleness under stress (McArthur and others 1992), browsing could promote sex phenotype shifts in fourwing saltbush stands. Both these processes, potentially driven by cattle browsing, could be responsible for the sex ratio differences found by Cibils and others (1997) between exclosures and grazed pastures.

The objective of our work was to investigate whether cattle browsing could trigger processes that lead to sex ratio alterations. We addressed the following questions in a field and greenhouse study: (1) are female fourwing saltbush shrubs at our site browsed more intensely than are male shrubs? (2) does cattle browsing promote sex phenotype shifts toward maleness in fourwing saltbush at our site? and (3) are clones from female fourwing saltbush shrubs affected more negatively by defoliation than are clones from male or monecious shrubs?

Materials and Methods

Field Study

We conducted the field study at the USDA-ARS Central Plains Experimental Range (CPER), approximately 60 km NE of Fort Collins, Colorado (40° 49' N 107° 47' W) at 1,650 m elevation. We set up the experiment at a shrub-dominated site, on a floodplain area with loamy to sandy loam soils. Fourwing saltbush, blue grama (*Bouteloua gracilis* [H.B.K.] Lag. Ex Griffiths), and western wheatgrass (*Agropyron smithii* Rydb.) are the dominant plant species at the site (Liang and others 1989). Mean annual precipitation is

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320 mm, most of which occurs between the months of April and September.

We set up 14 half hectare experimental pastures in two blocks of seven pastures each, described in detail by Cibils (1999). We conducted three 2-year browsing experiments (in 1997 and 1998) that consisted of grazing four pastures with cattle for a period of 4 days in winter (January), early spring (April), and late summer (September). Two pastures were grazed moderately (four animals) and two were grazed heavily (12 animals). Two of the 14 pastures remained as exclosures. We tagged 20 female and 20 male shrubs in each experimental pasture before the onset of the experiments in 1996. In June 1997 we tagged an additional 20 monecious shrubs in each pasture. Tagged shrubs that had shifted phenotypic sex expression in 1997 or 1998 were replaced in order to keep numbers of male, female and monecious shrubs constant. Shortly before each experiment, we marked and measured the length of four stems on all tagged shrubs. We re-measured marked stems immediately after removing cattle, and thus calculated percent length removed by browsing. Utilization was expressed as a proportion of biomass removed from each marked stem, derived from length/mass equations described in detail by Cibils (1999). In June 1997 and 1998 we determined sex constancy on all tagged shrubs by comparing present and previous season's sexual phenotype. We also determined shrub sex ratios in each experimental pasture by recording phenotypic sex expression on 100 shrubs. To do this, we set up two transects per pasture and recorded sexual phenotype on the closest adult shrub to each 3 m interval.

Shrub utilization data from each experiment were analyzed separately using a mixed effects repeated measures analysis of variance. We studied the effects of shrub gender, stocking density, year and block (of experimental pastures) on shrub utilization. Utilization data were arcsin transformed and the overall level of significance was set at P = 0.05. SAS (1996) Proc GLM was used for the statistical computations.

Sex change on tagged shrubs was analyzed by grouping shrubs into one of three categories on the basis of their current season's floral phenotype, namely: 1) changing towards maleness (→♂); 2) changing toward femaleness (→♀); and 3) constant sexual phenotype expression (constant). Nonflowering shrubs were not included in this analysis. We used a two-way contingency table to analyze these results by considering two classes of shrubs, namely: browsed or protected. We built separate tables for 1997 and 1998 and then related them by using the Cochran-Mantel-Haenzel test of general association. Level of significance was set at P = 0.05. SAS (1996) PROC FREQ was used for the statistical computations.

Sex ratios of experimental pastures were also collapsed into two groups (browsed or protected), and were compared to the 35♂:55♀:10[♂♀] tetraploid *Atriplex canescens* sex ratio described by McArthur (1977) using χ^2 goodness-of-fit tests. We set the level of significance at P = 0.05 and used Statgraphics (1994) to perform the statistical computations.

Greenhouse Study

During the fall of 1996 we collected cuttings from 30 fourwing saltbush shrubs (10 female, 10 male, and 10 monecious) at five fairly distant sites within the CPER. Stem-cutting collection, handling, and rooting techniques used in this study (described in detail by Cibils 1999) matched specifications proposed by Wiesner and Johnson (1977) and McArthur and others (1984). Overall, close to 30 percent of clippings rooted and survived through the first growing season (1997). We were therefore able to use clones taken from 18 parent fourwing saltbush shrubs in an 8-month experiment beginning in December 1997, designed to measure the effects of winter defoliation and water stress on several plant productivity-related variables.

We imposed three defoliation treatments (control, moderate and heavy), and two watering treatments (control and water stress). The former consisted of one clipping event at the beginning of the experiment that removed either 40 percent (moderate) or 70 percent (heavy) of the length of all stems 5 cm or longer. Water stress was imposed by varying watering intervals. Water in the control pots was replenished when soil water potential reached a value of –1.3 bars. In the water stressed pots, water was replenished when soil water potential reached a value of –6.5 bars. The experiment included a total of 108 clones. Treatments were randomized within parental origin (hereafter referred to as genotype). Surviving clones did not flower either before or during the experiment. This frustrated the corroboration of clone gender by floral phenotype observation. Therefore, clone gender in this paper must be interpreted as meaning "clones taken from a donor shrub exhibiting that gender."

In mid August 1998 we finalized the experiment and harvested aboveground biomass from all 108 clones, and root biomass from a subset of 54 clones. Aboveground biomass was harvested, oven-dried and weighed. Roots were washed and separated from pot soil (using 10 mm, 2 mm, and 1 mm sieves), oven-dried and weighed. In this paper we discuss the response to the experiment treatments in terms of total above- and belowground biomass of the subset of 54 clones. Aboveground biomass of defoliated clones included the biomass removed by the clipping treatments that had been oven-dried and weighed immediately after defoliation.

We used a mixed effects analysis of variance to analyze the impact of shrub gender, defoliation regime, watering regime, and genotype (nested within gender) on total above and belowground biomass. Significance level was set at P = 0.05. Means were compared using the LSM method controlling for comparisonwise error rates. We used SAS (1996) proc GLM and proc MIXED to perform the statistical computations.

Results

Field Study

In January and September percent biomass removed by cattle from marked leaders on tagged female shrubs was significantly higher than that removed from male shrubs (fig. 1). In both of these experiments female-biased browsing occurred in both years and across a three-fold increase in cattle density. In April we did not observe any significant differences in the levels of utilization of male and female shrubs (fig. 1).

Sex change in tagged shrubs was not significantly associated with browsing when monecious shrubs were excluded

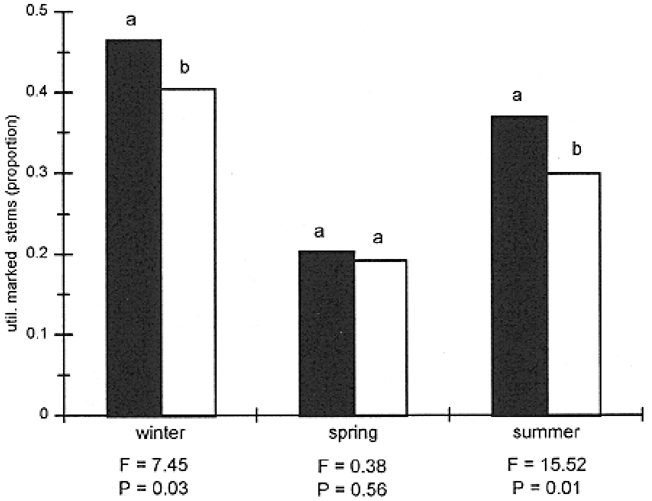

Figure 1—Mean utilization of tagged female (solid bars) and male (open bars) shrubs in the January, April and September experiments. F and P values for the "shrub gender" factor in the repeated measures ANOVAS are given below each pair of bars. Different letters indicate significant differences. Comparisons were made within experiments.

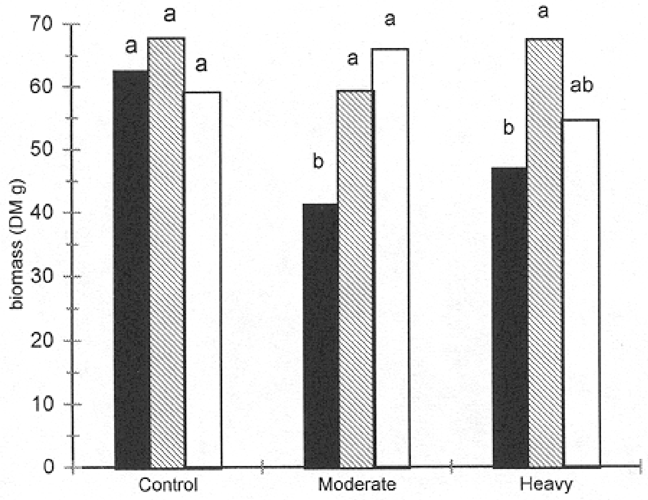

Figure 2—Overall means of total above- and belowground biomass for female (solid bars), monecious (slashed bars), and male (open bars) clones under 3 defoliation levels. Different letters indicate significant differences. Comparisons were made among genders within levels of defoliation.

from the analysis (table 1). However, in 1998 when monecious shrubs were included, the association was highly significant (table 1). Whereas sex shifts towards maleness were the most common, only shifting toward femaleness (that occurred much more frequently in exclosures) was significantly associated with cattle browsing (table 1). Shrub sex ratios in both browsed and protected pastures did not differ significantly from the 35♂:55♀:10[♂♀] phenotypic frequency, empirically derived for tetraploid fourwing saltbush (McArthur 1977).

Greenhouse Study

Total above- and belowground biomass was significantly affected by the defoliation-by-gender interaction (F = 2.713; P = 0.049). Whereas control female, monecious, and male clones produced similar amounts of total biomass, defoliated female clones consistently produced less biomass than clones of the other genders (fig. 2). Under heavy defoliation, however, differences between males and females were not statistically significant (fig. 2). Whereas the water stress treatment we imposed had an overall significant effect on total above- and belowground biomass (F = 6.846; P = 0.014), its effect did not depend on the gender of the clone (shrub gender X water stress: F = 0.886; P = 0.423). It did have, however, different effects depending on the level of defoliation considered (water stress X defoliation: F = 5.455; P = 0.01). Water-stressed non defoliated clones produced less than the controls, however such differences disappeared with defoliation. We found a considerable amount of genotypic variation within genders (F = 2.332; P = 0.057).

Table 1—Contingency table with counts of shrubs that either changed sex phenotype or exhibited constant sex phenotype in 1997 and 1998 under cattle browsing or in exclosures.

		Shrub counts			
Year	Treatment	→♀	→♂	Constant	P
1997 ([♂♀] excluded)	browsed	1	9	90	
	protected	1	13	86	0.672
1998 (including [♂♀])	browsed	1	30	69	
	protected	13	20	67	0.001**
Overall	(C.H.M. Test)				0.001**

Discussion and Conclusions

In January and September female shrubs were browsed more heavily than were males. In April, when overall shrub utilization was lowest, we detected no gender bias in utilization. Our results are only partially consistent with sheep-browsing patterns observed by Maywald and others (1998) in a fourwing saltbush transplant garden. Sheep preferred to browse male fourwing saltbush shrubs in June, and showed no gender-related preferences in March, a date that is comparable to our April experiment. While we did not find any instances of significant male-biased browsing, patterns involving greater use of males relative to females did occur in some plots of the April experiment in 1997. Our results tend to match the pattern observed in sheep browsing bladder saltbush (*Atriplex vesicaria* Heward ex Benth). Sheep preferentially browsed female shrubs irrespective of season and phenological stage (Maywald 1998). In bladder saltbush stands, female-biased herbivory by sheep is thought to cause greater mortality among female shrubs thus altering overall shrub sex ratios (Williams and others 1978). This may also be the case in the stands of fourwing saltbush that we studied. In a previous study of crown and stem dimensions of browsed and protected fourwing saltbush shrubs at this site, Cibils (1999) found that whereas female shrubs were apparently younger than males under grazing, in exclosures such apparent age differences were absent. The gender-biased browsing pattern we observed could be causing higher mortality of female shrubs at our site as well. This could ultimately lead to situations of sex ratio alterations.

Experimental pastures that were protected from cattle browsing exhibited a larger number of tagged shrubs that shifted toward femaleness than did the pastures that were browsed. If browsing is in fact a source of considerable stress to fourwing saltbush shrubs, then our results are consistent with the trend described by McArthur and Freeman (1982). In that study, release from stress caused labile shrubs that had previously shifted toward male sex expression under stress to return to female flowering status. However, sex phenotype shifts observed at the level of tagged shrubs did not translate into detectable deviations of overall shrub sex ratios at the level of experimental pastures. Labile shrubs may have been over-represented in our sample of tagged shrubs. This could account for the apparent lack of consistency between results obtained at the level of tagged individuals and the level of experimental pastures. Browsing-induced sex shifting may not be an important source of sex ratio alteration in fourwing saltbush stands at our site.

Defoliated female clones produced less above- and belowground biomass than either male or monecious clones. Whereas defoliation experiments conducted with dioecious species have not shown a consistent pattern of gender-specific response (Elmqvist and Gardfjell 1988; Oyama and Mendoza 1990; Delph and others 1993) female plants are generally assumed to grow more slowly than their male counterparts (Jing and Coley 1990). Should this be the case with fourwing saltbush, it is reasonable to speculate that female clones were not able to compensate the biomass removed by clipping in a growing season. This could explain differences in biomass production between genders observed in our greenhouse experiments. Our results suggest that defoliation may put female shrubs at a competitive disadvantage.

Overall, differences in sex ratios between exclosures and adjacent grazed pastures at our site reported by Cibils and others (1997) may have been the result of greater mortality rates in female shrubs. Both female-biased browsing by cattle, and possibly higher susceptibility to defoliation in female fourwing saltbush shrubs may have promoted differences in mortality rates of males and females. Browsing-triggered sex phenotype shifts of labile shrubs are possibly not important in driving alterations in phenotypic sex ratios of fourwing saltbush at our site.

Acknowledgments

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Ecological and Population Genetics of Locally Rare Plants: A Review

Simon A. Lei

Abstract—Plant species with limited dispersal ability, narrow geographical and physiological tolerance ranges, as well as with specific habitat and ecological requirements are likely to be rare. Small and isolated populations and species contain low levels of within-population genetic variation in many plant species. The gene pool of plants is a product of phenotype-environment interaction. The effects of inbreeding mating systems, geographical ecotypes, phenotypic plasticity, microhabitat differentiation, and stochasticity on genetic variability in locally rare plants are considered. The emphasis of this review paper is on recapitulation of original data and conclusions of results from a variety of research studies that approach locally rare plants from ecological and population genetics perspectives.

Introduction

Temporal and spatial variations in plant population sizes are detected both within and among species. Some plant species occur in wide ranges (cosmopolitan), while others are restricted to only a specific habitat (endemic). This variability is the result of complex interactions among the life history features of populations, local environmental conditions, and ecological and physiological requirements of particular species (Barnett and Kohn 1991). One often assumes that rare and endangered species occur in small populations that are geographically isolated from one another. Rare plants may be locally common but occur in only a few places because their habitat is geographically restricted (Kruckeberg and Rabinowitz 1985). Rare plants may be locally scarce but geographically widespread. They may also be both scarce and geographically restricted, reflecting specific adaptation to habitats that are rare (Rabinowitz 1981). The ecological and evolutionary processes that give rise to rarity are so complex that one cannot assume all locally rare plants exhibit the same patterns (Kruckeberg and Rabinowitz 1985). Likewise, some locally rare plants appear to be genetically depauperate due to their relatively small population size. It may be premature to assume that this is a universal feature of all locally rare species (Stebbins 1980; Griggs and Jain 1983).

The distribution and amounts of genetic diversity within and among populations of locally rare plants depend on whether a species is naturally rare or whether it has recently become rare as a result of stochastic events. Stochastic events may be environmental or anthropogenic. Plant populations that are naturally small may show genetic systems adjusted to close inbreeding, as well as adaptations that offset the disadvantage of rarity, as opposed to species that have experienced severe reductions in population numbers owing to habitat destruction, fragmentation, or degradation through anthropogenic activities (Barnett and Kohn 1991).

The role of ecological and population genetics in locally rare plants has been increasingly appreciated in recent years. This paper reviews and discusses some of the genetic and evolutionary consequences of small population size and the ecological significance of genetic diversity in locally rare plants.

Genetic Consequences of Mating in Small Populations

Differences in survivorship are detected between progeny from selfed and outbred matings within a population (Barnett and Kohn 1991). They (1991) further state that some plant species are capable of exhibiting both cleistogamous and chasmogamous flowers. Outcrossed offspring are expected to be more genetically diverse than the progeny of self-fertilization. A significant reduction in survivorship is found for selfed progeny in normally outcrossed plants (Schoen 1982). Similarly, differences in the relative fitness of sexually produced offspring versus vegetative (asexually) produced progeny have also been observed. An intense exploitation and interference competition would favor sexual offspring (Case and Taper 1986). Under changing environment, the competitive advantage obtained by the occasional rare genotype would give the sexual groups competitive dominance over the asexual (genetically identical) group, despite the initial advantages of asexual reproduction (Case and Taper 1986).

Heterozygosity seems to have a fitness advantage, and is often affiliated with increased growth rates and survivorship in many plant species. Although heterozygosity may not be advantageous with superior performance when environmental conditions remain relatively stable, heterozygosity may provide the ability to cope with fluctuating environments, and may play such a buffering role (Grant 1981).

Genetic Variation

Inbreeding

The frequency and intensity of inbreeding are often far greater in plants than in most animal groups. Unlike most

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animals, mature plants are sessile organisms. Seeds, pollen, and vegetative dispersal structures (for example, rhizome and stolon) are the only motile stages in the life cycle of a higher vascular plant. Because of limited gene flow through pollen and seeds, offspring plants usually germinate and establish fairly close to the parent, creating small neighborhood sizes. Populations structured into small neighborhoods appear to be inbred and contain low levels of within-population genetic variation compared to those in larger neighborhoods (Barnett and Kohn 1991). The level of inbreeding in a plant population increases over time at a rate dependent on the effective population size, and populations become inbred more rapidly when they are small in size (Barnett and Kohn 1991).

In plant breeding, it is often useful to know how rapidly the inbreeding coefficient increases when propagating by a regular system of mating, such as repeated self-fertilization, sib mating, and half-sib mating (Hartl 1988). Among the three mating systems, self-fertilization leads to an extremely rapidly increase in the inbreeding coefficient (fig. 1). As expected of highly self-fertilizing species, each individual plant is highly homozygous for alleles (Hartl 1988). Some population geneticists propose that self-fertilizing in locally rare species contain fewer deleterious recessives than do outcrossing species, presumably because the increased homozygosity permits harmful recessives to be eliminated from the population by natural selection (Hartl 1988).

Alternatively, other population geneticists argue that the potential consequences of inbreeding in locally rare species include a significant reduction in genetic variability (decreased heterozygosity) and a significant increase in the frequency of lethal or highly deleterious recessive alleles. Mating patterns are prime determinants of the levels of inbreeding in both large and small plant populations (Barnett and Kohn 1991). In an outcrossing population, these are maintained by the balance between mutation and selection. Nevertheless, when an individual self-fertilizes or inbreeds with a relative, these alleles are often homozygous, resulting in inbreeding depression (Barnett and Kohn 1991). Plant populations with a long history of inbreeding due to specific adaptations to selfing, leading to small population sizes, would be expected to show a relatively little inbreeding depression (Templeton and Read 1984). In theory, inbreeding depression usually occurs in normally outcrossing plants, leading to a substantially lower yield and relative fitness (fig. 2). Conversely, inbreeding depression is less severe in species that are partially self-fertilizing, and may be absent altogether in species that are highly selfed (Wright 1977). In some cases, plant species may be adapted to further inbreeding (Huenneke 1991). Alternatively, inbreeding depression may occur even in species with a history of selfing or inbreeding (fig. 3), yet is difficult to accurately determine the level of inbreeding that a species is likely to suffer or sustain.

Although plants growing under optimal conditions in a greenhouse or botanical garden tend to show little or no inbreeding depression, the effects of inbreeding depression may be more severe when seeds are released back into the wild. Seeds produced under uncompetitive conditions may have relatively low "ecological value," and small samples of locally rare plants maintained in botanical gardens may be inbred and of inferior genetic quality (Barnett and Kohn 1991). For this reason, conservation of wild plants growing in greenhouses or botanical gardens may lead to unintentional

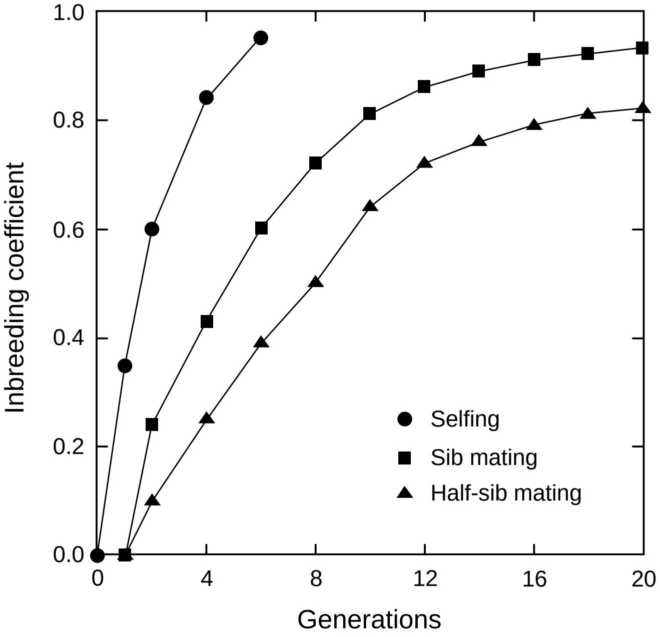

Figure 1—Theoretical increase in inbreeding coefficient *F* for regular systems of mating: selfing, sib mating, and half-sibing mating (redrawn from Hartl 1988).

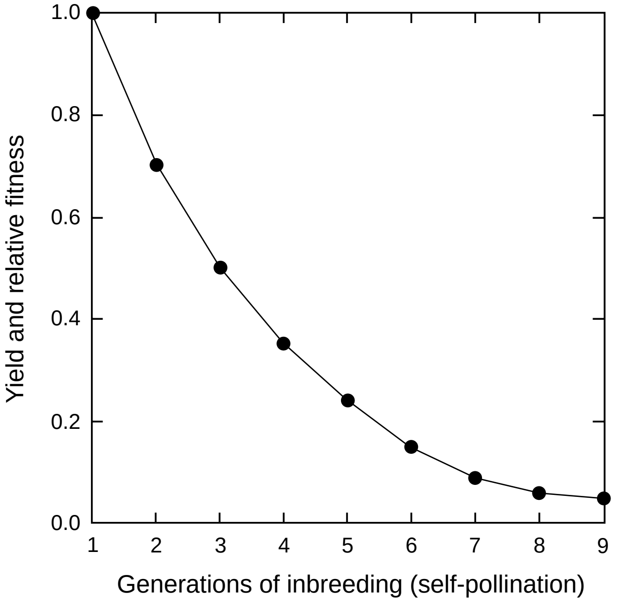

Figure 2—Characteristic loss of yield and relative fitness associated with inbreeding in a normally cross-pollinated plant species. This phenomenon of yield and relative fitness loss typically occurs with each successive generation of inbreeding (redrawn from Kaufmann 1989).

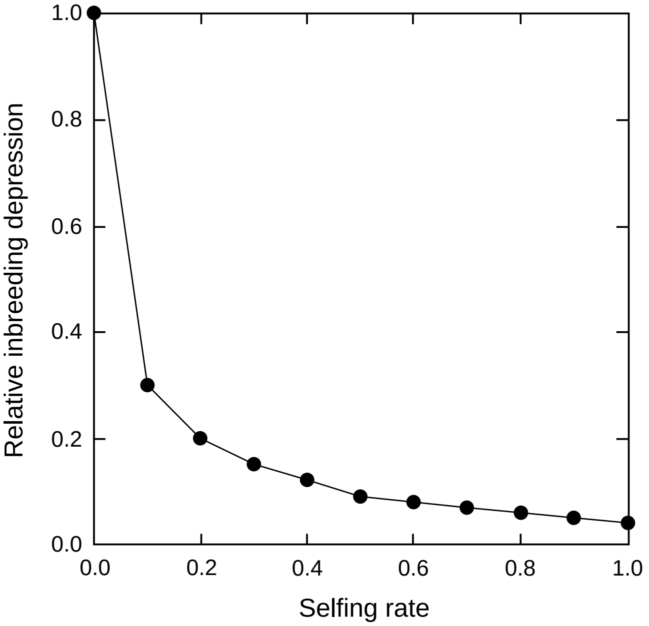

Figure 3—Relationships between inbreeding depression and the selfing rate assuming lethal or highly deleterious recessive alleles in a normally cross-pollinated plant species (redrawn from Barrett and Kohn 1991).

"domestication," particularly if many sexual generations under optimal conditions are allowed to occur (Barnett and Kohn 1991) at the expense of losing some genetic diversity.

Geographical Ecotypes

Plant species occupying a wide geographical range are frequently associated with environmental and ecological conditions. In general, plant species with a wide geographical or ecological range exhibit considerable genetic heterogeneity and phenotypic plasticity (Jain 1979).

Distinct ecotypic variations in growth form have been observed in plants that are geographically widespread. Distinct ecotypes presumably represent discontinuous genetic variation, relating to specific habitats. Local ecotypes, varying in morphology or physiology with environmental conditions, reflect genetic differences among populations (Huenneke 1991). Each plant population is a unique realization of the phenotype-environment interaction (Schwaegerle and Bazzaz 1987). In many plant populations, ecological performance associated with genetic differences exists; such differences are often responses to unusual edaphic, climatic, geomorphic, or other specific ecological conditions (Huenneke 1991). For instance, metal tolerance ecotype is ubiquitous in mine populations, but is nearly absent in adjacent populations growing on non-mine soils. Despite some gene flow across the abrupt environmental boundary, ecotypic variation is maintained by natural selection (McNeilly and Bradshaw 1968). In general, plants would have lower growth rate and survivorship than their "resident" ecotypes if they were transplanted to considerably different environments (Huenneke 1991). Hence, genetic differentiation among and within populations is frequently tied to variation in environmental factors, as well as to geographical and ecological ranges.

Response to Microhabitat Differentiation

Plants experience fine-scale microhabitat differentiations. Environmental variation influences population parameters, such as rates of mortality, growth, and reproductive output among individuals and among populations (Huenneke 1991). Microsite variation acts to buffer populations from environmental stochasticity, and is especially important for seeds, seedlings, and small plants (Huenneke 1991).

Some seedlings establishing several meters from their parent plant may have lower mortality and more rapid growth than seedlings establishing only 50 m from the parent (Huenneke 1991). Genetic variability may allow more efficient exploitation of a heterogeneous and changeable environments than would be possible for a genetically uniform population. However, not all plant species can utilize multiple microsite types efficiently and be buffered from environmental stochasticity. Such multiple microsite types require a higher genetic variation or phenotypic plasticity.

Response to Stochasticity

Stochastic occurrences play a vital role in determining the viability of small plant populations. These occurrences may be genetic or environmental. In general, great heterozygosity characterizes species establishing in variable environments (Beardmore 1983; Loveless and Hamrick 1984; Brown and Burdon 1987).

Genetic uniformity of a plant population may make the population highly susceptible to negative biotic interactions, such as herbivory and invasion by insects, pathogens, parasites, and exotic species. Populations may maintain genetic polymorphism in defense against biological invasions (Bremermann 1980). Variation in resistance to particular herbivores, pathogens, parasites (biological invasions) appears to be an important evolutionary response to promote genetic variation. The existence of a range of genotypes in a population may result in the survival of a few individuals after insect or pathogen attack (Bremermann 1980). The presence of genes for resistance or tolerance within a population may determine the chance of persistence in the face of insect outbreaks or other herbivory episodes (Bremermann 1980).

However, some stochastic events act on members of a plant population regardless of their genetic composition. Major catastrophic disturbances, such as fire, tornado, hurricane, typhoon, avalanche, landslide, earthquake, tsunami, and volcanic eruption, may be devastating to all genotypes in the population. Nevertheless, if disturbances are more moderate in intensity, genetic variability may lead to the survival of at least a few individuals in the population (Huenneke 1991).

Phenotypic Plasticity

A clear distinction between genetic variation and phenotypic plasticity of plants in nature are often difficult to determine. Plasticity allows a single genotype to succeed in a range of environments, and may conceal the true extent of genetic differentiation (Huenneke 1991). Plasticity has a genetic basis that varies among individuals and among populations (Huenneke 1991). Perhaps as a consequence of being restricted to microsites, plants have evolved remarkable levels of phenotypic plasticity (Schlichting 1986). Plasticity presumably buffers populations from stochastic environmental conditions and enhances population viability. Patterns of phenotypic plasticity in individual species appear to have adaptative significance, and plasticity can be responsible for a significant amount of life-history diversity and is often a vital product of life-history evolution (Real 1994). Phenotypic plasticity accounts for some of the natural variation in life history, but the site-origin interactions indicate an extensive array of genetic variation in the actual sensitivity and response to environmental effects (Real 1994).

Although phenotypic plasticity with little genetic heterogeneity would retard the rate of evolution, abundant plasticity has permitted successful germination and establishment of many plants whose principal mode of reproduction is vegetative (clonal) propagation. Whether phenotypic plasticity can fully compensate for low genetic variability of a plant species establishing in a heterogeneous environment is difficult to determine. However, when a species does not possess phenotypic plasticity or when a species periodically experiences environmental stochasticity, genetic variation can promote population viability.

General Conclusions and Ecological Implications

It is imperative to determine to what extent local plant populations are genetically differentiated, whether such differences have adaptive value, and whether the mixing of gene pools from different populations would increase or decrease successful establishment and long-term survival. Most plant populations are genetically differentiated from one another. However, population ecologists and geneticists are unable to make accurate predictions on whether such differences would be of adaptive value in the face of changing environments, or how new genetic combinations are likely to fare in nature.

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New Plant Releases From the USDA-NRCS Aberdeen, Idaho, Plant Materials Center

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Abstract—The Plant Materials Center at Aberdeen, Idaho, is operated by the United States Department of Agriculture, Natural Resources Conservation Service. The purpose of the Plant Materials Center is to evaluate and release plant materials for conservation use and to develop and transfer new technology for the establishment and management of plants. The Center serves portions of Nevada, Utah, California, Oregon and Idaho. 'Rush' intermediate wheatgrass was released in 1994 and was chosen for superior seedling emergence, high forage production and drought tolerance. In 1995, two selected ecotypes of penstemon were released. The Richfield Selection of firecracker penstemon has bright red flowers on upright racemes. The Clearwater Selection of alpine penstemon has bright lavender flowers on narrow panicles. Native penstemons provide soil stabilization, plant diversity and beautification. 'Bannock' thickspike wheatgrass was released in 1995 to be used as a component of seed mixes for rangeland and pasture seedings. The Aberdeen Selection of Laurel willow was released in 1997. The original material was collected in the upper Midwest from naturalized stands. The medium to tall shrub has lustrous, dark green foliage and is very attractive. It shows great promise for use throughout the Intermountain West in irrigated windbreaks and as an ornamental.

The Plant Materials Center (PMC) at Aberdeen, Idaho, is part of the national plant materials program operated by the United States Department of Agriculture, Natural Resources Conservation Service. The purpose of the plant materials program is to develop and transfer new technology for the establishment, use and management of plants.

Plant Materials Centers assemble, evaluate and release plant materials for conservation use. The Aberdeen PMC was established in 1939 and has been the primary breeder and releasing organization for 15 cultivars and 27 alternative releases, and has cooperated in the release of 12 additional cultivars. The Aberdeen PMC serves portions of Nevada, Utah, California, Oregon, and Idaho. The PMC works cooperatively with private landowners as well as State and Federal land management agencies. The PMC Farm is owned by the South Bingham Soil Conservation District and is leased to the PMC.

In 1995, the PMC in cooperation with the Idaho Agricultural Experiment Station released two selected ecotypes of *Penstemon*. Except for one minor species, the genus *Penstemon* does not occur naturally outside of North America. There are approximately 150 species and most are found in the Western United States. Penstemons are perennial plants with opposite leaves, and usually showy, often two-lipped flowers. The conservation value of these penstemons is soil stabilization, plant diversity, and beautification of many different sites. The two penstemons were selected from a collection of 119 penstemons that were evaluated at the PMC from 1981 to 1985. They were chosen for their natural beauty, hardiness and seed production.

The "Richfield Selection" of Firecracker penstemon (*Penstemon eatonii*) was collected near Richfield, Utah. Its natural habitat is the sagebrush, juniper, and ponderosa pine zones at 3,000 to 8,000 ft (914 to 2,438 m) elevation and an annual precipitation zone from 10 to 16 in (254 to 406 mm). It is best adapted to loamy, well-drained soils and can survive full sunlight, but will not tolerate hot, dry areas. It is not adapted to areas with poor drainage. Firecracker penstemon is a perennial, cool-season forb with a fibrous root system and the stems are often decumbent or reclining. The leaves are large and slightly pubescent. The flowers are bright red on upright racemes 24 to 36 in (60 to 91 cm) tall.

The "Clearwater Selection" of alpine penstemon (*Penstemon venustus*) was collected near the Dworshak Reservoir on the Clearwater River in northern Idaho. Its natural habitat is at elevations of 1,000 to 6,000 ft (305 to 1,829 m) and an annual precipitation zone from 20 to 35+ inches (508 to 889+ mm). Alpine penstemon is best adapted to loamy, well-drained soils and can survive full sunlight on open, rocky slopes, but does not do well in areas with poor drainage. It is a perennial, cool-season forb, 12 to 24 inches (30 to 60 cm) tall with a strong taproot and woody base. The leaves are oblong and sharply serrate. The flowers are bright lavender to purple-violet and appear in one or more narrow terminal panicles 12 to 20 inches (30 to 51 cm) long.

The PMC and the Idaho Agricultural Experiment Station released 'Rush' intermediate wheatgrass (*Elytrigia intermedia*) in 1994. Rush was selected from a collection received from the German Botanical Garden, Berlin, in 1962. It was chosen for superior seedling emergence, seedling vigor, high forage production and drought tolerance. The reason for naming it Rush is because after planting, seedlings tend to emerge from the soil 3 to 5 days earlier and in greater numbers than other currently released varieties of intermediate wheatgrass. Rush has been compared to many other varieties of intermediate wheatgrass at multiple locations. It was evaluated for emergence, seedling vigor, forage production, and drought tolerance.

Rush was found to be superior or equal in all of these factors on sites with annual precipitation of 12 inches

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(300 mm) or more. Rush is moderately rhizomatous and densely tillering, with abundant stems and wide leaves. Seed is large, averaging 66,000 seeds per pound as compared to other intermediate wheatgrass varieties which average 80,000 to 90,000 seeds per pound. It prefers well-drained, loamy to clay textured soils.

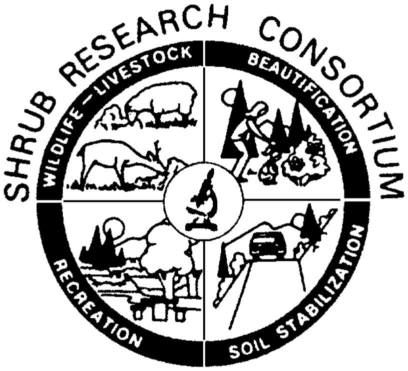
Rush can be used to solve a wide variety of conservation problems including erosion control, forage and cover on sites receiving 12 to 20 inches (300 to 500 mm) annual precipitation. Rush is protected by Plant Variety Protection (PVP) so that seed can be marketed only as a class of certified seed. This will help protect and maintain the characteristics for which it was released.

The PMC and the Idaho Agricultural Experiment Station cooperatively released 'Bannock' thickspike wheatgrass (*Elymus lanceolatus* ssp. *lanceolatus*) in 1995. Bannock is a composite of six seed collections from Washington, Oregon and southeast Idaho. The best performing plants were selected, isolated and increased to create Bannock. The grass was developed to be used as a component of a seed mix for rangeland and pasture seedings. Bannock is especially adapted to sandy areas with a minimum of 6 inches (152 mm) annual precipitation. It also provides wildlife cover and nesting.

Bannock has been thoroughly tested and compared to other varieties of thickspike wheatgrass in the Western United States. It was named in honor of the Bannock Indian Tribe that inhabited the Great Basin. Bannock is a long lived, leafy, rhizomatous, vigorous, sod-producing, cool season grass. Thickspike wheatgrass is native to most of the Northern and Western United States and southern Canada. The PMC has applied for PVP for Bannock so that seed can be marketed only as a class of certified seed. This will help protect and maintain the characteristics for which it was released.

The "Aberdeen Selection" of Laurel willow (*Salix pentandra*) was cooperatively released by the PMC and the Idaho Agricultural Experiment Station in 1997. The original plant material was obtained from the Rose Lake Plant Materials Center in Michigan. It was collected in the upper Midwest from naturalized stands. Laurel willow is native to central and western Europe where it has been cultivated for many centuries. The Aberdeen Selection was made from a collection of potential windbreak plants evaluated at the PMC from 1981 through 1996. This plant was also tested at locations near Mountain Home, Idaho, and Winnemucca, Nevada. It shows great promise for use throughout the Intermountain West in irrigated windbreaks and as an ornamental.

Laurel willow has lustrous, dark green foliage. The shiny leaves are 2 to 5 inches (5 to 13 cm) long and very attractive. The bark on the young twigs is green to yellow green and gray on older branches. It requires deep, moist soils or supplemental irrigation. The medium to tall shrub has a dense round top, and symmetrical crown. It has multiple trunks and grows to heights of 20 to 40 ft (6 to 12 m) with average canopy coverage of 15 to 25 ft (4 to 8 m). Since it is an introduced plant from Europe, it is not an appropriate component for use in natural riparian or wetland areas.



Disturbance Ecology and Biodiversity

What Makes the Desert Bloom? Contribution of Dust and Crusts to Soil Fertility on the Colorado Plateau

Jayne Belnap
Richard Reynolds
Marith Reheis
Susan L. Phillips

Abstract—Eolian dust (windblown silt and clay) and biological soil crusts are both important to ecosystem functioning of arid lands. Dust furnishes essential nutrients, influences hydrology, contributes to soil formation, and renders surfaces vulnerable to erosion. Biological soil crusts contribute directly to soil fertility by fixing carbon and nitrogen, and indirectly by trapping newly-deposited dust and stabilizing already-present soil. Results from crust-stabilized, unconsolidated sandy sediments on prominent rock exposures and grasslands show dust inputs have significantly increased all bio-essential nutrients in soils of SE Utah, including P, K, Mg, Na, and Ca. As plants can be P and K-limited in these soils, dust may be essential for plant growth. Evidence for eolian dust comes from magnetic, chemical, and mineralogic properties of the soils that contrast greatly with those of local bedrock. For example, magnetite, which formed originally in igneous rocks, is common in soils but absent in the local sedimentary bedrock. In view of the regional geology, particle-size distribution of soils, and patterns of properties, the magnetite represents long-distance transport of eolian dust. Dust in the biological soil crusts, when compared to underlying sediment, shows higher magnetite, Zr, and Zr/Ti, suggesting that dust sources have changed over the past few decades. It is suggested that recent human disturbance in areas surrounding the Colorado Plateau may be responsible for this change in dust source. Because most of the fertility in these soils is due to dust input, it is of concern to land managers when soil loss via wind and water erosion exceeds this input. Ever-increasing use of these desert landscapes by recreation, military and agricultural activities generally destroys the biological soil crusts that are critical for nitrogen, carbon, and soil stability. Thus, increased erosion, and reduced dust retention, may be a result of these activities.

Introduction

The source of desert soil fertility has long been a question for many scientists. Weathering of soils from parent material in this region is generally very slow, taking 5,000–10,000 years (Dregne 1983). Rainfall is low, and thus nutrient input via wet deposition is limited. Few nitrogen-fixing plants are found in these regions (Wullstein 1989), and sparse vascular vegetation limits carbon inputs. Eolian dust has recently been demonstrated to be an important source of nutrients for a wide range of ecosystems (Chadwick and others 1999). Eolian dust has been identified, primarily on the basis of chemical, mineralogic, and textural properties, in several types of surficial deposits in arid environments (McFadden and McAuliffe 1997; Reheis and others 1995). However, because such dust is wind-transported, it also renders the soils and sediment in which it resides vulnerable to subsequent wind erosion.

Biological soil crusts can contribute to soil fertility in deserts in many ways. They have high C fixation rates, and significant amounts of C can be fixed during seasons when soils remain wet for extended periods (Beymer and Klopatek 1991; Belnap and Lange 2001). Much of the C fixed by crust organisms is used for extracellular polysaccharide production or leaked into surrounding soils. Because desert microbial populations are generally C-limited (Follett 2001), soil crusts may be critical in sustaining decomposition in these soils. Biological soil crusts influence soil temperature, moisture levels, aeration and porosity (Harper and Marble 1988; Belnap 1995; George and others, unpublished data). Soil crusts influence vascular plant productivity by being a dominant source of N (Evans and Ehleringer 1993), mostly due to N fixation by the soil lichen *Collema* (Belnap 1996). Cyanobacteria secrete powerful metal chelators and other substances that maintain nutrients in plant-available forms despite the high pH of desert soils (Belnap and Lange 2001). Crusts are also critical for soil stability and aggregate formation (Belnap and Gardner 1993; Williams and others 1995a; Belnap and Gillette 1997, 1998).

Most lands in the Western United States, once isolated and seldom visited, have undergone escalating use since the late 1800s. Historically, most of the land use was limited to livestock grazing in areas where free surface water was available; more recently, substantial increases in recreation, military activities, and agriculture have expanded human use (both spatially and temporally) of arid and semiarid regions. The current combination of land use is leading to unprecedented levels of surface disturbance on many of these lands. Generally, soil surface disturbance and/or the invasion of annual grasses results in the loss of lichens and mosses, leaving cyanobacterial-dominated crusts (Belnap 1995; Harper and Marble 1988), which is expected

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to alter many aspects of nutrient cycling and soil stabilization (Belnap and Gillette 1998).

This study documents the presence of eolian silt in surficial sediment on part of the Colorado Plateau. We show how the biological soil crusts in this region enhance and maintain soil fertility through C and N fixation, dust trapping, and soil stabilization. We then discuss how soil surface disturbance alters this situation.

Sampling and Methods

Dust Inputs

Sediment was collected from potholes on slickrock, mesa tops, and grassland settings. Bedrock consisted of either red sandstone, brown to gray sandstone, or limestone. We analyzed sediment both within the biological soil crust and below to depths of 5 cm. We used a combination of reflected-light petrographic and magnetic techniques to determine the amounts, types, and origins of magnetic minerals. Magnetic property measurements included: (1) magnetic susceptibility (MS), a measure of the amount of all magnetic material but mainly ferromagnetic minerals (such as magnetite) when present; (2) frequency-dependent MS (FDMS; from measurements at 600 Hz and 6000 Hz), a measure of the amount of ultrafine grained magnetite, or magnetite-like maghemite, commonly attributed to pedogenic origins; (3) “hard” isothermal remanent magnetization (HIRM), a measure of the amount of hematite; and (4) the S parameter [the ratio of backfield isothermal remanent magnetization (IRM) at 0.3 Tesla (T) and IRM at 1.2 T], in this setting an indication of relative amounts of magnetite and hematite.

Trace and minor-element chemistry was determined using energy-dispersive X-ray fluorescence (XRF). Changes in Fe (commonly mobilized via primary mineral alteration), Ti (chemically immobile and associated with certain magnetic Fe oxide minerals), and Zr (also chemically immobile) are especially useful in evaluating potential post-depositional alteration of magnetite and possible shifts in sediment sources.

Biological Crust Inputs and Soil Retention

The site of this study was the Needles District of Canyonlands National Park, located 125 km south of Moab, UT. Annual rainfall averages 215 mm, with approximately 35 percent falling as summer monsoons. To estimate N inputs, we used data from a datalogger that has continuously recorded amount and time of rainfall, and air and soil temperatures, since April 1998. Using this data, we grouped precipitation events into six temperature categories (–4 to 4 °C, 5–8 °C, 9–17 °C, 18–23 °C, 24–27 °C, and 28–35 °C). We used a combination of manual dry-down curves and TDR results (that measured soil moisture in the top 1 cm of soil) to determine how long 1 mm of precipitation at different seasons and different air temperatures lasted in study soils for each temperature category. We then multiplied the precipitation received at a given temperature by the time soils took to dry at that temperature to estimate the number of hours soils are wet. We used a combination of laboratory and field-obtained N fixation values for each of the temperatures and multiplied this by the number of hours soils were wet at each temperature (Belnap 2001a). Because crusts are able to fix 4-6 hours during the dark, 50 percent of the nighttime hours were considered available for N fixation.

Studies of N fixation utilized the acetylene reduction technique, which requires conversion to absolute N values using $^{15}N_2$ calibration. This was done for soil *Nostoc* from the Moab, UT area by Phillips and Belnap (unpublished data); a conversion ratio of 0.31 was obtained, and is used for estimates of N inputs. A similar value for the same organism was measured by Liengen (1999) from arctic soils. It should be noted that this low conversion ratio gives much higher values for N inputs than is commonly reported in the literature. Most of these studies did not do the necessary experiments to find the appropriate conversion ratio, and so relied on the theoretical ratio of $3C_2H_4$:1N. However Liengen showed that this value is only accurate for cultured cyanobacteria and that for field-collected organisms, a much lower conversion ratio should be used.

Data from studies previous published (Belnap and Gillette 1997, 1998) and unpublished (Belnap and others) were used to estimate accelerated soil losses due to conversion of lichen crusts to cyanobacterial crusts. This data was also used to estimate losses from wind and water immediately following surface disturbance on sandy soils.

Results and Discussion

Dust Inputs

The MS of the host sedimentary rock was very low at all sites tested (11 sites, 2.4×10^{-10} to 1.1×10^{-8} m^3/kg). In contrast, MS values of the surficial sediment were between one and three orders of magnitude greater than the corresponding site bedrock (site averages, 3.5×10^{-8} to 1.5×10^{-7} m^3/kg), with MS at most sites highest in the biological soil crust (fig. 1a). The S parameter values indicate that there is a much greater concentration of magnetite relative to hematite in the soil crusts than below the surface (fig. 1b). While such patterns in MS and S parameters suggest the presence of eolian dust, they are not sufficient proof, as enhanced MS in upland soils and sediments (away from alluvial input) may result from other factors such as pedogenic production of ultrafine grained iron oxide minerals, concentration of residual minerals, and bacterially mediated reactions (Dearing and others 1996). Moreover, diagenetic or pedogenic alteration of magnetite at depth may produce a pattern of highest MS and S values at the surface.

However, the eolian origin of the observed MS enhancement is supported by other magnetic properties and geochemical results seen in these soils. Hematite content was much greater in surficial sediment than in the underlying bedrock, even including hematite-bearing redbeds (fig. 1c), as would be expected for eolian addition of hematite with magnetite. Moreover, FDMS values were small, implying pedogenic iron oxide contributed only a small amount (fig. 1d). Large differences in elemental content were seen between the surficial sediment and bedrock (fig. 2). For example, surficial sediment had higher average contents of Fe (≈1 wt. percent), Ti (≈0.15 wt. percent), and Zr (≥200 ppm) than local bedrock (Fe, 0.7 wt. percent; Ti, 0.08 wt. percent; Zr<100 ppm). Nearly constant Fe/Ti values (fig. 2), along with textural evidence, indicate a lack of magnetite destruction below the

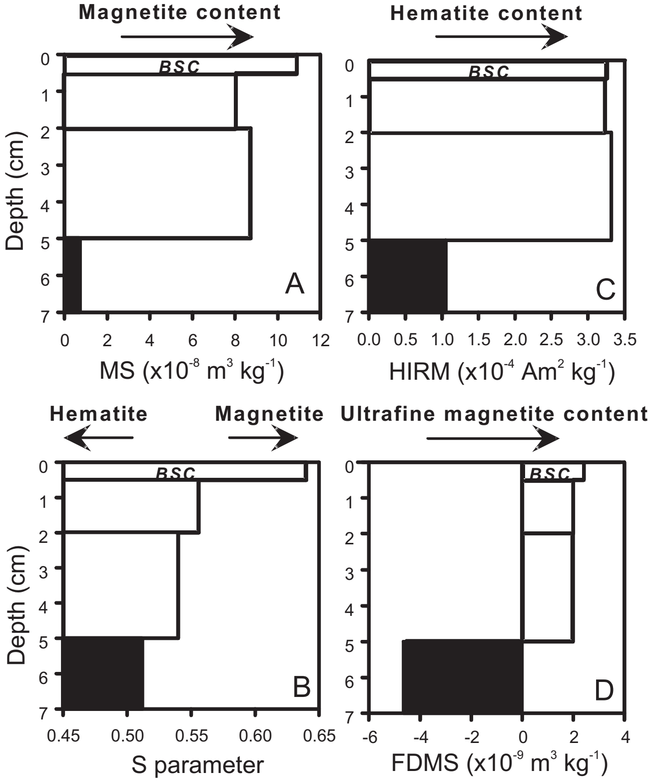

Figure 1—Plots of depth versus magnetic properties, as averages from sandstone sites. (A) magnetic susceptibility; (B) S parameter; (C) "hard" isothermal remanent magnetization; (D) frequency-dependent magnetic susceptibility. Uppermost sample represent biologic soil crust values. Solid pattern represents bedrock values.

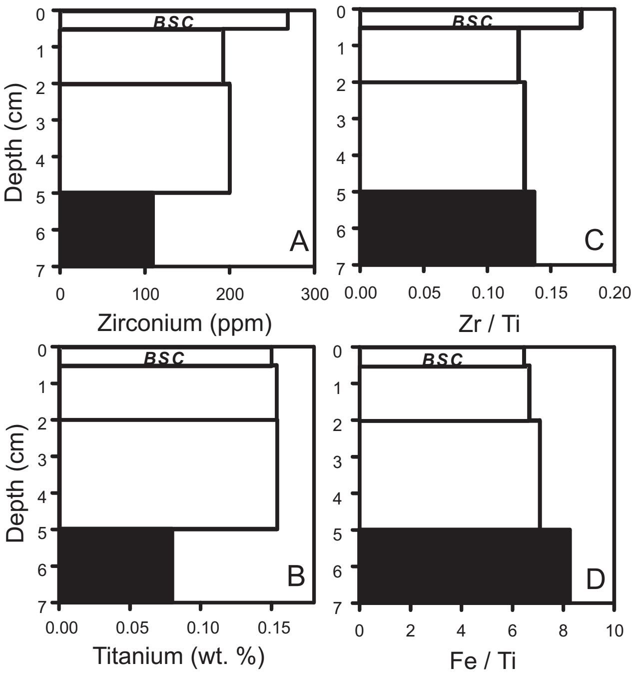

Figure 2—Plots of depth versus zirconium. (A) Titanium; (B) Zr/Ti; (C) Fe/Ti; (D) Patterns as in figure 1.

BSC biologic soil crust
☐ surficial sediment or soil
■ bedrock

biological soil crust. The overall thinness of layers, magnetic mineralogy, and resistant underlying bedrock preclude magnetic and elemental enrichment of the surficial layers by chemical weathering and residual accumulation.

The definitive test for the origin of magnetite and hematite in this setting is petrographic comparison of grains extracted from the sediment and bedrock. In these sediments, magnetic minerals include mainly silt-sized (5–60 mm) magnetite and associated oxides, such as ilmenite, hematite, and varieties of other Fe-Ti oxides that result from high-temperature oxidation of magnetite and ilmenite. These associated minerals, and the internal textures of magnetite with ilmenite lamellae, indicate that the magnetic Fe-Ti oxide minerals originated in igneous rocks. Such magnetite and associated minerals are absent in sandstone at the sampling sites, although limestone may contain only very rare magnetite or maghemite formed via oxidation of pyrite.

Combined, this evidence suggests that a major component of the surficial deposits must be eolian to account for their high content of strongly magnetic minerals, which are absent or sparse in the underlying bedrock. Moreover, fly-ash magnetite, produced via coal combustion in power plants, is observed in the biological soil crust, but has not been found in the underlying surficial sediment. Silt plus clay content typically ranges between 20 and 50 percent, implying a similar range in eolian dust content.

The biological soil crust, which stabilizes the surficial material, is a natural dust trap and appears to have documented a change in dust source over the past several decades. Relative to underlying sediment, this crust layer has higher magnetite (both absolute and relative to hematite), higher Zr/Ti, and nearly constant Fe/Ti (fig. 2). These shifts in magnetic and chemical properties are consistent with increased eolian input from desert regions (much underlain by granitic and rhyolitic rocks) west and southwest of the Colorado Plateau. The shifts may also represent more input from the mildly alkaline intrusive rocks that form the Henry, Abajo, and La Sal Mountains of the central Colorado Plateau. Either way, the magnetic and chemical shifts recorded in the biological soil crusts may reflect recent, intensive human disturbance of arid lands.

In light of the above evidence, the contribution of dust to soil fertility in this region is striking. As can be seen in figure 2, the deposition of dust has enhanced most plant-essential nutrients in these soils. Enriched nutrients include phosphorus (2x), potassium (1.2x), magnesium (4.4x), sodium (3.8x), calcium (10.5x, except in calcite-cemented sandstone sites), iron (1.6x), copper (1.4x), manganese (2.1x) and molybdenum (13x). Amounts and distribution patterns of enrichment are similar between sites, and magnesium, sodium, calcium, copper and zinc are consistently higher in the biological soil crust relative to underlying sediment.

Biological Soil Crust Inputs and Soil Retention

Biological soil crusts have long been known to fix carbon and nitrogen, and estimates of their annual contributions have been made by multiple authors (Jeffries and others 1993; Belnap 2001a; Evans and Lange 2001). Beymer and Klopatek (1991) estimated potential annual C contribution of lichen soil crusts to be 12–37 gC m^{-2} $year^{-1}$. Lange and others (1994) estimated lichen crusts in Namibia to contribute 32 gC m^{-2} $year^{-1}$ lower range. Lower rates have been reported for cyanobacteria-dominated crusts (0.4–2.3 gC m^{-2} $year^{-1}$; Garcia-Pichel and Belnap 1996). Because short wet-dry cycles in summer lead to C deficits due to drying of soils before net photosynthesis can be reached (Jeffries and others 1993), most C inputs occur during the cooler seasons.

Less is known about N fixation in this region. Our recording datalogger showed that rainfall events were surprisingly common in SE Utah during the measurement period. Between June 15, 1998, and September 15, 2000, 129 soil-wetting events were recorded (intermittent rains during consecutive days were considered one event if the soils did not dry between rain showers), an average of 4.8 events each month. The number of rain events in any given season, and the amount of rainfall, was highly variable, and within the 2-year measurement period, showed no obvious pattern among seasons (table 1). The number of rain events at night relative to those occurring during the day was also highly variable. Combining these results with average N fixation rates at a given temperature, we were able to estimate seasonal and annual N inputs for 2 measured years: 41 kgN/ha/yr for lichen crusts, and up to 13 kgN/ha/yr for cyanobacterial crusts (depending on biomass of a given crust). This represents a major input of N to soils of these ecosystems.

All crust components secrete extracellular C within minutes to a few days of C acquisition, and the presence of soil-crust organisms can increase soil polysaccharides and total carbon by up to 300 percent (Rao and Burns 1990; Rogers and Burns 1994), benefitting surrounding heterotrophic microbes which are often carbon limited. In addition, this input of carbon can lower soil C:N ratios, thus increasing decomposition rates (Kleiner and Harper 1972).

Table 1—Amount of precipitation (mm) by time of day and season for 1998–2000. Spring = March 16–June 15; Summer = June 16–September 15; Fall = September 16–December 15; Winter = December 16–March 15.

	Day	Night	Total
Spring 1999	129	318	447
Spring 2000	162	19	181
Summer 1998	40	49	89
Summer 1999	121	61	183
Summer 2000	8	10	18
Fall 1998	308	271	579
Fall 1999	128	70	199
Winter 1998	183	56	239
Winter 1999	206	146	352

Up to 70 percent of the nitrogen fixed by cyanobacteria and cyanolichens is released immediately into the surrounding soil environment, and is available to associated organisms including vascular plants, mosses, fungi, and other microbes (Belnap 2001a). Multiple studies have reported that the presence of soil crusts increases surrounding soil N by up to 200 percent (Shields and Durrell 1964; Rogers and Burns 1994; DeFalco 1995; Harper and Belnap 2001), and stable isotopes show soil crusts can be the dominant source of N for desert soils and plants (Evans and Ehleringer 1993; Evans and Belnap 1999).

Crusts affect soil nutrients in many other ways as well. Microbial exopolymers both add carbon to soils as well as create a mosaic of polyfunctional metal binding sites that bind both cations and anions (Greene and Darnall 1990), thus preventing them from leaching from sandy soils. Most of these polymers also concentrate plant-essential nutrients such as Na, K, Mg, Ca, Mn, Fe, Ni, Cu, and Zn (Lange 1976; Geesey and Jang 1990). As they are adsorbed to the extracellular sheath, and are not absorbed by the cells, they remain available to plants (Geesey and Jang 1990). Cyanobacteria, green algae, fungi, lichens, and bacteria also secrete powerful metal chelators such as siderochromes (Lange 1974; McLean and Beveridge 1990; Schelske 1962) that can maintain metals in bio-available forms, and can concentrate essential trace metals found at exceedingly low ambient concentrations (Paerl 1988). Cyanobacteria secrete peptide nitrogen and riboflavin which, together with siderochromes, keep P, Cu, Zn, Ni, and Fe plant-available. These secreted chelators are water soluble, and capable of being translocated in soil and water. Consequently, chelated compounds are made available to associated plants or microbes (Bose and others 1971; Lange 1974; Geesey and Jang 1990; Gadd 1990a). Cyanobacteria also secrete glycollate, which stimulates the uptake of P in cyanobacteria (Fogg 1966), as well as various vitamins such as B_{12}, auxin-like substances, and other substances that promote growth and cell division in plant and animal tissue (Fogg 1966; Venkataraman and Neelakantan 1967). Biological crusts are also important in trapping dust and stabilizing soils. Studies have shown that the top few mm of soil contain a much higher percentage of soil fine particles than underlying soils, indicating that crusts trap and entrain falling dust particles (Danin and Ganor 1991; Verrecchia and others 1995). Because dust can be a critical component of soil fertility, as discussed above, this capture and retention is an essential part of soil building in deserts.

Over 30 studies worldwide have shown that biological soil crusts reduce soil loss by wind and water (Belnap 2001b; Warren 2001a,b). Cyanobacterial and microfungal polysaccharides entrap and bind soil particles together, creating soil aggregates, which are then further linked together into larger aggregates (Belnap and Gardner 1993). These larger, linked aggregates require greater wind and water velocity to move than single soil particles (Gillette and others 1980; Marticorena and others 1997). Resistance to erosion increases with biological crust development (Belnap and Gillette 1998), with cyanobacterial crusts showing the least, and lichen crusts showing the greatest, resistance to erosive forces. In most cases, lichen crusts can withstand winds well above those recorded at field sites, and so offer complete protection from wind erosion, even in coarse soils (Leys

1990; Williams and others 1995a; Belnap and Gillette 1997, 1998; Leys and Eldridge 1998). Exhaustive field and lab studies show that increasing crust cover and/or development also significantly reduces sediment loss via water erosion (Booth 1941; Loope and Gifford 1972; Rushforth and Brotherson 1982; Brotherson and Rushforth 1983; Harper and St. Clair 1985; Williams and others 1995b).

Effects of Soil Surface Disturbance on Soil Fertility

Overall, disturbance generally results in loss of species diversity, biomass, and surface cover of cyanobacteria, lichens, and mosses. The more severe the disturbance, the greater the loss. Thus, after severe disturbance, the resulting crust community is greatly simplified from a community with multiple species of cyanobacteria, lichens, and mosses to a community often dominated by one or a few species of cyanobacteria. A shift from a lichen to a cyanobacterial-dominated crust will reduce C inputs, as cyanobacteria fix less C than lichens and mosses per unit soil surface area (Phillips and Belnap 1998). As discussed above, much of this C is released into the surrounding soils (Lewin 1956); thus, reduced C fixation is expected to reduce soil C available for microbial populations, decomposition rates and soil nutrient levels (Paul and Clark 1996).

Soil surface disturbance and/or a shift from a lichen to a cyanobacterial-dominated crust also decreases N inputs. Our annual input estimates are four times higher for lichen crusts than cyanobacterial crusts. Laboratory and field studies have consistently shown that lichen crusts have higher N fixation rates than cyanobacterial crusts (Jeffries and others 1993 a,b; Belnap and others 1994; Belnap 1995, 1996; Belnap 2001a). Multiple studies have shown less N input from crusts following disturbance. Vehicles, human foot traffic, mountain bikes, and raking reduced N input from crusts 25-89 percent, with a drop of 80-100 percent over time due to subsequent death of buried material (Belnap and others 1994; Belnap 1995, 1996). Grazing reduces N inputs by 50-95 percent (Brotherson and others 1983; Johansen and St. Clair 1986; Jeffries and others 1992; Terry and Burns 1987). Burning can reduce N inputs by 64 percent and tilling by 99 percent (Terry and Burns 1987). Evans and Belnap (1999) showed N fixation was still 2.5 times less than an adjacent, never-grazed area 30 years after grazing had ceased. Decreased N inputs from crusts can have long-term impacts on soil N levels. On the Colorado Plateau, Jeffries (1989) found 50 percent less N in non-crusted soils compared to adjacent crusted soils. Evans and Belnap (1999) found a 42 percent decrease in soil N and a 34 percent decrease in plant tissue N when comparing a cyanobacterial-moss dominated crust (previously grazed) to an adjacent lichen-dominated (ungrazed) area. In the same area, stable N isotopes showed that both soil and plants in the lichen-dominated area contained less newly fixed N than the cyanobacteria-moss dominated area. This has large implications for ecosystems that are dependent on soil crusts for N inputs, such as found on the Colorado Plateau (Evans and Ehleringer 1993).

As noted above, disturbance also results in increased soil loss (and thus reduced fertility) via wind and water erosion, as compressional disturbance breaks apart soil aggregates formed by the polysaccharide connections. Recent studies have shown that disturbance of crusted soils increases sediment loss by up to 300 percent (Belnap and Gillette 1997, 1998; Belnap, unpublished data). After disturbance and once a soil is stabilized by cyanobacteria, less erosion is expected compared to the bare soils; however, cyanobacteria are less able to protect soils from erosion than lichens or mosses, and thus accelerated losses are expected until the moss and lichen components recolonize the site. In addition, burial of nearby biological soil crusts from wind-blown sediments generally means death for the photosynthetic components of the soil crusts, further reducing fertility and stability of these soils. Most of the soil photosynthetic productivity and nitrogen fixation in desert soils is concentrated within 3 mm of the surface (Garcia-Pichel and Belnap 1996).

Conclusion

Accelerated soil loss is of great concern to land managers worldwide. Based on this study, soil fertility on the Colorado Plateau is dependent on the retention of atmospherically deposited dust and N inputs from lichen-dominated biological soil crusts. Well-developed biological soil crusts reduce erosional losses. In addition, the crusts contribute substantial amounts of C and N. Current dust deposition rates in the Colorado Plateau region are low, and when soils are disturbed, loss rates may exceed deposition (Gillette and others 1980; Offer and others 1992; Belnap and Gillette 1997, 1998; Reynolds and others 1998). Biological soil crusts are easily disturbed by soil surface disturbances, and recovery is very slow in this region (Belnap 1993). Thus, it is recommended that soil surface disturbance be kept to a minimum to maintain long-term soil fertility and productivity.

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Components of Spatial and Temporal Soil Variation at Canyonlands National Park: Implications for P Dynamics and Cheatgrass (*Bromus tectorum*) Performance

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Abstract—From January 1997 through October 1998, research was conducted at Canyonlands National Park to investigate soil traits responsible for distinct spatial patterns of cheatgrass (*Bromus tectorum)* occurrence. Field experiments were conducted at sites representing a broad range of soil conditions and cheatgrass abundances. Standard physicochemical soil measures in combination with innovative ion-exchange resin capsules and bags were used to describe spatial and seasonal soil variations. Cheatgrass performance varied along a complex, multivariate soil gradient, with the strongest cheatgrass-soil relationship occurring during winter. Biogeochemical principles, soil measures, growth rates, and leaf-tissue analyses support the hypothesis that this complex soil gradient represents a gradient in P dynamics for cheatgrass. A seasonal increase in the solubility of carbonate and calcium-phosphate (Ca-P) compounds should theoretically occur in winter, when cold-moist soil conditions favor the reaction of CO_2 and soil H_2O to generate carbonic acid, H_2CO_3. The magnitude of this seasonal acidification phenomenon should vary spatially in relation to pH buffer capacity (acid-neutralizing potential)—an important component of soil variation that affects Ca-P dynamics. Insights concerning the significance of pH buffer capacity for P dynamics and cheatgrass nutrition have several implications for research and management.

Introduction

Distinct soil-vegetation patterns are particularly evident in arid and semiarid landscapes. In low-precipitation environments, the scarcity of water results in slow rates of weathering, leaching, and soil formation (Cooke and others 1993). As a consequence, the relative importance of parent material as a factor determining physicochemical soil properties generally increases with aridity (Birkeland 1999), and many arid-land vegetation patterns are attributable to parent-material contrasts (Whittaker and Niering 1968). In addition, geomorphic processes such as erosion and deposition can produce mosaic landscapes composed of soil patches differentiated on the basis of pedogenic age and degree of profile development. Resultant among-soil variations in profile characteristics can strongly influence vegetation patterns through effects of pedogenic horizons on spatiotemporal soil-resource dynamics (McAuliffe 1994). Distinct vegetation patterns also may result from topographic variations (for example, aspect, slope gradient, and slope position) that affect microclimate, pedogenic processes, and the redistribution of water and mineral elements among landscape units positioned along a soil catena (Birkeland and Gerson 1991).

Although vegetation patterns often are correlated with parent materials, profile development, and topography, identification of the ultimate mechanisms underlying these plant-soil relationships is more problematic and illusive. Soil variation is complex and multivariate in time and three-dimensional physical space, but most plant-soil studies focus on a very limited set of soil measures (see Hammer 1998 for critique). Because of the significance of water in arid environments, soil effects on plant water relations often are emphasized (Comstock and Ehleringer 1992). Nutritional aspects of plant-soil patterns in arid environments have received comparatively little attention, despite increasing evidence for the importance of nutrient relations on population and community dynamics in arid systems (Bilbrough and Caldwell 1997). Water and nutrient uptake by plants are not independent (Barber 1995), and Chapin (1991) has argued that the effects of low soil moisture on nutrient availability to plants may be almost as significant as the direct effects of water stress on plant performance. Additional complexity can arise from strong seasonal variations in soil conditions, such that the availability of limiting soil resources may vary asynchronously with other limiting resources or conditions as well as with plant phenology and resource demand (Bilbrough and Caldwell 1997). Complex, multi-factor variations in space and time render the elucidation of mechanistic plant-soil relationships a major challenge for ecologists.

A mechanistic understanding of plant-soil patterns is particularly important with respect to the applied problem of invasive exotic species. The prediction of potential invasion patterns as well as the ecological restoration of ecosystems degraded by invasive exotics both depend for

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their success on a solid understanding of the mechanisms underlying observed invader-environment relationships (Crawley 1987). In this paper, we examine the plant-soil mechanisms responsible for distinct spatial patterns in the distribution and abundance of the invasive exotic grass cheatgrass (*Bromus tectorum* L.) in arid landscapes of Canyonlands National Park, Utah. This research was designed to address two questions. First, what are the major components of soil variation in the study area? Second, how does cheatgrass performance vary in relation to identified components of soil variation? We approached these questions through extensive soil characterization and by conducting field experiments to assess the effects of altered soil-resource conditions on seasonal aspects of cheatgrass performance along a calcareous soil gradient.

Methods

Study Species

Cheatgrass is an autogamous winter annual grass native to Eurasia (Mack 1981). Following its introduction to North America in the late nineteenth century, cheatgrass spread to most of North America north of Mexico, with the exception of the southeastern region of the United States (Stubbendieck and others 1992). It is most abundant in the Intermountain West, where it reached its present distribution within 50 years of introduction; currently it is the most common species on >410,000 km^2 of the region (Mack 1981). Cheatgrass seeds typically germinate in response to autumn precipitation, but recruitment can occur at any time from autumn through late spring (Mack and Pyke 1983). Germination has been recorded at temperatures just above freezing (Evans and Young 1972). Seedlings have high rates of root elongation, and root growth occurs at soil temperatures as low as 2 to 3 °C (Harris 1967). Comparatively rapid winter root growth has been cited as a major factor responsible for cheatgrass' competitive advantage over native grass seedlings (Harris 1967).

Study Sites

In September 1997, 17 study sites measuring approximately 40 m x 40 m were selected at Canyonlands National Park (fig. 1). Sites were selected to represent a range in abundances of cheatgrass and the native C_3 bunchgrass Indian ricegrass (*Stipa hymenoides* R. & S). Grassland communities dominated the vegetation at all sites. In addition to cheatgrass and Indian ricegrass, other common taxa were galleta (*Hilaria jamesii* [Torr.] Benth.) and dropseeds (*Sporobolus* R. Br. spp.). All sites were located at approximately 1550 m in elevation, aspects varied, and slopes ranged from 0 to 8 percent (Miller 2000). Soils were classified as mesic Ustollic Camborthids (Begay series) and mesic Typic Torripsamments (Sheppard series) (USDA Soil Conservation Service 1991).

At each of the 17 sites, six circular ricegrass-centered plots measuring 1.2 m in diameter were established (102 plots total). Plots were centered on ricegrass clones to control for micro-scale soil conditions among the four sets of companion studies. All litter and plants including the center ricegrass were removed by hand, and plot interiors (0.8 m diameter) were seeded with 1150 cheatgrass seeds (~2300 seeds/m^2) collected at Canyonlands. Seeds were mixed by hand in the top 1 to 2 cm of soil, and plots were caged with fencing to exclude vertebrate herbivores and granivores.

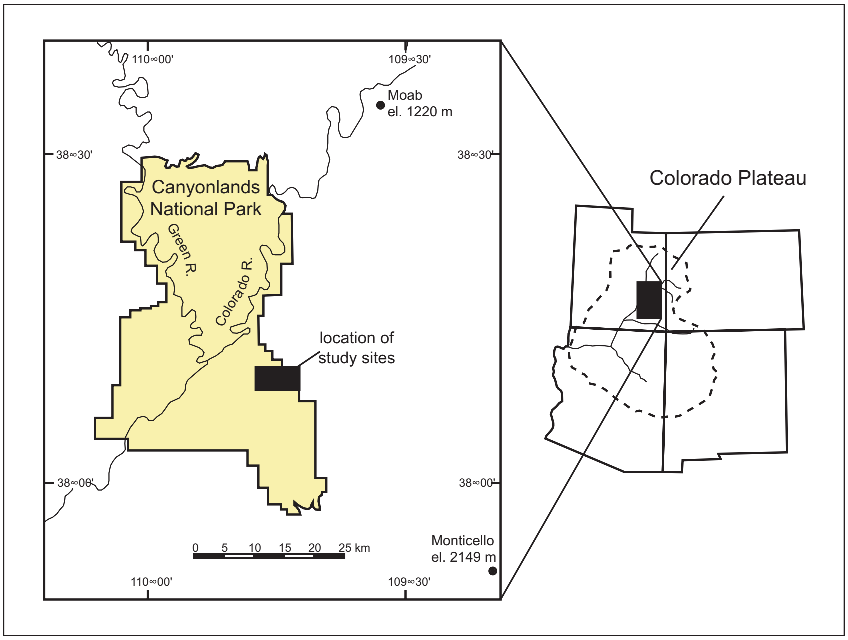

Figure 1—Map showing location of study sites in Canyonlands National Park, Utah.

Soil Measures

At each site, 10 soil samples were collected systematically with an 8-cm-diameter bucket auger from each of three depths 0 to 10, 20 to 30, and 50 to 60 cm. Samples were composited by depth, air dried, and analyzed by the Plant and Soil Analysis Laboratory at Brigham Young University (BYU) for electrical conductivity (EC), pH, cation exchange capacity (CEC), organic matter content, $NaHCO_3$-extractable P, NH_4OAc-extractable K^+ ("K-EX"), and acid-neutralizing potential (ANP) following the acid-neutralizing method of carbonate analysis described by Allison and Moodie (1965). Measurement of ANP involves reaction of a sample with dilute HCl, followed by titration to pH 7.0 with NaOH to determine the quantity of neutralized acid. In soils where the only acid-neutralizing compounds are carbonates and bicarbonates (for example, $CaCO_3$ and $Ca(HCO_3)_2$), ANP estimates soil carbonate levels. However, to the degree that soil constituents other than carbonates (for example, oxides, hydroxides, and $CaSO_4$) also react with the HCl, this measure is best viewed as a general index of the sample's total acid-neutralizing potential (Allison and Moodie 1965). ANP is the most reactive component of the soil's total acid-neutralizing capacity (ANC) as discussed by van Breemen (1983), and is conceptually analogous to pH buffer capacity (Nye 1986).

All macronutrients K^+, HPO_4^{2-}, NH_4^+, NO_3^-, Ca^{2+}, Mg^{2+}, SO_4^{2-}, and micronutrients Mn^{2+}, Zn^{2+}, Fe^{2+}, Cu^{2+}, and Na^+ were extracted simultaneously with mixed-bed (cation + anion) ion-exchange resin "capsules" (acquired from UNIBEST, Inc., P.O. Box 5095, Bozeman, MT 59717, http://www.wecsa.com/) at BYU following methods described by Miller (2000). Each manufactured resin capsule consisted of a 2-cm-diameter spherical ball with 4 ml of mixed-bed resin beads (H^+ - OH^- saturated) contained within a plastic screen mesh. Ion-exchange resin beads and membranes have been used for laboratory and in-situ nutrient measurements for over 40 years (see Skogley and Dobermann 1996 for review). The approach used here, with a simultaneous resin extraction of multiple elements from a saturated paste, has been referred to as the "phytoavailability soil test" (PST) (Skogley and Dobermann 1996). The PST provides an integrated index of nutrient bioavailability because it is sensitive to ion activities in the soil solution, as well as to ion diffusion and other soil properties that are important components of soil nutrient buffering capacity (Skogley and others 1990).

Soils were analyzed by the U.S. Geological Survey (USGS) Central Region Geology Laboratory, Denver, for particle size, carbonate content, and magnetic susceptibility. Particle size was measured with a Malvern laser particle sizer following the removal of carbonates and organic material by acid digestion. Carbonate content was determined gasometrically by measuring the volume of evolved CO_2 produced by reacting a sample with acid (Dreimanis 1962). Magnetic susceptibility (MS) measurements were conducted with a susceptometer. MS is a rapid, non-destructive measure that provides an index of the concentration of magnetic grains in a sample (Mullins 1977). Among-soil variations in MS have been interpreted to result from pedogenic processes (Singer and Fine 1989) or aeolian deposition of silt-sized particles bearing magnetic minerals (Reynolds and King 1995; Hanson 1999).

To assess in-situ nutrient dynamics, at five sites four nylon-mesh bags containing 10 g of moist, mixed-bed ion-exchange resins (H^+ - Cl^- saturated) were buried in all experimental plots at depths of 5 to 10 cm (Lajtha 1988). Ion-exchange resin bags were first placed at the beginning of experimentation in January 1997 and were replaced seasonally thereafter (approximately 3-month intervals). After replacement, exposed resin bags were extracted with HCl and analyzed for macro- and micronutrients at BYU.

Cheatgrass Measures

Cheatgrass measurements were made once following germination in October, at the onset of winter in early December, and monthly in spring from mid-March to mid-May. Fall establishment was estimated in December by counting the number of live plants occurring in a rectangular 250-cm^2 quadrat frame aligned with each of the four cardinal directions in each plot (1000 cm^2 sampled per plot). Ten individual plants per plot (1020 total) were marked with numbered sticks in late October. Total leaf lengths (sheaths plus blades) of all marked plants were measured to the nearest mm, averaged to obtain a single measure per plot per growth period, and used to calculate relative growth rates (mm/mm/day). In spring, foliar tissues were collected from plants in a subset of plots. Tissues were air dried, ground, and analyzed at BYU for tissue concentrations (percent dry weight) of mineral elements following wet digestion. At the end of the growing season, above-ground tissues were harvested, air dried, and weighed to obtain total biomass per plot.

Statistical Analyses

To describe among-site soil variation, 40 soil variables were analyzed by principal components analysis (PCA) with varimax factor rotation (Kent and Coker 1992). Included in the analysis were soil measures from 0 to 10 cm, total profile values for macro- and micronutrients (sum of resin-capsule values for 0 to 10, 20 to 30, and 50 to 60 cm samples within a single core), and the surface:depth ratio for ANP (0 to 10 cm:50 to 60 cm ratio), the latter measure providing an index of profile development. Simple linear correlation (Zar 1999) was used to assess relationships between seasonal measures of cheatgrass performance and spatial components of soil variation identified through PCA. All statistical analyses were conducted using the software package STATISTICA™ v5.5 on a PC platform (StatSoft 1999).

Results

Soil Variation

Table 1 summarizes selected soil characteristics of the 17 study sites considered together as a group. In general, study area soils were sandy and calcareous. Soil ANP tended to be slightly higher and more variable than carbonate content, suggesting the presence of acid-neutralizing compounds in addition to carbonates. Soils had low organic-matter (OM) content, low CEC, and low levels of $NaHCO_3$-extractable P. Resin-capsule data indicated that Ca^{2+} was the most active cation in the soil environment, with values 8-9 times higher

Table 1—Descriptive statistics for selected soil characteristics of 17 study sites at Canyonlands National Park, Utah.

Variable (units)	Mean	Min.	Max.	s.d.	CV[a]
0 to 10 cm					
Acid-neutralizing potential (% $CaCO_3$ equiv.)	7.35	4.41	11.03	2.08	28.27
Carbonate content (% $CaCO_3$ equiv.)	6.45	5.02	8.20	1.02	15.80
Magnetic susceptibility (m^3/kg x 10^{-8})	7.26	2.59	14.83	3.94	54.27
Coarse sand (%)	15.26	7.70	24.23	4.48	29.33
Fine sand (%)	70.74	61.93	77.60	4.06	5.74
Total sand (%)	86.01	77.30	90.38	3.86	4.49
Silt (%)	9.97	6.03	17.00	3.07	30.80
Clay (%)	4.02	2.83	5.74	0.89	22.10
pH	7.50	7.17	7.99	0.22	2.96
EC (dS/m)	0.38	0.28	0.46	0.05	13.10
CEC ($cmol_c$/kg soil)	4.52	1.74	8.74	1.82	40.21
Organic matter (%)	0.26	0.04	0.42	0.10	40.73
K-EX (ppm)	168.46	86.92	323.60	61.49	36.50
$NaHCO_3$-P (ppm)	7.98	4.02	14.34	2.43	30.45
K (μmol_c/capsule)	39.64	23.42	61.80	10.15	25.60
HPO_4 (μmol_c/capsule)	10.87	4.91	18.02	4.46	41.01
NH_4 (μmol_c/capsule)	14.40	6.51	21.49	5.22	36.25
NO_3 (μmol_c/capsule)	2.79	0.33	6.18	1.82	65.23
Ca (μmol_c/capsule)	990.55	491.03	1973.42	423.64	42.77
Mg (μmol_c/capsule)	111.48	40.92	252.39	63.54	57.00
SO_4 (μmol_c/capsule)	27.66	15.98	48.88	10.14	36.65
Mn (μmol_c/capsule)	2.00	0.84	3.63	0.95	47.75
Zn (μmol_c/capsule)	0.25	0.10	0.64	0.15	59.26
Fe (μmol_c/capsule)	4.90	3.41	6.73	1.06	21.61
Cu (μmol_c/capsule)	0.12	0.06	0.20	0.04	35.27
Na (μmol_c/capsule)	9.25	1.79	16.08	5.30	57.36
Surface:depth (0 to 10 : 50 to 60 cm)					
Acid-neutralizing potential	0.76	0.32	1.07	0.21	27.59
K	1.20	0.47	2.50	0.61	50.67
HPO_4	2.73	1.21	8.14	1.55	57.00
NH_4	1.33	0.54	3.00	0.68	50.89
NO_3	1.72	0.14	10.01	2.33	135.47
Ca	0.94	0.41	2.28	0.40	42.52
Mg	1.05	0.54	2.31	0.38	36.37
SO_4	0.89	0.18	2.08	0.37	41.77
Mn	2.28	0.86	5.28	1.13	49.66
Zn	1.37	0.45	3.05	0.64	47.16
Fe	1.08	0.75	1.37	0.18	17.04
Cu	1.19	0.70	1.91	0.31	25.97
Na	1.20	0.02	7.21	1.62	134.94
HPO_4:Ca	3.06	1.52	6.99	1.50	49.07
Mn:Ca	2.69	1.01	7.23	1.68	62.31

[a] CV = coefficient of variation (100*s.d./mean).

(on a charge basis) than Mg^{2+}, the second most active cation. Together, these two accounted for approximately 94 percent of measured cation charges. Of the measured anions, SO_4^{2-} was the most active. Measured anions reported in table 1 provided less than 5 percent of the charges required to balance measured soil cations. Based on water analysis (Miller 2000), it is probable that HCO_3^- was the major charge-balancing anion in the soil.

Surface:depth ratios in table 1 indicate several soil-profile trends. On average, ANP, Ca^{2+}, and SO_4^{2-} tended to increase with depth whereas K^+, HPO_4^{2-}, N, and micronutrients tended to have higher values at the surface than at depth. HPO_4^{2-}:Ca^{2+} and Mn^{2+}:Ca^{2+} ratios also tended to be much higher at the surface than at the 50 to 60 cm depth. NO_3^- levels were extremely variable in the sampled profiles. Of the single-ion measures, average, minimum, and maximum surface:depth ratios were greatest for HPO_4^{2-} and Mn^{2+} (with the exception of the maximum value for NO_3^-), indicating a strong tendency for resin-extractable P and Mn both to be concentrated at the soil surface.

The first four axes derived from the PCA of soil variables explained 62 percent of the variation in the analyzed data set (table 2). Variables with highly significant ($p<0.01$) positive loadings for the first axis included 0 to 10 cm carbonate content, HPO_4^{2-}, Ca^{2+}, Mg^{2+}, SO_4^{2-}, Mn^{2+}, and Na^+; and total-profile HPO_4^{2-}, Ca^{2+}, Mg^{2+}, and Mn^{2+}. The second PCA axis was characterized by high positive loadings for 0 to 10 cm ANP and sand content, as well as for the ANP surface:depth ratio. Variables with high negative loadings for axis II included 0 to 10 cm MS, percent silt and clay, CEC,

Table 2—Summary of the first four axes derived from principal-components analyses (PCA) of soil data describing 17 study sites at Canyonlands National Park, Utah. For surface:depth variables, only significant correlations are reported.

	PCA Axes			
	I	II	III	IV
Proportion of variation explained	**0.23**	**0.17**	**0.13**	**0.09**
Variable correlations (loadings for included variables)				
0 to 10 cm				
Acid-neutralizing potential	0.18	0.78***	–0.22	–0.14
Carbonate content	0.86***	0.22	0.15	0.11
Magnetic susceptibility	–0.24	–0.91***	0.07	–0.07
Coarse sand	0.17	0.48	–0.10	–0.08
Fine sand	0.02	0.25	0.06	0.37
Total sand	0.21	0.82***	–0.05	0.30
Silt	–0.13	–0.82***	0.09	–0.28
Clay	–0.44	–0.71***	–0.08	–0.31
pH	–0.16	–0.12	0.17	0.81***
EC	–0.25	–0.30	–0.06	–0.21
CEC	–0.34	–0.74***	–0.13	–0.17
Organic matter	0.09	–0.56*	0.50*	0.11
K-EX	–0.10	–0.88***	–0.12	0.11
K	0.39	–0.35	0.33	0.66**
HPO_4	0.63**	–0.14	0.45	0.05
HPO_4:Ca[1]	–0.33	–0.78***	0.12	0.06
NH_4	0.22	–0.04	0.91***	0.19
NO_3	–0.40	0.20	0.40	–0.03
NH_4+NO_3	0.07	0.03	0.93***	0.16
Ca	0.65**	0.18	0.37	0.03
Mg	0.91***	0.27	–0.01	0.15
SO_4	0.70**	0.17	0.35	0.05
Mn	0.85***	0.17	0.14	0.03
Mn:Ca[1]	0.58*	–0.01	–0.19	0.01
Zn	0.40	0.19	0.12	0.81***
Fe	0.30	0.21	0.14	0.02
Cu	0.44	0.13	0.48	0.15
Na	0.75***	0.02	0.46	–0.07
Total profile sum (sum 0 to 10, 20 to 30, and 50 to 60 cm)				
K	0.37	0.19	0.25	0.68**
HPO_4	0.71***	0.06	0.33	0.13
NH_4	0.44	–0.07	0.66	0.14
NO_3	–0.07	0.01	0.58	0.06
NH_4+NO_3	0.33	–0.06	0.70***	0.13
Ca	0.70**	0.16	0.23	0.18
Mg	0.86***	0.30	–0.05	0.20
SO_4	0.42	0.10	0.28	0.05
Mn	0.88***	0.32	0.06	0.07
Zn	0.08	0.32	0.06	0.79***
Fe	0.46	0.26	0.33	0.14
Cu	0.36	0.15	0.44	0.27
Na	0.14	0.04	0.25	–0.05
Surface:depth ratio (0 to 10 : 50 to 60 cm ratio)				
Acid-neutralizing potential	0.31	0.76***	0.25	–0.17
K[1]	–0.38	–0.68**	0.03	0.13
HPO_4:Ca[1]	–0.33	–0.80***	–0.23	0.07
NH_4[1]	–0.26	0.09	0.52*	0.27
Ca[1]	0.03	0.13	0.53*	–0.26
Mn[1]	–0.36	–0.51*	0.10	–0.06
Mn:Ca[1]	–0.40	–0.69**	–0.33	0.14
Zn1	0.37	0.08	0.30	0.74***

[1] Not included in PCA; * p <0.05; ** p <0.01; *** p <0.001

K-Ex. Other soil measures that were significantly inversely correlated with axis II (though not included in the PCA) were the 0 to 10 cm HPO_4^{2-}:Ca^{2+} ratio, as well as surface:depth ratios for K^+, HPO_4^{2-}:Ca^{2+}, and Mn:Ca^{2+}. Correlations of surface:depth HPO_4^{2-} with PCA axes were highly influenced by a single outlier. Removal of the outlier also resulted in a significant inverse correlation of surface:depth HPO_4^{2-} with axis II ($r = -0.71$, $p < 0.05$). Variables with highly significant loadings for axis III were 0- to –10-cm and total-profile NH_4^+ and NH_4^++NO_3^-. The fourth axis was characterized by high loadings for 0- to –10-cm pH, K^+, and Zn^{2+}, as well as total-profile K^+ and Zn^{2+}. The surface:depth ratio for Zn^{2+} also was correlated with axis III, although not included in the PCA.

Cheatgrass performance measures were most highly and consistently correlated with axis II (table 3). Performance also was correlated with axis IV, though to a lesser degree. A plot of significant soil variables in relation to these two PCA axes shows that axis II can be conceptualized as a complex soil gradient (fig. 2). At one end of the conceptual soil gradient (high axis-II scores) were sandy sites characterized by high ANP and high surface:depth ANP. Maximum surface:depth ANP in the data set was 1.07 (table 1), indicating a lack of profile differentiation at that end of the gradient. At the other end of the conceptual gradient (low axis-II scores) were sites with higher silt and clay content, as well as greater CEC, K-EX, OM, and HPO_4^{2-}:Ca^{2+} values at 0 to 10 cm. At this extreme of the gradient, low surface:depth ANP was associated with high surface:depth HPO_4^{2-}:Ca^{2+}, K^+, Mn^{2+}, and Mn^{2+}:Ca^{2+}. These measures, all indicative of profile differentiation, tended to covary with MS in 0 to 10 cm soils. Variations in profile differentiation along the conceptual gradient were consistent with taxonomic identity. Soils with differentiated profiles generally were classified as Camborthids, whereas soils without profile differentiation generally were classified as Torripsamments (USDA Soil Conservation Service 1991).

Cheatgrass Performance

Figure 3 summarizes seasonal variations in cheatgrass performance in relation to selected soil variables and PCA axes II and IV. Net cheatgrass establishment in fall was greatest at relatively fine-textured sites with low ANP and high HPO_4^{2-}:Ca^{2+} values. Among-soil patterns in fall growth rates tended to parallel establishment patterns. Winter (early December to mid-March) growth rates varied linearly along the conceptual soil gradient described by PCA axis II (Pearson's $r = -0.78$, $p < 0.001$, table 3). It was during this 3-month winter period that the greatest relationship of cheatgrass performance to measured soil variation was found, with the highest growth rates found in low-ANP, fine-textured soils. Relative growth rates increased markedly in early spring, but sites with the highest winter growth rates consistently had the lowest growth rates during both the early and mid-spring periods (Miller 2000). Spring growth was greatest at sites that were intermediately positioned along PCA axis II and high on PCA axis IV (fig. 3). By the end of the growing season, whole-plot biomass tended to be greater at these intermediate sites, but the biomass difference between sites where cheatgrass performed best during fall and winter and sites where cheatgrass performed best during spring was statistically insignificant (Miller 2000).

Data from resin bags in plots at selected study sites provide information concerning in-situ nutrient dynamics during the fall-winter-spring cheatgrass growing season. During the January to April winter period when cheatgrass performance varied inversely with soil ANP and PCA axis II, resin-bag Mn^{2+}, HPO_4^{2-}, K^+, and Mg^{2+} also varied inversely with soil ANP (fig. 4). Ca^{2+} and Fe varied positively with ANP during this period, and correlations of NH_4^+ and NO_3^- with ANP were insignificant (fig. 4).

In figure 5, leaf-tissue nutrient concentrations for cheatgrass in this study are compared with concentrations reported for cheatgrass in shrubsteppe environments of south-central Washington (Rickard and Vaughan 1988), values for the native winter-annual grass sixweeks fescue (*Festuca octoflora* Walter) in sandy, calcareous soils of southeastern Utah (Belnap and Harper 1995), and average mineral contents reported to be adequate for unrestrained plant growth (Epstein 1965, cited in Marschner 1995). Average tissue N (2.02 percent) and K (1.28 percent) for cheatgrass in this study were higher than or similar to values reported for cheatgrass in Washington, sixweeks fescue in Utah, and average values for unrestrained plant growth. In contrast, concentrations of the carbonate-related minerals P (0.08 percent), Ca (0.35 percent), Mg (0.09 percent), and Mn (0.004 percent) all were lower in this study than in the comparative data sets. Of these, P content was the lowest in comparison with concentrations reported elsewhere. Tissue Fe (0.04 percent), N:P, and K:P documented in this study all tended to be much higher than comparative values.

Table 3—Correlation coefficients (Pearson's r) describing relationships among cheatgrass performance measures and axes I to IV derived from principal components analyses of soil characteristics, Canyonlands National Park, Utah. Performance measures used in the analyses were site averages with all manipulative treatments combined (n = 17). (RGR = relative growth rate.)

	PCA Axes			
Performance measure	**I**	**II**	**III**	**IV**
Net fall establishment	–0.38	–0.51*	0.31	0.02
RGR, Oct. to Dec.	0.15	–0.53*	–0.12	–0.07
RGR, Dec. to Mar.	–0.40	–0.78***	0.14	0.17
RGR, Mar. to Apr.	0.38	0.10	0.03	0.55*
RGR, Apr. to May	0.44	0.49*	0.11	0.34
End-of-season biomass	0.06	–0.35	0.10	0.44

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

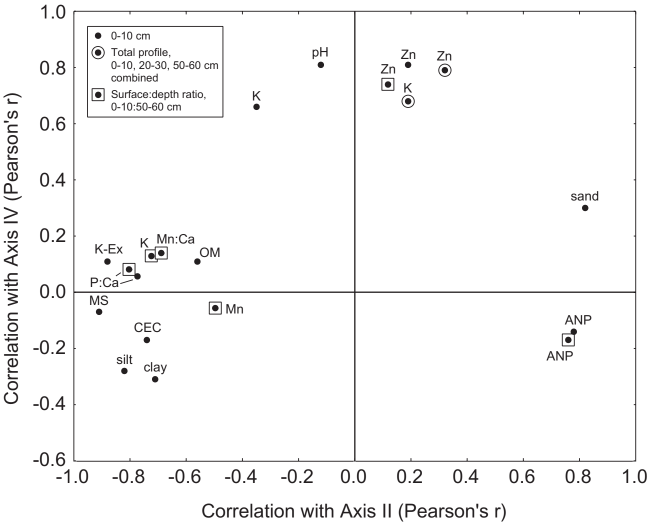

Figure 2—Plot of soil variables significantly correlated with PCA axes II and IV, Canyonlands National Park.

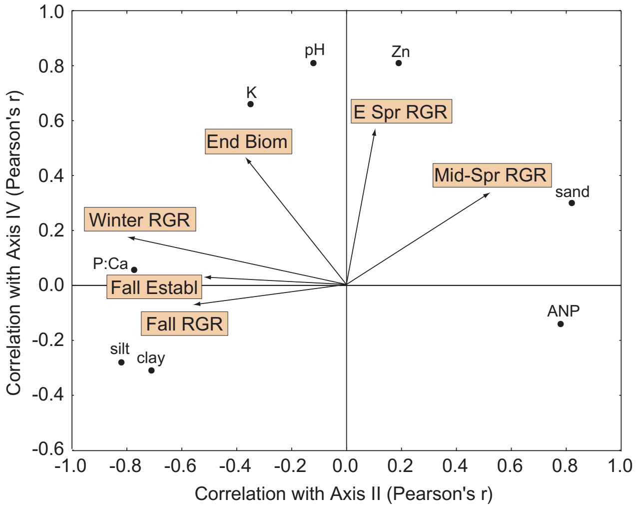

Figure 3—Vector plot illustrating correlations of seasonal cheatgrass measures with soil PCA axes II and IV, Canyonlands National Park.

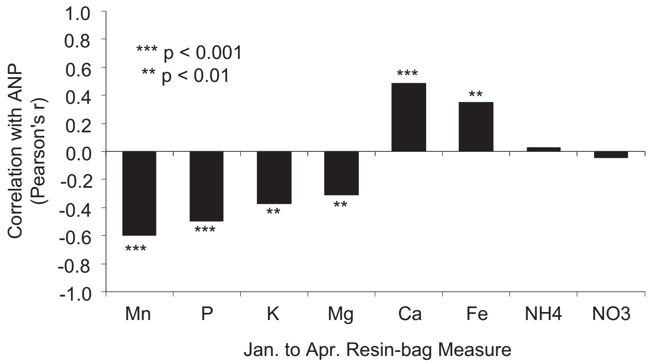

Figure 4—Correlations of in-situ resin-bag measures with soil acid-neutralizing potential, January to April 1998, Canyonlands National Park.

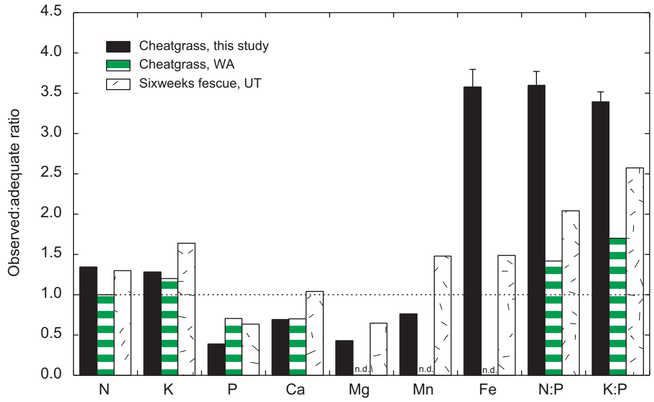

Figure 5—Comparison of average mineral contents of cheatgrass at Canyonlands National Park (this study) with those of cheatgrass in shrubsteppe environments of south-central Washington (Rickard and Vaughan 1988) and those of the native annual grass sixweeks fescue (*Festuca octoflora*) in southeastern Utah near Canyonlands (Belnap and Harper 1995). Values on the y-axis were derived by dividing observed mineral contents by average mineral contents reported to be adequate for unrestrained plant growth (Epstein 1965, cited in Marschner 1995). For cheatgrass in this study, error bars extend 1 SE above means (n = 30).

Discussion

Results presented here demonstrate the complex, multivariate nature of soil variation and plant-soil relationships. Cheatgrass-soil relationships varied by season and performance measure, but the most significant pattern occurred during the 3-month December to March period when cheatgrass growth varied strongly in relation to PCA axis II. Winter growth varied positively with 0 to 10 cm silt and clay content, CEC, K-Ex, MS, and resin-capsule HPO_4^{2-}:Ca^{2+}, whereas growth varied inversely with both 0 to 10 cm and surface:depth ANP. Which of these variables, either alone or in combination, best explains winter variations in cheatgrass growth along the conceptual soil gradient described by PCA axis II?

CEC is considered an important component of soil fertility (Brady and Weil 1996). In this study, CEC and K-EX both covaried with silt and clay content, consistent with the pattern observed for most soils (Brady and Weil 1996). However, with the important exceptions of NH_4^+ and K^+, the availabilities of most nutrient cations (Ca^{2+}, Mg^{2+}, Mn^{2+}, Cu^{2+}, Zn^{2+}, Fe^{2+}) to plants in calcareous soils are likely to be more strongly influenced by carbonate reactions (including sorption, desorption, precipitation, dissolution, and pH buffering) than by ion-exchange properties of soil colloids (Knight 1991). On the basis of resin-capsule data, it can be inferred that Ca^{2+} and Mg^{2+} together occupied approximately 94 percent of the exchange sites on soil colloids. Resin bags buried at five study sites indicated that in-situ NH_4^+

adsorption did not vary in relation to CEC or axis II during winter. In-situ K^+ was weakly correlated with CEC and axis II during the winter period, but KCl additions did not enhance cheatgrass performance during any period (Miller 2000). These observations suggest that variations in CEC and K-Ex cannot alone explain winter variations in cheatgrass performance along axis II. MS, because it simply serves as a proxy indicator of variations in aeolian silt content (Reynolds and King 1995; Hanson 1999) and/or pedogenic profile development (Singer and Fine 1989), by itself cannot provide a mechanistic explanation for spatial variations in cheatgrass performance.

In contrast with CEC, K-Ex, and MS, ANP can provide a mechanistic explanation for winter variations in cheatgrass performance due to the importance of rhizosphere acids for plant nutrition in calcareous soils. Chemical conditions in the rhizosphere are known to be drastically different than bulk-soil measures as a consequence of biotic processes (Hinsinger 1998). In calcareous soils, solubilities of nutrients P, Mn, Zn, and Fe typically are low due to one or more of the following interrelated geochemical factors: (1) sorption reactions with carbonate minerals, (2) the formation of insoluble Ca and/or carbonate compounds, and (3) the presence of high Ca^{2+} and HCO_3^- levels which further inhibit nutrient dissolution due to common-ion effects and/or acid-neutralization reactions (Barber 1995). Rhizosphere acidification due to the combined activities of roots, mycorrhizal symbionts, and associated rhizosphere microbes is a common means by which nutrient dissolution and acquisition can be enhanced in calcareous soils (Hinsinger 1998). Rhizosphere acidification most often is caused by protons excreted to balance uptake of cations such as NH_4^+ and Ca^{2+} (Haynes 1990), but respiratory CO_2 also can be an important acidification mechanism through its reaction with H_2O to form carbonic acid, H_2CO_3 (Hinsinger 1998).

The generation of H_2CO_3 in the soil environment depends on (1) the partial pressure of CO_2, (2) soil water content, and (3) CO_2 solubility in H_2O (Krauskopf and Bird 1995). CO_2 solubility in H_2O, like that of other gases, is greater at cold temperatures than at warm temperatures (Krauskopf and Bird 1995). Thus, all else being equal, H_2CO_3 formation in the soil environment should exhibit a seasonal increase during winter when soils are moist and cold. Cheatgrass also exhibits considerable below-ground growth during winter (Harris 1967), presumably producing respiratory CO_2, enhancing rhizosphere H_2CO_3 generation, and facilitating the dissolution and acquisition of carbonate-bound nutrients.

The enhancement of nutrient dissolution and acquisition due to rhizosphere H_2CO_3 generation is a temporal phenomenon, and the magnitude of this temporal phenomenon should vary spatially in relation to soil characteristics. The major soil properties influencing soil susceptibility to plant-induced rhizosphere acidification are initial soil pH and soil pH buffer capacity (Marschner and Römheld 1996), the latter measured here as ANP. Rhizosphere pH, which cannot be measured from bulk soil samples, is strongly dependent on pH buffer capacity (Marschner and Römheld 1996). Accordingly, ANP or other indices of pH buffer capacity should be more widely applied in studies of plant-soil relationships because they describe a dynamic, plant-relevant soil property that cannot be inferred from static pH measurements alone. Measured pH can vary due to differences in soil texture (as it effects soil water capacity), salt concentrations, and technique; pH buffer capacity can vary widely among soils in which pH varies only slightly (van Breemen and others 1983; Bache 1984).

Data from in-situ resin bags and leaf tissues suggest that the conceptual soil gradient associated with ANP and PCA axis II was a gradient in P and Mn bioavailability for cheatgrass. Resin-bag HPO_4^{2-} and Mn^{2+} covaried in relation to PCA axis II and ANP similar to the among-site pattern observed for winter cheatgrass growth. Although average tissue P and Mn concentrations for cheatgrass in this study both were lower than “adequate” levels reported by Epstein (1965, cited in Marschner 1995), Mn concentrations were 3 to 4 times greater than those “critical” for growth of agronomic monocots (Hannam and Ohki 1988). DeLucia and others (1989) found experimentally that cheatgrass was P-limited in hydrothermally altered soils possessing $NaHCO_3$-extractable-P levels similar to those found in Canyonlands soils. Thus the evidence suggests that PCA axis II, in association with ANP, primarily was a gradient in P limitation for cheatgrass.

Conclusions

Findings of this study emphasize the complex nature of plant-soil interactions and the importance of temporal plant-soil dynamics for understanding spatial plant-soil patterns. Cheatgrass performance varied along a complex, conceptual soil gradient characterized by variations in particle size, acid-neutralizing potential (pH buffer capacity), exchangeable K, and several profile indices indicative both of pedogenesis and of plant-soil feedbacks. Cheatgrass-soil relationships were strongest during winter when relative growth rates were inversely correlated with acid-neutralizing potential and positively correlated with silt and clay content and exchangeable K. Biogeochemical principles, as well as evidence from in-situ resin bags, tissue chemistry, and experimental manipulations of K availability suggest that this conceptual soil gradient primarily was a gradient of P limitation for *Bromus*. We hypothesize that spatial variations in soil acid-neutralizing potential affected the degree to which P dissolution and acquisition were enhanced in winter by the formation of carbonic acid in cold, moist soils. The complex space-time dynamics described here indicate the need for ecological plant-soil studies to expand and investigate a broader range of resources and relationships.

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Equilibrium Theory of Island Biogeography: A Review

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Simon A. Lei

Abstract—The topography, climatic pattern, location, and origin of islands generate unique patterns of species distribution. The equilibrium theory of island biogeography creates a general framework in which the study of taxon distribution and broad island trends may be conducted. Critical components of the equilibrium theory include the species-area relationship, island-mainland relationship, dispersal mechanisms, and species turnover. Because of the theoretical similarities between islands and fragmented mainland landscapes, reserve conservation efforts have attempted to apply the theory of island biogeography to improve continental reserve designs, and to provide insight into metapopulation dynamics and the SLOSS debate. However, due to extensive negative anthropogenic activities, overexploitation of resources, habitat destruction, as well as introduction of exotic species and associated foreign diseases (biological invasions), island conservation has recently become a pressing issue itself. The objective of this article is to analyze previously published data, and to review theories from numerous research studies that attempt to explain species patterns on islands. In effect, this analysis brings insight into current issues of continental reserve design and island conservation efforts.

Introduction

The equilibrium theory of island biogeography (ETIB), proposed by MacArthur and Wilson, is a relatively recent development that has sparked a tremendous amount of scientific controversy. Initially introduced to the public in 1963 as “An Equilibrium Theory of Insular Zoogeography,” the idea was expanded in 1967 into a book publication. The ETIB implies that island fauna and flora (biota) eventually reach an equilibrium point between extinction and immigration. Although species rarely reach equilibrium due to the extremely dynamic island system, MacArthur and Wilson note that the ETIB permits general predictions of future island biodiversity patterns. In this article, the theory of island biogeography is examined in reference to island environments, including topographic origins and characteristics, as well as climatic patterns. A comprehensive analysis of the theory is discussed, such as species-area relationship, dispersal mechanisms and their response to isolation, and species turnover. Additionally, conservation of oceanic and continental (habitat) islands is examined in relation to minimum viable populations and areas, metapopulation dynamics, and continental reserve design. Finally, adverse anthropogenic impacts on island ecosystems are investigated, including overexploitation of resources, habitat destruction, and introduction of exotic species and diseases (biological invasions). Throughout this article, theories of many researchers are re-introduced and utilized in an analytical manner. The objective of this article is to review previously published data, and to reveal if any classical and emergent theories may be brought into the study of island biogeography and its relevance to mainland ecosystem patterns.

Island Environments

Island Formation and Topography

Island topography is primarily determined by the geophysical origins of the island. Marine islands may be subdivided into two geophysically distinct categories: continental shelf islands (land-bridge islands) and oceanic islands. Continental shelf islands are likely to be physically connected to the mainland during low sea level periods. Due to their connection, these islands have similar geological structure to the nearby mainland (Williamson 1981). This similar topography, coupled with the island’s close proximity to the continent, results in the proliferation of similar flora and fauna (biota).

Oceanic islands are typically more isolated, and may have never been physically connected to a continental landmass. There are three main types of oceanic islands: oceanic ridge islands, hot-spot islands, and the individual islands of island arcs. Oceanic ridge islands and hot-spot islands are volcanic islands because they are formed from ocean-floor volcanoes. Islands that are part of island arcs also have a volcanic origin, involving the collision of continental and oceanic plates, resulting in islands that consist of both basalt and granite rock (Williamson 1981).

All of the geological processes occurring volcanic islands can produce islands with high elevations, with peaks of at least 2,000 m (fig. 1) (Williamson 1981). Volcanic islands are typically steeper and become increasingly dissected with age. This phenomenon has important implications for island biota because a wide range of elevational gradients and associated ecological attributes allows for the persistence of diverse habitats. The elevation of islands also has important influences on the climatic regime.

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Figure 1—A map indicating all islands with a peak of 2000 m or higher. Larger islands are shaded, smaller islands are denoted by Δ (Williamson 1981).

Island Climate

Island climate is determined by both external influences, such as ocean circulation and atmospheric circulation, and internal influences, such as island size, shape, and topography. Ocean circulation and atmospheric circulation consist of water currents and air currents, respectively, that have similar movements of upwelling and sinking. If an island is in the path of a moving current or is located where two currents intersect, this can alter the climate significantly. In addition to circulation influences, the proximity of an island to a continental landmass also affects the island's climate. Islands located close to a mainland, such as land-bridge islands, are likely to be influenced by the continental climate. Remote oceanic islands, on the contrary, are influenced by the maritime climate.

Internal influences, such as island size and elevation, can have a substantial impact on the precipitation regime on the island. Whittaker (1998) states that low islands typically have relatively dry climates and high islands are wetter through orographic rainfall, resulting in the creation of extensive arid regions due to the rain shadow effect. These higher islands often contain diverse habitats within a relatively small area. Due to the impact of elevation on island climate, research studies have indicated that elevation is a critical variable in analyzing species diversity on islands. Telescoping, a compression of elevational zones, is fairly common on small tropical islands. Leuschner (1996) proposes that forest lines on islands are generally 1,000 to 2,000 m lower than forest lines on continents. Hence, telescoping creates smaller patches from a variety of habitats favorable to many species, and permits high- and low-elevation inhabiting species to coexist in a relatively small area (Whittaker 1998).

Island Patterns

The Equilibrium Theory of Island Biogeography (ETIB) revolutionizes the way in which biogeographers and ecologists viewed island ecosystems. Prior to the ETIB was the static theory of islands (Dexter 1978), which hypothesizes that island community structures remain relatively constant over geological time. The only mechanism for biological change was the gradual evolutionary process of speciation. Few successful colonization events would occur due to a limited number of ecological niches on the island (Lack 1976). Once these niches are completely filled, no space and resources are available for new immigrants, and they may not become successfully established on the island. The ETIB refutes the static theory, indicating that island communities exhibit a dynamic equilibrium between species colonization and extinction, or species turnover. The immigration curve is descending and is shaped concavely because the most successful dispersing species would colonize initially, followed by a significant decrease in the overall rate of immigration (fig. 2). The extinction curve, on the contrary, is an ascending curve because as more species inhabit the island through time, more species would become extinct exponentially (fig. 2). Such a trend is amplified due to a combination of population size and negative biotic interactions among

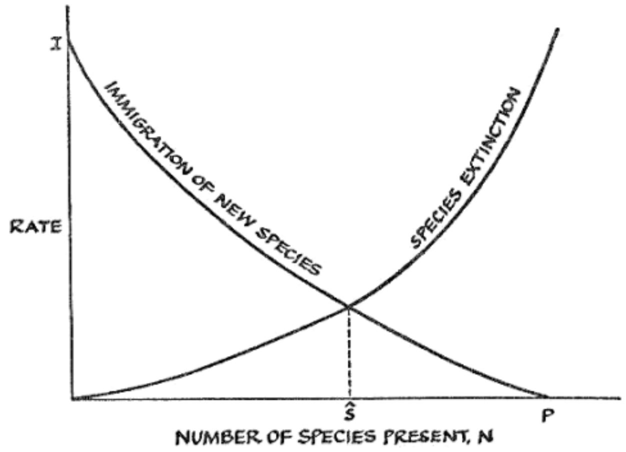

Figure 2—The equilibrium model of species present on a single island. The equilibrium number of species is reached at the point of intersection between the rate of immigration and the rate of extinction (MacArthur and Wilson 1967).

different species. This model graphically and mathematically represents an equilibrium point, S, in which the immigration and extinction curves intersect (fig. 2). This point represents the actual number of species present on an island at equilibrium. Moreover, figure 3 accounts for trends in island size and degree of island isolation (distance from mainland). Patterns regarding the species-area relationship and the species-isolation relationship have been acknowledged by biogeographers since the beginning of the 19th century. Therefore, the contribution made to island ecosystem study by MacArthur and Wilson was a compilation of these well-known ideas into one, integrated paradigm (Brown and Lomolino 1998).

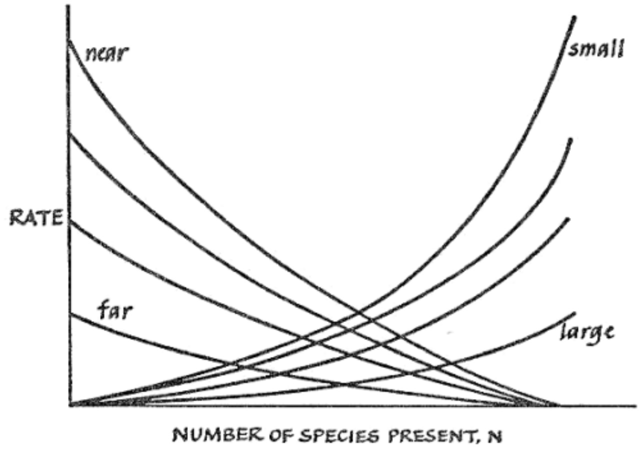

Figure 3—The equilibrium models of species of several different islands with a various degrees of isolation and size. An increase in isolation (near to far) decreases the immigration curve, while an increase in area (small to large) decreases the extinction curve (MacArthur and Wilson 1967).

Species-Area Relationship

A positive relationship exists between island size and island species richness (fig. 4). These two variables, nevertheless, do not always exhibit a linear correlation. Arrhenius represented this non-linear trend in mathematical form in 1920 with the following equation:

$$S = cA^{Z}$$

In this equation, S = the species richness on an island, c = a constant depending on biotic and biogeographic region, A = the area of the island, and z = a constant representing the slope of S and A on a logarithmic scale (z changes very little among different taxa or same taxon from different regions.).

There are two potential explanations for the positive correlation between island size and species diversity. First, large islands generally contain more diverse habitats and, thus, more biota compared to small islands. Although this is a logical explanation, ecologists and biogeographers have a difficulty to prove in the field because habitat diversity has no distinct parameters and is a challenge to measure. Many parameters are approximated to determine the number of species inhabiting various islands. Second, the island size, rather than the habitat diversity, is the main factor in determining the number of species on islands. This theory is also difficult to prove in the field because habitat diversity and island size are strongly correlated, and it is nearly impossible to distinguish the two.

Species-Isolation Relationship (Distance Effect)

Isolation is a critical component when examining evolutionary processes since it allows for allopatric speciation to occur. Islands offer prime examples of isolation effects on biota (Cox and Moore 1993). Specific adaptations, such as seed parachutes, are necessary for plants to disperse across large bodies of water. Such dispersal invokes survival of a sweepstakes route, an extensive barrier permitting only a

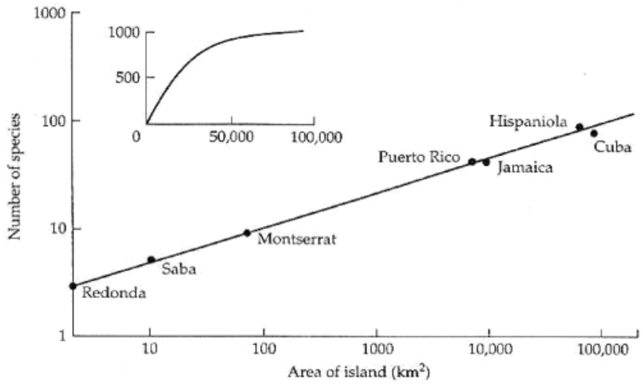

Figure 4—The correlation between species number, S, and island area, A, for reptiles and amphibians of the West Indies. Both axes are logarithmic and a best-fit line is used. The inset represents this relationship arithmetically (Brown and Lomolino 1998).

stochastic set of immigrants to successfully colonize the island (Brown and Lomolino 1998). The more remote the island is from a continental landmass, the more severe the sweepstakes route and the smaller the number of species that would successfully colonize and become established on the island. This is known as the species-isolation relationship on islands. The number of species would decrease exponentially as a function of isolation because the species-isolation correlation should account for a pool of species (fig. 5) (Brown and Lomolino 1998). Successful colonization over large bodies of water is potentially easier for plants than for animals. Many species of plants possess dispersal mechanisms, such as "parachutes and "wings," to allow new generations of plants to be carried far from the parent plant by wind currents. Without having a mate to reproduce, plants only require one fertile seed or spore to colonize a remote island. Other mechanisms, such as sticky seeds, permit seeds to be transplanted by animals. Through animal assistance, the chance for successful plant immigration is greatly enhanced. In addition, some plants are able to withstand long periods of seawater immersion, and successfully colonize remote islands. Such adaptive characteristics are essential in creating plant communities on both nearby and remote islands.

Species Turnover

Species turnover on islands is also critical to the ETIB model. The cycle of extinction of certain established species and the immigration of new species permit the equilibrium point to maintain its value over geological time. Such species turnover, however, can be extremely difficult to quantify in the field. Whittaker (1998) detects two main problems with quantifying extinction and immigration rates on islands. Firstly, species turnover is a situation in which surveys on islands are at irregular intervals. This phenomenon allows for some species to become extinct and possibly re-migrate during periods between the surveys, resulting in a depression of turnover rates (Simberloff 1976). Secondly, there is potential for pseudoturnover on islands, implying that information with regard to breeding conditions is fragmentary or incomplete. Under such circumstances, species appear to have turned over when, in fact, they have simply been overlooked. With such potential inaccuracies, the ETIB requires an extensive attention to census detail, causing it to be a relatively difficult theory to prove under natural island conditions.

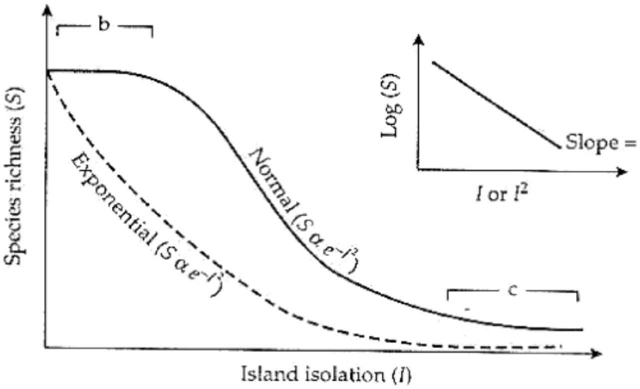

Figure 5—Display of a negative relationship between species richness (S) and island isolation (I). The inset represents the log-transformed equivalent of this relationship (Brown and Lomolino 1998).

ETIB Strength and Weaknesses

In addition to the limitations in detecting species turnover, Brown and Lomolino (1998) note a number of major weaknesses in the theory initially proposed by MacArthur and Wilson. First, many island species rarely achieve equilibrium. The number of species at the equilibrium point may change over geological time, especially when immigration and extinction coincide with periods of anomalous climatic and geological (disturbance) events. Second, not all species have identical immigration and extinction rates. For instance, birds generally have a higher immigration rate than large, heavy reptiles and mammals. Third, the ETIB model regards immigration and extinction as being independent variables when, in many cases, they are closely related. For example, when there is a depression or extinction of a population on an island, a rescue effect may occur, thus increasing species numbers once again. Fourth, the model does not consider specific characteristics of species, such as species fitness and dispersal ability. Fifth, species inhabiting a single island may be derived from several mainland and island sources. It may be challenging to determine the source pool for a species on an island without a comprehensive study on the historical and current distribution of the species. Sixth, the ETIB model does not incorporate speciation, which may exceed immigration rates as a potential mechanism affecting an island system. Species present by speciation do not add to the overall species diversity of the island. This model should include the effects of both speciation and immigration. Seventh, anthropogenic-induced habitat fragmentation or destruction may isolate once massive and continuous ecosystems on an island. Eighth, the ETIB model does not consider periodic rescue effect and target area effect. The rescue effect reduces species extinction, while the target area effect enhances immigration on large islands. Finally, the use of island size is extremely general and does not consider the impact of habitat heterogeneity (complexity of habitats and natural landscapes) on species diversity.

These main arguments against the ETIB are important to examine. However, modifications of the ETIB are a possibility to account for such problems. Despite such flaws, the ETIB is still acceptable by some modern scientists in at least three ways. Firstly, the theory may be graphically simplified, and makes logical sense to a wide array of audiences. Secondly, this theory forms a link between traditional notions of ecology and biogeography, thereby enriching the information of both types of study. And, thirdly, this theory provides a clear and testable strategy for population pattern predictions not only on islands, but also on localized continental systems.

Island Conservation

The initial objective for the ETIB was to gain a better understanding of island ecosystems and their dynamic processes. Nevertheless, as studies continued, many ecologists, biogeographers, and conservation biologists discovered a parallel between oceanic islands and fragmented habitats on continental landmasses. Most species have a range of habitat in which they prefer to live, yet it has become evident that human activities such as deforestation, habitat destruction, and urban and suburban development, have all contributed to a significant fragmentation of natural habitats. The continuation of such fragmentation has resulted in species extinction from local to global scales (Whitmore and Sayer 1992). The remaining patches of these relatively natural areas may be perceived as habitat islands (fig. 6). From the similarities between habitat islands and actual oceanic islands, biogeographers utilize the ETIB as a guideline to preserve biodiversity in these patches (Whittaker 1998). This notion, ironically, spawned a great controversy in the field of biogeography and conservation biology. Janzen (1983) argues that natural habitats such as parks and nature preserves vary significantly from true oceanic islands, and thus the ETIB would not be completely applied to continental reserves. Unlike continental parks, Janzen (1983) points out that islands are encompassed by water, an extremely different type of habitat. Habitat islands can be surrounded by a landscape containing a variety of species that are potentially capable of establishing populations within the habitat patch. This event often introduces negative biotic interactions, such as competition, predation, and parasitism, within the habitat island that is not experienced by true oceanic island ecosystems. Likewise, species within the habitat island are capable of escaping the patch and influencing populations of species within the degraded or fragmented landscape. These are important biotic interactions that do not occur on oceanic islands, and must be considered when attempting to apply theories of island biogeography to habitat islands on continents. The scale and degree of insularity are critical components when making such comparisons. For these reasons, in addition to theories concerning oceanic island biogeography, issues such as minimum viable population and area, along with metapopulation dynamics must be evaluated when determining the most effective continental reserve design.

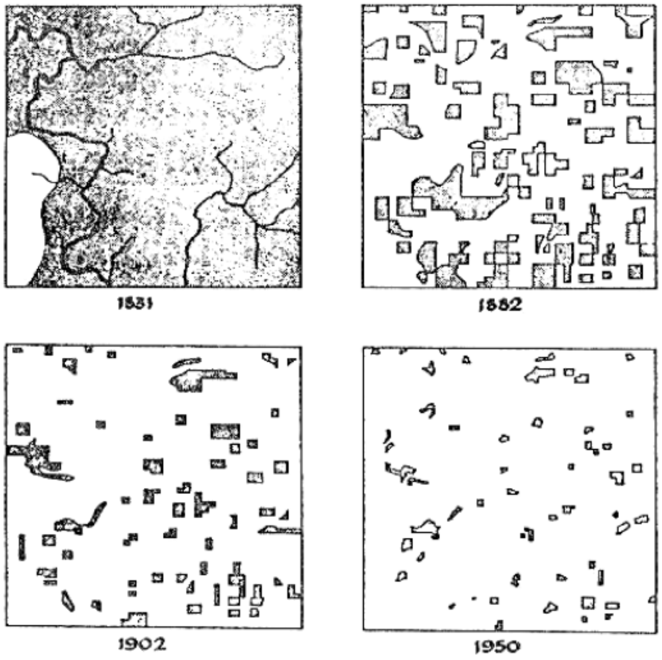

Figure 6—The fragmentation of forested land in Cadiz Township Green County, Wisconsin (94.93 km^2), into habitat "islands" during the era of European settlement (Shafer 1990).

Minimum Viable Population and Minimum Viable Area

The study of population dynamics of a species is critical when attempting to support the future success of the species' population. When evaluating populations of species inhabiting a reserve, survival pressures on these populations are compounded. Smaller areas tend to support smaller numbers of species as noted by the species-area concept. Consequently, the proposal of the minimum viable population (MVP) concept emerged. Shaffer (1981) tentatively defines the minimum viable population for a given species in a given habitat regardless of the impacts of demographic stochasticity, environmental stochasticity, genetic stochasticity, and natural catastrophes. Under this definition, the survival of the species must not only endure normal conditions, but also endure episodic catastrophes in order to persist through geological time.

Shaffer (1981) attempts to give a definitive measure in order to conserve species living within a restricted area because this would allow conservation biologists to have a framework in which to proceed. However, Thomas (1990) argues that the MVP theory is not realistic with regard to actual population dynamics within a limited geographical range. Additionally, Thomas (1990) states that in certain large-scale, remote areas, the MVP concept would be too difficult to quantify due to the paucity of available information.

The theory of minimum viable area (MVA) resembles the theory of minimum viable population. If a determined area of minimum size is conserved, the species inhabiting such area is conserved as well. The MVA often corresponds to the range size in which this particular species is found. Species located higher on the trophic level generally require more area or space to ensure maximum survival. Hence, for certain species, the MVA is considerably large in order for a MVP to persist within the designated area (Whittaker 1998).

The MVA approach may be effective to help preserve entire ecosystems since various species coexist and interact closely within the MVA. However, this concept assumes that each area is discrete, and has no biotic (genetic) exchange with other surrounding areas. The MVA must account for the immigration and colonization of species in and out of the area (Whittaker 1998). Consequently, the MVA is difficult to quantify due to its extremely dynamic nature.

Metapopulation Dynamics

Metapopulation models first emerged in 1969, and have since evolved into a dynamic concept involving wildlife conservation and population turnover. A metapopulation is a discontinuous distribution of a population of species. This population is geographically spread over disjunct fragments of suitable habitat separated by intermixed fragments of unsuitable habitat through which little migration occurs (McCullough 1996). As a result, there is a limited movement of population among suitable patches, and populations remain spatially separated. However, when a metapopulation becomes environmentally and physiologically stressed, the population crashes; the patch may be recolonized by a nearby metapopulation, and may eventually bring the population back up to threshold (fig. 7). Therefore, although populations of the same species are spatially separated, migration and gene flow still occur among suitable patches to ensure long-term survival of the species (Whittaker 1998).

Gotelli (1991) realizes two main dilemmas in studying metapopulation models. Firstly, the dynamics of metapopulations may be difficult to replicate, especially when considering the temporal-scale in which metapopulation changes may occur under natural settings. Secondly, the subdivision of populations may occur at many levels, and the degree of separation in metapopulations is often subjective.

Despite potential weaknesses as suggested by Haila (1990), the metapopulation concept forms a link between population ecology studies and island biogeography theory. Metapopulation models are comprised of dynamic, interdependent island systems in which population fluctuations are determined by the degree of isolation (Gotelli 1991; Whittaker 1998). These geographically distinct metapopulations may be viewed as habitat islands due to an extensive human colonization and development (McCullough 1996). Such metapopulation pattern is evident in both population ecology and island biogeography studies. Hence, the research used for island biogeography study may allow for the postulation of a unified concept concerning isolation, area, and species number on mainland metapopulation systems (McCullough 1996). However, the application of island biogeography theory to the patch dynamics of metapopulations has many flaws. Most importantly, habitat patches on a continental landscape rarely, if ever, resemble true oceanic islands. Ecotones and edge effects tend to be less dramatic gradients of habitat than distinct changes from terrestrial landscapes to seascapes. This dissimilarity introduces two additional differences between these seemingly analogous habitats. First, the surrounding area represents a gradient of habitat, rather than a distinct boundary. The surrounding habitat may simultaneously offer both advantages, such as additional food sources, and disadvantages, such as competitors, predators, and pathogens. Second, through properly designed corridors, the surrounding matrix permits periodic migrations among suitable patches; the degree of spatial isolation is considerably less on habitat islands than on true oceanic islands.

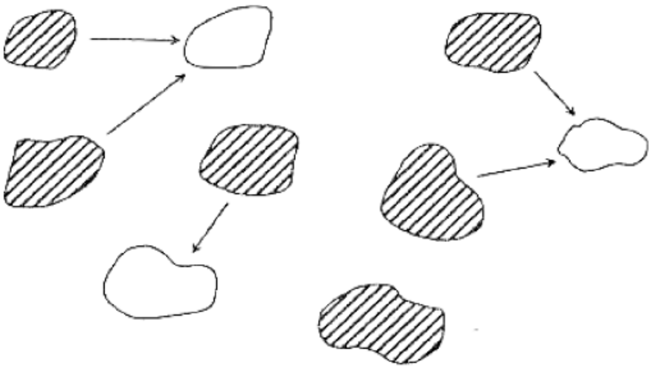

Figure 7—The classic metapopulation model in which occupied patches (shaded) will re-supply patches in which the population has decreased or vanished (unshaded). Movement is denoted by the arrows (Whittaker 1998).

Continental Reserve Design and the SLOSS Debate

Metapopulation dynamic theory is utilized to find the most effective and efficient strategies for continental reserve design, and has allowed for a better understanding of population ecology. Many opinions exist concerning the most effective and "natural" design theory, the size and shape of reserves, and the number of reserves necessary to maintain the optimum amount of biodiversity. The SLOSS debate (Single Large or Several Small) emerged in 1976, and proposed two schools of thoughts regarding reserve design. One extreme option was to create a single large reserve. The other option was to create several small reserves that, combined, would equal the same area as the large reserve. Diamond (1981) supports large reserves, using managerial considerations as a main determining factor. Nilsson (1978) is also in favor of large reserves, using field data on plant and bird observations as support. Conversely, Simberloff and Gotelli (1984) argue that several small reserves would maximize local biodiversity. Shafer (1990) and Simberloff and Gotelli (1984) utilize plant data to reveal that small reserves are as effective as a large reserve in maintaining biodiversity. Like true oceanic islands, a higher degree of isolation on continental reserves would result in decreased migration levels to and from the reserve. Furthermore, the destruction and degradation of habitat surrounding the reserve would increase extinction rates, as habitat becomes unsuitable to sustain high biodiversity. A new equilibrium number would be reached as suitable habitats become less available (fig. 8). While the reserve is being properly designed and developed, supersaturation may result primarily due to an excess of species as displaced populations flee into the still relatively pristine reserve system. The reserve may not have the capacity to sustain such high biodiversity, and relaxation of species numbers into a new point of equilibrium may eventually occur (fig. 8). The new equilibrium number may be estimated after information regarding area and degree of isolation is gathered. Diamond and May (1981) use the equilibrium point from ETIB to determine what type of reserve would maximize the species richness and abundance. Whittaker (1998) postulates that larger reserves are

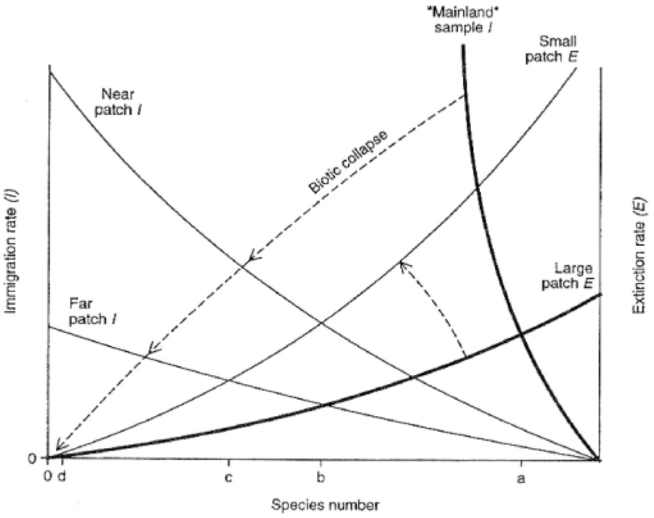

Figure 8—According to the assumptions made by the ETIB, as reduction in area will cause supersaturation as immigration rates decrease and extinction rates increase. This causes a "relaxation" into a lower species equilibrium point. Under extreme circumstances, "biotic collapse" may occur and the results may be an immigration rate so low that the equilibrium number is zero.

more effective than smaller reserves, shorter distances between reserves are better than longer distances, circular shaped reserves are better at maintaining reserve species than elongated shaped reserves due to a reduction of edge effects, and corridors connecting large reserves would be more favorable than without corridors (fig. 9).

The use of island biogeography theory has two main limitations when applying it to the continental reserve design. Firstly, the ETIB focuses on overall species richness of a habitat island by using species-area equations. The ETIB does not allow for the prediction of species with the highest probability of becoming extirpated from the remaining patch (Saunders and others 1991; Whitmore and Sayer 1992; Whittaker 1998; Worthen 1996). This approach then does not permit the investigation of specific species circumstances within the reserve, and may prove harmful if requiring in-depth analysis. Secondly, the ETIB model itself is flawed. Any application of this concept to the continental reserve design and conservation policy also contains such flaws (Whittaker 1998). If the use of this theory is not meticulously studied on a case-by-case basis, certain flaws are not only represented in reserve design, but also perhaps even amplified.

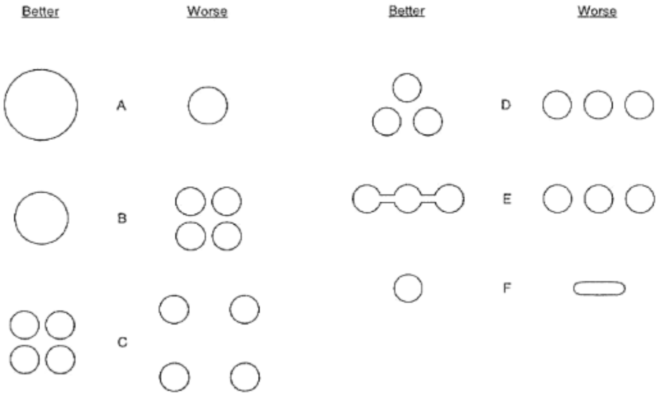

Figure 9—The simplified geometric principles for nature reserve designs derived from island biogeography research (Diamond 1975; Whittaker 1998).

Human Impact on Island Ecosystems

The utilization of island biogeography theory in determining the most effective reserve design has recently been an important issue in conservation. Yet, islands themselves have also been an issue in conservation biology, mainly due to detrimental human impacts in island environments. There are numerous heated debates as to what type of impact the earliest human colonizers had on island ecosystems. Some ecologists and biogeographers argue that most of the earliest island colonizers were respectful of the island ecosystem, and that negative impacts occurred only after secondary arrivals of colonizers conflicted with the interests of the initial inhabitants. Others argue that earliest inhabitants of some islands devastated the environment because of their ignorance and negligence concerning island ecosystems. One rather undisputed fact is that as human communities on islands reached the carrying capacity, humans often modified island landscapes to support the rapidly growing population. A classic example is the terracing of steep terrain on islands in order to maximize agricultural productivity (Nunn 1994). Through history and into the modern age, negative anthropogenic impacts have continued and increased. Humans can easily damage pristine island environments in four ways: overexploitation and predation by humans, habitat loss, fragmentation, and degradation, as well as introduction of exotic species and diseases (biological invasions).

Overexploitation and Predation by Humans

Many islands contain unique endemic species because the remote quality of islands allows for the speciation of flora and fauna to be considerably different from mainland taxa. A classic example of predation of island species by humans is that of the dodo bird (*Raphus cucullatus*), once populated on the island of Mauritius, located east of Madagascar in the Indian Ocean. Dodo birds were endemic and were highly adapted to island conditions. By the early 17th century, Dutch settlers began to colonize the island, hunting both dodo birds and tortoises as food sources. Dodo birds became extinct by the year 1690. Predation of species by humans not only occurred for food sources, but also for tribal (in other words, vibrantly colored bird feathers) and exportation reasons. Moreover, fruit bats are currently being exported from the Polynesian islands. Not only is the declining population of fruit bats an issue of conservation, but also these bats play an imperative role in pollination and seed dispersal of island flora. Therefore, the absence of fruit bat population can also harm the proliferation of many plant species (Whittaker 1998). A secondary extinction can occur under extreme cases.

Habitat Loss, Fragmentation, and Degradation on Island Systems

For centuries, island ecosystems have been the target for habitat loss, fragmentation, and degradation primarily for agricultural reasons. In addition, the wood from the forested trees was used for fuel and residential cooking (Heywood 1979). Such habitat destruction not only directly damages the island flora, but also reduces the faunal biodiversity. As forested areas are diminished, suitable habitats and food resources for fauna also diminish. As habitat fragmentation (deforestation) continues at an alarming rate, it creates major ecological dilemmas on islands such as Madagascar.

Another mechanism of habitat degradation or simplification is human-induced fires. Fires are often utilized for hunting purposes or to clear a plot for agricultural purposes. Frequent fires in areas with a low natural fire frequency can be tremendously destructive. Such prescribed burning can clearly destroy the present island ecosystem and permanently transform the island landscape.

Impact of Exotic Species and Associated Diseases on Island Ecosystems

As humans travel the globe, different species have been intentionally and inadvertently introduced into new ecosystems. Many island species, also known as the native biota, are particularly vulnerable to biological invasions due to their isolation through evolutionary time. The absence of herbivory, for instance, has resulted in the persistence of many island flora with no defensive mechanisms against grazing pressures. Isolation, in a sense, has protected such plant species that, otherwise, would have become extinct on the mainland (Melville 1979). Nevertheless, the presence of abundant herbivores, such as cattle, sheep, goats, and pigs, has led to extreme habitat degradation. Historically, humans intentionally introduced these grazing animals to ensure abundant food supply, without even considering the negative ecological consequences. However, many of these animals have become feral and extremely detrimental to the island landscape. Overgrazing has caused massive erosion on the hillsides, leading to large-scale landslides. Similarly, heavy grazing has encouraged the proliferation of exotic species. The introduction of exotic species into an island ecosystem is typically irreversible. Some exotic species, in fact, are more successful in these foreign environments than in their native landscape. Once those exotic species have established, their populations rapidly proliferate, making it nearly impossible to completely extirpate them from the island.

Foreign diseases on islands are closely associated with biological invasions onto islands. An exotic species is frequently infected with a disease, and can introduce additional harmful diseases onto the island. If island biota is immune to the ill effects of the disease, there is little or no negative impact on the native biota. Conversely, if native island biota is susceptible to foreign diseases, the results can be disastrous. The entire island biota is adversely affected, and many species can be extinguished from the island. If this species is endemic with a narrow geographic range, the entire population of this species is likely to become extinct.

Conclusions and Implications

This article re-examines the equilibrium theory of island biogeography initially proposed by MacArthur and Wilson in 1963. Island environments including topographic origins and characteristics, along with climatic patterns have been discussed. The ETIB is analyzed using essential components, such as species-area relationship, island isolation, dispersal mechanisms, and species turnover. The strengths and weaknesses of the ETIB model are evaluated. Additionally, continental conservation theories that apply the ETIB concept are assessed in terms of minimum viable populations and areas, metapopulation dynamics, continental reserve design, and the SLOSS debate. Lastly, adverse anthropogenic impacts on island ecosystems, such as overexploitation of resources, habitat destruction, and introduction of exotic species and diseases, are examined. This article has primarily re-investigated the research performed by ecologists, biogeographers, and conservation biologists at the forefront of island study. The ETIB has been an issue of heated debate since its emergence nearly four decades ago, and still today, the vitality of the concepts is evolving as researchers gain better understanding of island ecosystems and their pertinence to mainland habitats. This trend will undisputedly continue, but hopefully researchers will be able to unlock all of the knowledge to be gained by these delicate ecosystems before they become relics of the past.

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Vegetation Response to Natural and Anthropogenic Disturbances in the *Larrea-Ambrosia* and *Coleogyne* Shrublands

Simon A. Lei

Abstract—Vegetation response to various types of disturbances was quantitatively investigated in the *Larrea tridentata-Ambrosia dumosa* (creosote bush-white bursage) and *Coleogyne ramosissima* (blackbrush) shrublands of southern Nevada. Between the two control (undisturbed) habitats, the *Larrea-Ambrosia* vegetation zone had a greater plant species richness, but had a lower percent vegetation cover than the *Coleogyne* zone. Mean plant species richness and percent vegetation cover were significantly reduced in edge (disturbed) habitats compared to adjacent undisturbed habitats in both vegetation zones. A major shift in species composition to favor weedy (pioneer) species was observed in all disturbed habitats. Mean ratios of weedy to nonweedy species were significantly higher in disturbed relative to undisturbed habitats. Among the heavily disturbed habitats, roadside corridors exhibited the greatest, while human trail corridors exhibited the least invasion of weedy species. Woody and succulent (climax) species are highly vulnerable to habitat destruction and fragmentation as a result of natural and anthropogenic disturbances in the *Larrea-Ambrosia* and *Coleogyne* vegetation zones of southern Nevada.

Introduction

Habitat alteration and destruction are direct habitat removal when an ecosystem is converted to residential, recreational, commercial, agricultural, and industrial areas. Habitat destruction and fragmentation typically begin with gap formation or perforation of the vegetation matrix as humans colonize a Mojave Desert landscape or begin extracting resources there (Lord and Norton 1991; Meffe and Carroll 1997). As the gaps get bigger and more numerous, the original Mojave Desert woody vegetation is broken. Roads and powerline corridors as narrow as 8 m may produce significant edge effects by attracting weedy and exotic plant species (Meffe and Carroll 1997). Habitat destruction, fragmentation, and degradation can alter species richness initially, but often favors weedy and exotic species. Metapopulation dynamics suggest that even once common native desert plant species are not completely immune to the adverse effects of widespread habitat fragmentation and degradation (Brown and Lomolino 1998; Meffe and Carroll 1997; Noss 1983). Weedy plants are initially found along the edges, and these plants can become well established in desert interiors and outcompete natives at certain areas through time (Lei, personal observation 1998).

The internal fragmentation of once pristine natural areas by roads, trails, powerlines, fences, and other anthropogenic activities has not been well studied, but it has potentially dramatic effects on native biodiversity (Meffe and Carroll 1997).

The Las Vegas Valley and vicinity have experienced a rapid urbanization, economic growth, and recreational activities in recent years. Yet, a comparative vegetation response to various natural (fire and soil erosion) and anthropogenic (human/jeep trail, roadside, powerline, fence, and construction site) disturbances remain poorly understood. The objectives of this article were to compare changes in plant species richness, percent vegetation cover, and weedy/nonweedy species ratio among edge (disturbed) habitats of the *Larrea-Ambrosia* and *Coleogyne* vegetation zones in Las Vegas and the adjacent Spring Mountains of southern Nevada.

Methods

Study Site

Field studies were conducted in the Las Vegas Valley and the adjacent Spring Mountains (roughly 36°30' N, 115°30' W; fig. 1) in southern Nevada during Fall 1998.

Figure 1—A sketch map showing location of study sites in southern Nevada. The Spring Mountains lie just to the west of the Las Vegas Valley.

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The *Larrea-Ambrosia* vegetation zones occur at low elevations of the Las Vegas Valley, while the *Coleogyne* zones occur directly above the *Larrea-Ambrosia* zones at mid-elevations of the Spring Mountains.

The natural Mojave Desert woody vegetation occurred throughout the Las Vegas Valley and the Spring Mountains several centuries ago (fig. 2A). Gaps were gradually formed several decades ago, but became highly intensified in recent years as humans rapidly colonize this desert landscape (figs. 2B-C). At the present time, a substantial portion of the natural desert vegetation is broken (fig. 2D). Considerably more habitat destruction through fragmentation is expected in the near future due to rapid urbanization through residential, recreational, commercial, and industrial (economic) development. Eventually, the Las Vegas Valley and vicinity will become an immense anthropogenic habitat, with relatively little remaining of the native Mojave Desert woody vegetation.

The four seasons are well defined. Summers display desert conditions, with a maximum air temperature usually in the 40 °C range. Winters are generally mild and pleasant, with a minimum temperature just below the freezing range (Local Climatological Data, Las Vegas). The spring and fall seasons are considered most ideal, although sharp temperature changes can occur during these months. The precipitation patterns include summer storms and winter rains. Summer rainfalls generally occur in July through early September, and come from the Gulf of California, drawn into the Mojave Desert by strong convectional currents (Rowlands and others 1977). Conversely, winter rains are mild and widespread, and come from the Pacific Ocean. Winter rainfalls may last several days. Winter and summer precipitation contribute significantly to the annual precipitation (table 1), which varies considerably from year to year. In general, precipitation is positively correlated with elevation (Rowlands and others 1977). Relative humidity of 20 percent or less is common in the summer months, resulting in exceedingly high evaporation (Lei and Walker 1997a,b).

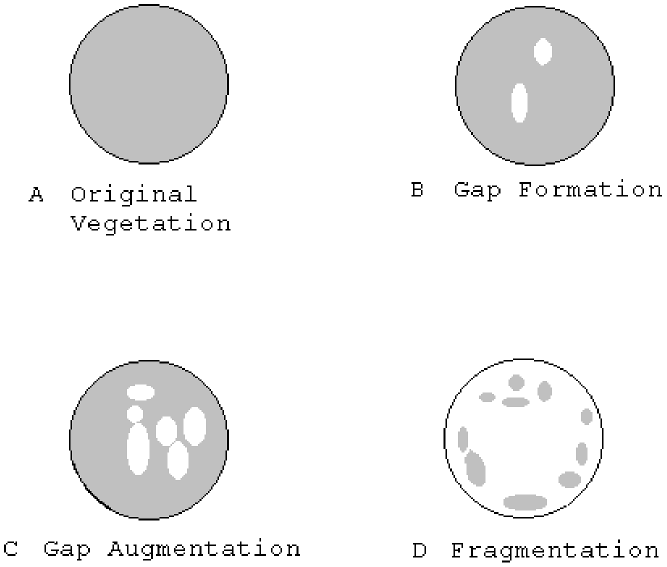

Figure 2—A schematic diagram showing a temporal sequence of habitat destruction through fragmentation starting from an original Mojave Desert woody vegetation (A) to a massive anthropogenic habitat (D).

Table 1—Mean monthly precipitation and mean monthly maximum and minimum air temperature based on the 1936-1997 data in the Las Vegas Valley. The climatological data (National Weather Service) were obtained collectively from multiple long-term weather stations in Las Vegas of southern Nevada.

	Air temperature (°C)		
Month	**High**	**Low**	**Precipitation (mm)**
January	14.4	1.1	12.7
February	17.2	3.9	11.4
March	20.6	6.7	10.2
April	25.6	10.6	5.1
May	31.1	15.6	5.1
June	37.7	20.6	5.1
July	41.1	23.3	11.4
August	39.4	23.3	14.0
September	35.0	18.9	7.6
October	27.8	12.2	6.4
November	19.4	6.1	11.4
December	14.4	1.1	7.6

Field Surveys and Statistical Analyses

Three transects were established along each of the eight types of natural and anthropogenic disturbances (a total of 24 transects) in the *Larrea-Ambrosia* and *Coleogyne* vegetation zones. Three transects were also established in the adjacent undisturbed (control) habitats in each of the two vegetation zones. Each transect was 400 m in length. Within each transect, 10 (20 x 20 m) plots were randomly placed to avoid biased vegetation sampling. Within each plot, species richness was quantified, and vegetation cover was visually quantified in 10 percent increments. Ratios of weedy to nonweedy species were also computed.

Within each type of disturbance, vegetation data from three transects were pooled. One-way Analysis of Variance (ANOVA; Analytical Software 1994) was conducted to detect differences in vegetation attributes among the eight types of disturbed habitats in the *Larrea-Ambrosia* and *Coleogyne* shrublands. Tukey's Multiple Comparison Test (Analytical Software 1994) was performed to compare mean species richness, percent vegetation cover, and ratio of weedy to nonweedy species when a significant habitat effect was detected. Mean values are expressed with standard errors, and statistical significance is determined at $p \leq 0.05$.

Results

The *Larrea-Ambrosia* vegetation zone was considerably more disturbed and fragmented by anthropogenic activities than the *Coleogyne* zone in recent years in southern Nevada. Mean species richness declined significantly ($p \leq 0.001$; fig. 3) across the six types of disturbed habitats

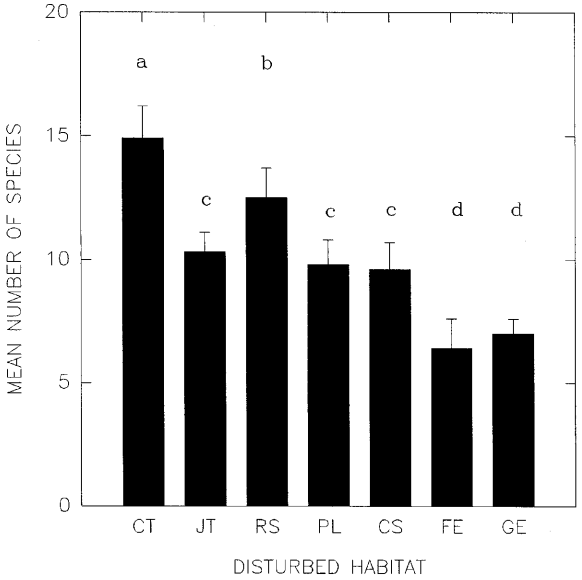

Figure 3—Species richness (mean ± S.E., n = 30 plots in each type of disturbance) in disturbed and undisturbed (control) habitats in the *Larrea-Ambrosia* shrublands. Symbols of disturbed habitats: Control (CT); jeep trail (JT); roadside (RS); Powerline (PL); construction site (CS); fence (FE); and gully erosion (GE).

compared to adjacent undisturbed habitats in the *Larrea-Ambrosia* vegetation zone. Among the edge habitats, roadside corridors had the greatest, while fence corridors had the lowest mean species richness (fig. 3). Mean percent vegetation cover also decreased significantly ($p \leq 0.001$; fig. 4) in these disturbed habitats relative to undisturbed habitats. Roadside corridors revealed the greatest, whereas gully erosion corridors revealed the lowest mean percent vegetation cover (fig. 4). However, mean ratio of weedy to nonweedy species increased significantly ($p \leq 0.001$; fig. 5) in disturbed habitats compared to undisturbed habitats in the *Larrea-Ambrosia* shrubland. Roadside corridors exhibited the highest mean ratio with a variety of weedy, herbaceous species (fig. 5).

Furthermore, mean species richness was significantly lower ($p \leq 0.001$; fig. 6) across the five types of disturbed habitats compared to adjacent undisturbed habitats in the *Coleogyne* shrubland. Conversely, mean species richness between the roadside and undisturbed habitats did not differ significantly (fig. 6). Mean percent vegetation cover was significantly lower ($p \leq 0.001$; fig. 7) in disturbed than undisturbed habitats. Roadside corridors exhibited the greatest, while fence corridors exhibited the lowest mean percent vegetation cover (fig. 7). In contrast, mean ratio of weedy to nonweedy species was significantly higher ($p \leq 0.001$; fig. 8) in disturbed relative to undisturbed habitats in the *Coleogyne* vegetation zone. Among the highly disturbed habitats, roadside corridors showed the highest mean ratio with abundant weedy, herbaceous individuals (fig. 8).

Discussion

The Las Vegas Valley and the Spring Mountains of southern Nevada have recently experienced a severe habitat destruction through fragmentation largely due to rapid urbanization, economic growth, and recreational activities. Ecological impacts of disturbance on vegetation of the *Larrea-Ambrosia* and *Coleogyne* vegetation zones have been conspicuous. The Mojave Desert habitats disturbed by natural and anthropogenic forces contributed to significant shifts in plant species richness, percent vegetation cover, and ratio of

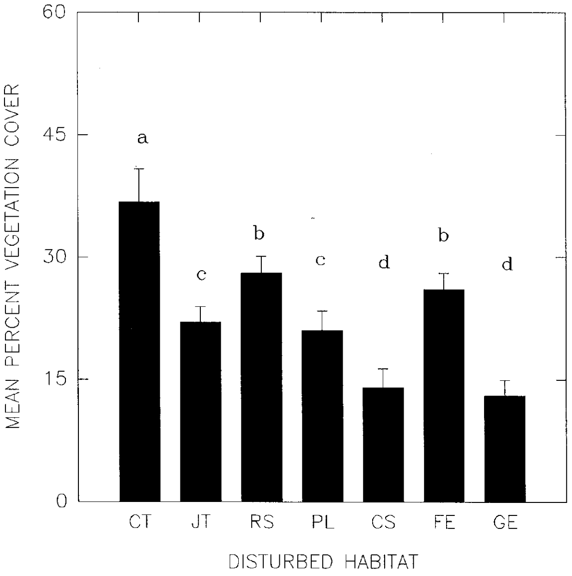

Figure 4—Percent vegetation cover (mean ± S.E., n = 30 plots) in disturbed and undisturbed (control) habitats in the *Larrea-Ambrosia* shrublands. Symbols of disturbed habitats are explained in figure 3.

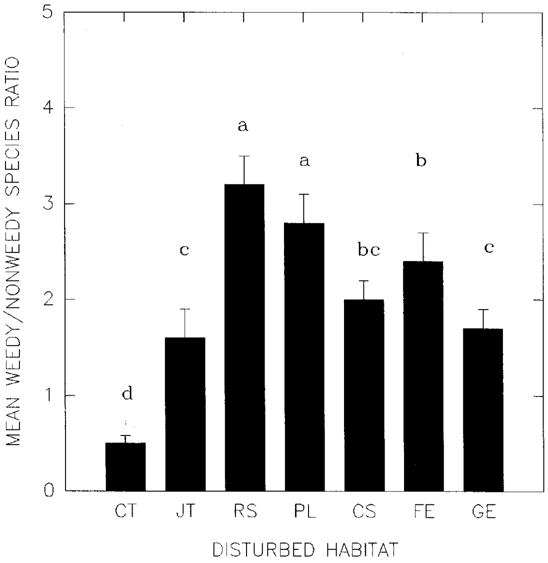

Figure 5—Ratio of weedy to nonweedy species (mean ± S.E., n = 30 plots) in disturbed and undisturbed (control) habitats in the *Larrea-Ambrosia* shrublands. Symbols of disturbed habitats are explained in figure 3.

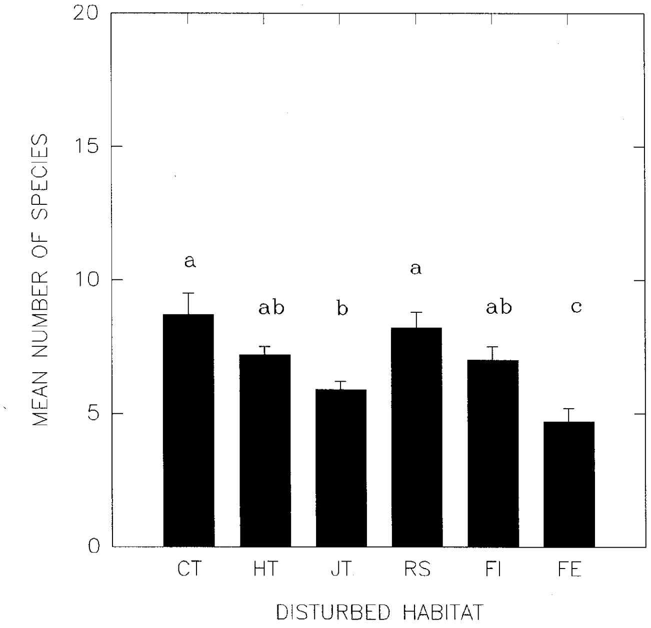

Figure 6—Species richness (mean ± S.E., n = 30 plots in each type of disturbance) in disturbed and undisturbed (control) habitats in the *Coleogyne* shrublands. Symbols of disturbed habitats: Control (CT); human trail (HT); jeep trail (JT); roadside (RS); fire (FI); and fence (FE).

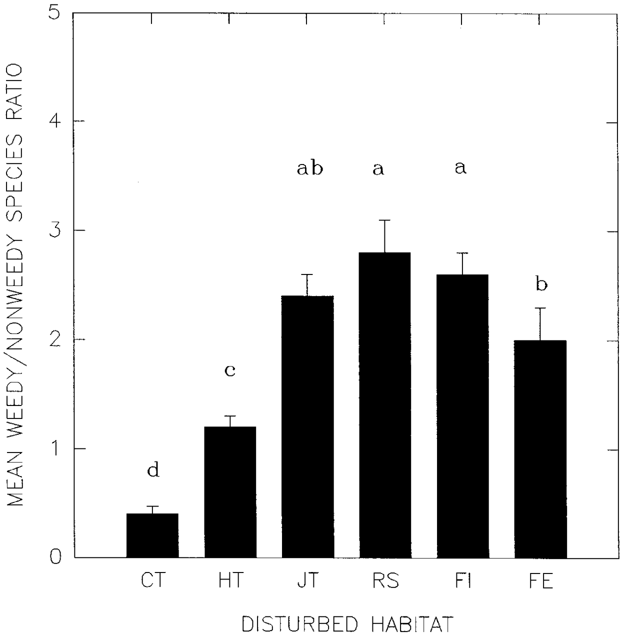

Figure 8—Ratio of weedy to nonweedy species (mean ± S.E., n = 30 plots) in disturbed and undisturbed (control) habitats in the *Coleogyne* shrublands. Symbols of disturbed habitats are explained in figure 6.

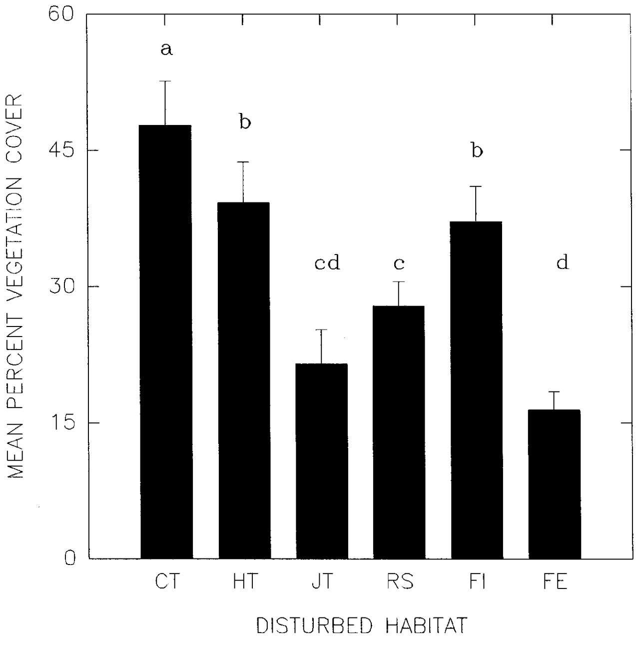

Figure 7—Percent vegetation cover (mean ± S.E., n = 30 plots) in disturbed and undisturbed (control) habitats in the *Coleogyne* shrublands. Symbols of disturbed habitats are explained in figure 6.

weedy to nonweedy species to favor weedy and opportunistic species.

From casual observations, weedy species, such as Russian thistle (*Salsola kali*), *Pectis papposa*, red brome grass (*Bromus rubens*), and *Eriogonum* spp., colonize within two months after initial disturbances. In this study, species richness and percent vegetation cover decreased significantly at highly disturbed sites, primarily due to the complete or nearly complete removal of native woody vegetation in the *Larrea-Ambrosia* and *Coleogyne* zones. Conversely, native woody, subwoody, and succulent plants contribute substantially to species richness and percent vegetation cover at undisturbed sites. Disturbance and fragmentation are not isolated events; rather, they are ongoing processes and may lead to a complete replacement of the native vegetation by many weedy and exotic plants along the edge habitats (Soule and others 1992). The ratio of weedy to nonweedy species was significantly higher at disturbed than undisturbed sites in this study, and such ratio is often more useful than species abundance and richness (Meffe and Carroll 1997). In both *Larrea-Ambrosia* and *Coleogyne* vegetation zones, roadside disturbance exhibited the highest ratio of weedy to nonweedy species, presumably due to an excess moisture supply (surface water run-off) along the gutter after major storm events. Nevertheless, human trail disturbance exhibited the lowest ratio of weedy to nonweedy species since the trails were typically less than 1.5 m wide and the extent of disturbance beyond the trails was minimal in this study.

Natural and anthropogenic disturbances through fragmentation in the *Larrea-Ambrosia* and, to a lesser extent, *Coleogyne* shrublands have led to a substantial habitat loss, and have created edge habitats and spatial heterogeneity. Edge zones subject to more disturbance than interior core zones, favoring weedy and opportunistic (edge) species (Murica 1995; Soule and others 1992). In general, the greater the structural contrast between adjacent undisturbed habitats, the more intense the edge effects (Meffe and Carroll 1997). The Mojave Desert landscape in Las Vegas has abundant edge zones and may gradually become dominated by edge-adapted species. The edge effect studies suggest that species composition and abundance patterns change in disturbed landscapes because some species are more vulnerable than others to increased isolation (metapopulation), edge effects, reduced interior core areas that contain critical resources, and other factors that accompany the disturbance process (Meffe and Carroll 1997; Murica 1995). As cosmopolitan plant species invade more and more disturbed areas, local vegetation types are likely to become homogenized by losing their floristic and ecological distinctness through time.

Implications and Future Directions

Habitat destruction and fragmentation are a major threat to biodiversity without significant changes in climatic, edaphic, and geomorphic conditions. Significant alterations in species diversity and vegetation cover at a local scale due to invasions by weedy and exotic species were evident in the Las Vegas Valley and vicinity. Although not quantitatively investigated in this study, biotic interactions, along with ecological processes and attributes, may change substantially as a result of edge effects and other accompaniments of habitat destruction and fragmentation. As urbanization, economic growth, and recreational activities intensify through time, considerably more conversion of a native Mojave Desert woody vegetation to an immense anthropogenic habitat is fully expected. Landscape restoration and large-scale revegetation to the original, pristine level are virtually impossible. In recognition of the alarming yet largely unmeasured destruction and conversion of native desert habitats, future research is required to properly address the biological underpinnings of ecological and conservation issues. Such issues may include ecological processes and attributes, biotic interactions, biodiversity, invasive and endangered species, metapopulation dynamics, as well as reserve size and design in a fragmented landscape caused by natural and anthropogenic disturbances in the southern Nevada region of the Mojave Desert.

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Plant Community Dynamics of Burned and Unburned Sagebrush and Pinyon-Juniper Vegetation in West-Central Utah

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Stewart C. Sanderson

Abstract—Fire ecology of sagebrush and pinyon-juniper vegetation in the Great Basin has been influenced by human disturbances and exotic plant introductions. Late-seral woody vegetation, which increased following Euro-American settlement, is now decreasing because of wildfire and exotic annuals. Multiple successional pathways following fire have been observed in these vegetation types. Following the 1996 wildfires in west-central Utah, burned and unburned vegetation were compared at four sites. Measures of frequency, cover, and density of vascular plant species were used to show fire effects and to follow population dynamics over a period of 3 years. Woody species characteristic of the unburned areas were generally absent from the burned areas. Native herbaceous species, particularly annual forbs, were abundant in the burned areas 1 year after the fires, but many of these declined by the second and third year, as exotic species, particularly cheatgrass (*Bromus tectorum*), increased. Cheatgrass became dominant in the interspaces among burned trees by the second year following the fires, a period of high precipitation. In the subcanopy zones of burned trees, cheatgrass did not become dominant until the third year following the fire, and was preceded by exotic annual forbs. Community composition and structure differed by site as well as by fire history. Cheatgrass cover was lowest at a site where perennial grasses and forbs had become established through aerial broadcast seeding.

Introduction

Large portions of the semiarid Great Basin region of Utah, Nevada, and surrounding states are occupied by vegetation types that are referred to as sagebrush and pinyon-juniper. These vegetation types are named for their dominant woody plant species, including big sagebrush (*Artemisia tridentata*), Utah juniper (*Juniperus osteosperma*), singleleaf pinyon (*Pinus monophylla*), and Colorado pinyon (*Pinus edulis*) (West 1988). These species occur in association with a variety of other species of shrubs, grasses, and forbs (Bunting and others 1999; Rust 1999). The vegetation structure and floristic composition of sagebrush and pinyon-juniper communities are variable over the wide geographical and ecological ranges of these vegetation types. At some locations, sagebrush vegetation has historically included a significant perennial grass component, and is described as sagebrush steppe (West 1988). Mature pinyon-juniper woodlands often have sparse herbaceous understory, and are common on steeper, rockier, and higher elevation sites than sagebrush vegetation (West 1988; West 1999). At many sites, however, the distinction between sagebrush and pinyon-juniper is blurred because either could potentially occur. Pinyon-juniper is capable of invading sagebrush (Miller and Wigland 1994), and sagebrush often occurs in the early successional stages of pinyon-juniper (Barney and Frischknecht 1974). Tausch (1999) described shrub and steppe communities as a matrix within which pinyon-juniper woodlands of various successional stages are present.

Fire is an important ecological factor in the sagebrush and pinyon-juniper vegetation types. Estimates of fire return intervals prior to Euro-American settlement range from 20 to 25 years for the sagebrush steppe of Yellowstone National Park (Houston 1973) to 50 to 100+ years for the xeric pinyon-juniper woodlands of Great Basin National Park (Gruell 1999). The historical impact of fire has differed by region, due to differences in factors such as the occurrence of summer thunderstorms (Billings 1994). In fire-prone areas, selective pressure has favored plants that are either capable of surviving fire, or able to occupy the environments of successional stages that follow fire (Wright and others 1979; Bradley and others 1992).

Early successional stages following fire are often characterized by herbaceous species, because the primary woody dominants (big sagebrush, Utah juniper, and pinyon) are easily killed by fire and require long fire-free periods to reestablish and mature (Billings 1994; Miller and Wigland 1994). Barney and Frischknecht (1974) described a sequence of successional stages following fire in juniper woodlands of west-central Utah, based on examination of several burns of different ages. An annual phase lasting 3 to 4 years was succeeded by a perennial grass/forb stage, which then gradually became occupied by maturing shrubs and trees. Sagebrush generally became dominant after 35 years, and juniper after 70 years. These authors noted that the rate and character of succession may vary, due to factors such as seed availability, pre-burn vegetational composition, and grazing. At locations where fire-tolerant perennial species, such as bluebunch wheatgrass (*Elymus spicatus*), were abundant prior to the fire, the annual stage could be shortened or

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bypassed. Heavy grazing had the potential to inhibit perennial grasses and increase the rate of sagebrush establishment (Barney and Frischknecht 1974).

Other successional sequences are also possible because of widespread disturbances and exotic plant invasions that have occurred in the sagebrush and pinyon-juniper vegetation types since the time of Euro-American settlement. Prolonged livestock grazing and fire suppression practices have contributed to a decline of perennial grasses and an increase in shrubs and trees at many sites (Tausch and others 1981; Laycock 1991). Currently, there is a reversal in this trend, with shrubs and trees being lost as a result of an increased number of large, high-intensity fires (Tausch 1999). One of the factors contributing to this increase in fire is the presence of invasive exotic annuals, particularly the widespread annual cheatgrass (*Bromus tectorum*) (D'Antonio and Vitousek 1992). Following fire, cheatgrass readily reestablishes from seed, and alters successional trajectories by interfering with native plant seedling establishment (Stewart and Hull 1949) and shortening the interval between fires (Whisenant 1990). The exotic annual forbs Russian thistle (*Salsola pestifer*) and tumblemustard (*Sisymbrium altissimum*) often dominate early post-fire successional stages on disturbed sites where cheatgrass will later become dominant (Piemeisel 1951).

To account for such alternative successional patterns, state-and-transition models (Westoby and others 1989) have been applied to the sagebrush and pinyon-juniper vegetation types (Jameson 1987; Laycock 1991). According to the state-and-transition model of Laycock (1991) for sagebrush steppe, fire, grazing, and annual invasion can lead to a threshold beyond which the climax steady state becomes an annual grassland. After such a threshold has been crossed, intensive human intervention in the form of weed control and revegetation treatment may be necessary to restore the system to its former state, or to an alternative state containing desirable perennial species. Artificial seeding of perennial species such as crested wheatgrass (*Agropyron cristatum*) is commonly carried out following wildfire on managed lands to preclude the development of undesirable cheatgrass stands and to meet other management objectives (Evans and Young 1978; MacDonald 1999).

During the summer of 1996, several large lightning-caused wildfires occurred in western Utah, burning thousands of acres of sagebrush and pinyon-juniper (MacDonald 1999). The study presented here was carried out following these fires to document the effect of the fires on plant community composition and structure, and successional changes over a period of 3 years. Attention was given to the distribution and dynamics of individual species, and groups of species organized according to origin (native or exotic), life form (grass, forb, shrub, or tree), and longevity (annual or perennial). This report is part of a broader study of wildfire rehabilitation following the 1996 fires (Ott 2001).

Study Sites and Methods

Four study sites were selected in 1997, at locations in west-central Utah where wildfires had occurred the previous year (fig. 1; table 1). The Gilson and Jericho sites were part the Leamington complex fire, which burned during early August 1996. The Twin and Cunningham sites represent separate fire complexes, which burned during early July and August 1996, respectively (BLM, personal communication). At each of these sites, unburned vegetation occurred adjacent to burned vegetation of similar composition and structure. The burned portion of the Cunningham site had been rehabilitated through aerial broadcast seeding during the fall of 1996 by the Bureau of Land Management. Rehabilitation treatments including aerial seeding, chaining, and rangeland drill seeding were carried out by the Bureau of Land Management at the Jericho, Gilson, and Twin sites. In addition, burned but untreated controls were present at the foregoing sites on non-BLM lands (highway right-of-ways, state, and private lands). The data presented in this paper for the Jericho, Gilson, and Twin sites were collected on these untreated burned areas.

At each study site, a cadestral survey marker or other reference point was located, and transect lines were directed from the reference point into areas of burned and unburned vegetation, which we refer to as burned and unburned treatments. Within each treatment/site combination, four permanent plots were established at tape-measured intervals of 50 m (Twin and Gilson sites) or 60 m (Cunningham and Jericho sites). A metal rebar was used to mark the center of a circular plot of area 100 m^2 (0.025 acre), and also served

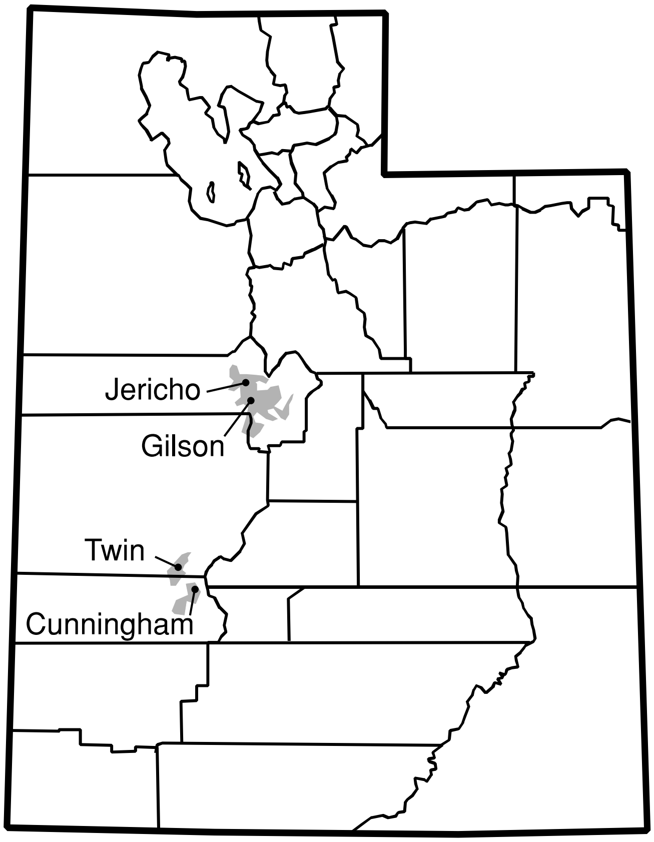

Figure 1—Location of study sites in relation to 1996 wildfire complexes (shading) in west-central Utah.

Table 1—Description of study sites in west-central Utah where burned and unburned plant communities were sampled following 1996 wildfires.

Site name	Location (marker)	Elevation	Range of slopes	Soils	Site description
		ft	*percent*		
Cunningham	Rebar at canyon mouth, T27S R7W S34 S35 S2 T27S	6,400–6,500	20–35	Red Butte very rocky loam[a]	Rocky east-facing slopes
Gilson	Section marker T13S R3W S35 T14S R3W S1 S2	5,320–5,400	4–15	Borvant cobbly loam[b]	Eastern foothills of Gilson Mountains
Jericho	Milemarker 124, US Hwy. 6, T12S R3W S28	5,420–5,480	4–16	Jericho gravelly fine sandy loam[b]	South side of Tintic Valley
Twin	Quarter-section marker T25S R7W S29 S32	5,900–5,940	1–6	Kessler-Penoyer very cobbly loam[a]	Basalt plains

[a] Stott, L. H.; Olsen, M. E. 1976. Soil survey of Beaver-Cove Fort area, Utah. U.S. Department of Agriculture, Soil Conservation Service.
[b] Trickler, D. L.; Hall, D. T. 1984. Soil survey of Fairfield-Nephi area, Utah. U.S. Department of Agriculture, Soil Conservation Service.

as the southwest corner of a square-shaped 1 m^2 plot (McArthur and Sanderson 1996).

Composition and foliar cover of vascular plant species were recorded for both plot sizes. Species nomenclature followed Welsh and others (1993). For the large (100 m^2) plots, each species present (having canopy within the plot boundary) was assigned a cover class, based on classes proposed by Daubenmire (1959), with an additional cover class added to accommodate species having less than 1 percent cover (McArthur and Sanderson 1996). For the small (1 m^2) plots, a whole-number percent cover estimate was made for each species. Total cover of understory plants (excluding trees), and any bare soil, rock (>1 cm diameter), litter, or cryptobiotic crust exposed beyond the understory cover, were also estimated for the small plots. The number of rooted individuals of each species was also counted for small plots; counts were rounded to the nearest 5 or 10 when the number of individuals exceeded 50.

Plot data as described above were collected each year for 3 consecutive years (July to August 1997, June to early July 1998, and late June to early August 1999). In 1998, additional data were collected using a step-point technique modified from Evans and Love (1957). A step-point transect consisting of 40 points was extended from the edge of each large plot along the transect line upon which the plot had been placed. At paced intervals of 1 m, a pin (2 mm diameter wire attached to a meterstick) was lowered to the ground directly in front of the recorder's boot. Basal cover at the intersection of the pin and the ground was identified as bare soil, rock, litter, cryptobiotic crust, or a species of vascular plant. Litter was defined to include dead wood at ground level and dead herbaceous material from a previous year. Tree canopy above each point was also recorded, with canopy above dead burned trees estimated as if they were foliated. If a tree or shrub became an obstacle along a transect line, the line was maintained by extending the meterstick, from point to point, beneath or through the canopy of the tree or shrub, then resuming paced steps on the opposite side. If the boundaries of the treatment area were reached before a transect line was complete, the direction of the transect was redirected by 135° to complete the sample within the treatment of concern.

Recorded plant species were variously organized into groups based on life form (tree, shrub, grass, or forb), origin (native or exotic), and longevity (perennial or annual), as indicated by Welsh and others (1993). Species that had been used in the rehabilitation seedings were also segregated. Biennial species were considered perennial unless the species also typically grows as an annual. For each of the resulting groups (native shrubs and trees, native grasses, exotic grasses, seeded grasses, seeded shrubs and forbs, exotic forbs, native annual forbs, and native perennial forbs), synthetic percent-cover values were created by adding the cover values of all species within the group. Synthetic percent-cover values for large plots were computed using the midpoints of cover classes.

Cover data for synthetic species groups were analyzed statistically using SAS statistical software (SAS Institute, Inc. 1990). Large and small plots were analyzed separately. The Cunningham site, which had been aerially seeded, was excluded from this analysis in order to highlight the response where seeding had not been done. SAS PROC MIXED was used to run a mixed model, first order autoregressive repeated measures analysis (Littell and others 1996). Site and the interaction of site with treatment and year were treated as random effects, while treatment, year, and their interaction were treated as fixed effects. The Tukey adjustment was used to test differences between treatment, year, and treatment by year means. The PROC UNIVARIATE procedure in SAS was used to test for normality of residuals (considered normal if the Shapiro-Wilk statistic was greater than or equal to 0.05). Percentage variables failing to meet this test of normality were retested following an arcsine transformation of the square root of the percentage value (Snedecor 1956).

Other data were examined and used to make comparisons, but were not analyzed using parametric statistics. Cover and density of individual species were averaged across the three nonseeded sites by treatment and year. Frequency, here defined as the number of plots where a species was present, was tabulated by year and treatment, across all sites, for each species. Basal cover, based on the 1998 step-point transects, was averaged by treatment and site for each synthetic species group.

Results and Discussion

First-Year Burned/Nonburned Comparison

Species frequencies among sites and years in burned and unburned treatments are shown in table 2. Some species were recorded much more frequently in either the burned or the unburned treatment, while others occurred more uniformly in both treatments or were too rare to reveal differences. Species with the greatest difference in frequency between burned and unburned large plots in 1997 are highlighted in table 3. Species with the highest frequency in burned plots relative to unburned were primarily annual forbs, including the native species pinnate tansymustard (*Descurainia pinnata*), floccose gilia (*Gilia inconspicua*), groundsmoke (*Gayophytum lasiospermum*), whitestem blazingstar (*Mentzelia albicaulis*), and coyote tobacco (*Nicotiana attenuata*); and the exotic species prickly lettuce (*Lactuca serriola*), African mustard (*Malcolmia africana*), and tumblemustard (*Sisymbrium altissimum*). Seeded species, not shown in table 3, also had greater frequency in the burned areas. The species with the highest frequency in the unburned plots relative to the burned included native trees and shrubs such as Utah juniper (*Juniperus osteosperma*), big sagebrush (*Artemisia tridentata*), viscid rabbitbrush (*Chrysothamnus viscidiflorus*), and native perennial forbs such as desert phlox (*Phlox austromontana*) and Holboell's rockcress (*Arabis holboelii*). Species with high frequencies in both burned and unburned plots, not shown in table 3, included cheatgrass (*Bromus tectorum*), bottlebrush squirreltail (*Elymus elymoides*), bluegrass (*Poa* spp.), Indian ricegrass (*Stipa hymenoides*), bluebunch wheatgrass (*Elymus spicatus*), Douglas' dustymaiden (*Chaenactis douglasii*), sego lily (*Calochortus nuttallii*), longleaf phlox (*Phlox longifolia*), and bur buttercup (*Ranunculus testiculatus*).

When mean percent cover, based on the cover-class midpoints for the large plots, was used to identify species with different abundances in the burned and unburned treatments, results were similar to those for frequency, with some notable exceptions (table 3, right). Cheatgrass (*Bromus tectorum*) was present in all plots, burned and unburned, but its mean percent cover 1 year following the fire was 7.3 percent higher on burned than on unburned plots. The exotic annual forb desert alyssum (*Alyssum desertorum*) had higher frequency in the unburned plots but higher cover in the burned. The native perennial grasses bottlebrush squirreltail, muttongrass (*Poa fendleriana*), and Indian ricegrass also had higher cover in the unburned plots. Most species had only slight differences (less than 1 percent) in mean percent cover between burned and unburned plots.

Although the comparison of plots in adjacent burned and unburned areas is not as conclusive as would be a comparison of a single set of plots before and after a fire, these results are nevertheless instructive. We assume that the differences in frequency and cover between the burned and unburned treatments are in large measure due to the effects of the fires. Perennial species with lower abundance in the burned treatments likely suffered mortality or direct damage from the fires, or were indirectly affected because they were better adapted to the late-seral than to the early-seral environments.

The fires at our study sites were of sufficient intensity to kill nearly all individuals of nonbase-sprouting perennial species, including Utah juniper, pinyon, and big sagebrush. Viscid rabbitbrush also appeared to have been eliminated by the fires at our study sites, even though the typical response of this species is vigorous resprouting (Wright and others 1979; Everett and Ward 1984). Zschaechner (1985) observed mortality of viscid rabbitbrush following fire and suggested that this was the result of high amounts of fuel in the vicinity of the plants, which raised the heat load to lethal levels. Herbaceous perennials with lower abundance in the burned treatments, such as desert phlox, Holboell's rockcress, and bottlebrush squirreltail, may have likewise been damaged because of the high intensity of the fires. In the unburned treatments, bottlebrush squirreltail was observed most commonly in the zone beneath juniper trees. Similar concentrations of this species beneath trees prior to the fire in the burned treatments would have likely suffered high mortality because of the high intensity of fire that typically occurs in subcanopy zones (Klebenow and others 1977).

The timing of a fire relative to periods of growth and dormancy is another important variable affecting fire response (Wright and others 1979). Most perennial grasses encountered in our study were cool-season species, which were probably less damaged by the late-summer 1996 fires than they might have been if burned earlier in the growing season. Residual patches of bluebunch wheatgrass and western wheatgrass (*Elymus smithii*) were present in the burned treatment, even at the Twin site, which had burned in early July.

Many of the native and exotic annual forbs that we recorded in the burned treatments, including members of the genera *Chenopodium, Collinsia, Descurainia, Gilia, Lactuca, Mentzelia, Nicotiana, Sisymbrium, Salsola,* and *Polygonum*, have been reported by other authors studying early succession following fire in sagebrush and pinyon-juniper areas (Young and Evans 1978; Everett and Ward 1984; Koniak 1985). Seeds of these annuals were either part of the seedbank that survived the fires, or arrived through rapid dispersal following the fires. Koniak and Everett (1982) found that most of the seedbank in a mature pinyon-juniper stand consisted of annuals, many of which were not present in the community as mature plants. Fire may promote the germination of dormant seeds by consuming litter containing allelopathic compounds (Jameson 1970; Schott and Pieper 1987), and altering the nutrient, water, microbial, temperature, and light regimes of the seedbed (Koniak 1985; Blank and others 1995). Chemical factors in wood smoke or burned soil have been found to promote germination of certain species, including coyote tobacco (Baldwin and others 1994) and Indian ricegrass (Blank and Young 1998).

Three-Year Community Dynamics

For some species, frequency remained roughly constant across years, while for other species, frequency changed in the burned and/or unburned plots (table 2). Slight changes may represent error due to species being overlooked or misidentified, or sampling at different periods of phenological development in different years. For the majority of

Table 2—Frequency (number of plots in which species were present) by treatment and year for vascular plant species recorded at four sites in west-central Utah following 1996 wildfires. Values without parentheses are for 100 m^2 plots; values in parentheses are for 1 m^2 subplots, shown if greater than zero. Maximum frequency per treatment/year combination is 16.

Species name	Common name	Sites[a]	Unburned			Burned		
			1997	1998	1999	1997	1998	1999
Native shrubs and trees								
Artemisia tridentata	Big sagebrush	C G J T	12 (7)	12 (5)	12 (7)	1	1	1
Chrysothamnus nauseosus	Rubber rabbitbrush	——J—	0	0	0	1	1	1
Chrysothamnus viscidiflorus	Viscid rabbitbrush	——J T	8 (5)	8 (4)	8 (5)	0	0	0
Cercocarpus montanus	Mountain mahogany	C———	1	1	1	1	1	1
Ephedra nevadensis	Nevada ephedra	——J T	5	5	5	1	1	1
Eriogonum corymbosum	Fremont's buckwheat	C———	1	1	1	0	0	0
Eriogonum ovalifolium	Cushion buckwheat	———T	2	3	2	0	0	0
Gutierrezia sarothrae	Broom snakeweed	C G J T	5	5	5	5	6	6
Juniperus osteosperma	Utah juniper	C G J T	15 (3)	15 (3)	15 (3)	1	1	1
Leptodactylon pungens	Prickly phlox	C G——	1 (1)	1 (1)	1 (1)	1	1	0
Opuntia polyacantha	Pricklypear	C—J T	5	5	5	1	1	1
Pediocactus simpsonii	Simpson's footcactus	———T	1	0	0	0	0	0
Pinus edulis	Colorado pinyon pine	C———	3	4	4	0	0	0
Purshia mexicana	Cliffrose	——J—	1	1	1	0	0	0
Purshia tridentata	Bitterbrush	C G——	4 (1)	4 (1)	4 (1)	0	0	0
Quercus gambelii	Gambel oak	C———	1	2	1	2	2	2
Symphoricarpos oreophilus	Mountain snowberry	C———	1	0	0	0	0	0
Tetradymia canescens	Gray horsebrush	——J—	2	2	2	0	0	0
Native grasses								
Elymus elymoides	Bottlebrush squirreltail	C G J T	16 (12)	16 (11)	16 (9)	14 (3)	13 (3)	13 (3)
Elymus smithii	Western wheatgrass	—G—T	0	0	0	3	2	2
Elymus spicatus	Bluebunch wheatgrass	C G—T	8 (5)	8 (4)	8 (4)	6 (1)	6	6 (1)
Festuca octoflora	Sixweeks fescue	——J—	1	1	0	0	0	0
Koeleria macrantha	Prairie junegrass	C———	4	3 (2)	4 (2)	2	3	3
Poa fendleriana	Muttongrass	C G J T	7 (4)	12 (4)	7 (4)	6 (1)	6 (1)	3
Poa secunda	Sandberg bluegrass	C——T	5 (2)	4 (2)	2 (2)	4 (2)	4	2 (1)
Stipa comata	Needle-and-thread	— J—	0	0	0	1	1	1
Stipa hymenoides	Indian ricegrass	C G J T	11 (1)	11 (1)	10 (1)	8 (1)	8 (1)	8 (1)
Exotic grasses								
Bromus japonicus	Japanese brome	C——T	1	1 (1)	0	3	4	0
Bromus tectorum	Cheatgrass	C G J T	16 (15)	16 (16)	16 (16)	16 (13)	16 (16)	16 (16)
Hordeum jubatum	Foxtail barley	C———	0	0	0	1	1	0
Secale cereale	Cultivated rye	——J—	0	1	0	0	0	0
Setaria viridis	Green bristlegrass	C———	0	0	0	1	0	0
Seeded grasses								
Agropyron cristatum	Crested wheatgrass	C G J—	2	1	2	5 (3)	6 (4)	7 (5)
Bromus inermis	Smooth brome	C—J—	0	0	0	4 (4)	5 (4)	5 (4)
Dactylis glomerata	Orchardgrass	C———	0	0	0	0	1	0
Elymus elongatus/hispidus	Tall/Intermediate wheatgrass	C G J—	0	0	0	4 (1)	7 (1)	10 (1)
Elymus junceus	Russian wildrye	C G——	0	0	0	0	5 (2)	5 (2)
Seeded shrubs and forbs								
Atriplex canescens	Fourwing saltbush	—G——	0	0	0	1	0	0
Medicago sativa	Alfalfa	C———	0	0	0	4 (1)	4 (2)	1 (1)
Melilotus officinalis	Yellow sweetclover	C———	0	0	0	4 (1)	4	0
Sanguisorba minor	Small burnet	C———	0	0	0	4 (1)	4 (1)	3 (1)
Exotic forbs								
Alyssum desertorum	Desert alyssum	C G J T	12 (9)	13 (11)	13 (12)	6 3	7 4	7 2
Camelina microcarpa	Falseflax	—G——	1	3 (2)	3 (3)	3	4 (1)	3 (2)
Chenopodium album	Lambsquarter	C G J—	0	1	0	2	1	0
Erodium cicutarium	Storksbill	——J—	0	0	0	1	3	3 (1)
Lactuca serriola	Prickly lettuce	C G J T	0	6 (4)	5 (1)	12	11 (7)	12 (7)
Malcolmia africana	African mustard	—G J T	1	0	0	6	3	0
Polygonum aviculare	Knotweed	C ——	0	0	0	0	1	0
Ranunculus testiculatus	Bur buttercup	C G—T	8 (6)	8 (6)	7 (6)	8 (5)	4	4 (2)
Salsola iberica	Russian thistle	—G J—	0	1 (1)	0	0	0	1
Salsola paulsenii	Barbwire Russian thistle	———T	0	0	0	1	0	0
Sisymbrium altissimum	Tumblemustard	—G J T	1	6 (2)	7 (1)	2	9 (7)	11 (6)
Tragopogon dubious	Yellow salsify	C G J T	4	1	3 (1)	7	8 (2)	8 (5)
Native annual forbs								
Camissonia boothii	Booth's camissonia	——J—	0	0	0	1	0	0
Collinsia parviflora	Blue-eyed Mary	C———	1	2 (1)	0	4 (1)	0	0
Collomia grandiflora	Large collomia	C———	0	0	0	2	0	0

(con.)

Table 2—Cont.

Species name	Common name	Sites[a]	Unburned			Burned		
			1997	1998	1999	1997	1998	1999
Cryptantha ambigua	Wilke's cryptanth	C———	0	0	0	1	0	0
Cryptantha cineria	James' cryptanth	—G——	1 (1)	1 (1)	0	0	0	0
Cryptantha micrantha	Dye cryptanth	——J—	0	1	0	0	0	0
Cryptantha nevadensis	Nevada cryptanth	C G —	1	0	0	3	2	0
Cryptantha (unidentified)	Cryptanth	C—J T	0	1	3 (1)	2	1	2
Descurainia pinnata	Pinnate tansymustard	C G J T	3 (1)	4 (3)	2 (1)	12 (3)	16 (2)	3
Draba verna	Spring draba	—G——	0	0	0	1	0	0
Epilobium brachycarpum	Autumn willowherb	C——T	0	1	0	2 (1)	2	4 (1)
Eriogonum deflexum	Skeleton buckwheat	—G J—	5 (1)	1	0	5 (2)	3 (1)	1
Eriogonum palmeranum	Palmer's buckwheat	—G——	0	0	0	1	0	0
Galium aparine	Common bedstraw	C———	0	0	0	2	0	0
Gayophytum decipiens	Deceptive groundsmoke	——J—	1	0	0	0	0	0
Gayophytum lasiospermum	Hairyseed groundsmoke	C G—T	0	0	0	8 (1)	0	0
Gilia giliodes	Collomia gilia	C——T	0	0	0	5 (4)	0	0
Gilia inconspicua	Floccose gilia	C G J T	4	6 (1)	5 (2)	15 (8)	4 (1)	5
Gilia polycladon	Spreading gilia	——J—	0	0	0	2	0	0
Helianthus annuus	Common sunflower	C———	0	0	0	1	0	0
Lappula occidentalis	Western stickseed	C—J—	1	0	0	1	1	0
Mentzelia albicaulis	Whitestem blazingstar	C G J T	0	0	0	8 (3)	1	0
Microsteris gracilis	Little polecat	C———	4 (3)	4 (3)	3 (3)	3	0	0
Mimulus rubellus	Monkey-flower	C———	0	0	0	2	0	0
Nicotiana attenuata	Coyote tobacco	C G—T	0	0	0	7 (1)	2	0
Phacelia ivesiana	Ives' Phacelia	—G——	0	0	0	2	0	0
Polygonum douglasii	Douglas' knotweed	C———	3 (1)	4 (1)	3 (1)	4	2	3
Solanum triflorum	Cutleaf nightshade	C———	0	0	0	2	0	0
Verbena bracteata	Prostrate verbena	C—J—	0	0	0	2	2	2
Native perennial forbs								
Agoseris glauca	Mountain dandelion	C——T	2 (1)	3	0	4	2	2 (1)
Allium acuminatum	Acuminate wild onion	C——T	0	0	0	2	1 (1)	0
Antennaria dimorpha	Low pussytoes	C———	0	2	0	0	0	0
Arabis drummondii	Drummond's rockcress	———T	1	2	0	2	0	0
Arabis holboellii	Holboell's rockcress	C G J T	8 (1)	7 (1)	3	3	3	0
Argemone munita	Prickly-poppy	C G——	0	0	0	5	5	3
Astragalus calycosus	Torrey's milkvetch	—G J T	9 (1)	9 (1)	8 (2)	4 (2)	3 (1)	2
Astragalus convallarius	Rush milkvetch	—G——	1 (1)	1 (1)	1 (1)	1	0	1
Astragalus eurekensis	Eureka milkvetch	—G J—	1	1	2	0	0	1
Astragalus lentiginosus	Freckled milkvetch	—G J—	3	4	4	5	5	3
Astragalus piutensis	Sevier milkvetch	C——T	4 (1)	4 (1)	2	3	1	0
Astragalus utahensis	Utah milkvetch	C——T	2 (1)	4	1	2	0	0
Astragalus (unidentified)	Milkvetch	———T	0	0	0	0	0	1
Calochortus nuttallii	Sego lily	C G—T	7 (2)	4 (1)	3 (1)	7	3	3
Castilleja chromosa	Common paintbrush	——J—	1	1	1	0	0	0
Chaenactis douglasii	Douglas' dustymaiden	C G J T	10 (2)	11 (2)	10 (2)	9 (2)	8 (1)	2 (1)
Chaetopappa ericoides	Rose-heath	———T	2 (1)	2 (1)	2 (1)	0	0	0
Cirsium wheeleri	Wheeler's thistle	C———	0	1	0	1	2	2
Comandra umbellata	Bastard toadflax	———T	2 (1)	1 (1)	1 (1)	2	1	2
Crepis occidentalis	Western hawksbeard	C——T	4	0	0	4 (1)	4 (1)	4 (2)
Cryptantha humilis	Dwarf cryptanth	—G—T	5	3 (1)	5 (2)	1	1	1
Erigeron aphanactis	Hairy daisy	C——T	1	2	0	3	2	3
Erigeron engelmanii	Engelmann's daisy	—G J—	0	0	1	0	0	1
Linum perenne	Blue flax	—G—T	2	2	2 (1)	1	1	1
Lygodesmia grandiflora	Showy rushpink	——J—	2	2	1	0	0	0
Machaeranthera canescens	Hoary aster	—G—T	5 (1)	5 (1)	5 (2)	3	3	2
Oenothera caespitosa	Tufted evening primrose	——J—	1	1 (1)	2 (1)	0	0	0
Orobanche multiflora	Cancerroot	——J T	1	4	1	0	0	0
Petradoria pumila	Rock goldenrod	C——T	3 (1)	2 (1)	2 (1)	0	0	0
Phlox austromontana	Desert phlox	C G—T	8 (5)	6 (6)	8 (6)	2	2	2
Phlox longifolia	Longleaf phlox	C G J T	11 (5)	9 (2)	7 (4)	10 (2)	3 (1)	3 (1)
Physaria chambersii	Chamber's twinpod	———T	0	0	0	1	1	0
Senecio multilobatus	Uinta groundsel	C G J T	7 (1)	9 (2)	6 (2)	2	3 (1)	0
Sphaeralcea coccinea	Common globemallow	—G——	3 (1)	2 (1)	3 (1)	3	3	3 (1)
Sphaeralcea grossulariifolia	Gooseberry globemallow	——J T	2	2	2	4 (1)	3 (1)	5
Stanleya pinnata	Prince's plume	——J—	1	1	1	0	0	0
Streptanthus cordatus	Twistflower	—G J—	4 (2)	4 (2)	4 (2)	3	2 (1)	0
Vicia americana	American vetch	—G——	3 (2)	3 (2)	3 (2)	4 (2)	4 (2)	2
Viola spp.	Violet	———T	0	1	0	0	0	0
Zigadenus paniculatus	Foothills death camas	C G—T	3 (1)	2	2 (1)	1	0	0

[a] Study sites where species was recorded; C = Cunningham, G = Gilson, J = Jericho, T = Twin.

Table 3—Species with greatest difference in frequency and cover between burned and unburned treatments across four sites in west–central Utah following 1996 wildfires. Based on 1997 data from 100 m^2 size plots. Early-seral species have low value for frequency index (unburned frequency minus burned frequency) and cover index (mean unburned cover minus mean burned cover); late–seral species have high values for these indices. Seeded species are omitted.

	Frequency index		Cover index
Early-seral		**Early-seral**	
Lactuca serriola (EAF)	–15	*Bromus tectorum* (EAG)	–7.3
Descurainia pinnata (NAF)	–12	*Gilia inconspicua* (NAF)	–3.3
Gilia inconspicua (NAF)	–11	*Nicotiana attenuata* (NAF)	–1.3
Gayophytum lasiospermum (NAF)	–8	*Descurainia pinnata* (NAF)	–1.2
Mentzelia albicaulis (NAF)	–8	*Lactuca serriola* (EAF)	–0.8
Nicotiana attenuata (NAF)	–8	*Alyssum desertorum* (EAF)	–0.7
Argemone munita (NPF)	–5	*Ranunculus testiculatus* (EAF)	–0.7
Malcolmia africana (EAF)	–5	*Crepis occidentalis* (NPF)	–0.5
Sisymbrium altissimum (EAF)	–4	*Mentzelia albicaulis* (NAF)	–0.4
Tragopogon dubius (EAF)	–4	*Sisymbrium altissimum* (EAF)	–0.4
Late-seral		**Late-seral**	
Alyssum desertorum (EAF)	4	*Arabis holboellii* (NPF)	0.2
Astragalus calycosus (NPF)	4	*Gutierrezia sarothrae* (NS)	0.2
Ephedra nevadensis (NS)	4	*Petradoria pumila* (NPF)	0.3
Opuntia polyacantha (NS)	4	*Oryzopsis hymenoides* (NPG)	0.4
Purshia tridentata (NS)	4	*Poa fendleriana* (NPG)	0.4
Arabis holboellii (NPF)	5	*Phlox austromontana* (NPF)	2.7
Phlox austromontana (NPF)	6	*Sitanion hystrix* (NPG)	3.8
Chrysothamnus viscidiflorus (NS)	8	*Chrysothamnus viscidiflorus* (NS)	4.5
Artemisia tridentata (NS)	10	*Artemisia tridentata* (NS)	13.8
Juniperus osteosperma (NT)	15	*Juniperus osteosperma* (NT)	17.0

Key to abbreviations: Origin: E = exotic, N = native; Longevity: A = annual, P = perennial; Form: F = forb, G = grass, S = shrub, T = tree.

species encountered, cover and density were low and followed approximately the same trends as frequency. Widespread species (or genera) having high mean cover or density are shown in tables 4 and 5. Note that the means in these tables are based on only three sites (Jericho, Gilson, and Twin) where burned treatments had not been aerially seeded. Some seeded species were found in plots at the Jericho and Gilson sites, probably because of drift from nearby aerial seedings. However, cover of these seeded species was low (less than 1 percent) and their contribution to community dynamics was minimal.

In general, fewer changes were observed in the unburned treatment than the burned treatment, as would be expected because of the slower rate of successional change in late seral stages (Austin 1987). Frequency, density, and cover remained relatively stable for most perennial species in the unburned treatment, although some perennial forbs, such as Holboell's rockcress, sego lily, and longleaf phlox, showed a trend of decreasing frequency over time (table 2). Some annuals, such as the exotic forbs tumblemustard and falseflax (*Camelina microcarpa*), increased in frequency and density over time in the unburned treatments (tables 2, 5). Certain other annual and short-lived perennial species (such as, floccose gilia, Douglas' dustymaiden, Uinta groundsel (*Senecio multilobatus*), prickly lettuce, and desert alyssum) had slightly higher frequency, density, and/or cover in 1998 in the unburned treatment than in other years (tables 2, 4, 5). These fluctuations of short-lived species in the unburned, late-seral vegetation are likely related to climatic fluctuations, such as the observed higher precipitation during the winter and spring of 1998 (NOAA 1998; fig. 2). Another potential factor is increased dispersal from the nearby burned areas. Prickly lettuce was absent from the unburned plots in 1997, but present in six unburned plots in 1998, possibly as a result of seed dispersal from the 1997 crop of this species in the burned areas.

In the burned treatment, most species of native grasses, shrubs, and trees changed little in frequency, density, and cover between years. Muttongrass (*Poa fendleriana*) and Sandberg bluegrass (*Poa secunda*) fluctuated in frequency (table 2), but these species are easy to overlook when dormant and may have sometimes been missed at some plots. Some exotic species (such as, cheatgrass, tumblemustard, falseflax, and prickly lettuce) showed an increasing trend over time in the burned treatment, while other exotic species (such as, Japanese brome (*Bromus japonicus*), bur buttercup (*Ranunculus testiculatus*), desert alyssum, and African mustard) showed declining trends (tables 2, 4, 5). On the other hand, most native forbs decreased over time, with exceptions such as *Crepis occidentalis, Erigeron aphanactis, Epilobium brachycarpum, Machaeranthera canescens, Phlox austromontana, Sphaeralcea coccinea, S. grossulariifolia,* and *Verbena bracteata*, which remained stable or increased in frequency, density, and/or cover over time in the burned treatment (tables 2, 4, 5).

Table 4—Mean percent cover of synthetic species groups and selected species or genera, in burned and unburned treatments across 3 years, averaged across three sites in west-central Utah. Values without parentheses are for 100 m^2 plots; values in parentheses are for 1 m^2 subplots. Letters following species group means show statistical significance according to a mixed model, first order autoregressive analysis with mean separation by the Tukey adjustment. Across rows, means with the same letter were not significantly different at alpha = 0.05.

Species	Unburned						Burned					
	1997		1998		1999		1997		1998		1999	
Native shrubs and trees	**40.6^{a}**	**(11.5)**	**33.9^{a}**	**(14.5)**	**33.7^{a}**	**(14.3)**	**0.4^{b}**	**(0)**	**0.5^{b}**	**(0)**	**0.7b**	**(0)**
Artemisia tridentata	18.1	(7.9)	14.4	(11.5)	14.2	(10.6)	+	(0)	+	(0)	+	(0)
Chrysothamnus viscidiflorus	6.0	(3.5)	4.9	(3.0)	4.9	(3.6)	0	(0)	0	(0)	0	(0)
Juniperus osteosperma	15.7	(+)	13.8	(+)	13.8	(+)	+	(0)	+	(0)	+	(0)
Native grasses	**8.5^{a}**	**(8.2^{e})**	**9.6^{a}**	**(9.4^{e})**	**6.3^{a}**	**(9.3^{e})**	**3.2^{a}**	**(1.0^{e})**	**4.4^{a}**	**(3.2^{e})**	**4.1^{a}**	**(1.5^{e})**
Elymus elymoides	5.9	(6.5)	5.5	(6.8)	4.5	(6.9)	1.1	(0.2)	1.3	(1.0)	1.1	(1.0)
Elymus smithii	0	(0)	0	(0)	0	(0)	0.5	(0)	0.5	(0)	1.5	(0)
Elymus spicatus	0.6	(0.3)	0.8	(0)	0.6	(0)	0.8	(0.1)	0.8	(0)	0.8	(+)
Poa spp.	1.2	(1.4)	2.7	(2.6)	0.9	(2.3)	0.5	(0.5)	1.5	(2.1)	0.1	(+)
Stipa hymenoides	0.8	(+)	0.6	(+)	0.4	(0.2)	0.3	(0.1)	0.3	(0.1)	0.5	(0.3)
Exotic grasses*	**19.0^{b}**	**(9.7^{f})**	**22.0^{bc}**	**(16.8^{f})**	**17.0^{b}**	**(9.1^{f})**	**28.6^{bd}**	**(28.0^{fg})**	**69.8^{a}**	**(75.7^{e})**	**54.7^{acd}**	**(54.6^{eg})**
Exotic forbs	**1.8^{a}**	**(2.4^{e})**	**1.3^{a}**	**(2.8^{e})**	**1.6^{a}**	**(1.8^{e})**	**4.4^{a}**	**(3.6^{e})**	**7.8^{a}**	**(11.0^{e})**	**8.5^{a}**	**(5.4^{e})**
Alyssum desertorum	0.3	(0.4)	0.4	(1.5)	0.6	(1.2)	0.7	(0.6)	0.2	(0.5)	0.2	(+)
Lactuca serriola	0	(0)	0.2	(0.2)	0.2	(+)	0.8	(0)	0.8	(0.4)	1.3	(2.3)
Sisymbrium altissimum	+	(0)	0.3	(0.8)	0.3	(+)	0.3	(0)	5.6	(9.7)	4.8	(2.1)
Native annual forbs	**0.5^{ab}**	**(0.2^{f})**	**0.5^{ab}**	**(0.3^{ef})**	**0.3^{b}**	**(0.1^{f})**	**8.3^{a}**	**(8.2^{e})**	**1.3^{ab}**	**(0.5^{f})**	**0.4^{b}**	**($+^{f}$)**
Gilia spp.	0.2	(0)	0.3	(+)	0.2	(0.1)	3.7	(3.9)	0.1	(0.3)	0.2	(0)
Mentzelia albicaulis	0	(0)	0	(0)	0	(0)	0.5	(1.3)	0	(0)	0	(0)
Nicotiana attenuata	0	(0)	0	(0)	0	(0)	1.7	(1.3)	0.1	(0)	0	(0)
Native perennial forbs	**8.1^{a}**	**(5.6^{e})**	**9.5^{a}**	**(6.3^{e})**	**8.5^{a}**	**(7.5^{e})**	**5.0^{a}**	**(3.8^{e})**	**3.8^{a}**	**(2.4^{e})**	**2.1^{a}**	**(0.6^{e})**
Astragalus spp.	0.9	(0.3)	1.0	(0.6)	0.6	(0.3)	0.9	(0.1)	0.8	(0.3)	0.3	(0)
Phlox austromontana	3.1	(2.3)	4.1	(1.8)	4.2	(2.6)	+	(0)	+	(0)	+	(0)
Sphaeralcea spp.	0.4	(0.1)	0.4	(+)	0.4	(0.1)	0.9	(0.2)	0.5	(+)	0.6	(0.1)
Vicia americana	0.6	(0.5)	0.5	(1.5)	0.3	(1.4)	0.4	(0.8)	0.6	(1.5)	0.1	(0)

*Exotic grass mean cover is equivalent to mean cover of *Bromus tectorum*

Table 5—Mean density per m^2 of selected species, based on counts in 1 m^2 plots, in burned and unburned treatments across 3 years, averaged across three sites in west-central Utah.

Species	Unburned			Burned		
	1997	1998	1999	1997	1998	1999
Native grasses						
Elymus elymoides	9.1	8.8	7.2	0.2	0.6	0.3
Elymus spicatus	0.4	0	0	0.1	0	0.2
Poa fendleriana	1.4	2.6	7.5	2.5	0.7	0
Stipa hymenoides	0	0	0.2	0.1	0.1	0.1
Bromus tectorum	84.1	76.3	89.2	55.3	157.5	345.8
Exotic forbs						
Alyssum desertorum	14.8	27.3	19.8	3.0	10.3	0.4
Camelina microcarpa	0	0.2	2.1	0	0.3	2.3
Lactuca serriola	0	1.4	0.3	0	1.5	26.8
Ranunculus testiculatus	?	?	9.0	62.3	0	1.0
Sisymbrium altissimum	0	0.5	0.6	0	5.2	6.2
Native annual forbs						
Gilia inconspicua	0	0.2	0.3	3.6	0.4	0
Mentzelia albicaulis	0	0	0	3.5	0	0
Native perennial forbs						
Astragalus calycosus	0.3	0.3	0.2	0.3	0.1	0
Phlox austromontana	3.8	2.3	3.7	0	0	0
Sphaeralcea coccinea	0.3	0.3	0.3	0	0	0.2
Sphaeralcea grossulariifolia	0	0	0	0.6	0.1	0
Vicia americana	3.8	2.8	2.9	2.6	4.5	0

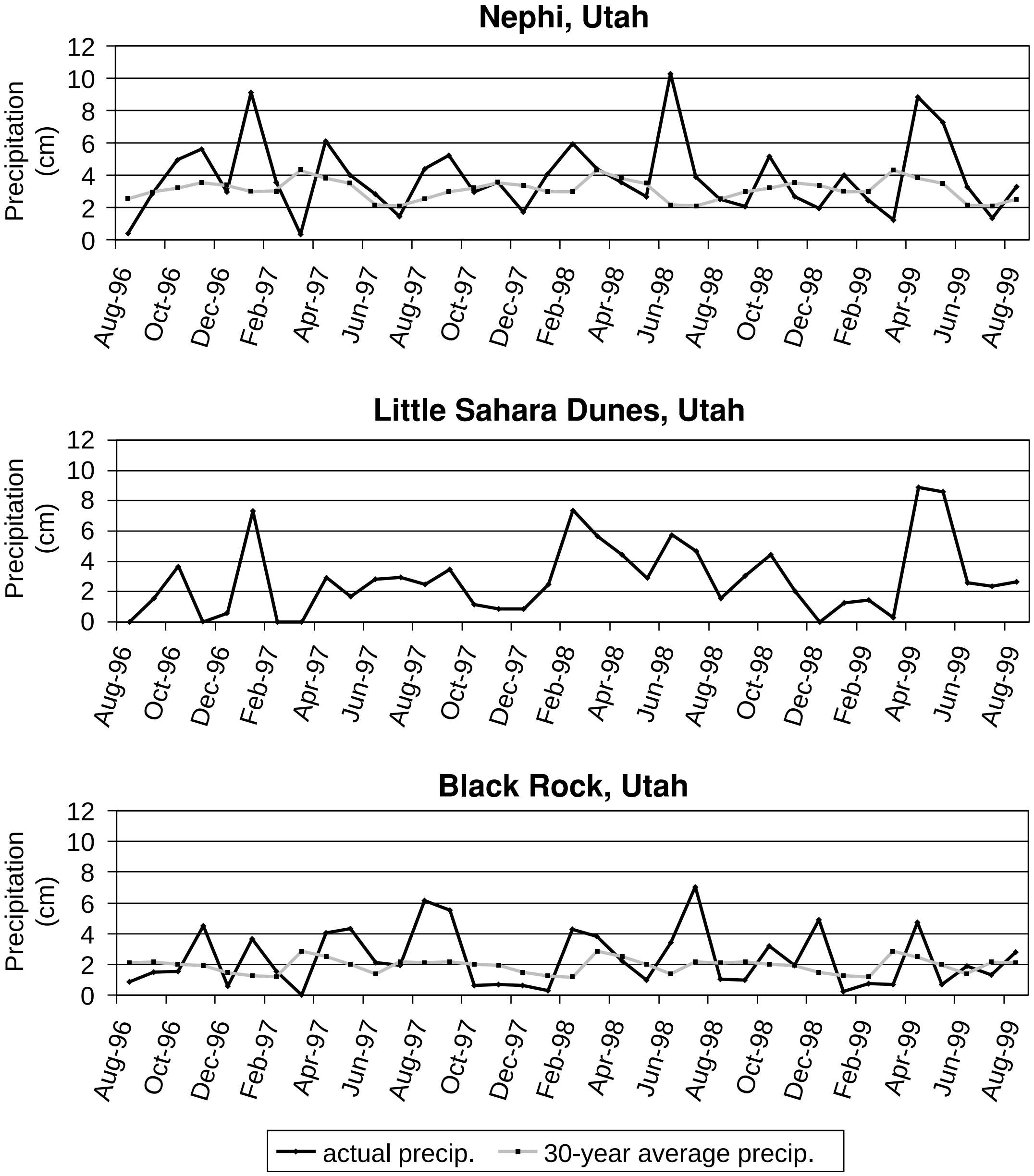

Figure 2—Monthly precipitation from August 1996 to August 1999 at three weather stations in west-central Utah (source: National Oceanic and Atmospheric Survey).

Results of mixed model analysis of synthetic cover for species groups are shown in table 4. Although, in the burned treatment, synthetic cover of native perennial forbs had a decreasing trend over time, and synthetic cover of exotic forbs had an increasing trend over time, these trends were not statistically significant. The decrease in native annual forb cover between 1997 and 1999 in the burned treatment appeared statistically significant, although the native annual forb group did not meet the assumption of normality according to the Shapiro-Wilk statistic. Only the native shrub and tree, exotic grass, and native perennial forb groups clearly met the assumption of normality for this model. Native shrubs and trees had significantly greater cover in the unburned treatment than the burned treatment for all years.

The most notable trend observed was a more than two-fold increase in exotic grass cover in the burned areas between 1997 (ca. 28 percent) and 1998 (ca. 70 percent in large plots and 76 percent in small plots). The trend was statistically significant (table 4). Cheatgrass density likewise increased between 1997 (55 per m^2) and 1998 (157 per m^2), and continued to increase to 345 per m^2 in 1999 (table 5). These data indicate that cheatgrass, the principal exotic grass, had an explosive population increase in the early-seral environment. Other authors have reported similar responses for this species following fire (Young and Evans 1978; Hosten and West 1994).

The decline of certain species over time in the burned treatment, concurrent with the increase of cheatgrass and other exotic species, suggests that competition may have shaped the observed dynamics. Factors such as climatic events and soil changes brought about by the fire may have interacted with competition to cause some populations to increase and others to decline. High precipitation during the cool season of the 1997 to 1998 period (fig. 2) undoubtedly contributed to the explosive increase of cheatgrass. Cheatgrass then appeared to displace or subdue many native forbs, which otherwise might have increased and reached peaks of cover during the second to fifth growing season following the fires (Everett and Ward 1984). Forb declines could also be related to periods of low precipitation, such as late summer of 1998 (fig. 2).

Comparison of Tree Canopy and Interspace

The successional dynamics described above did not proceed uniformly in all portions of the burned areas. Dynamics occurred at different rates in interspace and subcanopy areas. Although we did not detect delayed invasion of cheatgrass into the haloes of burned shrubs, as reported by Young and Evans (1978), we did observe a delay under the skeletons of juniper trees. Figure 3 illustrates this observation through a depiction of the spatial relationship between cheatgrass basal cover and tree canopy along the 1998 burned and unburned step-point transects at the Gilson study site. Along the unburned transects, cheatgrass was relatively rare, and was found most frequently beneath the canopy of living trees. This pattern may have been the result of more favorable nutrient, water, or seedbed characteristics in the subcanopy litter zone. The pattern also suggests that cheatgrass was resistant to allelopathic compounds in the juniper litter at that site. Along the burned transects, cheatgrass cover was much greater, but was concentrated in the interspaces rather than beneath the dead trees, even after two seasons of population increase.

As noted previously, heat loads appeared to have been high beneath most burned trees at our study sites. Plants, seeds, and litter were consumed beneath the trees, and hydrophobic soil conditions may have been generated (Blank and others 1995). Cheatgrass, which germinates best on surfaces with litter or microtopographic relief (Young and others 1976), did not immediately recolonize areas beneath burned trees. Factors inhibiting the establishment of cheatgrass in the subcanopy zones of dead junipers began to break down by the second year following the fire, when rings of newly established cheatgrass were frequently observed around the edges of burned juniper canopies. To the inside of these cheatgrass rings, we typically observed a ring of exotic annual forbs, dominated by mustards (family Cruciferae) such as tumblemustard, desert alyssum, and falseflax. Both the mustard and cheatgrass fronts had moved concentrically inward by the third season following the fire.

The foregoing successional pattern is illustrated for a 1 m^2 plot in the subcanopy zone of a dead juniper at the Gilson site (fig. 4). Density and cover data for this plot are shown in table 6, along with data for another meter-square plot that was located in an interspace zone. The plot in the subcanopy zone (fig. 4; table 6a) consisted primarily of bare soil and two species of native annual forbs (coyote tobacco and floccose gilia) in 1997. These species were replaced in 1998 by exotic species, primarily tumblemustard. By 1999, cheatgrass was the dominant species in the subcanopy plot, with cover of 85 percent. Even though cheatgrass invasion was delayed by a year in the subcanopy plot compared to the interspace plot (table 6b), density of this aggressive, exotic grass was approximately 400 per m^2 in both plots by 1999. In the interspace

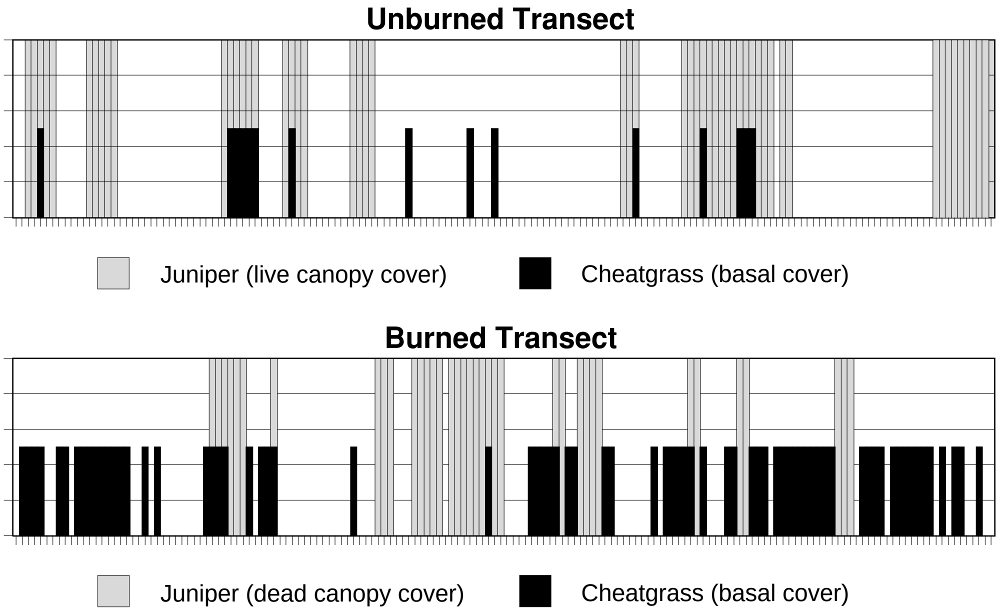

Figure 3—Spatial relationship between cheatgrass and juniper canopy along step-point transects in burned and unburned treatments of the Gilson study site in 1998 (second year post-fire). For each treatment, a composite of four transects of 40 points each, at intervals of 1 m is shown.

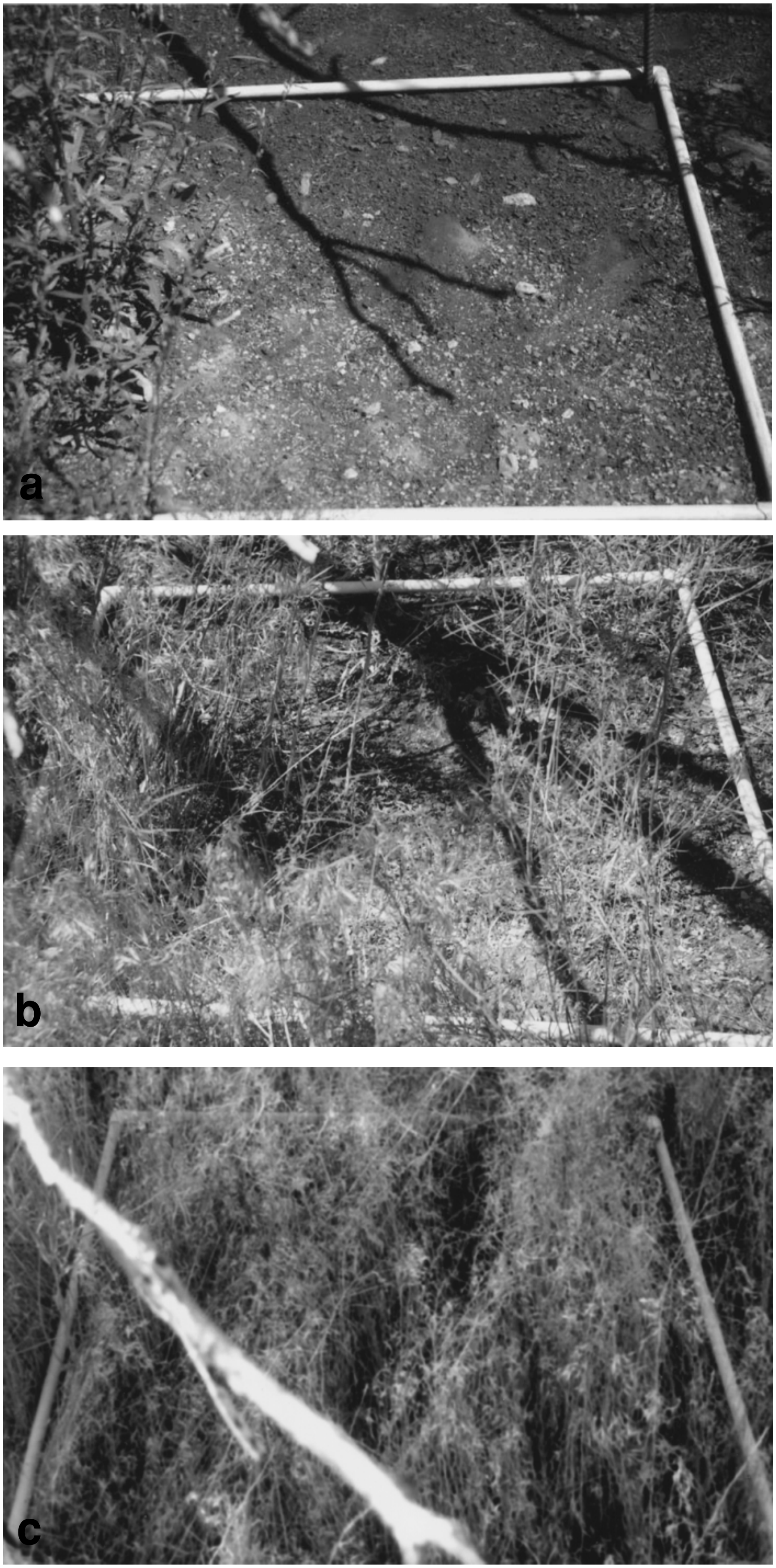

Figure 4—Photographic record of a 1 m^2 plot at the Gilson burned area, showing a representative sequence of changes occurring in the subcanopy zone of a burned juniper tree: (a) 1997 (first year after fire) bare ground/ native annual forbs; (b) 1998 (second year after fire) tumblemustard dominant; (c) 1999 (third year after fire) cheatgrass dominant. Also see table 6.

Table 6—Three-year post-fire trends of cover and density count by species for two representative 1 m^2 plots of the Gilson study site burned treatment.

	1997		1998		1999	
Species/category	Count	Percent cover	Count	Percent cover	Count	Percent cover
Tree canopy plot (see also fig. 2)						
Bromus tectorum	0	0	20	10	~400	85
Camelina microcarpa	0	0	0	0	25	5
Descurainia spp.	0	0	2	2	0	0
Gilia inconspicua	1	2	0	0	0	0
Lactuca serriola	0	0	1	<1	4	<1
Nicotiana attenuata	1	15	0	0	0	0
Sisymbrium altissimum	0	0	18	70	4	<1
Tragopogon dubius	0	0	0	0	1	1
Exposed litter	—	1	—	15	—	10
Exposed rock	—	14	—	10	—	<1
Exposed bare soil	—	70	—	45	—	<1
Tree interspace plot						
Alyssum desertorum	29	5	~100	5	0	0
Bromus tectorum	~150	30	~400	98	~400	65
Eriogonum deflexum	10	5	0	0	0	0
Gilia inconspicua	12	8	0	0	0	0
Lactuca serriola	0	0	0	0	6	1
Mentzelia albicaulis	40	15	0	0	0	0
Ranunculus testiculatus	40	10	0	0	0	0
Sisymbrium altissimum	0	0	4	1	1	<1
Vicia americana	10	5	22	8	0	0
Exposed litter	—	15	—	1	—	35
Exposed rock	—	10	—	<1	—	0
Exposed bare soil	—	5	—	<1	—	<1

plot, the 1998 cheatgrass crop contributed to the 1999 litter cover, with the result that cheatgrass litter and new cheatgrass growth together occupied nearly 100 percent of the plot surface in 1999. The decline of species such as American vetch (*Vicia americana*) in the interspace plot may have been related to the expansion of cheatgrass and/or drier conditions in 1998 and 1999.

Comparison of Study Sites

While some patterns and trends were common to all study sites, the uniqueness of each site was also evident. Step-point transect results illustrate some of the differences in composition and cover between sites in 1998 (table 7). One of the categories with the highest variability between sites was tree canopy cover, which was highest at Cunningham and lowest at Twin. Cunningham also had several woody species not recorded elsewhere (table 2), including pinyon (*Pinus edulis*), gambel oak (*Quercus gambelii*), mountain mahogany (*Cercocarpus montanus*), and mountain snowberry (*Symphoricarpos oreophilus*). Compared to the other study sites, Cunningham has higher elevation, steeper slopes, and rockier substrate (table 1). These characteristics indicate that Cunningham is probably a "true" pinyon-juniper site, whereas the other sites are probably sagebrush or sagebrush steppe that have been more recently invaded, to different degrees, by juniper.

The unburned communities at all sites had greater cover of exotic annual grass than native perennial grass (table 7). Prolonged grazing of livestock has probably occurred at these sites and contributed to the observed pattern. Of the unburned treatments, Cunningham had the lowest basal cover of native grass (2 percent) relative to exotic grass (12 percent) in the 1998 step-point results (table 7). The disparity between native grass and exotic grass cover was even greater in the Cunningham burned treatment (2 percent native, 22 percent exotic), but not as high as the burned treatments of other sites, where exotic grass cover ranged from 45 to 60 percent (table 7). The lower exotic grass cover at Cunningham appears to have been directly related to the presence of seeded species, particularly seeded grasses, which had 17 percent cover in 1998 (table 7). Crested wheatgrass (*Agropyron cristatum*), intermediate wheatgrass (*Elymus hispidus*), and smooth brome (*Bromus inermis*), the primary seeded grasses at the Cunningham site, have been shown to be good cheatgrass competitors (Francis and Pyke 1996; Wicks 1997; Whitson and Koch 1998). To a lesser degree, native perennial grasses such as bluebunch wheatgrass and bottlebrush squirreltail are also competitive with cheatgrass (Reichenberger and Pyke 1990; Stevens 1997). Evidence suggests that cheatgrass proliferation following fire can be suppressed by a good cover of native perennial grasses (West and Hassan 1985). These findings highlight the importance of perennial grasses for rehabilitation or restoration of cheatgrass-infested areas.

Table 7—Mean percent cover of species groups and other categories in 1998 (second season following fires), in burned and unburned treatments at four sites in west-central Utah. Based on percentage of hits from four step-point transects of 40 points each per treatment/site combination.

	Unburned					Burned				
	Cunningham	**Gilson**	**Jericho**	**Twin**	**Mean**	**Cunningham**	**Gilson**	**Jericho**	**Twin**	**Mean**
Basal cover										
Native shrubs	0	0	2.5	1.3	0.9	1.9	0	0	0	0.5
Native grasses	1.9	3.1	2.5	7.5	3.8	1.9	1.9	1.9	3.8	2.3
Exotic grasses	12.5	9.4	11.3	18.1	12.8	21.9	45.6	56.9	55.6	45.0
Seeded grasses	0	0	0	0	0	17.5	0	0.6	0	4.5
Seeded forbs	0	0	0	0	0	1.3	0	0	0	0.3
Exotic forbs	1.3	2.5	0.6	0.6	1.3	0	1.3	0.6	0	0.5
Native annual forbs	0.6	0	0	0	0.2	0.6	0	0	0	0.2
Native perennial Forbs	0.6	1.3	0	8.1	2.5	1.9	0	0	0.6	0.6
Cryptogams	0	13.8	10.0	1.9	6.4	0	0.6	1.9	0.0	0.6
Litter	39.4	35.0	23.8	21.9	30.0	6.3	19.4	15.0	16.9	14.4
Rock	31.9	11.9	12.5	13.1	17.3	30.6	3.8	4.4	11.9	12.7
Bare soil	11.9	23.1	36.9	27.5	24.8	16.3	27.5	18.8	11.3	18.4
Canopy cover										
Live trees	59.4	33.8	10.6	7.5	27.8	0	0	0	0	0
Dead trees	0	0	0	0	0	40.0	23.1	5.0	1.3	17.3

Conclusion

The study presented here offers a rough glimpse of fire effects and successional characteristics of numerous species occurring in the sagebrush and pinyon-juniper communities of west-central Utah. We found many native species in late-seral sagebrush and pinyon-juniper communities at our study sites, even though these sites had been disturbed by prolonged livestock grazing and the introduction of exotic species. Fire in these communities resulted in a shift in dominance from woody to herbaceous species, especially annual species. The post-fire community continued to change over the 3-year period of observation. Certain species increased while others declined or remained relatively stable. Exotic species, particularly cheatgrass, appear to have strongly influenced the character and rate of succession observed. Beneath burned juniper trees, exotic annual mustards displaced native annual forbs, and may have created conditions leading to their own displacement by cheatgrass. Although exotic species undoubtedly had an impact, not all exotic species were aggressive intruders, and not all native species appeared to be adversely affected by the presence of exotics.

An understanding of the dynamics and interactions among the species that currently occupy these communities is important for effective management and restoration efforts. Complete restoration of degraded sagebrush and pinyon-juniper communities will be difficult because of the presence of exotic species. Nevertheless, communities in which exotic species are subordinate to competitive or tolerant native species can perhaps be attained through restoration efforts. The period immediately following fire is a window of opportunity in which intervention could favor native species. Failure to seed burned sites will usually permit exotic annuals to proliferate. The result may be stable systems dominated by exotic annuals and a short fire-return cycle.

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Response of Residual Native Species After Two-Way Chaining and Seeding in Utah

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Abstract—Pinyon-juniper woodlands have dramatically increased in both tree density and distribution over the last 150 years. This change led to depleted native herbaceous understory in pinyon-juniper woodlands. One method to increase herbaceous understory is to remove the trees and aerially seed. The objective of this study was to determine how variations of seed mixes used in past revegetation projects have affected residual native species.

Native herbaceous understory diversity and abundance were significantly greater in chained and seeded sites than in non-chained sites ($p \leq 0.02$ and $p \leq 0.05$ respectively), although diversity and abundance were low in both. Native herbaceous understory richness was similar between chained/seeded sites and non-chained pinyon-juniper sites. Seeding rates and mixtures showed low correlation with post-treatment native species diversity and abundance. The post treatment combined abundance of crested wheatgrass [*Agropyron cristatum* (L.) Gaertner] and intermediate wheatgrass [*Elymus hispidus* (Opiz.) Meld.] was negatively associated with native herbaceous understory diversity after two-way chaining and seeding with exotic species ($r^2 = 0.76$).

Future revegetation projects, on sites similar to those in central and southern Utah, should include a more site-specific approach to increasing native herbaceous understory diversity or abundance than the broad approach previously used in the revegetation efforts examined here. If increasing native species diversity or abundance are objectives in future revegetation projects, inclusion of adapted native species in conjunction with decreasing the proportion of exotic species in seed mixtures may be required.

Introduction

Pinyon-juniper [*Pinus edulis* Engelm. and *Juniperus osteosperma* (Torr.) Little] woodlands cover approximately 18 million hectares throughout the Intermountain West and approximately 6 million hectares in Utah (West 1984; O'Brien and Woudenberg 1999). Over the last 150 years pinyon-juniper woodlands have dramatically changed in tree density (from an open savanna type with scattered trees to a closed canopy community) and distribution (movement of woodlands into lower and higher elevations) (Tausch 1999; West 1999).

The principal factors believed to contribute to the changes in tree density and distribution of pinyon-juniper woodlands include: (1) heavy livestock grazing following European settlement (West 1984), (2) an increase in fire suppression and corresponding decrease in fire frequency (West 1984; Bunting 1994), (3) a change in climate with rising mean annual temperatures (Ghil and Vautgard 1991), (4) cessation of the hunting, gathering and burning by populations of indigenous people that occurred during the Little Ice Age (Creque 1996; Tausch 1999), and (5) increasing atmospheric CO_2 levels that change community competitive interactions in favor of dominance by large woody perennials (Polley and others 1996; Farquhar 1997).

As pinyon-juniper woodlands become more dense and spread into adjacent sagebrush-grass plant communities, interspecific competition between trees and the understory species increase. Pinyon and juniper trees influence understory plants in several ways: by shading, sub-canopy litter accumulation and by the competition for soil moisture through the development of an extensive and competitive shallow root system (Schott and Pieper 1985). As mature trees obtain dominance, the remaining understory species are severely suppressed. Hurst (1975) and Dye and others (1995) report that understory suppression generally varies inversely with the tree overstory density. Additionally, Arnold and others (1964) found that as canopy cover increases, basal cover of grasses and forbs decrease.

Beginning in the early 1950s, earnest efforts were undertaken to improve the depleted pinyon-juniper ranges in the Western United States through mechanical removal of the pinyon-juniper overstory and replacement with a desirable shrub-herbaceous understory. Early efforts focused on increasing forage for livestock, while later objectives were expanded to include wildlife habitat restoration and watershed protection (Fairchild 1999; Roundy 1996). Early improvement techniques included: anchor chaining, cabling, hula dozing, bulldozing, windrowing and burning, and chemical treatments. After extensive research, two-way anchor chaining was most commonly employed because it was cost efficient, effectively reduced pinyon-juniper tree densities (Aro 1971; Parker 1971; Phillips 1977; Stevens 1999) and prepared an excellent seedbed (Plummer and others 1968; Stevens 1999). Two-way chaining entails dragging an anchor chain between two tractor crawlers one direction, aerially seeding, and then back chaining in the opposite direction to cover the seed and increase pinyon and juniper tree mortality (Plummer and others 1968; Aro 1975; Stevens and others 1975; Stevens 1999).

Due to understory suppression, pinyon-juniper woodlands usually lack sufficient seed of grass, forb and browse species

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for natural recovery of the community after treatment. To establish desired vegetation cover, seeds of desired species are often sown during treatment. Many successful revegetation projects in the Western United States resulted in replacement of degraded plant communities with substitutes containing mostly exotic species.

Requirements for establishing native species from seed in a rangeland setting were not fully understood in these early revegetation efforts. Native species showed poor establishment, seed availability was low and the seed that was available was relatively expensive (Pyke 1995). Additional factors prohibiting native species from being included in seed mixes were the inability of native plants to compete with exotic weeds such as cheatgrass [*Bromus tectorum* L.] and the susceptibility of native species to grazing (Anderson and Marlette 1986; Roundy and Call 1988; Chambers and Norton 1993). Extensive research was initiated on the establishment requirements of native plants, as well as several species from Europe, Russia and Asia (Plummer and others 1968; Kilcher 1969; Monsen 1975). Through this research, many exotic species demonstrated a better ability than native species to successfully establish and persist under arid conditions following chaining and seeding pinyon-juniper woodlands.

As a result of the success of selected exotic grasses, large tracts of treated pinyon-juniper woodland were seeded; generally with only a few exotic grass species dominating seed mixtures. Species diversity following treatment was not as much of a concern as the establishment of some type of vegetation, whether native or exotic (Pyke 1995). Two grasses in particular, crested wheatgrass [*Agropyron cristatum* L.] and intermediate wheatgrass [*Elymus hispidus* (Opiz) Meld], were used extensively for seeding rangelands throughout the Western United States because they were easily established and seed was readily available at low cost. Additionally, with the aggressive habits of these grasses, land managers felt they had found a tool to control weeds, reduce soil erosion and maintain or increase grazing capacities.

Plummer and others (1968) recognized several advantages for rangeland seedings to contain diverse seed mixtures rather than single species for several reasons. First, many of the areas that are seeded have varying terrain, micro-surface reliefs and climatic conditions. A diverse seed mixture will allow adapted species to excel and persist in different niches within the treated site. Second, a variety of forage species can extend the season of use for both livestock and wildlife. Third, a diverse community provides better overall ground cover than single species stands. Fourth, higher species diversity makes the community more resilient and shortens recovery time from long term disturbance. Although the aforementioned recommendations were made with respect to seed mixes in the late 1960s, few Federal land managers prescribed diverse seed mixes in chaining treatments until the mid to late 1980s.

Pyke and Archer (1991) asserted that competitive relationships of species used in rangelands need to be identified to determine if species can coexist and thereby facilitate greater species diversity on the site. Furthermore, a diversity of species and growth forms would provide more stable cover and more dependable productivity than a monoculture, because most sites are characterized by environmental variability. Pyke (1995) points out that even though competitive exotic species may be effective in suppressing weedy species, this same aggressive value may exclude desirable native species as well. Compatibility and competitive relationships among plants in mixtures appear to be rarely considered and research providing quantitative evidence is lacking.

Our objectives in this study were to determine whether native species diversity, richness and abundance differ between two-way chained and seeded plots and adjacent non-chained pinyon-juniper woodlands in Utah. Secondly, are there variables that can predict or explain these differences?

Methods

Study Sites

Ten sites were chosen for study throughout central and southern Utah that represent typical pinyon-juniper chainings. Study sites were located on state and Federal lands where the treatments had been conducted by Bureau of Land Management, U.S. Forest Service and/or Utah Division of Wildlife Resources personnel. Seed mixtures varied across sites with respect to seeding rate, number of species/mix and the proportions of individual species within each mix.

Chained sites ranged in age from 10 to 21 years since treatment. Non-chained sites are best characterized as climax pinyon-juniper woodlands with high canopy cover and sparse herbaceous understory. A few scattered shrubs were present and dominant overstory species were pinyon pine and Utah juniper. Chained sites contained mostly exotic grasses with the majority of sites exhibiting some reencroachment of pinyon-juniper trees. Trees that were uprooted in the chaining treatment had been left on the ground as litter. Plant composition on chained sites included some native species that were present in the non-chained woodlands as well as exotic species that were seeded as part of the two-way chaining and seeding treatments.

A pair of study plots were established at each site. One of the paired plots was placed in pinyon-juniper woodland that had been two-way chained and aerially seeded between chaining passes with exotic grasses and forbs. The second of the paired plots was placed in adjacent non-chained pinyon-juniper woodland. To reduce any confounding effects due to placement of study plots, specific criteria for elevation, aspect and slope were used. The range of acceptable values for these variables were: (1) slopes below 20 percent, (2) aspects of south or west exposure, and (3) elevations from 1,800 to 2,400 m.

Only native grass and forb species (hereafter referred to as native herbaceous understory) were considered for native diversity, richness and abundance. Native shrubs were often included in seed mixtures, and inclusion of these shrubs in data analysis would confound interpretations about natural occurrences. Soil samples were collected at each site and analyzed for physical and chemical properties at Brigham Young University's Soil and Plant Analysis Laboratory. Although soil texture at the study sites varied, the majority had soil texture characterized as sandy loam or sandy clay loam.

Data Collection

Vegetation at each site was sampled along a 150 m transect. A 1 m^2 quadrat was placed on alternating sides of the transect, beginning on the left at the zero meter mark, and continuing at each 3 m interval for a total of 50 quadrats per transect. Percent cover of vegetation and cryptogamic crusts were estimated within each quadrat using a modified Daubenmire cover class method (Daubenmire 1959; Bailey and Poulton 1968). Nested frequency was determined for each species and cover type following Smith and others (1986, 1987). Nested frequency value were summed for each species over all quadrats (50) to get a total value for the site (a maximum value of 250).

Density of pinyon and juniper trees at 30 m intervals along each transect sites was estimated using the point-centered quarter method (Cottam and Curtis 1956). Canopy cover of pinyon and juniper trees was measured along each transect using the line-intercept method (Canfield 1941). Cover and nested frequency data for non-vegetation variables were also collected using the methods previously described. Non-vegetation variables include: litter, bare ground, rock and pavement.

Species richness (S) was defined as the total number of species encountered at a site. The Shannon-Weiner index was used to determine species diversity (S´) because it is more sensitive to the abundance of rare species (Peet 1974). S´ is the number of species of equal abundance in a community and equates to the antilog of $H' (\sum(p_i)(\log_2 p_i))$, which is often used as the index of species diversity when using the Shannon-Weiner index (Krebs 1999).

Analysis

Differences in native herbaceous understory abundance, richness and the percent change in diversity between treated and native sites were tested using paired t-tests. The percent change in native species diversity was used so that relative comparisons could be made across all sites. Additionally, differences in individual native species abundance between chained and non-chained sites were also examined.

Regression analysis was used to develop predictive models for post-treatment changes in native species diversity and abundance. In the models, percent change in native species diversity and abundance between chained and non-chained woodlands were used as response variables. Time since chaining is a continuum and was used as a predictor variable to examine how time after treatment affects diversity and abundance across sites. Similarly, seeding rates are a continuum and were used as predictor variables to examine the effect of different seeding rates on native species diversity and abundance.

Several seed mix variables were examined including: total lbs/acre of seed, total number of seeds/m^2, total number of grass seeds/m^2, the proportion of the seed mix that was composed of crested and intermediate wheatgrasses seed (both individually and combined) and the individual and combined abundance of crested and intermediate wheatgrass after treatment.

Individual and combined abundance values for crested and intermediate wheatgrasses after treatment, as measured by sum of nested frequency, were used as predictor variables to examine possible post-treatment species effects. Pure live seed (PLS) information was unavailable for most sites. Therefore, data analysis concerning seed mixes was estimated using bulk seed rate information obtained from *Range Development and Improvements* (Vallentine 1989).

Results

Vegetation

Herbaceous understory cover was significantly greater (p = <0.001) for the chained sites than for the non-chained sites. Mean cover values were 18.9 percent and 1.9 percent respectively. Native herbaceous cover was different (p = 0.192), with 1.9 percent cover on the non-chained sites and 4.6 percent cover on the chained sites. Seeded grasses were not encountered on the non-chained sites.

Abundance, Diversity, and Richness

Native herbaceous understory abundance was significantly greater (p = 0.054) in the non-chained sites as compared to chained sites (fig. 1). Non-chained sites had 1.5 times greater sum of nested frequency values than chained sites. Native herbaceous understory richness was similar (p = 0.570) in the chained and non-chained sites averaging 11.4 species and 10.5 species respectively (fig. 2). Native herbaceous understory Shannon-Weiner diversity values were significantly greater (p = 0.022) in the non-chained than in chained sites (fig. 3). Non-chained sites had mean Shannon-Weiner diversity values nearly 2 times greater than the chained sites. Differences in individual species abundance were examined across all sites, however, individual native species were not encountered frequently enough to allow for statistical analysis.

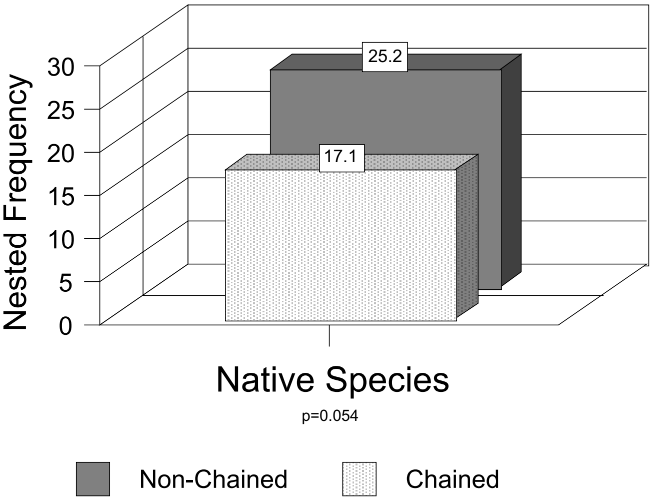

Figure 1—Native herbaceous understory species abundance.

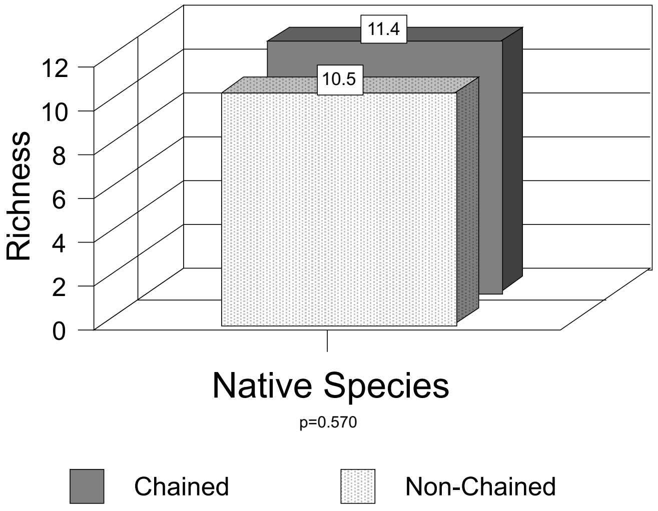

Figure 2—Native herbaceous understory species richness.

Time Since Treatment

Regression analysis was completed for time since treatment with native herbaceous understory diversity and native herbaceous understory abundance as response variables. Low correlation between native herbaceous understory abundance or diversity and time since treatment indicated no significant differences.

Seed Mixtures and Post-Treatment Abundance

Regression analysis was completed for several seed mixture variables, the abundance of crested and intermediate wheatgrasses after treatment as predictor variables with native herbaceous understory abundance and diversity as response variables (table 1). Native herbaceous understory abundance was negatively associated with the proportion of crested wheatgrass in the seed mix with an r^2 value of 0.55. Additionally, abundance of crested wheatgrass after treatment was negatively associated with native herbaceous understory abundance with an r^2 value of 0.61.

All seed mix variables examined showed poor correlation with native herbaceous understory diversity after treatment. However, the combined abundance of crested and intermediate wheatgrass after treatment best predicted the percent change in native herbaceous understory diversity after treatment. The combined abundance is negatively associated with an r^2 value of 0.76 (table 2).

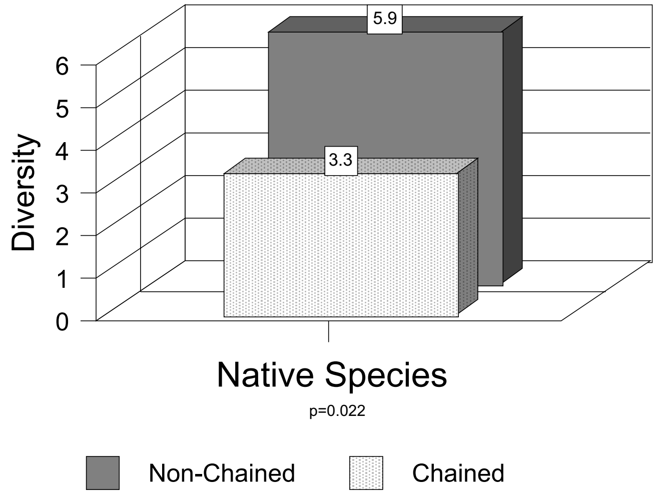

Figure 3—Native herbaceous understory species diversity.

Discussion

In this study, the non-chained sites had significantly greater native herbaceous understory diversity and abundance than the chained area. Although analysis indicated this was statistically significant, native herbaceous understory plants were rarely encountered and made up only a small portion of the cover in both the chained and non-chained woodland. The response of native species after two-way chaining and seeding pinyon-juniper sites can be influenced by several factors. These include: (1) plant density, condition and age of the plants left on the site following treatment, (2) competition from any seeded species, (3) grazing by wildlife and livestock, and (4) climatic conditions following treatment (Walker and others 1995). These influences could effect native herbaceous understory diversity and/or abundance after treatment.

Native species abundance, although significantly greater in the non-chained sites, was considered very low across all sites to begin with. Different factors can influence abundance of native species in both non-chained and chained sites, but residual effects of the pinyon and juniper trees may affect the native species in the chained area well after the treatment was completed. The subsequent community changes and the impact of competitive exotic species on desirable and undesirable species after treatment with crested and intermediate wheatgrass are generally well known and can provide insight about the results of our study.

Studies conducted by Heinrichs and Bolton (1950) in Saskatchewan lead them to conclude that crested wheatgrass was a strong competitor and eventually excluded some native species when seeded into areas of established introduced and native species. Hull and Klomp (1966) reported crested wheatgrass exhibited continued high production over a 33-year period. It persisted and even spread in some locations under adverse conditions. This included: heavy use, disease and extremes in temperature and moisture. Additionally, Hull and Stewart (1948) found crested wheatgrass to survive and spread into stands of cheatgrass.

Pavlychenko and Kirk (1946) conducted a study to determine if crested wheatgrass could control perennial weeds on dryland farms in Saskatchewan, Canada. Plots containing well established stands of perennial sow thistle [*Sonchus arvensis* L.], blue lettuce [*Lactuca tatarticas* L.], toad flax [*Linaria canadensis* (L.) Dum.-Cours.], Canada thistle

Table 1—Significance of seeding variables on native herbaceous understory abundance for chained pinyon-juniper woodlands in Utah.

Variable	F-value	Prob>F	r^2-value
Total seed lbs/acre	2.10	0.19	0.23
Total seed/m^2	3.25	0.11	0.29
Grass seed/m^{2*}	8.11	0.02	0.50
Proportion of crested wheatgrass in mix (seeds/m^2)*	9.71	0.01	0.55
Proportion of intermediate wheatgrass in mix (seeds/m^2)	1.18	0.31	0.13
Proportion of crested and intermediate wheatgrass in mix (seeds/m^2)*	8.00	0.02	0.50
Crested wheatgrass abundance after treatment*	12.63	0.01	0.61
Intermediate wheatgrass abundance after treatment*	0.14	0.72	0.02
Crested and Intermediate wheatgrass abundance after treatment*	5.07	0.05	0.39

* Negatively associated with response variable.

[*Cirsium arvense* (L.) Scop.], field bindweed [*Convolvulus arvense* L.], leafy spurge [*Euphorbia esula* L.], poverty weed [*Iva axillaris* L.], white top [*Cardaria draba* (L.) Desv.] and Russian knapweed [*Centaurea repens* L.] were hand seeded with crested wheatgrass at a rate of 28 kg/ha. After 5 years, all plants of perennial sow thistle, blue lettuce, toad flax and Canada thistle were eliminated from the plots. All other species were greatly reduced with field bindweed showing the least suppression. Crested wheatgrass was also recommended for seeding abandoned farmland occupied by Russian thistle [*Salsola iberica* A. Nels.] and tumble mustard [*Sisymbrium altissimum* L.] by Reitz and others (1936).

Intermediate wheatgrass has similar traits as crested wheatgrass with the exception that it is a sod former and is not as drought tolerant. It is able to compete very well with other species for resources and quickly established after seeding on treatments in Utah (Plummer and others 1970). Plummer and others (1970) also reported that a seed mixture containing crested wheatgrass, intermediate wheatgrass and Russian wildrye essentially eliminated cheatgrass on a site in Central Utah. Similarly, Skousen and others (1989) showed crested wheatgrass, intermediate wheatgrass and Russian wildrye to establish and persist over a long period of time in the Intermountain region.

Plant nutrients are essential for plant communities to establish and persist after treatment. Pinyon and juniper trees that have invaded a site and are now dominant in communities claim much of the water and nutrient resources that were previously used by the herbaceous species (Doughty 1987). Tiedemann (1987) reported that invasion of grass/forb and sagebrush/grass areas by pinyon and juniper was accompanied by a greater nutrient accumulation in

Table 2—Significance of seeding variables on percent change in native herbaceous species diversity (Shannon-Weiner Index) after treatment for chained pinyon-juniper woodlands in Utah.

Variable	F-value	Prob>F	r^2-value
Total seed lbs/acre	0.48	0.51	0.07
Total seed/m^{2*}	0.00	0.99	0.00
Grass seed/m^{2*}	1.08	0.33	0.12
Proportion of crested wheatgrass in mix (seeds/m^2)*	2.59	0.15	0.25
Proportion of intermediate wheatgrass in mix (seeds/m^2)*	0.96	0.36	0.11
Proportion of crested and intermediate wheatgrass in mix (seeds/m^2)*	2.50	0.15	0.24
Crested wheatgrass abundance after treatment*	4.62	0.06	0.37
Intermediate wheatgrass abundance after treatment*	6.77	0.03	0.46
Crested and Intermediate wheatgrass abundance after treatment*	25.56	0.00	0.76

* Negatively associated with response variable.

aboveground biomass. The native woodland sites investigated in this study were considered to be mature with a lack of herbaceous understory. Due to the lack of herbaceous understory species and the associated poor seed bank, seeds of exotic, perennial species were seeded during treatment to enhance the herbaceous vegetation component. Resources redistributed by removing the dominant pinyon-juniper overstory would be available for seedling establishment and plants that were present at the time of treatment. Exotic species may benefit more than natives species due to the shear abundance of exotic species seed on site. Furthermore, aggressive species, such as crested and intermediate wheatgrass, would have an even greater advantage due to less stringent germination requirements, more competitive seedlings and post-establishment competitiveness as compared to native species. Not surprisingly, seeded species abundance (sum of nested frequency) was significantly greater than native species abundance (66.5 and 17.1 respectively) after treatment on the sites examined in this study.

Another factor perhaps influencing the significant difference in diversity and abundance between chained and non-chained sites may be site potential changes imposed by the new assemblage of species on the treated sites. Several studies suggest that there may be long term negative impacts by crested wheatgrass stands on soil. Lesica and DeLuca (1999) provide a comprehensive review of literature regarding soil changes that can be attributed to crested wheatgrass stands in a mid-grass prairie. For instance, crested wheatgrass stands have a lower below ground biomass than the native prairie grasses (Dormaar and others 1995; Smoliak and Dormaar 1985). This can lead to lower energy input into the soil as compared to the native range and alter physical and biochemical processes (Dormaar and others 1978). Stands of crested wheatgrass are associated with higher bulk density, fewer water stable aggregates and lower levels of organic matter and nitrogen compared to stands of native grasses (Redente and others 1989; Dormaar and others 1978; Smoliak and others 1967). Crested wheatgrass also provides the soil with a relatively high concentration of carbohydrates and little organic nitrogen (Klein and others 1988). Klein and others (1988) suggest that these alterations to soil quality may prevent native species from invading crested wheatgrass monocultures. Mid-grass prairies obviously have different soil and site potentials, but it is worth pointing out the influences crested wheatgrass exhibits in some situations that were not examined in this specific situation. Similar soil chemical and physical changes may be occurring to soil in the Intermountain region after chaining and seeding with crested wheatgrass and may be restricting native species expansion or persistence.

Another influence listed by Walker and others (1995) affecting the recovery of residual native species following treatment is livestock and wildlife grazing. While livestock access and utilization of treated sites can be somewhat controlled, wildlife utilization, and its' measurement, is another matter.

Some variables that were presumed to influence native species response prior to this study ultimately showed low correlation. For instance, it was hypothesized that as time passed since chaining, native species would increase in density relative to when it was seeded. Our data indicate that this is not the case as seeded species values were similar for all sites regardless of time since treatment. Similarly, Walker and others (1995) reported that although native grass abundance responded positively for 3 years following chaining, the native grasses slowly started showing negative response and declined over time, presumably from competition with exotic grasses. They also report that 23 years after chaining and seeding, the exotic grasses became more dominant in the communities and that plant dominance had not yet stabilized.

Seed mixes used in the revegetation projects examined in this study varied with respect to total seeding rate and the proportion of various species such as crested and intermediate wheatgrass within the mixture across all sites. One objective of this study was to determine if variations of seed mixtures affected native species diversity and abundance. Data from this study indicated that both native species abundance and diversity were significantly lower in the chained plots versus the non-chained plots. However, these differences were best correlated with the abundance of crested and intermediate wheatgrass after chaining and seeding rather than the specific seed mixtures used on the sites. This raised the question whether a correlation exists between the seed mixes used on these sites and the resulting abundance of species following treatment. If a significant correlation existed, seed mixes might be tailored for improved native species response.

Regression analysis showed low association between proportions of species in the seed mixes and the relative abundance of crested and intermediate wheatgrass after treatment. These results are similar to those of Davis and Harper (1990). They reported that it is difficult to maintain a stand of specified composition after treatment because each species responds differently to natural and imposed environmental factors. Pyke (1995) also points out that although many species are included in a seed mix, establishment and persistence of each species depends on many biotic and abiotic factors. With this in mind, it should not be surprising that the assemblage of plants on a site would not necessarily correlate to the seed mix applied to the site and would vary through time in response to various external factors.

The judgement of success or failure of the treatments reviewed in this study should not be solely based on the diversity or abundance of native species following treatment. The goals and objectives for the revegetation projects examined in this study were generally to protect the soil resource, increase forage for livestock and/or restore big game ranges; not to enhance native species diversity or abundance. The approach used by these land managers was to get desirable plants, whether they be exotic or native, to establish under arid conditions following chaining pinyon-juniper woodlands. If increasing native species diversity or abundance is to be considered an objective in the future, this study indicates that a different approach than previously used should be taken on sites similar to those examined in this study.

Conclusions

Native species diversity and abundance were significantly lower after chaining and seeding. Varying combinations of introduced species in the seed mix showed some association with the resulting native herbaceous understory diversity and abundance. However, post-treatment abundance of crested and intermediate wheatgrass combined was the best indicator of native herbaceous understory diversity. This association was negative. Although this may lead one to believe that if the proportion of crested and intermediate wheatgrass were decreased in the seed mix, the abundance of these species after treatment would decrease as well. This was not the case as the proportion of crested and intermediate seeds in the seed mix had low correlation with crested and intermediate wheatgrass abundance at the point in time when these sites were sampled.

Inclusion of adapted native species in the seed mix in conjunction with decreased proportions of introduced species may be one alternative to enhance the native species community after treatment. This does not necessarily mean excluding exotic species from seed mixes entirely, but determining the correct balance of exotic and native species. Because site potential is potentially altered after pinyon-juniper invasion and the ensuing treatment, native species alone in a seed mix may be inadequate to satisfy desired goals or objectives, especially in light of the abundance of invasive annual and secondary perennial weeds spreading throughout the Intermountain West. Initially, protection of the site may be the prudent course of action with follow up treatments designed to increase native species diversity.

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Winterfat Decline and Halogeton Spread in the Great Basin

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Abstract—Winterfat (*Ceratoides lanata*) is a long-lived shrub with excellent drought tolerance and good to moderate tolerance for herbivory. It often occurs as near monocultures in deep fine-textured soils of alluvial fans and valley bottoms. Winterfat communities are second only to those of shadscale (*Atriplex confertifolia*) in dominance of the 16 million ha of salt-desert shrublands found in Western North America. In spite of improved grazing practices, winterfat is declining in many areas of the Great Basin. The Eurasian summer annual, halogeton (*Halogeton glomeratus*), is well adapted to the soils and climate associated with winterfat communities and is invasive, replacing winterfat on degraded sites. Recolonization of halogeton stands by winterfat is rare. Subsequently, distinct winterfat- and halogeton-dominated communities often occur side by side. At the Desert Experimental Range (Utah), episodic winterfat mortality at the ecotone has been observed particularly after flood events and periods of higher than average precipitation. The upward translocation and accumulation of cations, particularly sodium, in the soil by halogeton may account, at least in part, for the lack of winterfat establishment in halogeton stands. Other evidence suggests that a possible halogeton-induced change in soil microbiota may also be unfavorable for winterfat. The development of viable management options to restore winterfat communities will require a greater understanding of plant-soil interactions for these species.

Winterfat

Winterfat, or white sage (*Ceratoides lanata*), is a long-lived short- to medium-statured chenopod shrub with excellent drought tolerance (Chambers and Norton 1993) due in part to an extensive fibrous root system and deep penetrating taproot (Stevens and others 1977). It occurs in near monocultures on fine textured lacustrine deposits found in dry valley bottoms and as a more or less primary component of mixed communities on deep alluvium derived from calcareous substrate. Until recent decades, winterfat dominated the 'island' communities associated with rodent burrow clusters, which are scattered within otherwise mixed shrub/grass communities of valley alluvium (Kitchen and Jorgensen 1999).

Winterfat communities are second only to those of shadscale (*Atriplex confertifolia*) in dominance of the 16 million ha of North American salt-desert shrubland found primarily in the Great Basin (Blaisdell and Holmgren 1984). Common native associates include shadscale, budsage (*Artemisia spinescens*), low rabbitbrush (*Chrysothamnus greenei*), black sagebrush (*Artemisia nova*), Indian ricegrass (*Oryzopsis hymenoides*), galleta (*Hilaria jamesii*), and gooseberryleaf globemallow (*Sphaeralcea grossulariifolia*). Within the context of currently accepted models incorporating multiple stable states, successional pathways, and interstate thresholds (Friedel 1991; Laycock 1991), a species that is represented in multiple stable states might be safely considered late seral. Winterfat is such a species (Comstock and Ehleringer 1992). Consistent with a late seral strategy (Grime 1977; Tilman 1988) are winterfat traits of plant longevity (Chambers and Norton 1993), inconsistent seed production (Blaisdell and Holmgren 1984), and absence of seed dormancy mechanisms necessary to preserve a soil seed reserve (Stevens and others 1977; Kitchen and Jorgensen 1999). It is, therefore, no surprise that winterfat stands are slow to rebound following disturbance.

Winterfat is palatable and provides nutritious forage for wildlife and livestock in all seasons. Although moderately tolerant of herbivory (Harper and others 1990; Chambers and Norton 1993), significant Great Basin reductions in winterfat are attributed to abusive grazing practices by domestic livestock from the 1870s to the 1930s, and later in some locations (for example, Murdock and Welsh 1971). Winterfat is most susceptible to grazing damage during spring months when physiological activity is greatest (Blaisdell and Holmgren 1984; Harper and others 1990). On many locations, the condition of winterfat communities improved somewhat as grazing frequency and intensity were reduced consistent with implementation of the Taylor Grazing Act of 1934. However, despite improved grazing practices, Great Basin winterfat communities today show patterns of continued, or perhaps, renewed decline (Harper and others 1990; Alzerreca-Angelo and others 1998; Kitchen and Jorgensen 1999).

Halogeton

Halogeton, (*Halogeton glomeratus*) is a succulent halophytic annual native to central and southwestern Asia and southeastern Europe. It is a prolific seed producer, even under drought stress (Eckert 1954). Tisdale and Zappetini (1953) reported yields of 25,000 seeds for larger plants and 800 seeds per plant in crowded stands where plant maturation height was only 76 mm. They found that vigorous stands

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produced from 220 to 450 kg of seed per ha. Halogeton seed are small (1 to 2 million per kg) and easily dispersed by wind, animal vectors, and vehicles. The production of both nondormant/short-lived black seed and dormant/long-lived brown seed (Cronin and Williams 1966) provides the means for both rapid spread and long-term persistence.

Although the timing and mode of introduction to the United States are unknown, the first documented collection of halogeton was made near Wells, Nevada, in 1934 (Dayton 1951). Although a weak competitor in perennial communities (Eckert 1954; Blaisdell and Holmgren 1984), this weed is well adapted to the soils and climate associated with salt-desert shrublands and is quick to invade disturbed sites, often resulting in near monocultures. Natural spread is facilitated by human-caused disturbances, in particular, the inadvertent creation of invasion corridors produced by road construction and maintenance activities (Dayton 1951; Stoddart and others 1951). After introduction, halogeton spread rapidly through the overgrazed rangelands of the semiarid West, infesting 4 million ha in the Western United States within 30 years of first collection (Cronin and Williams 1966). Once a salt-desert shrubland community is converted to halogeton, natural regeneration of native shrubs, such as winterfat, generally does not occur (Eckert 1954; Harper and others 1996).

The poisonous nature of halogeton for all classes of livestock, but more particularly for domestic sheep, was first recognized in 1942 (Dayton 1951). This awareness, in combination with the rapid rate of spread that was observed, captured the attention of the western range management community and resulted in substantial research effort on various aspects of halogeton biology during the 1940s and 1950s. One focus of that research was to examine the effect of halogeton litter on the chemical and physical properties of salt-desert soils. Eckert and Kinsinger (1960) conducted controlled studies using Nevada soils collected from three salt-desert community types and multiple levels of halogeton mulch. They demonstrated that the primary effect of halogeton leachate was an increase in cations, primarily sodium, at or near the soil surface with corresponding increases in soil pH and electrical conductivity. Secondary effects associated with the chemical changes included changes in soil physical properties, including increased crust strength and decreased percolation rate, and capillary rise of water associated with halogeton soils.

Today, halogeton stands are common on sites previously occupied by winterfat and are often found adjacent to remnant winterfat communities throughout the Great Basin. Using 1998 and 1999 road surveys in central and eastern Nevada and western Utah, we observed moderate to extensive displacement of winterfat by introduced annuals (primarily halogeton) in 16 central Great Basin drainage systems: specifically, Jakes, Monitor, Newark, Railroad, Spring, Steptoe, and White River Valleys of central and western Nevada, and Antelope, Escalante, Ferguson Desert, Pine, Rush, Sevier Desert, Snake, Tule, and Wah Wah Valleys of western Utah. Displacement had occurred in both low-diversity valley bottom communities and in the 'island' vegetation associated with rodent burrow clusters scattered in the more diverse alluvial community types. We concluded that the probability of surveying winterfat habitat in the Great Basin without observing significant displacement by halogeton was probably quite low. Goodrich (2000) reported a similar phenomenon in the Green River Basin of southwestern Wyoming, where halogeton is replacing stands of Gardner saltbush (*Atriplex gardneri*). It is apparent that a complete list of impacted communities will require additional reconnaissance.

Desert Experimental Range

In 1933, President Herbert Hoover set aside as an "agricultural range and experiment station" 22,500 ha (87 sections) located in western Millard County, Utah (Clary and Holmgren 1982). Pastures and reference areas of the Desert Experimental Range (DER), the Station's current name, were soon fenced for use in grazing and ecological studies, which continue to the present. Today, research and monitoring activities at the DER are coordinated by the Forest Service, Rocky Mountain Research Station, under the care of the Shrub Sciences Laboratory in Provo, Utah.

The DER is located primarily within the northwest quarter of Pine Valley, a north/south trending closed basin with a bottom elevation of 1,547 m and with several surrounding peaks ranging from 2,400 to 2,900 m elevation. During the late Pleistocene, the valley held a small lake with a maximum size of approximately 10,600 ha and an upper shore line at about 1,570 m (Snyder and others 1964). A mostly barren playa and remnants of old shorelines are the most visible evidence of the lake.

Approximately 75 percent of the DER is coalescing alluvial fans, or bajadas, and valley bottom, including about half of the playa. The remainder is steeper uplands and outcrops made primarily of Paleozoic limestone and dolomite with lesser amounts of quartzite and early tertiary volcanics. Soils are mostly gravelly loams, sandy loams, and gravelly sandy loams (Aridisols and Entisols; Tew and others 1997). Soil series located on alluvium above ancient shorelines are deep to very deep, with rapid to moderate permeability, and moderate to well developed calcic horizons (Tew and others 1997). Soil series below these shorelines are very deep, with moderate to moderately slow permeability and high levels of exchangeable sodium (15 to 40 percent) in subsurface horizons (below 40 cm).

Precipitation at the DER is highly variable within and between years. Mean annual precipitation at the headquarters complex (1,600 m) for the period of 1934 to 1981 was 157 mm with approximately half occurring from October through April (Clary and Holmgren 1982). Annual precipitation for the last 25 years (1975 to 1999) averaged near 200 mm (Alzerreca-Angelo and others 1998; data on file at the U.S. Forest Service, Shrub Sciences Laboratory, Provo, Utah). Mean temperatures for January and July are –3.5 and 23.3 °C, respectively.

Vegetation on alluvial fans is salt-desert shrubland with shadscale, winterfat, low rabbitbrush, bud sagebrush, Nevada ephedra (*Ephedra nevadensis*), and various perennial grasses and forbs dominating. Multi-scaled patchiness in the vegetative matrix reveals variability in species dominance, a reflection of the heterogeneity in soil composition, structure, and disturbance. Valley bottom vegetation is less diverse than that found on alluvial fans (Kitchen and others 1999) and is comprised primarily of winterfat (sometimes in near monocultures), Indian ricegrass, gray molly (*Kochia americana*), Bonneville saltbush (*Atriplex bonnevillensis*), and halogeton. Black greasewood (*Sarcobatus vermiculatus*) and Nuttall saltbush (*Atriplex falcata*) are conspicuous additions on colonized portions of the playa.

Halogeton Research at the Desert Experimental Range

The early history of halogeton at the DER is recorded in unpublished documents on file at the U.S. Forest Service, Shrub Sciences Laboratory, Provo, Utah, and is summarized here. Halogeton was first observed at the DER in 1952 as a small (approximately 1 ha) patch near the playa. At the time, populations were known to exist in all basins surrounding Pine Valley. Although the means of seed transport to the DER is unknown, it was believed that seed might have come by way of contaminated bales of hay dropped as emergency feed in the winter of 1948 and 1949. A monitoring plan was developed to assess the condition of this population as well as to survey the remainder of the DER for new infestations in coming years. New populations were identified in 1953 both inside and near DER boundaries. Small plots with and without perennial vegetation were seeded to halogeton in June of 1954 to assess establishment with and without competition from perennials. Halogeton plants grew in all plots the same year. During the next 4 years, halogeton spread in Pine Valley from an increasingly greater number of source populations. Subsequently, by 1958 halogeton was widespread at the DER and surrounding lands. Within the DER, halogeton was concentrated mostly within the more open communities near the playa and on upland communities associated primarily with disturbance (rodent diggings, roads, and so forth).

Boundaries between nearly pure stands of winterfat and halogeton are generally well defined by a rather narrow ecotone. This results from the inability of winterfat to invade halogeton stands and the weak competitive attributes of halogeton in healthy perennial communities. At the DER, no natural regeneration of winterfat has occurred for up to 30 years following conversion to halogeton. However, halogeton advances have been observed following unexplained winterfat die-off events preceded by either summer flooding (Harper and others 1996) or extended periods of abnormally high precipitation.

Harper and others (1996) observed changes in soil chemistry associated with halogeton conversion at the DER similar to those observed in Nevada (Eckert and Kinsinger 1960). They also found evidence that halogeton conversion had altered the soil microbial community as was predicted by Eckert and Kinsinger. In greenhouse experiments using treated (methyl bromide fumigation) and untreated soils collected from the halogeton and winterfat communities, winterfat seedling survival in treated halogeton soil (50.3 percent) was significantly higher than that for untreated halogeton soil (36.6 percent) and not significantly different than that of treated (55.9 percent) and untreated (47.4 percent) winterfat soils. These results suggest possible enhanced pathogenic activity associated with halogeton soils.

In 1998, additional soil samples were taken at four DER sites near the playa. Samples were collected from adjoining winterfat and halogeton stands, the ecotone between the stands, and bare areas (<1 percent cover) located within halogeton stands. These bare areas had supported solid stands of halogeton in 1997 as determined by the condition of standing litter. Three replicated samples were taken from the top 10 cm for each site/plant community combination (n = 12). Increases in sodium associated with halogeton (table 1) were consistent with that reported by Eckert and Kinsinger (1960) and Harper and others (1996). Halogeton-related increases in potassium and magnesium were also significant. Our results also show that, although exchangeable concentrations of these cations were not significantly higher at the ecotone than in the winterfat community, they were trending upward and clearly were being affected by halogeton litter. Change in cation concentration between halogeton and winterfat soils, when expressed as a ratio, was greater for sodium (3.7:1) than for potassium (2.3:1) or magnesium (1.3:1). Eckert and Kinsinger (1960) suggested that disproportionate increases in sodium could cause reduced uptake of other cations resulting in nutrient stress for affected plants. Whether by the direct affect of increased sodium on plant growth, negative alteration of the physical properties of soils, disruption of soil micro flora, changes of cation ratios, or some combination of the above, halogeton is clearly effective at rendering intolerable, soils previously occupied by winterfat.

Because of the cumulative nature of these soil-chemistry changes, it seems reasonable to assume that the length of time a site is occupied by halogeton and the chemical, physical, and perhaps biological condition of that soil as it pertains to winterfat growth are inversely related. We believe that this is largely true, at least until conditions are so poor that halogeton growth also becomes restricted. It is possible that this occurred on the bare areas we observed at the DER in 1998. Cation concentrations were clearly greater in these soils than in other soils tested, including those associated with dense halogeton stands (table 1). Interestingly, a full and vigorous stand of halogeton grew on the previously bare areas in 1999. The 1998 boundary between the halogeton stand and bare ground remained clearly visible due largely to greater stand vigor (height, color, biomass) associated with previously bare areas. This would

Table 1—Exchangeable concentrations (ppm) for four cations in top 10 cm of soil in adjoining winterfat and halogeton communities, ecotone, and bare areas at four sites on the Desert Experimental Range, Millard County, Utah (1998). Within columns, means followed by the same letter are not significantly different at the $p < 0.05$ level (SNK).

Community type	Ca	Mg	K	Na
	- - - - - - - - - - - - - -	- - - - - - *ppm*	- - - - - - - -	- - - - - - -
Winterfat	8,736a	490c	636c	102c
Ecotone	8,359b	509c	793c	149c
Halogeton	8,371b	650b	1,455b	373b
Bare	8,644a	725a	1,633a	450a

seem to suggest that halogeton rendered these sites unfavorable for halogeton (or most any other species present), and that it remained so until soil conditions improved. For example, the above average precipitation that occurred in 1998 (215 mm) could have been sufficient to partially leach salts from near the soil surface, improving conditions on bare soils. At the same time, such improvements might not have occurred on soils with active halogeton stands due to the extra halogeton biomass (and, therefore, salted litter) produced in response to abundant soil water. Research that could document and quantify this hypothesis has not been done.

Conclusion

Winterfat decline is widespread in Great Basin salt-desert communities. Presently, our knowledge of the processes by which introduced annuals, particularly halogeton, displace and exclude winterfat is deficient. Before we can assess the probable effectiveness of potential management strategies in preventing continued expansion of halogeton and in restoring winterfat community stability, a more complete understanding of interactions among winterfat and halogeton and associated soils and soil microbiota must first be developed. Failure to respond to this challenge will likely result in further degradation of winterfat-dominated communities in the Great Basin.

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Predicting First-Year Bare-Root Seedling Establishment With Soil and Community Dominance Factors

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Abstract—The usefulness of measuring community dominance factors and the soil parameters of geometric mean particle size and percent fines as predictors of first-year bare-root establishment of Wyoming big sagebrush seedlings was investigated. The study was conducted on six sandy soils in south-central Washington. Soil parameters that could affect the distribution of Sandberg's bluegrass and cheatgrass as dominants in seral plant communities were also examined. Plant health was inversely related to increasing geometric mean particle size and directly related to increasing percent fines. Percent fines were also directly related to cheatgrass cover on these sandy soils. The highest sagebrush survival occurred on the alien-dominated sites.

Introduction

Mitigation for impacts to mature sagebrush habitat on the Hanford Site was conducted during fall 1998 on the semiarid sagebrush steppe of south-central Washington. Restoration in this area usually relies in part on transplanting Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) seedlings into post fire habitats where the shrub component is absent. Bare-root seedlings are inexpensive to produce and plant, and have been shown to establish as readily as container-grown stock under good conditions (Whisenant 1999). However, bare-root seedling establishment in poor or more variable conditions has not been as successful (Barnett and McGilvray 1997; McKell and Van Epps 1980; Lohmiller and Young 1972). In conjunction with the 1998 habitat mitigation effort, a field study was initiated to investigate environmental and vegetational elements of the landscape that might be associated with successful establishment of bare-root seedlings. This research was conducted in the Lower Cold Creek valley on the Fitzner/Eberhardt Arid Lands Ecology Reserve (ALE) adjacent to the Department of Energy's (DOE) Hanford nuclear reservation.

Landscapes are sometimes described as a blend of resource patches that support a mosaic of plant communities associated with changes in slope, aspect, and soil type (Whisenant 1999). In the sagebrush steppe of south-central Washington, resource patches are often the result of soil water availability, which is one of the most significant edaphic features affecting the distribution of habitat types across this semiarid landscape (Daubenmire 1974; Franklin and Dyrness 1988; Hironaka 1979).

Soils with high water holding capacity allow plants to survive periods of drought (Larcher 1995). While temporary physiologically induced water deficits often occur mid day when it is hot and sunny, long-term deficits are mainly caused by decreasing soil water availability (Kramer 1983). As the water content within the root zone decreases, the remaining water becomes less available to plants (Bristow and others 1984; Larcher 1995). The degree to which this availability is limited is strongly dependent on the soil's texture, or particle size distribution (Larcher 1995). Coarse sandy soils exhibit a low affinity to water (which makes it easier for plants to obtain); however, they also have a low water holding capacity. This is evident as farmers are forced to irrigate at much higher (less negative) soil water potentials in sands than in silts or clays (Bristow and others 1984).

It is reasonable to expect that planted seedlings would be affected by environmental gradients. Because shrub transplanting can be expensive, careful site selection that considers these gradients is an important and reasonable approach to achieving a high level of success.

Shiozawa and Campbell (1991) have shown that soil texture in terms of a geometric mean particle diameter and a geometric standard deviation are associated with the soil hydraulic property of moisture retention. If a significant association exists between geometric mean particle diameter and first-year seedling establishment, then these modeled parameters could be useful in selecting appropriate sites for planting in sandy areas.

Community competition on a site may also be a factor to consider in the prediction of restoration success. One of the more prominent plant species across the study area is cheatgrass (*Bromus tectorum* L.). While this ubiquitous winter annual maintains a competitive edge across most of the study area, its distribution and abundance varies in response to environmental gradients (Rickard 1975). Across

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much of the lower elevations of Hanford and ALE, cheatgrass has replaced the small native bunchgrass, Sandberg's bluegrass (*Poa secunda* Presl.), as the dominant understory species (Daubenmire 1970; Rickard 1975), yet Sandberg's bluegrass is still found to dominate or co-dominate on this habitat type in many areas. Link and others (1990) determined that the dominance of one or the other of these species was not a direct result of phenological differences or plant water status, but suggested it might depend on some other abiotic or biotic factors.

The purpose of this study was to find a practical approach to the prediction of bare-root seedling establishment on sandy sites in varying competitive environments, and to investigate the soil parameters that might be affecting the distribution of Sandberg's bluegrass and cheatgrass as dominants in seral plant communities on the Wyoming big sagebrush/Sandberg's bluegrass habitat type. The specific objectives were to characterize the relationships that exist between: (1) modeled geometric mean particle sizes and corresponding percent fines (percentage of particle sizes less than 53 μm) to first-year survival and health of bare-root Wyoming big sagebrush seedlings; (2) modeled geometric mean particle sizes and percent fines to community composition; and (3) community composition to first-year bare-root seedling survival.

Methods

Six 20-m x 30-m study plots were positioned on ALE along a sandy drainage of the Lower Cold Creek valley. The sites were in a post-burn seral condition with the shrub component lacking due to fire. The sites had not burned in at least 10 years. Three sites (A1, A2, A3) were selected to represent alien communities dominated by cheatgrass, while three other sites (N1, N2, N3) were selected to represent native communities dominated by Sandberg's bluegrass. Elevation at the study sites is about 134 m (440 ft). The potential native vegetation is Wyoming big sagebrush/Sandberg's bluegrass. Normal effective precipitation (October through May) is 126 mm (4.9 inches), with summer precipitation averaging 33 mm (1.3 inches) at the Hanford Meteorological Station (HMS) located about 22.5 km (14 mi) NNW of the study areas (Hoitink and others 1999). The soils were mapped into the Burbank series, which is made up of coarse-textured sands and loamy sands underlain by gravel (Hajek 1966).

Soil Measurements

Soils were sampled systematically at each site. Five cores were extracted at two depths (0.3 m and 1.0 m respectively) from each site. Samples from each core (30 cores, 60 samples) were sent to Soiltest Farm Consultants in Moses Lake, Washington, where nutrient content, soluble salts, organic matter, pH, and cation exchange capacities (CEC) were determined. Sand, silt and clay fractions were determined using hydrometer and wet sieve methods (Gee and Bauder 1986) on the 0.3-m soil samples. Prior to hydrometer measurements, soil samples were soaked in sodium-hexametaphosphate solution and placed on a shaker table overnight for particle dispersion. Soil drying methods and soil water calculations were conducted following Gardner (1986).

The parameters of geometric mean particle diameter and the associated standard deviation were estimated based on the two-parameter Sirazi and Boersma (SB) model described by Shiozawa and Campbell (1991):

$$d_g = \exp(5.756 - 3.454m_t - 7.712m_y) \qquad (1)$$

and,

$$\sigma_g = \exp\left\{\left[33.14 - 27.84m_t - 29.31m_y - \left(\ln d_g\right)^2\right]^{1/2}\right\} \qquad (2)$$

where: d_g is the geometric mean particle diameter, σ_g is the geometric standard deviation (both in μm), and the silt and clay fractions are represented by m_t and m_y respectively.

Community Measurements

Percent cover, species composition (based on relative cover), and frequency were determined during May 1999, following the coverage class method described by Daubenmire (1959), using a modified 0.2-m x 0.5-m sampling frame. Fifty samples were obtained from each site by splitting the 20-m x 30-m planting areas into two 10-m x 30-m halves. Five 10-m lines were then randomly positioned along the interior long axis and the flip of a coin determined if the lines would be positioned to the left or right of the tape. The sampling frame was then systematically positioned every meter along each of the five lines and ocular estimates of percent cover, percent species composition, and percent frequency for each species were determined.

Seedling Measurements

During November 1998, each 20-m x 30-m planting area was divided into 120 sections. Bare-root seedlings were randomly assigned (60 at each site) within each planting area. Seedling roots were dipped into a solution of water and fine-grade Terra-Sorb™ hydrogel (acrylamide coploymer) before planting. The following summer, during late July 1999, plant survival and health were qualitatively ranked according to the plant's overall appearance and phenological development (Caldwell and others 1973; Daubenmire 1975), and the following guidelines:

0 Dead, no live leaves left on the plant.
1 Plant displays low vigor (for example, no apparent new growth, no bud or reproductive stem elongation, and so forth) and at least 61 percent of the foliage is missing, chlorotic, or otherwise unhealthy in appearance.
2 Plant displays good vigor (for example, new growth and relatively green turgid leaves) and only displays between 11 and 60 percent of the unhealthy characteristics listed above.
3 Plant displays very good vigor (for example, ephemeral leaves growing on reproductive shoots) and displays no more than 10 percent of the unhealthy characteristics listed above.

All seedlings were identified (alive or dead), and measures of seedling height and two widths were recorded. Data for second-year survival, health, and growth, were not obtained because the test sites were destroyed by a large range fire that occurred in June 2000.

Analysis

Logistic regression and analysis of deviance were used to analyze the relationship between environmental and community characters and the multinomial ordinal response of the bare-root seedlings. The SAS Genmod procedure (SAS Institute, Cary, North Carolina) was used to perform the calculations.

Results and Discussion

Effective precipitation recorded at the HMS for the 1998–1999 (October through May) growing season totaled 99 mm (3.9 inches), which is about 78 percent of normal (Hoitink and others 1999, 2000). Summer precipitation received during the two months prior to seedling health and survival measurements totaled 10 mm (0.38 inches).

Soil and Seedling Measurements

Although there were several notable differences between the soil properties of the alien study plots and the native study plots (table 1), native plot N2 was more similar to the three alien plots in terms of soil properties than to the other two native plots. The alien plots exhibited higher percent fines and lower geometric mean particle sizes, than the native plots. In addition, alien plots had higher magnesium contents and higher CEC than the native plots (table 1). All sampled soils were considered alkaline, exhibiting pH values from 7.9 to 8.6 and increasing at depth to a maximum pH of 9.2. Soluble salts were also low across all plots (0.2 dSm^{-1}), indicating no hinderance to plant growth (Cline and others 1977).

Modeled geometric mean particle size was related to plant health ($X^2 = 13.41$, $p = 0.0003$, $df = 1$). Plant survival was inversely related to increasing geometric mean particle size (fig. 1). Mean particle sizes ranged from 97.1 to 213.3 µm. Modeled means across all sites were classified as fine sands based on the USDA classification system.

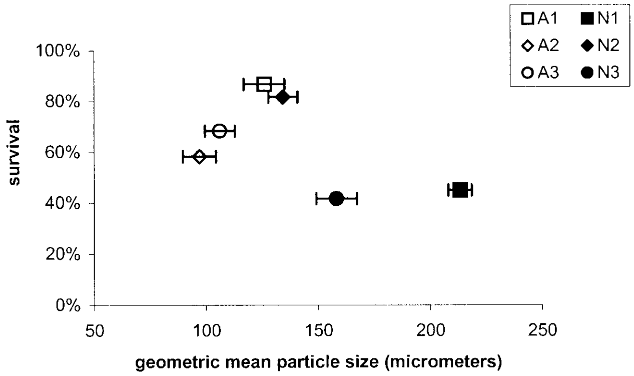

Figure 1—Percent survival of Wyoming big sagebrush seedlings relative to modeled geometric mean particle diameters for the six study sites. Bars represent ± one modeled standard deviation (n = 5 soil cores from each planting site).

Percent fines were also shown to be related to plant health ($X^2 = 12.22$, $p = 0.0005$, $df = 1$) with plant survival directly associated with increasing percent fines (fig. 2). Percent fines ranged from 5 to 27 percent. Seedling survival ranged from 42 to 87 percent (figs. 1, 2, 3).

Soil and Community Measurements

Percent fines were directly related to cheatgrass cover indicating that this component of soil texture was a good predictor of community dominance in the samples measured for this study ($X^2 = 245.83$, $p < 0.0001$, $df = 1$). Lower cheatgrass cover was observed on soils exhibiting less than 15 percent fines (tables 1 and 2). Nevertheless, native site N2 was found on soils similar to the soils found on the alien-dominated sites (table 1), indicating that community dominants on that site were affected by factors other than soil texture and available water.

Table 1—Summary of selected physical and chemical properties measured on the six study sites. Data are presented as means with ± one standard deviation (n = 5 soil cores from each site).

	Alien-dominated plots			**Native-dominated plots**		
	A1	**A2**	**A3**	**N1**	**N2**	**N3**
Texture						
Percent sand	82.8 ± 1.7	70.6 ± 3.7	71.6 ± 1.0	94.3 ± 1.0	79.6 ± 5.0	89.8 ± 3.5
Percent fines	17.2 ± 1.7	29.4 ± 3.7	28.4 ± 1.0	5.7 ± 1.0	20.4 ± 5.0	10.2 ± 3.5
Mean particle size (µm)	126 ± 9.1	97 ± 7.4	106 ± 6.6	213 ± 5.2	134 ± 6.5	158 ± 9.0
Nutrients						
Calcium (ppm)	964 ± 62.3	1136 ± 121	1136 ± 32.9	856 ± 388	1180 ± 130	764 ± 108
Magnesium (ppm)	174 ± 18.4	177 ± 38.8	186 ± 22	84.7 ± 24.2	201 ± 13.8	96.8 ± 28.4
Soluble salts (dSm^{-1})						
0.3 m depth	0.20 ± 2E-09	0.26 ± 0.089	0.20 ± 2E-09	0.20 ± 2E-09	0.20 ± 2E-09	0.20 ± 2E-09
0.9 m depth	0.46 ± 0.358	0.22 ± 0.045	0.20 ± 2E-09	0.22 ± 0.045	0.30 ± 0.228	0.22 ± 2E-09
Cation exchange capacity						
meq/100 g	6.5 ± 0.5	6.9 ± 0.5	7.0 ± 0.4	3.5 ± 0.5	7.2 ± 1.1	4.2 ± 0.3
pH 0.3 m depth	8.0 ± 0.1	8.4 ± 0.2	8.0 ± 0.2	8.2 ± 0.2	8.1 ± 0.2	8.4 ± 0.1
0.9 m depth	8.6 ± 0.5	9.2 ± 0.1	8.7 ± 0.4	8.7 ± 0.1	9.0 ± 0.1	8.9 ± 0.1

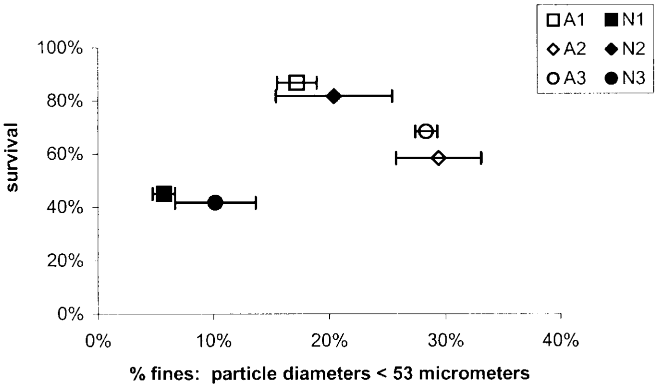

Figure 2—Percent survival of Wyoming big sagebrush seedlings relative to the percent fines across the six study sites. Bars represent ± one standard deviation (n = 5 soil cores from each planting site).

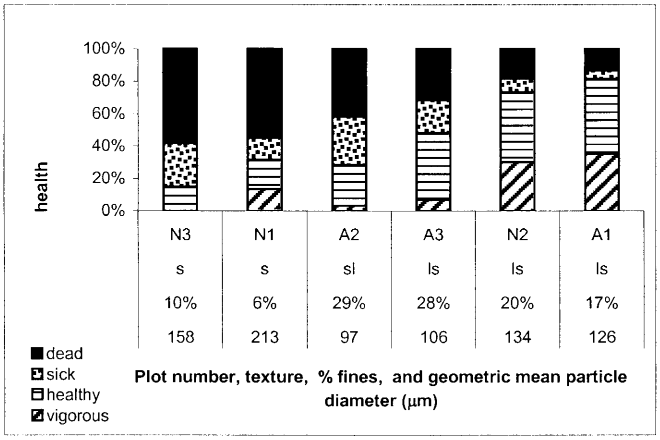

Figure 3— Health rankings in relation to alien [A] or native [N] dominated communities, texture, percent fines, and geometric mean particle diameters across the six study sites. Data are ordered by increasing survival (n = 60 bare-root Wyoming big sagebrush seedlings planted at each site). Textures were determined based on the USDA classification scheme (s = sand, sl = sandy loam, and ls = loamy sand).

Community and Seedling Measurements

Community factors of percent cover appear to be good predictors of bare-root seedling survival on these sandy sites ($X^2 = 7.12$, $p = 0.0076$, df = 1). Overall, the highest sagebrush survival occurred on the alien dominated sites with percent survival ranging between 58 and 87 percent (figs. 1, 2, and 3). This may be due to the increased percent fines and corresponding increased water-holding and cation-exchange capacities. On native sites N1 and N3, sagebrush survival was 42 and 45 percent respectively, while native site N2 exhibited an 82 percent survival (figs. 1, 2, and 3). Clear distinctions were evident with respect to percent cover and frequency between the native and alien plots (table 2). Sandberg's bluegrass cover on the native sites was between 30 and 39 percent and fell between 0.3 and 11.6 percent on the alien dominated sites. Likewise, cheatgrass cover on the native sites was between 16 and 22 percent and reached between 53 and 68 percent on the alien dominated sites. All sites exhibited low species diversity (table 2) which is consistent with the Wyoming big sagebrush/Sandberg's bluegrass habitat type (Daubenmire 1970).

Conclusions

Our study found that geometric mean particle size, percent fines, and community-dominance factors could be good indicators of potential bare-root seedling survival. With respect to soil texture, measuring geometric mean particle size was cumbersome and time consuming. The percent fines in a soil were much easier to measure, and can predict seedling establishment success just as well. Based on this data from the Lower Cold Creek valley, overall establishment success is more likely in soils containing greater than 15 percent fines. We recommend that percent fines, rather than geometric mean particle size, be used as an indicator of environments that would promote the successful establishment of bare-root seedlings on sandy locations. Furthermore, percent fines were found to be good predictors of community dominance, and community dominance factors were considered good predictors of seedling establishment. Often site selection guidelines restrict mitigation areas to high quality native sites. However, when quality native sites are not available, or if successful establishment of sagebrush is the only goal, the data provided in this study suggest that cheatgrass stands on sandy sites can be indicative factors that promote successful establishment of bare-root Wyoming big sagebrush seedlings.

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Table 2—Community measurements across the six study sites (n = 50, 0.2-m x 0.5-m plots from each 20-m x 30-m study site).

	Alien dominated plots			Native dominated plots		
Taxa	**A1**	**A2**	**A3**	**N1**	**N2**	**N3**
Shrubs	Percent cover * Percent species composition * Percent frequency					
Artemisia tridentata	–[1]	–	–	–	+[2]	+
Chrysothamnus nauseosus	–	–	–	–	–	+
Half shrubs						
Phlox logifolia	+	–	–	–	+	+
Antennaria dimorpha	–	–	–	–	+	–
Native perennial grasses						
Poa secunda	8.4 * 11.3 * 46	11.6 * 13.4 * 84	0.3 * 0.4 * 2	30.0 * 52.0 * 96	34.4 * 56.6 * 98	39.1 * 61.6 * 98
Pseudoroegneria spicatum	–	–	–	–	+	–
Sitanion hysterix	–	–	–	–	0.8 * 1.2 * 2	–
Stipa comata	+	–	–	+	–	–
Stipa thurberiana	–	–	–	–	0.8 * 1.2 * 2	–
Introduced annual grasses						
Bromus tectorum	53.0 * 71.7 * 100	67.6 * 76.7 * 100	62.6 * 83.0 * 100	16.0 * 27.7 * 82	21.9 * 36.0 * 96	18.9 * 29.7 * 96
Native perennial forbs						
Balsamorhiza careyana	–	+	–	–	+	+
Chaenactis douglasii	–	–	–	–	–	0.1 * 0.2 * 4
Crepis atrabarba	–	+	–	–	+	–
Erigeron poliospermus	–	–	–	–	+	+
Lomatium macrocarpum	–	–	–	–	+	–
Machaeranthera canescens	–	–	–	–	+	–
Native annual forbs						
Agoseris heterophylla	–	0.1 * 0.1 * 2.0	–	–	0.8 * 1.2 * 2	–
Ambrosia acanthicarpa	0.3 * 0.3 * 10	–	–	–	–	0.3 * 0.3 * 10
Amsinckia tessellata	0.1 * 0.1 * 2	–	+	0.1 * 0.1 * 2	–	–
Epilobium paniculatum	0.1 * 0.1 * 2	0.4 * 0.4 * 14	0.1 * 0.1 * 4	–	–	–
Microsteris gracilis	–	–	–	0.1 * 0.1 * 2	–	0.1 * 0.2 * 4
Introduced annual forbs						
Draba verna	0.8 * 1.1 * 32	3.9 * 4.4 * 86	4.3 * 5.7 * 62	8.4 * 14.6 * 96	1.1 * 1.8 * 44	3.6 * 5.6 * 54
Holosteum umbellatum	7.8 * 10.5 * 82	4.0 * 4.5 * 72	6.4 * 8.5 * 58	1.8 * 3.0 * 15	–	0.7 * 1.0 * 26
Salsola kali	1.9 * 2.5 * 54	0.5 * 0.6 * 20	0.7 * 0.9 * 26	1.2 * 2.0 * 46	1.2 * 3.5 * 48	0.3 * 0.5 * 12
Sisymbrium altissimum	1.3 * 1.8 * 22	0.1 * 0.1 * 2	0.2 * 0.3 * 8	0.2 * 0.3 * 6	–	–
Tragopogon dubius	0.6 * 0.7 * 12	0.1 * 0.1 * 4	0.9 * 1.2 * 6	0.2 * 0.3 * 6	–	+
Total native taxa and % cover	6 * 8.9%	6 * 12.1%	3 * 0.4%	4 * 30.2%	13 * 36.8%	10 * 39.6%
Total alien taxa and % cover	6 * 65.4%	6 * 76.2%	6 * 75.1%	6 * 27.8%	3 * 24.2%	5 * 23.5%

[1] – = not present on site.

[2] + = present but not sampled.

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Forage Kochia: Friend or Foe

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Abstract—Perennial forage kochia (*Kochia prostrata*) is a half-shrub valuable for reclamation, fire breaks, and livestock and wildlife forage on semiarid and saline rangelands. Interest is mounting about this species, but some are concerned that it will become an invader of perennial communities. Only one cultivar (Immigrant) has been released in the United States. Eighty-one forage kochia plantings (mainly Immigrant) were evaluated to document forage kochia's adaptation and spread. Ecological descriptions were taken for each site and multiple regression analyses were done to determine prediction equations for recruitment outside the original plantings. Our results indicated that forage kochia is well adapted to a wide range of semiarid and arid rangelands, but is not an aggressive spreader. However, it may recruit into playas, slick spots, and disturbed and/or degraded areas. The fringe of recruitment, defined as the marginal recruitment threshold, ranged from 0 to 100 ft with a mean and median distance of 20 ft. Regression only explained 22 percent of fringe threshold variation and consisted of the following factors: medium textured soils, lower elevation, and age of seeding. Unexplained variation may be due to factors not determined, such as the disturbed peripheral area surrounding each planting.

Introduction

"Immigrant" forage kochia [*Kochia prostrata* ssp. *virescens*], a half-shrub, has been seeded on over 200,000 acres of rangeland in 10 western states. Many scientists and rangeland managers consider forage kochia a prime candidate for western range rehabilitation and fire prevention. However, others are concerned about its potential to invade and suppress or eliminate native plant populations. Many are concerned that because forage kochia is an introduced species it may spread vigorously throughout western rangelands. We conclude that these concerns are largely unfounded. This investigation was undertaken to examine Immigrant forage kochia's competitive ability, invasiveness and potential effects on bio-diversity of native and introduced plant communities on semiarid rangelands.

During October 1999, two of the authors (Waldron and Harrison) participated in a forage kochia germplasm collection trip to Kazakhstan. They evaluated forage kochia's compatibility and aggressiveness in its native environment on 64 sites.

Immigrant forage kochia was released in the United States in 1984 (Stevens and others 1984). Immigrant is native to the arid and semiarid regions of Central Eurasia (Larin 1956; Keller and Bleak 1974; Plummer 1974). The parental accession (PI314929) of Immigrant, along with other accessions, was acquired in May 1966 in a search for plants to suppress halogeton [*Halogeton glomeratus*) on droughty and saline sites. Immigrant, the only North American cultivar of the ssp. *virescens* (green-stem forage kochia) is a diploid with a chromosome number of 2n = 18 (Pope and McArthur 1977; Herbel and others 1981).

The first known Immigrant (PI 314929) planting in the U.S. was made in l968 by Keller and Bleak (1974). Immigrant was jointly released in March l984 by the USDA Forest Service, USDA Soil Conservation Service, the Utah Division of Wildlife Resources and the Idaho, Nevada, Oregon, and Utah Agriculture Experiment Stations.

Forage kochia is a long-lived, semi-evergreen half shrub that averages 1 to 3 ft high at maturity. Individual plants may live 10 to 15 years (Balyan 1972). It develops an extensive fibrous root system with a tap root that may extend to a depth of 16 ft (Prianshnikov 1976). It does not tolerate flooding or soil with a water table (Balyan 1972).

Seeds ripen in October and November (Prikhod'ko and Prikhod'ko 1977), however, freezing temperatures hasten seed ripening. There are approximately 115,000 pure live seeds per lb (Stevens and others 1996). Forage kochia seeds germinate well for 6 to 8 months after harvest. It may maintain good germinability for up to 3 years if seed is properly dried to 7 percent or less moisture and stored at 36 to 50 °F (2.2 to 10 °C) (Jorgensen and Davis 1984).

Immigrant is widely adapted and has been successfully established on a range of soils including fine-to-coarse textured, shallow-to-deep, gravelly-to-stony and saline-to-alkaline and in numerous plant communities from mountain to desert shrub.

Uses

Immigrant has been seeded to improve plant community diversity, esthetics, plant cover, species richness, forage for domestic livestock and wildlife, fire prevention, and improved soil stability. Specific examples of its use are to (1) prevent accelerated soil erosion, flooding, and critical

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area treatment including blowout areas (Stevens and others 1984; Rassmussen and others 1992; Horton, unpublished data 1998); (2) supply livestock and wildlife forage during normal and critical periods (Otsyina and others l983; Gade and Provenza 1986; Kashkarov and Balyan 1989; Bake 1997); (3) provide food and cover for upland game birds, small mammals, reptiles, and insects (Stevens and others 1985); (4) readily provide ground cover on disturbed areas (Nemati 1986; Blauer and others 1993); (5) suppress or eliminate alien invasion of annual weeds like cheatgrass (*Bromus tectorum*), halogeton [*Hologeton glomeratus*], Russian thistle [*Salsola pestifer*], and medusahead rye [*Taeniatherum (Elymus) caput-medusae*], (Van Epps and McKell 1983; McArthur and others l990; Stevens and McArthur 1990; Monsen and Turnipseed 1990; Monsen 1994; Gutknecht 1996; Simper, personal communication, NRCS, Cedar City, UT, 1997; Turnipseed, personal communication, Idaho Fish and Game, Caldwell, ID, 1998); (6) reclamation of disturbed mine sites (Howard and others 1976; Frishchknecht and Ferguson 1984; Clements and others 1997); (7) beautify and stabilize road sides (Plummer 1970; Blauer and others 1993); (8) stabilize sand dunes (Krylova 1988); (9) increase species richness and biodiversity and assist in the reestablishment of desired perennials (Blauer and others 1993; Gutknecht 1996; Clements and others 1997); (10) provide green strips that suppress or prevent wild fires (Pellant 1990; Monsen 1994; Clements and others 1997); and (11) extract salts (sodium and chloride) from saline soils (Larin 1956; Francois 1976).

Competition, Invasiveness, and Biodiversity

Expression of a plant's competitive ability is a function of environmental and site conditions. Important environmental considerations are geomorphology, slope, aspect, soil type, climate, salinity, human impacts, seed sources, and existing or competing vegetation. All plants, both native and introduced, spread and compete in environments where they are best adapted and where there is little or no competition by other species for resources (Harrison and others 1996).

Immigrant forage kochia appears to have a competitive advantage over many other species in the cool shrub steppe because of its temporal and spatial capacity for water uptake (Romo and Haferkamp 1987). Under some conditions it can rapidly deplete soil moisture and become established in the presence of annual and perennial competitors (Keller and Bleak 1974; Van Epps and McKell 1983; Stevens and others 1985; Romo and Haferkamp 1987). The competitive advantage of Immigrant on disturbed sites over annuals like cheatgrass and halogeton is well documented (McArthur and others 1990; Monsen and Turnipseed 1990).

In its natural range in south-central Eurasia forage kochia is commonly associated with grasses and *Artemisia* species and contributes significantly to plant biodiversity. We concur with others that it generally does not grow in pure stands in its native habitats in Eurasia (Plummer 1970; McArthur and others 1974). In the U.S., Immigrant forage kochia appears to be best adapted within its ecological range when there is little competition from established perennial species. The Bureau of Land Management in Idaho found that Immigrant has spread a few meters in disturbed areas beyond the original seeded boundaries on several 1986 greenstrip seedings (M. Pellant, BLM, personal communication, Boise, ID, 1998). Several researchers (Blauer and others 1993; Stevens and others 1985; Pendleton and others 1992; Clements and others 1997; K. Gray, personal communication, Nevada Division of Wildlife, Elko, NV, 1998; M. Haferkamp, personal communication, USDA-ARS, Miles City, MT, 1998) have concluded from studies in the big sagebrush and desert shrub communities that Immigrant is not highly invasive and does not spread aggressively into healthy plant communities.

Clements and others (1997), (C. D. Clements, personal communication, USDA-ARS, Reno, NV, 1999) states, "In the sagebrush/bunch grass region of the Great Basin, forage kochia does not appear to be invasive." They found little to no movement outside of 17 established seedings ranging from 2 to 17 years old. They concluded that "areas must be reduced to bare soil before it successfully invades." Stevens and others (1984) reported that Immigrant out competes many annuals, fills in the inter spaces between perennials, and establishes well when co-seeded with other perennials. They noted its recruitment into a black greasewood [*Sarcobatus vermiculatus*]-shadscale [*Atriplex confertifolia*]-halogeton community, and into introduced plant communities of intermediate wheatgrass [*Thinopyrum intermedium*], crested wheatgrass [*Agropyron cristatum*], cheatgrass, and medusahead rye. A. DeBolt (personal communication, USDI BLM, Boise, ID, 1998) indicated that pepper plants (*Lepidium davisii* and *papillienum*) species may suffer due to Immigrant's tendency to colonize on saline and alkaline playas. Blauer and others (1993) noted that in higher precipitation zones, Immigrant does not compete well in a closed herbaceous plant community.

In 1998, Clements (personal communication, 1999) found in Immigrant seedings that the density of cheatgrass declined and that native species numbers were seven times greater than in adjacent unburned stands. Clements and others (1997) concluded that native plants will become established in Immigrant seedings if fires are infrequent. They reported the spread of Wyoming big sagebrush, thickspike wheatgrass [*Elymus lanceolatus*], native bunch grasses and forbs was common in the fourth growing season of a stand of Immigrant, which had first suppressed cheatgrass.

Materials and Methods

This study was designed to determine planting success, biodiversity, spread, and competition of Immigrant forage kochia on semiarid western rangelands. In our attempt to assess the responses of Immigrant to the varied rangeland conditions into which it has been seeded in the Intermountain West we: (1) sent questionnaires to personnel at state and national resource agencies and researchers at universities and other institutions who were, or had been, involved with forage kochia research; (2) visited representative seedings and/or transplantings throughout the West that were old enough to give some indication of long term responses. We received over 151 questionnaire responses describing forage kochia plantings. Information from the questionnaires and published reports was used to determine which plantings should be visited for further evaluation.

Onsite assessments were made, where possible, to all known Immigrant plantings that were unique or that were 10 years or older. More than 90 planting sites were visited and data was collected from 81 sites.

Because of the large number of field sites, the line-intercept method was used to evaluate Immigrant spread and percent composition. Transects were randomly located in plantings and a 100-foot tape was laid parallel to the original planting. Individual species, litter, bare ground and rocks were recorded. Percent plant composition was calculated for each species as the percentage of the total vegetation comprised by that species. A visual reconnaissance survey was made to assess the spread of forage kochia into fringe areas adjacent to the original planting, and the maximum distance from the seeding's edge where a single Immigrant plant had become established was recorded. The fringe distance was defined as the visual marginal or peripheral threshold of Immigrant encroachment from the original seeded boundary. In many instances, recruitment away from the seeding occurred in a pattern of fingers or pockets. At such sites a transect was taken within the finger or pocket at the visually observed threshold area of recruitment. If spread appeared to be mainly uniform around the planting then random transects were taken at the visually observed fringe. If no spread was observed then the fringe distance was recorded as zero. It should be noted the evaluation areas for each site were randomly selected and may not completely represent the entire planted area. Planting boundaries were shown to us by field personnel. Recruitment data were not taken when original seeding boundaries were unknown.

Statistical Analysis

Independent variables were treated as continuous (for example, elevation, precipitation, and so forth), interval categorical (for example, results = poor, fair, good, or excellent), or dichotomous categorical (yes or no) for correlation and regression analysis.

Questionnaire

Information obtained from the questionnaires was subjected to correlation analysis using SAS software (1989) to search for significant ($P < 0.10$) associations between independent environmental factors and the perceived degree of success in establishment and recruitment of forage kochia outside the planting area.

Onsite Assessment

All possible correlation coefficients (*r*) (SAS 1989) were calculated between dependent variables (maximum distance to a single plant, fringe of recruitment, percent Immigrant composition at the fringe, percent Immigrant composition inside original seeding) and independent environmental variables as determined by site visits or from the questionnaires and published literature.

Stepwise multiple regression procedures (SAS 1989) were performed on independent variables to identify the best multiple regression model for the dependent variables. Independent variables that failed to maintain significance were eliminated. Multiple regression was repeated using the MAXR option of SAS (1989) to determine the maximum R^2 obtainable using the independent variables estimated. The resulting R^2 from these multiple regression models is indicative of the proportion of total variation in forage kochia spread and composition explained by the independent variables. It is possible that interactions between independent factors may have significantly increased the predictive power of the regression models, but because of degree-of-freedom limitations and complexity of interpretation, we did not test interactions. Planting-method variables were not included in the stepwise regression procedures because of the limited number of sites for which that information was known.

Results

Adaptation and Stand Composition Within Orginal Seeding

Percent composition of Immigrant within original seedings ranged from 2 to 91 percent with an average of 50 percent and median of 53 percent . Factors favorably associated with higher Immigrant composition included seeding date, medium textured soils, Immigrant planted with no other species, prepared or disturbed seedbed, successful initial establishment, and predominantly annual competition (table 1). Stepwise regression analysis resulted in an R^2 of 44 percent (table 1). Including all independent variables in the regression model resulted in a maximum R^2 of 58 percent . Unexplained variation may be due to factors not determined such as quality of seed, seeding rate and date, or interactions among environmental variables.

Fringe of Recruitment

Fringe distance, or marginal or peripheral recruitment threshold, ranged from 0 to 100 ft. The mean and median were both 20 ft. These small values for the mean and median strongly suggest that in most environments, Immigrant is not an aggressive competitor with native or established vegetation. The best regression model, consisting of medium soil texture, elevation, and date of seeding, only explained 22 percent of variation in recruitment fringe distance (table 1). Even though date of planting was included in the multiple regression model, the plot of planting date versus fringe suggests a very weak association between the two (fig. 1). The maximum R^2 achievable using all estimated variables still only explained 48 percent of the variation. Unexplained variation may be due to factors that were not determined such as variations in annual precipitation during the life of the seeding.

Table 1—Correlation coefficients and associated P-value, P-value from stepwise multiple regression, and R^2 for multiple regression model for ecosite variables associated ($P \leq 0.10$) with percent forage kochia composition within seeding and fringe of forage recruitment outside of planting (58 sites included in analysis).

Variable	r	P-value (individual)	P-value (mult. reg.)
Forage kochia percent within seeding			
Monoculture seeding	0.43	0.001	0.001
Disturbed seedbed	0.41	0.001	0.020
Perennial competition	–0.42	0.002	.
Medium textured soils	0.29	0.026	.
Annual competition	0.29	0.034	.
Coarse textured soils	–0.27	0.038	.
Elevation	–0.25	0.057	0.018
Fire before planting	–0.28	0.058	.
Seeding date	0.24	0.065	.
Precipitation	–0.24	0.068	.
Successful establishment	0.23	0.077	.
Pinyon-juniper ecosystem	–0.23	0.087	.
Basin big sagebrush ecosystem	–0.23	0.087	0.010
			R^2 = 44 percent
Fringe of forage kochia recruitment			
Medium textured soils	0.30	0.021	0.018
Salt desert shrub ecosystem	0.24	0.067	.
Elevation	–0.22	0.090	0.4
Fire before planting	–0.22	0.098	.
Pinyon-juniper ecosystem	–0.21	0.100	.
Age of planting	.	.	0.063
			R^2 = 22 percent

Maximum Distance From Seeding to a Single Plant

Reconnaissance surveys of the perimeters surrounding 62 Immigrant plantings found individual plants at 0 to 1,265 ft from the seeding boundary. The mean and median distances were 93 ft and 50 ft, respectively. These numbers indicate that although individual plants were found at a considerable distance from the boundary at a few sites, the furthest single immigrant plant at half the sites was 50 feet or less from the original planting. The best multiple regression model only explained 6 percent of the variation among sites, further indicating the evaluated environmental variables could not be used to predict this measure of spread. No ecosite variables were significantly correlated with maximum distance to single forage kochia plants.

Immigrant Forage Kochia Composition at Recruitment Fringe

On average Immigrant comprised only 6 percent of the vegetation at the defined recruitment fringe (range was 0 to 26 percent). The median value for immigrant composition at the fringe was 4 percent . The most significant correlation found was with age of planting.

From the low R^2 values for these measures of recruitment it is obvious that unknown factors are important in determining the extent of forage kochia recruitment. Our observations suggest that the extent of severe soil disturbance around the planting may have a large impact on the recruitment.

Discussion and Summary

The complete report of this study can be found at (Harrison and others 2000). Our findings are in agreement with and generally confirm reports in literature. Immigrant will naturally recruit, like the majority of plants, mainly in disturbed soil or in areas lacking vegetation, especially perennial vegetation, both within and outside its seeding area. The major elements that influence the distance and amount a species will spread are its ecological adaptation, amount of soil disturbance, and plant competition from both annuals and perennials. Immigrant kochia has a broad diverse adaptability and therefore propagates itself in several western rangeland plant communities.

Sites with high annual precipitation supported less kochia spread than those with lower annual precipitation. High precipitation zones may have more closed plant communities and less open spaces for kochia establishment than lower rainfall areas. Immigrant establishes well in course, medium, and fine textured soils including sandy, gravely, stony, clay, silt, and loam soils.

Long-term research is needed to determine Immigrant's competitive interaction with perennials in the Wyoming big sagebrush, desert shrub (black sagebrush and shadescale), and salt desert shrub sites. Our observations suggest that over time native perennials, such as shadscale, winterfat, Wyoming big sagebrush, thickspike wheatgrass and western wheatgrass [Pascopyrum Smithi] may reestablish themselves in stands of Immigrant forage kochia. In many instances, resource mangers are currently faced with the persistence of alien annuals such as cheatgrass and

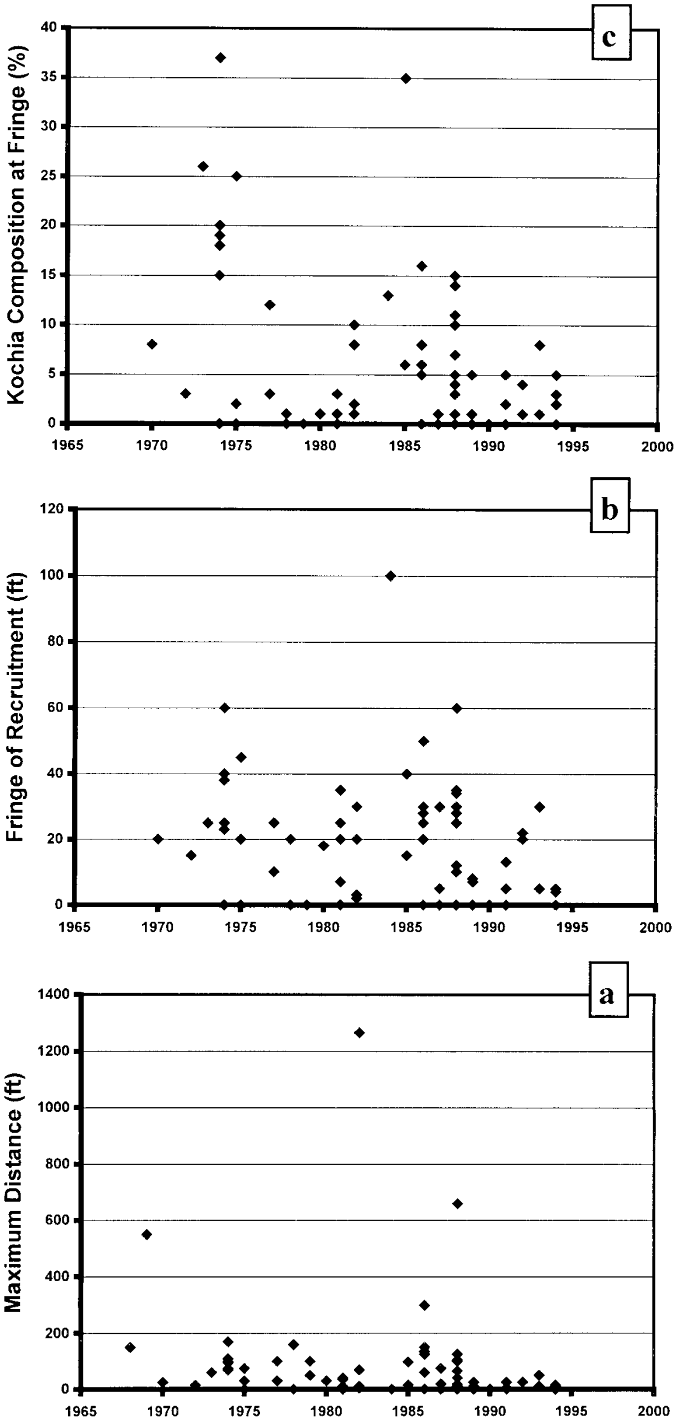

Figure 1—Date of forage kochia planting plotted against (a) maximum distance to a single kochia plant outside the planting boundary, (b) the fringe (threshold) of spread outside the planting boundary, and (c) the percent composition of forage kochia at the fringe. These graphs show that date of planting is not associated with distance of forage kochia spread.

medusahead rye that result in increased frequency of wildfires and degradation of the resource base through soil erosion. The establishment of Immigrant forage kochia helps protect these environmental resources and allows native perennial communities to become re-established. On many evaluated sites, biodiversity has been improved by the presence of Immigrant. Clearly, Immigrant can be established in a wide range of areas and environmental conditions. It successfully competes with annuals, such as cheatgrass, halogeton, Medusahead rye, and tumble mustard (Sisymbrium altissimum). Although Immigrant may spread into disturbed and bare areas, especially on sites with minimal productivity, low elevation, low precipitation, and saline/alkaline soils, including playas and slick spots, we found little evidence that Immigrant is an aggressive spreader in established perennial plant communities.

Our conclusions from evaluations in Kazakhstan and discussions with Russian and Kazakhstan scientists concerning the spread of forage kochia into native perennial plant communities are in full agreement with our assessments of its adaptation and aggressiveness in the U.S.A. Depending on the site and associated species, native perennial plant communities in Kazakhstan contained from 1 to 20 percent forage kochia. However, in disturbed areas along roadways, abandoned fields, and farmsteads, forage kochia made up from 15 to 60 percent of the plant community. Forage kochia was never observed to be the dominant species in the major plant communities compromised of sagebrush, saltbush, winterfat, crested and siberian wheatgrasses, and needlegrass. Nowhere did we observe sites where forage kochia had invaded from disturbed sites into adjacent perennial plant communities on the Kazakhstan steppes.

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Impact of Tebuthiuron on Biodiversity of High Elevation Mountain Big Sagebrush Communities

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Abstract—The objectives of this study were to determine tebuthiuron's (1) effectiveness at low application rates in thinning dense, high elevation stands of mountain big sagebrush, (2) impact on understory herbaceous plants and soil microflora, and (3) movement and stability in soil. Four study sites were established in the Fish Lake National Forest and adjacent Bureau of Land Management holdings. Tebuthiuron pellets were applied at one site in 1994, a second site in 1995, and two sites in 1996 at rates ranging from 0.2 to 0.7 pounds of active ingredient (AI) per acre (0.18 to 0.63 kg AI per ha). Data from the two sites treated in 1996 show that sagebrush canopy cover was reduced in annual increments from pretreatment levels of about 23 percent to11 percent (0.3 AI treatment), 6 percent (0.5 AI), and 4 percent (0.7 AI) by 1999 (control plots were 26 percent by 1999). Understory vegetation increased slightly or had no change over time depending on treatment and climatic factors. Tebuthiuron treatments at these rates did not have long-term adverse effects on soil microflora. Tebuthiuron was mobile and its concentration remained twice as high in the zero to 15 cm soil samples as compared to deeper soil samples (>15 to 30 cm). Overall, tebuthiuron levels dropped about six fold from the second to third year after application (to 0.1 ppm). The preliminary conclusion is that tebuthiuron applied at these low concentrations can maintain mountain big sagebrush cover at meaningful levels without damage to the understory and soil micoflora.

Introduction

Tebuthiuron, N[5-(1,1-dimethylethyl)-1,3,4-thidiazol-2-yl]-N-N'-dimethylurea, is an herbicide that is used to thin dense stands of woody plants in rangelands in order to increase access to forage plants in the understory. It has been used in many studies to control big sagebrush, *Artemisia* spp., (Britton and Sneva 1984; McDaniel and Balliette 1986; Whitson and Alley 1984). Tebuthiuron is applied to the soil surface as pellets and thus its movement through soil can be affected by soil type and moisture (Johnsen and Morton 1989). Studies have shown that tebuthiuron is highly mobile in soil and levels typically decrease rapidly in 1 to 4 years after treatment (Emmerich and others 1984; Johnsen and Morton 1989). Despite this initial rapid decrease, in one study Johnsen and Morton (1989) have shown that concentrations were detectable throughout the study and actually began to steadily increase 9 to 11 years after treatment (11 year study). It has been suggested that this may be due to slow release from soil particles or from slowly decaying litter (Garcia and Lee 1979). Long-term effects of residual tebuthiuron may be of particular importance in arid soils.

It is therefore important to determine if low doses of the herbicide can still be effective in thinning woody species while minimizing any possible detrimental effects on the community as a whole. This study examined the impact of tebuthiuron in low concentrations (0.18 to 0.63 kg AI per ha) on high elevation mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities. In addition to its effectiveness against the target species, this study sought to determine if tebuthiuron has an impact on understory plants or on soil microflora.

The functional composition and diversity of plant communities have been shown to be the principal factors controlling productivity (Hooper and Vitousek 1997; Tilman and others 1997). These findings suggest that management practices affecting plant diversity and composition can have a profound effect on ecosystem processes. Although compounds such as herbicides and insecticides are, in general, less detrimental to microbial activities, some soil microbial processes and properties may be affected (Hicks and others 1990; Nemes-Kosa and Cserhati 1995). This possible impact on soil microbial communities should be evaluated in view of their role in sustaining the global cycling of matter and their varied functions in supporting plant growth. Assessment of the impact of changes in plant communities on soil community structure is difficult because of the highly diverse nature of microbial communities in soil. This may be facilitated by investigation of specific groups of microorganisms or specific activities. Microorganisms involved in the nitrogen cycle are of particular concern since nitrogen is usually

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the limiting nutrient in soils and the rate of microbial activity is limited in arid ecosystems. Due to the limitations in scope and budget, efforts were concentrated on limited areas and methodologies. Hence, this study focused on determining the impact of tebuthiuron treatment on total heterotrophic microbial populations and aspects of nitrogen cycling.

Species abundance and diversity measurements are sensitive indicators of environmental conditions. However, the conventional methodologies investigating diversity of microbial communities have significant shortcomings. These include the time and resources required to quantify and identify microbial species of many different groups and extensive analysis of numerous samples from different treatments. Furthermore, a significant bias is invariably introduced by the selective cultivation, analysis, and interpretation of results. We acknowledge these shortcomings in this report.

The objectives of this study were (1) to evaluate the effectiveness of low application rates of tebuthiuron in thinning dense, high elevation stands of mountain big sagebrush, (2) to evaluate the impact of tebuthiuron on understory herbaceous plants and soil heterotrophic bacteria and fungi, ammonium oxidizing microflora, nitrifying/nitrate reducing (combined assimilatory and dissimilatory processes) microflora, photosynthetic microflora, and mycorrhizal associations, and (3) to examine the movement and stability of tebuthiuron in the soil.

Methods

Study Sites

Four study sites were established in the Fish Lake National Forest and adjacent Bureau of Land Management holdings: three were on the Monroe Mountain portion of the Sevier Plateau, designated as the Plateau, Big Flat and Burnt Flat treatment sites. The fourth site was on the nearby Fish Lake Plateau and is referred to as the Fish Lake treatment site. The elevations of the sites are: Plateau, 8,125 ft (2,508 m); Fish Lake, 8,800 ft (2,716 m); Burnt Flat, 9,300 ft (2,870 m); and Big Flat, 9,400 ft (2,901 m). All sites were dominated by mountain big sagebrush. Soils were characterized as loams with 40 to 48 percent sand, 20.56 to 26.56 percent clay, and 29.16 to 33.44 percent silt in all but the upper depths (zero to 15 cm) at Plateau, which was a clay loam (29.56 percent clay and 26.42 to 28.16 percent silt). Soil pH ranged from 5.9 to 6.6. Upper soils typically had more organic matter than did corresponding deeper soil (>15 to 30 cm). Overall percentages of soil organic matter are: Plateau, 2.34 to 3.88 percent; Fish Lake, 3.57 to 9.36 percent; Big Flat, 4.39 to 5.32 percent; and Burnt Flat, 9.46 to 10.70 percent.

Tebuthiuron Application

Study plots measuring 50 x 100 ft (15.24 x 30.48 m) were established in a random manner and tebuthiuron was applied as pellets in the following concentrations and times at the four sites: Plateau site, 0.0, 0.3, 0.5, and 0.7 pounds active ingredient (AI) per acre (0.0, 0.27, 0.45, and 0.63 kg AI per ha) applied Sept. 29, 1994; Fish Lake site: 0.0, 0.2, 0.4, and 0.6 pounds AI per acre (0.0, 0.18, 0.36, and 0.54 kg AI per ha) applied Sept.13, 1995; Big Flat site 0.0, 0.3, 0.5, and 0.7 pounds AI per acre (0.0, 0.27, 0.45, and 0.63 kg AI per ha) applied July17, 1996; and Burnt Flat site 0.0, 0.3, and 0.5 pounds AI per acre (0.0, 0.27, and 0.45 kg AI per ha) applied July17, 1996. Big Flat and Burnt Flat sites also included replicate plots.

Vegetation Study

Plant ecological data were collected in the summers prior to soil sampling. In 1996, vegetation surveys were conducted before tebuthiuron was applied to the Big Flat and Burnt Flat treatment sites. Vegetation data were collected over a 4-year period from 1996 to 1999.

Control and treatment plots (about 0.4 ha each) were set up in areas of level terrain and homogeneous vegetation and soil. Within each plot a circular 0.01 ha subplot was established in a random manner and centered on a steel rebar post. Subplot perimeters were at least two meters from the plot boundary. Data collected in the subplots included vascular plant species present and percent cover partitioned among shrubs, grasses, forbs, bare soil, liter, rock (>2 cm), and cryptogams (Daubenmire 1959; McArthur and Sanderson 1992, 1995). Density of plant species was determined from 4 m^2 quadrats located 1 m in each cardinal direction from the center of the circular subplots. Sagebrush cover was monitored along two 45 m diagonal line transects in each treatment and control plot. Means separations of data were performed using Proc Means procedures of the SAS statistical package (SAS 1989).

Soil Sampling

Soil sampling was done during site visits at the four sites in August 1996, 1997 and 1998. In 1996, soil samples were taken at two depths (0 to 15 cm and >15 to 30 cm) at the base of two selected healthy looking plants (healthy) in the control plots, and one healthy, two slightly unhealthy looking plants (medium affected), and one unhealthy looking plant (affected) in each of the treated plots at the Fish Lake and Plateau sites. The plants were tagged and samples were taken at the base of the same plants in subsequent years. In addition, pooled (composite) samples from each plot were taken each year. In 1996 only composite samples were taken at the Big Flat and Burnt Flat sites. In the subsequent 2 years, 1997 and 1998, a full sampling approach (healthy, medium affected, affected and composite) was taken at all treatment sites.

Two to four pounds of soil were collected per sample and put into plastic airtight bags. Each sample was then mixed thoroughly and split into two separate labeled bags and transported on ice to the laboratory. One set was used for soil chemical analysis and the other for microbial analysis. Soil samples were kept refrigerated until tests were conducted.

Tebuthiuron and Soil Analysis

Tebuthiuron and its metabolites were extracted from soil samples with acidified methanol. It was quantified using a

Waters HPLC (Loh and others 1980). Soil classification (texture class) was made based on percent sand, clay, and silt. In addition, percent organic matter, pH, and electrical conductivity were determined.

Microbial Analysis of Soil

Total Heterotrophic Bacteria and Mold Counts—Serial dilutions of soil samples were made and surface plated on Trypticase Soy Agar (TSA) and Sabouraud Dextrose Agar (SAB). Plates were incubated at 30 °C for 72 hours. Total bacterial and fungal counts were made. The plates were reincubated and checked again after 5 days to observe slow colony forming organisms. The counts were amended as required.

Estimation of Nitrifying and Nitrate-Reducing Microbial Populations—Soil samples were taken from the base of healthy plants in control plots, and healthy and affected plants in the highest treatment plot at each site. The MPN method described by Alexander (1982) was used and an estimation of nitrifying populations was made using the method described by Schmidt and Belser (1982). A total of 25 tubes of each medium, ammonium oxidizer and nitrite oxidizer media, for each soil sample were used. Samples were incubated at room temperature with light.

The presence of ammonium was determined in incubated samples using Nessler's reagent, nitrite and nitrate were detected using modified Griess-Ilosvay reagents, and diphenylamine, respectively (Schmidt and Belser 1982). A sample was considered positive for ammonium oxidation if nitrite and/or nitrate were detected after incubation in ammonium medium. A sample was considered positive for nitrite oxidation when all nitrite was exhausted from the medium or nitrate was detected in the total absence of nitrite in the nitrite medium. Complete oxidation to nitrate and subsequent removal of nitrate (assimilatory reduction by incorporation into cell material and/or dissimilatory reduction to N2 gas) could be concluded by the absence of nitrite and nitrate in nitrite medium.

Estimation of Photosynthetic Microbial Populations (Algae and Cyanobacteria)—During examination of plates and MPN tubes in 1996 and 1997, green colonies with mixed bacterial and photosynthetic microorganisms were seen on some plates and green-pigmented growth was observed in several MPN tubes. The most vigorous growth was found in nitrite medium when incubated in light. This provided an opportunity to compare the photosynthetic microbial communities in samples from control and the highest treated plots at each site using the MPN method. This was done using samples taken in 1998.

Mycorrhizal Association—In the first year (1996) root samples of more than 20 plant species from control plots at the Fish Lake and replicate Big Flat sites were collected and examined for the presence of mycorrhizal associations. Each root sample was washed thoroughly with tap water through a 1 mm sieve, retaining the roots on top of the sieve. The washed roots were preserved in FAA (5 percent Formalin, 5 percent Acetic acid, 40 percent Ethanol, 50 percent H_2O) until needed.

Ectomycorrhizae: Each root sample was spread out in a petri dish with enough FAA to keep roots immersed. Small pieces of root tips were stained in lacto-phenol-cotton blue, transferred to clear lacto-phenol, mounted on a slide in clear lacto-phenol under a coverslip, and examined under a microscope for the presence of ectomycorrhizal associations.

Endomycorrhizae and Vesicular-Arbuscular Mycorrhizae (VAM): Small pieces of root tip were placed in perforated microfuge tubes. The roots were placed in a beaker containing 10 percent KOH and autoclaved at 121 °C for 10 minutes. Roots were then rinsed in tap water, bleached in 30 percent hydrogen peroxide for 10 minutes, and rinsed with tap water three times. The roots were covered in 1 percent HCl for 3 to 4 minutes without rinsing and stained with Trypan Blue for 20 minutes in a hot water bath (90 °C). Roots were then placed in 40 percent glycerin and examined microscopically. Photomicrographs were taken for documentation.

In 1997 and 1998, the above procedure was used to examine the mycorrhizal associations in selected plant species in control and the highest treatment plots at all four sites.

Results

Soil Concentrations of Tebuthiuron

Soil chemical analyses from the Plateau and Fish Lake sites were pooled, as were those from the Big Flat and Burnt Flat sites (table 1). Tebuthiuron was detected up to 100 ft (30.48 m) from the areas of application after the first year. Tebuthiuron concentrations remained significantly higher (at least double) in the upper 15 cm of soil as compared with deeper soil samples throughout the duration of the study. The final measured tebuthiuron concentrations (2 years after application) were significantly (80 to 83 percent) less than those measured in the previous year. There was no significant difference in tebuthiuron concentrations among treatments.

Vegetation Study

Plant community sampling spanned a 4-year period (1996 to 1999). Results from the Big Flat and Burnt Flat sites are presented. Similar trends were seen at the other sites. The percent cover of mountain big sagebrush (table 2) was not

Table 1—Tebuthiuron concentrations (ppm); treatment is in pounds of active ingredient per acre.

Location	Time frame	Soil depth 0 to 15 cm		Soil depth >15 to 30 cm		Significance[a]
Plateau and Fish Lake	All years	0.40		0.16		NS
	1997–1998	0.50		0.09		*
	Treatment					NS
Big and Burnt Flat	All years	0.54		0.27		*
	1997–1998	0.69		0.11		*
	Treatment	0	0.3	0.5	0.7	
		0.14	0.38	0.38	0.33	NS

[a] * = $P < 0.05$, NS = not significantly different.

Table 2—Percent cover of mountain big sagebrush after tebuthiuron treatment at Big Flat and Burnt Flat treatment sites.

	Year[b]			
Treatment level[a]	1996	1997	1998	1999
0	22.9 A	24.6 A	24.9 A	25.9 A
0.3	23.3 A	15.2 B	12.3 B	11.0 B
0.5	24.9 A	13.1 B	7.2 B	6.3 B
0.7	19.2 A	7.0 B	5.1 B	4.3 B

[a] Active ingredient in pounds per acre.

[b] Different letters in rows and columns indicate significantly different mean values, $P < 0.05$.

significantly different among plots prior to herbicide application. In each subsequent year after tebuthiuron application sagebrush cover decreased with increasing tebuthiuron concentration, while remaining almost constant in control plots. Treated plots had significantly less sagebrush cover than did control plots.

The density of perennial grasses (table 3) was not significantly different with increased tebuthiuron concentrations. Overall, the density was highest in 1998, but there was no significant difference between years. The density of native perennial grasses also peaked in 1998, but again there was no significant difference among years (McArthur and Sanderson, data on file at Shrub Sciences Laboratory). There were, however, significantly fewer native perennial grasses in the highest herbicide treatment plots as compared with control plots. The densities of native perennial forbs and native annuals were not significantly different among treatments (McArthur and Sanderson, data on file at Shrub Sciences Laboratory). The density of native perennial forbs increased significantly while the density of native annuals decreased significantly in later years (1998 an 1999) as compared with earlier years.

Soil Microbial Study

Results from all four sites were similar. Total soil heterotrophic bacterial counts ranged from 10^6 to 10^7 as seen on TSA with the exception of 1998 (zero to 15 cm) at Big Flat, where all plots produced 10^4 to 10^5 bacteria (data not shown). Total soil mold counts ranged from 10^4 to 10^6. Data from Fish Lake will be presented and are representative of the other sites. Total heterotrophic bacterial counts (fig. 1) and total mold counts (fig. 2) did not differ significantly among treatments, years, or soil depth.

Table 3—Density of perennial grasses after tebuthiuron treatment at Big Flat and Burnt Flat treatment sites.

	Year[b]			
Treatment level[a]	1996	1997	1998	1999
0	180 B	287 AB	328 A	308 A
0.3	147 B	210 A	235 A	228 A
0.5	163 A	208 A	228 A	206 A
0.7	74 A	136 A	139 A	131 A
Year	155 A	225 A	251 A	236 A

[a] Active ingredient in pounds per acre.

[b] Different letters in rows indicate significantly different mean values, $P < 0.05$.

There was essentially no significant difference in the MPN of nitrite oxidizers (fig. 3) or in the MPN of nitrate reducers (fig. 4) isolated from soil near plants in control and heavily treated plots or in samples collected in different years. There were slightly more nitrite oxidizers and nitrate reducers in the soil samples from the base of healthy plants in the treated plot as compared with that of affected plants in the same plot and controls. There was virtually no difference in the detected MPN of ammonium oxidizers among treatments or between healthy and affected plants (fig. 5). The detected MPN of ammonium oxidizers varied slightly between years, but the results were very consistent among treatments and plants.

Mycorrhizal Study

There were essentially no differences found in the quantity or type of mycorrhizal associations found on root samples among control and treated plots or in different years (data not shown). Virtually all root samples examined had endomycorrhizal associations.

Photosynthetic Soil Microflora

In the last year of the study (1998), the MPN, based on green-pigmented growth in nitrite tubes, was used to compare and quantify photosynthetic soil populations. The MPN of control and the highest treated plots from all sites showed no persistent effect among treated and untreated plots on photosynthetic microbial populations.

Discussion

Tebuthiuron was shown to be mobile in the soils in this study. This concurs with a previous study by Whisenant and Clary (1987), which found that tebuthiuron is dispersed over greater lateral distances in loam soils of low organic content (such as those in this study) than those of high organic content. The results of this study are consistent with several other reports (Bovey and others 1978; Garcia and Gontarek 1975; Johnsen and Morton 1989; Whisenant and Clary 1987) showing that tebuthiuron is found in higher concentrations in upper soil levels. Emmerich and others (1984) found that tebuthiuron applied at 0.84 kg AI per ha decreased by 62 percent after 21 months. The results of the present work showed a similar trend, an 80 to 83 percent decrease 2 years after treatment. Johnsen and Morton (1989) showed that tebuthiuron can persist in the soil for many years (particularly in a semiarid environment) and exert herbicidal activity on vegetation for several years, it is therefore necessary to determine minimum dosages required to achieve the desired effects while avoiding over-dosing to prevent undesirable prolonged effects on an ecosystem.

The present study showed that low levels of tebuthiuron were extremely effective in decreasing the cover of mountain big sagebrush for at least 3 years. Overall, sagebrush cover

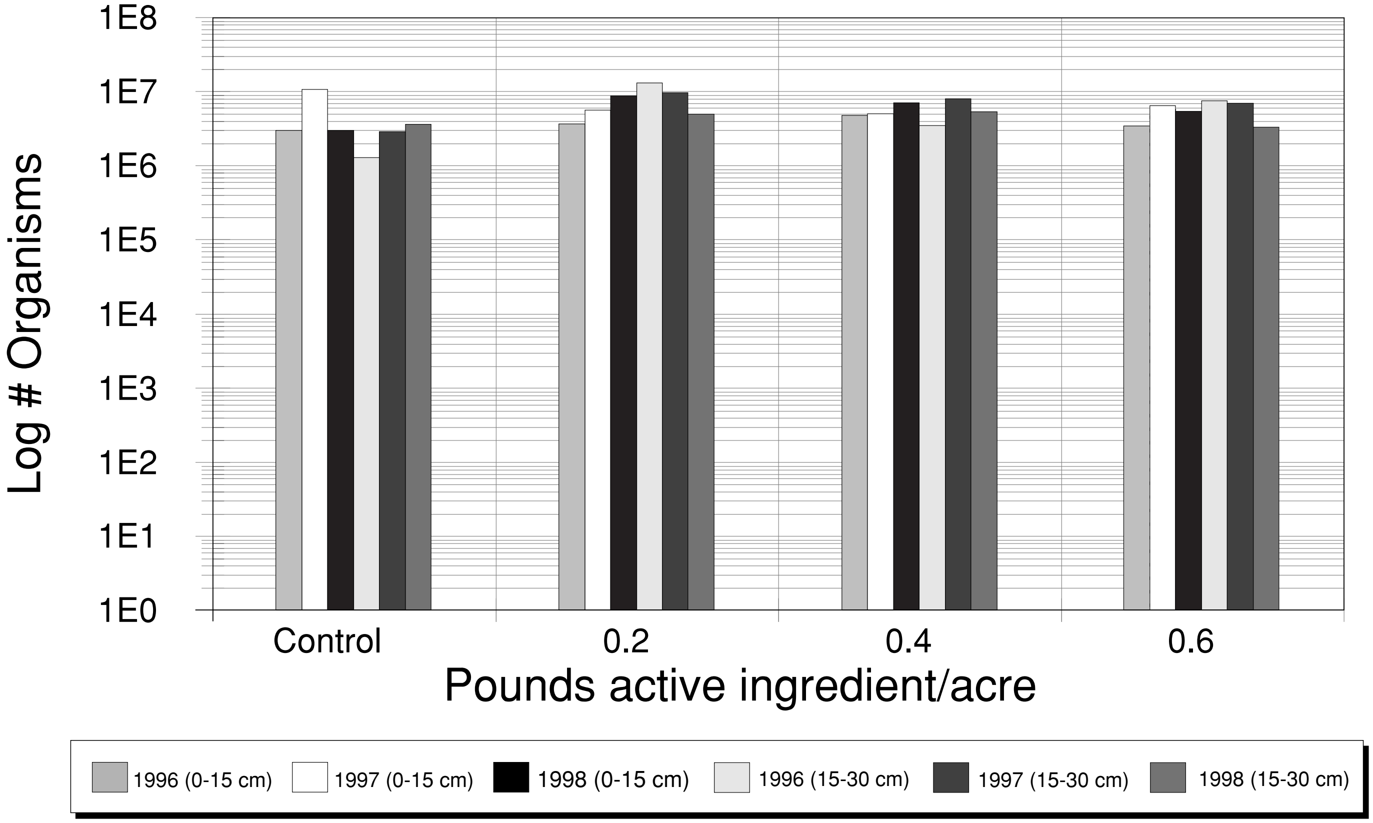

Figure 1—Total soil heterotrophic bacterial counts after tebuthiuron treatment at the Fish Lake treatment site. Data from soil near healthy, medium affected, and affected plants were similar and are pooled.

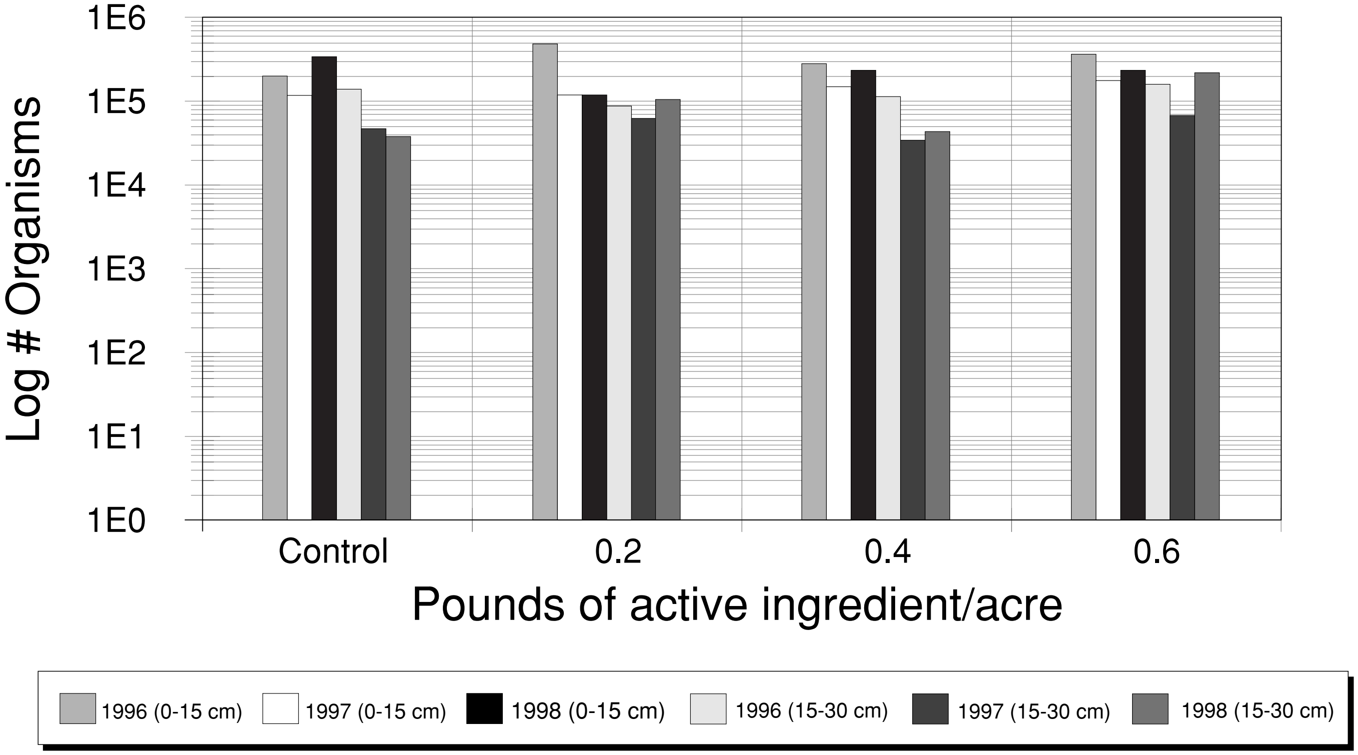

Figure 2—Total soil mold counts after tebuthiuron treatment at the Fish Lake treatment site. Data from soil near healthy, medium affected, and affected plants were similar and are pooled.

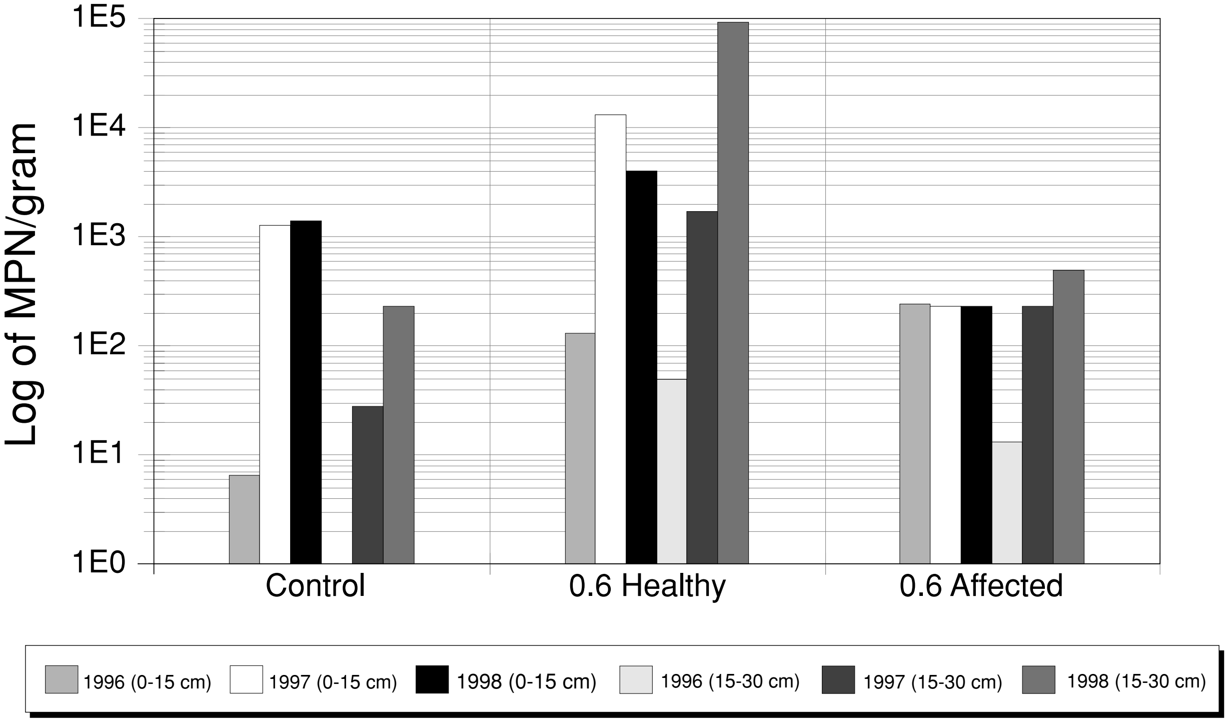

Figure 3—Most Probable Number (MPN) of nitrite oxidizers after tebuthiuron treatment at the Fish Lake treatment site. Soil samples were taken from the base of healthy control plants and healthy and affected plants in the highest treatment plot (0.6 pounds active ingredient per acre).

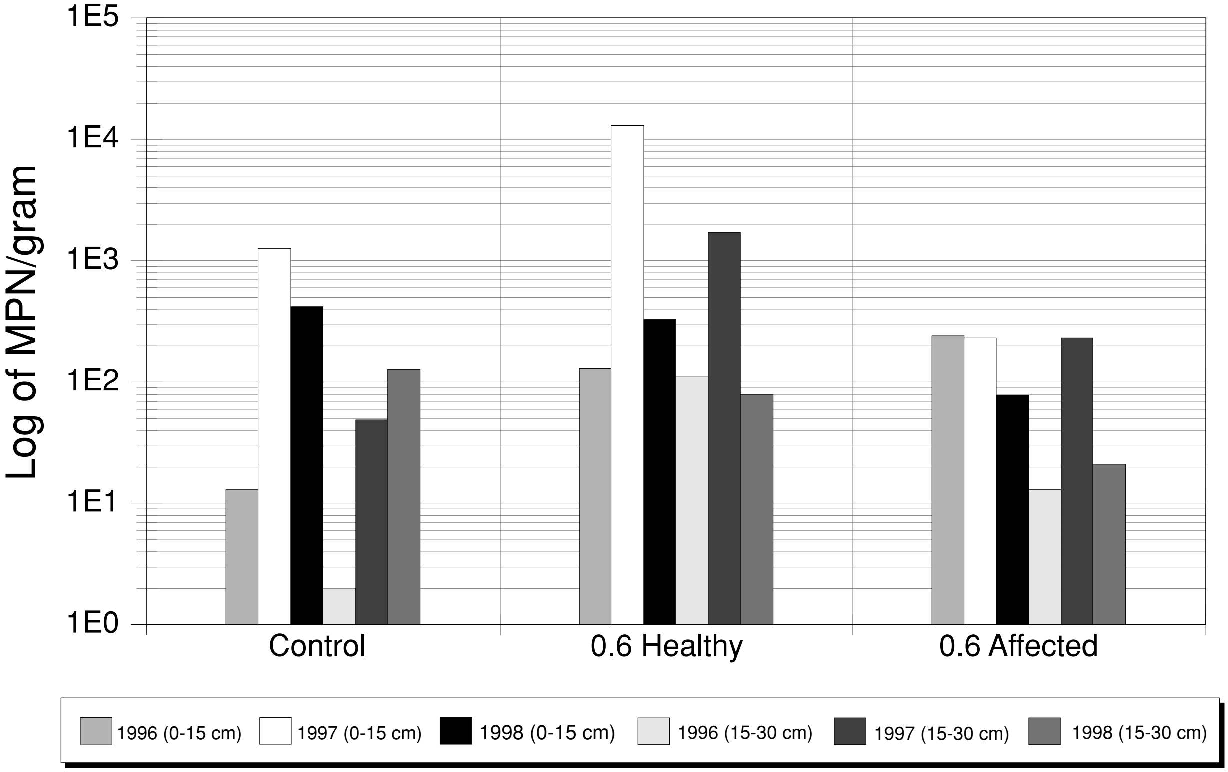

Figure 4—Most Probable Number (MPN) of nitrate reducers after tebuthiuron treatment at the Fish Lake treatment site. Soil samples were taken from the base of healthy control plants and healthy and affected plants in the highest treatment plot (0.6 pounds active ingredient per acre).

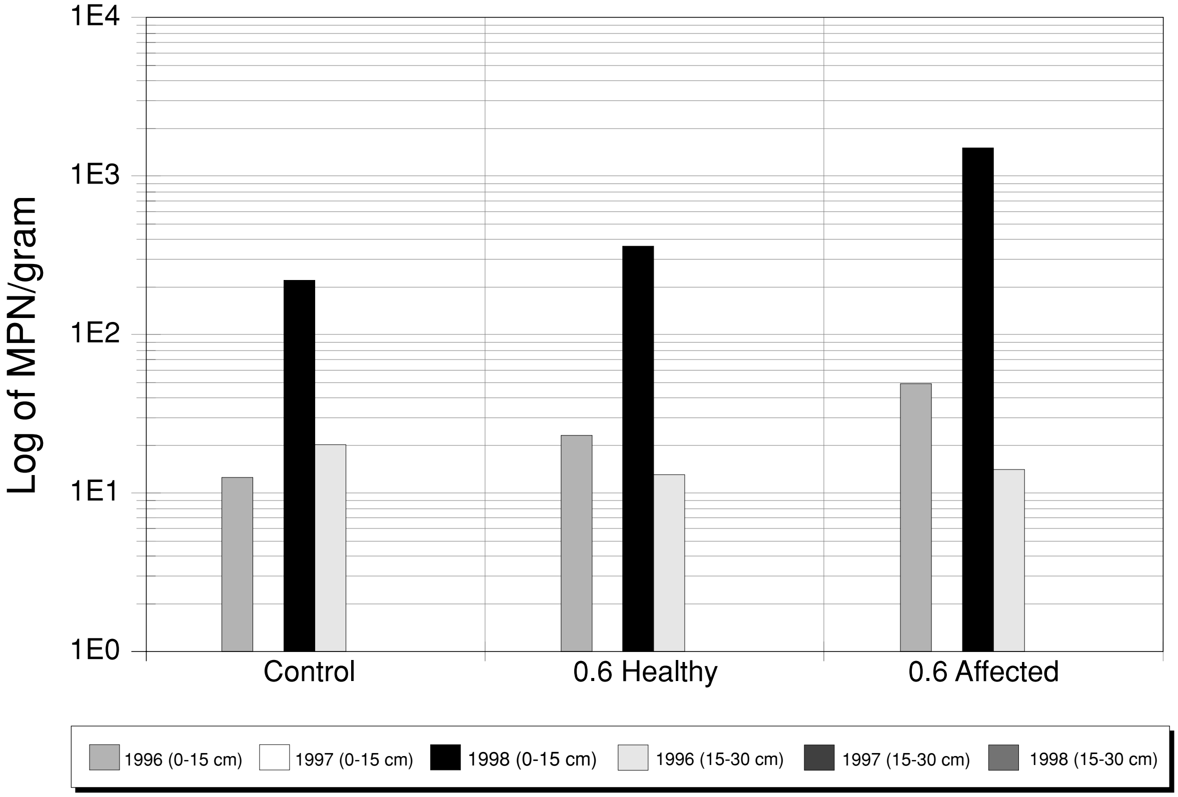

Figure 5—Most Probable Number (MPN) of ammonium oxidizers after tebuthiuron treatment at the Fish Lake treatment site. Soil samples were taken from the base of healthy control plants and healthy and affected plants in the highest treatment plot (0.6 pounds active ingredient per acre).

was less in treated plots as compared with controls. There was a trend, although not significant, for sagebrush cover to decrease with increased herbicide concentration. Considering the long-term study mentioned above it could therefore be a concern that tebuthiuron may continue to exert its effects for a long time and may decrease target species to lower levels than necessary or desired. The study also showed that concentrations above the lowest level used here may not be necessary and concentrations lower than those used in this study may actually achieve the desirable results.

The densities of perennial grasses and native perennial grasses were greater after treatment, though not significantly so. The concentration of tebuthiuron had no significant effect on these groups except that there were significantly fewer native perennial grasses in the highest treatment level. In the second and third years after treatment there were significantly more perennial forbs and significantly fewer native annuals than in earlier years. The level of tebuthiuron did not have any significant effect on these groups. It is probable that the annuals declined as competition with perennial understory plants increased. These results suggest that tebuthiuron concentrations as low as 0.27 kg AI per ha could be effective in reducing big sagebrush cover, while having very little adverse effects on herbaceous plants in the community.

It is widely accepted that analysis of changes in the composition of a community can be used to characterize its response to stress. In order to observe effects by quantifying changes in microbial biomass or in the general metabolic activities of microbial communities, a variety of tests have been recommended (Gerber and others 1991) and employed. Some may argue that species abundance and diversity are the most sensitive indicators of environmental conditions and that a community's composition and diversity are most significantly represented by the nucleic acid profiles of organisms present in the soil (Engelen and others 1998). We acknowledge that comprehensive studies employing the most advanced and proven methodologies are required to derive the most meaningful and accurate conclusions. However, in the absence of studies on the impact of tebuthiuron on microbial populations and activities, and a limited scope and budget, results generated from the present study are a step in the right direction.

Our work indicates that neither heterotrophic microbial populations (bacteria and mold) nor nitrifying activities at these sites were affected by tebuthiuron. This is in agreement with the general view that herbicides are less detrimental to microbial activity and, under certain conditions, may even stimulate certain activities (Hicks and others 1990).

The low ammonium oxidizer populations detected in the present study could be attributed to inhibition of ammonium-sensitive fractions (Phillips and others 2000; Suwa and others 1994) in the media used to determine MPN and the low number of ammonium oxidizers in semiarid land in general. Hence, our data do not represent total ammonium oxidizers, but only the populations that are not adversely affected by the 0.5 g/l ammonium used in the medium (Schmidt and Belser 1982). The apparent absence of ammonium oxidizers in some samples determined by MPN in ammonium medium could be misleading. It is likely that the removal of nitrate, as it is produced from further oxidation of nitrite, is responsible for these results. The consistency of data obtained from control and the highest treated plots indicate that tebuthiuron does not affect ammonium oxidizers.

Although the present study did not determine microbial composition of samples or a profile of microbial diversity, the results of the comparison of total heterotrophic counts and nitrifying activity contribute to the available data on the possible ecological impacts of tebuthiuron.

Due to the fact that tebuthiuron is an herbicide, there is reason to suspect that it may have possible adverse effects on photosynthetic microbial populations in treated soil. The role of cyanobacteria and algae in nitrogen fixation and the cryptogamic crust structure is well known. However, there is limited information regarding the impact of tebuthiuron on green algae. Price and others (1989) studied its effects on green algae found in playa lakes. This study indicated that runoff from agricultural fields treated with tebuthiuron concentrations greater than 2.24 kg AI per ha may adversely affect the green algae communities of playa lakes. To our knowledge, there are no studies addressing the effect of tebuthiuron on photosynthetic microorganisms in the soil. There were no significant differences between photosynthetic microbial population sizes at each site when the MPN of the highest treated and control plots were compared. The results may even suggest a slight increase in treated sites by the end of the third year. Therefore, in the absence of data to assess photosynthetic microbial populations in all 3 years, we could only conclude that tebuthiuron does not have a lasting effect at concentrations used in this study.

The results indicate that understory vegetation is not affected after 3 years and that all plant species sampled show mycorrihzal associations. Therefore, one could conclude that mycorrhizal fungi in the soil and their associations are not affected by tebuthiuron application.

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Factors Mediating Cheatgrass Invasion of Intact Salt Desert Shrubland

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Abstract—Cheatgrass (*Bromus tectorum*) has recently displaced salt desert shrubland in many areas of the Great Basin. We studied the dynamics of cheatgrass invasion into an intact shadscale-gray molly community in Dugway Valley, Utah, by adding seeds and manipulating disturbance regime and resource availability. Shrub clipping or cryptobiotic crust trampling on large plots increased cheatgrass recruitment and biomass production slightly in a favorable moisture year (1997 to 1998), whereas in a less favorable moisture year (1998 to 1999) these disturbance treatments had a significant negative effect. In 1998 to 1999 small plot studies, recruitment was similar in intact shrub clumps and openings, but biomass and, therefore, seed production was three times greater in shrub clumps. Disturbance decreased recruitment but had no significant effect on biomass per plant. Added water had no effect in openings, but added N increased and reduced N decreased biomass. In shrub clumps, fertility manipulation had little effect, but added water increased biomass. Shrub simulation (water + N + shade) increased biomass per plant in openings, whether intact or disturbed. It had no effect in shrub clumps where shrubs were intact, but caused a large increase in both recruitment and biomass per plant where shrubs were removed. Shrub clumps provide foci of invasion because of their higher resource availability, but the shrubs have competitive as well as facilitative effects. In a dry year (1999 to 2000), there was no survival to reproduction in any treatment. There are no intrinsic obstacles to cheatgrass invasion at this site, but the process will be very slow because of low site productivity and the high probability of drought years. Disturbance is not a necessary precondition for invasion, but may facilitate the process in favorable years.

Introduction

Shrub steppe ecosystems of the Great Basin are in the process of a massive type conversion to low diversity annual grasslands heavily dominated by the exotic annual cheatgrass (*Bromus tectorum*). Fire frequency is a key factor in this conversion. The importance of fire in shrub steppe ecosystems depends on several factors. The long-term importance of infrequent but recurring fire in maintaining mosaics of shrub and perennial grass domination has been established for sagebrush steppe ecosystems (Peters and Bunting 1994). But overgrazing accompanied by invasion of exotic annual grasses that form a continuous layer of fine fuel has drastically increased fire frequency in these ecosystems, with fire return times decreasing from 50 to 200 years to 3 to 5 years (Whisenant 1990). This has resulted in complete loss of the shrub overstory and establishment of an annual grass dysclimax that perpetuates itself through repeated burning on ever-increasing areas (Billings 1994; D'Antonio and Vitousek 1992).

Shadscale-dominated ecosystems, which generally occur in areas of lower precipitation than sagebrush steppe ecosystems, experienced fire very infrequently if at all prior to the introduction of exotic annuals in the understory (West 1994). These ecosystems have been heavily impacted by a century and a half of livestock grazing and weed invasion, and few if any truly pristine areas exist. But the impact of fire in salt desert shrublands has manifested itself only recently, within the last 25 years (West 1994). The relatively sudden appearance of fire as a factor was associated with an increase in density and biomass production of cheatgrass that may already have been present in the understory. No one knows exactly what happened to open shadscale communities to massive understory dominance by cheatgrass, but a sequence of years of exceptionally high precipitation in the early 1980s is implicated in the effect. The result has been a rapid and extensive type conversion to a cheatgrass dysclimax with short fire return times, similar to the type conversion so widespread in sagebrush steppe ecosystems.

The question addressed in the work described here is how shadscale communities are placed at risk for understory takeover by cheatgrass, and whether there is any way to minimize this risk. We need to know how difficult it will be to manage these ecosystems as shrublands in the long term, and whether it is possible to restore shadscale ecosystems to a state that can resist massive annual grass invasion. This study represents a necessary step toward answering those questions.

One problem with descriptive studies of plant community change is difficulty in separating the effects of multiple causal factors. For example, heavy livestock grazing in a shadscale community can have many effects, including destruction of the cryptobiotic soil crust through trampling, selective elimination of palatable understory perennials, prevention of shadscale seed banking through consumption of fruits, and introduction of weed seeds. These in turn may have different effects on weed invasion success. In our

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experimental study, we introduced each of several factors independently, making it possible to examine the effect of each factor on invasion success, both alone and in combination. The study had two principal objectives: first, to determine the effect of seed introduction and systematic disturbance of an intact shadscale community on cheatgrass success, and second, to determine whether the effects of disturbance on cheatgrass success are mediated through soil nitrogen and/or water availability.

Study Site Description

Shrub steppe ecosystems dominated by shadscale (*Atriplex confertifolia*) occupy millions of acres in the Great Basin (Stutz 1978; Blauer and others 1976). Although referred to as salt desert shrublands, shadscale communities occur on fine-textured soils that are variably saline, in the zone between the greasewood (*Sarcobatus vermiculatus*) communities of the playa bottoms and the sagebrush (*Artemisia tridentata* and *A. nova*) communities of less xeric upland sites with coarser soils (Billings 1949).

The Camelback study site is located at an elevation of 1,310 m in Dugway Valley, on the Dugway Army Proving Grounds, approximately 170 km west of the Wasatch Front urban area. The army facility at Ditto is approximately 3 km to the north, and Camelback Hill is a few kilometers to the south. The vegetation on the site is a shrubland with shadscale (*Atriplex confertifolia*) and gray molly (*Kochia americana*) as the dominant species, and with a vascular plant cover value of 22 percent (Meyer and Garvin, unpublished data). Herbaceous perennial understory is essentially lacking. All surfaces, whether under shrubs or in openings, are inhabited by a well-developed cryptobiotic crust made up of lichens, mosses, and cyanobacteria. Weedy annuals present on the study site include perfoliate pepperweed (*Lepidium perfoliatum*) and bur buttercup *(Ranunculus testiculatus*), principally in the openings. In summer 1997, the only evident cheatgrass was along gravelly road shoulders, though there was a large population in a flooding area next to a gravel road a few hundred meters away.

Table 1—Monthly long-term precipitation totals and 1998, 1999, and 2000 water year (October 1 to September 30) monthly totals in millimeters at the Ditto Weather Station.

Month	WY1998	WY1999	WY2000	Longterm
October	15	45	0	20
November	26	8	1	15
December	10	6	1	15
January	14	25	19	12
February	41	5	29	14
March	44	5	4	21
April	21	52	8	21
May	16	28	20	26
Season total[a]	187	174	82	144
June	60	27	—	15
July	25	3	—	14
August	13	8	—	15
September	18	12	—	20
Grand total	303	224	—	208

[a] Total for 8-month season of growth for cheatgrass, a winter annual that emerges in autumn, winter, or early spring and matures by early summer.

The average annual precipitation at the study site, based on a station at nearby Ditto, is 208 mm (8.19 inches; table 1). The site has a history of sheep grazing but has been protected from grazing by livestock for over 50 years. Feral horses and pronghorn have access to the area but rarely visit. There is minimal vehicular disturbance.

Soils at the site are generally calcareous clay loams of moderately alkaline pH and moderate salinity and sodicity. In samples collected in November 1997, salinity, clay content, and carbonate content increased significantly with depth, while pH and sodicity (as measured by sodium adsorption ratio) did not (table 2). None of these parameters

Table 2—Mean values and significance tests for 10 soil parameters measured at 0 to 15 cm and 15 to 30 cm depths under shrub canopies and in openings at the Camelback study site. N = 4 per treatment combination.

	Under shrubs		In openings		Probability of significance from ANOVA		
Parameter	Surface (0 to 15 cm)	Sub-surface (15 to 30 cm)	Surface (0 to 15 cm)	Sub-surface (15 to 30 cm)	Shrub versus opening	Surface versus subsurface	Shrub/opening x surface/subsurface
Nitrate-N (ppm)[a]	12.2	7.6	6.9	6.8	<0.02	<0.06	<0.07
P (ppm)[b]	14.3	14.0	16.4	9.8	ns	ns	ns
K (ppm)[a]	704	818	809	867	<0.05	<0.06	ns
Org. Matter (percent) [c]	1.17	1.38	0.99	1.30	<0.06	<0.01	ns
Elec.Cond. (mmhos/cm)[a]	5.4	8.9	5.1	10.3	ns	<0.001	ns
pH[a]	7.9	7.9	7.8	8.0	ns	ns	ns
Sodium AR[a]	27.1	34.2	28.8	37.0	ns	ns	ns
Carbonate (percent)[d]	35.0	41.3	33.2	41.4	ns	<0.0001	ns
Sand (percent)	36.2	24.9	38.4	21.8	ns	<0.0001	ns
Clay (percent)	44.4	62.1	41.6	63.3	ns	<0.0001	ns

[a] In saturation extract.
[b] Bicarbonate-extractable.
[c] Walkley-Black method.
[d] Calcium carbonate equivalent.

differed significantly between shrub clumps and openings. Organic matter was generally low but was higher in shrub clumps and increased with depth, probably because of the high root:shoot ratios of the dominant shrub species (Holmgren and Brewster 1972). Phosphorus and potassium were present in nonlimiting amounts. Phosphorus concentration was not related to position or depth, while potassium was significantly higher in the subsoil and in openings. Nitrate-N was present at low levels, as would be expected with the low organic matter content. It was higher in shrub clumps than in openings and higher in the surface soil than in the subsoil. Nitrate-N was 50 percent higher in the surface soil under shrubs than in the open or in the subsoil. Surface soils under shrub clumps were also less compacted than soils in openings, with more surface roughness and lower bulk density.

Materials and Methods

Field experiments were initiated in September of each year. Disturbance studies utilizing large plots were carried out in 1997 to 1998, 1998 to 1999, and 1999 to 2000, while small plot resource manipulation studies were performed for 2 years starting in September 1998. Cheatgrass seeds were collected on the Whiterocks Road in former shadscale vegetation, ca. 28 km northeast of the study site, in June of each year, cleaned to >95 percent purity, tested for viability, and allowed to after-ripen under laboratory conditions until the broadcast planting without any covering treatment in September.

The large plot study initiated in 1997 consisted of four disturbance treatments, two seeding treatments, and 10 blocks for a total of eighty 1 x 3 m plots. The disturbance treatments included: intact shrubs and crust, shrubs clipped and left in place, crust trampled in place, and shrubs clipped in combination with crust trampled. The seeding treatments were no additional seed and 100 viable seeds (florets) per 0.1 m^2. This design was repeated the following 2 years with the exception that unseeded plots were not harvested, so that the plot total was 40. The same plots were used each year, with reclipping of any resprouted shrubs and redisturbance of the crust.

The small plot study was also a randomized block design, with eight replications. The treatment design was factorial with two positions (shrub clumps and openings), two disturbance treatments (intact and removal), and six resource manipulation treatments, for a total of 24 treatment combinations and 192 plots. The manipulations included: control, added water, added shade, added nitrogen, reduced nitrogen (by adding sucrose to immobilize nitrogen into microbial biomass), and shrub simulation (added shade, nitrogen, and water). Plot size was 0.1 m^2; the same plots were used each year.

Living shadscale shrubs >50 cm in crown diameter were selected for the shrub clump treatments. For the removal treatment, shrubs were clipped at ground level. Cryptobiotic crust was left intact in the shrub removal plots. For the open removal treatment, the cryptobiotic crust was physically removed to a depth of ca. 2 cm.

For the supplemental water treatment, water was added to simulate 25 mm of extra rainfall in mid-October and mid-March by suspending water-filled ziplock bags on hardware cloth platforms over the plots and allowing the water to drip through holes punched in the bottoms. Application took approximately an hour and resulted in little or no runoff. Nitrogen was added at a rate of 5.3 g per m^2 per yr in the form of ammonium nitrate, while sucrose was added at a rate of 50 g per m^2 per yr (McLendon and Redente 1992). Fertility treatments were applied dry at the same time as supplemental watering in the fall and spring, and plots were watered with a few milliliters of water to help prevent removal by wind. Shade was continuously applied through the course of the study by surrounding each shade plot with a quadrangular frame covered with 2 mm fiberglass window screening to a height of 45 cm. The shade frame tops were open.

Harvest took place in May each year after the plants had turned red and the seeds had reached maximum dry mass, but before any seed shatter. The first year, plants in the large plot experiment were counted after harvest, then dried at 40 °C for 48 hours and weighed to obtain total biomass per plot. In following years, only total biomass per plot was measured. For the small plot study, plants for each plot were counted during harvest and separated into seed (floret) and vegetative fractions. Each fraction was then dried and weighed to obtain biomass as above. Biomass per plant was a good predictor of seed biomass and, therefore, of seed number ($R^2 = 0.965$, d.f. = 190, $p < 0.0001$)

All count and biomass data were log-transformed prior to analysis of variance to increase homogeneity of variance (Zar 1984). Dependent variables for all analyses included number of plants setting seed per 0.1 m^2, dry biomass per 0.1 m^2, and biomass per plant. For the small plot study, seed fraction (floret mass/total mass) was also included. After determining that the block effect was not significant for any variable, it was pooled into the error term, and the data were analyzed as completely randomized designs. Data for the 1998 and 1999 large plot harvests were analyzed separately using fixed-effects two-way (1999 and 2000) or three-way (1998) analysis of variance. Data for the 1999 small plot study were analyzed as three-way fixed-effects models using a general linear models procedure. Control treatments for the four shrub/open intact/removal small plot treatment combinations were then compared with each other and with their respective manipulation treatments using orthogonal contrasts (Steel and Torrie 1980).

Results

Large Plot Study

The 1997 to 1998 fall-winter-spring season was favorable for cheatgrass at the Camelback study site, with adequate autumn, winter, and spring precipitation (table 1). Estimated seed return on the seeded plots averaged 28 percent, with 28 plants reaching reproductive maturity and mean biomass production of 1.2 g per 0.1 m^2 on seeded plots. Cheatgrass success in 1997 to 1998 was clearly limited by seed supply (table 3). There were 10 times as many plants on the seeded plots, and they produced five times as much biomass as the plants on the unseeded plots (fig. 1). The plants on the unseeded plots averaged twice the size of those on the seeded plots, however.

Table 3—Analysis of variance for the 1998 and 1999 harvests of the large plot experiment. Data were log transformed to increase homogeneity of variance prior to analysis. The block effect was not significant for any dependent variable: therefore, block and block interactions were pooled as the error term. Error degrees of freedom: 1998 = 62, 1999 = 36.

		Plant number		Plant biomass		Total plot biomass	
	d.f.	**F**	**P**	**F**	**P**	**F**	**P**
1998 experiment							
Seeded/unseeded	1	197.8	0.0001	58.3	0.0001	121.0	0.0001
Shrubs intact/clipped	1	0.1	ns	3.71	0.06	1.06	ns
Crust intact/trampled	1	0.57	ns	0	ns	0.57	ns
Seeding x clipping	1	0.10	ns	1.44	ns	0.88	ns
Seeding x trampling	1	0.31	ns	0.85	ns	1.05	ns
Clipping x trampling	1	4.35	0.05	0.02	ns	4.30	0.05
Seed x clip x tramp	1	0.42	ns	0.48	ns	1.05	ns
1999 experiment							
Shrubs intact/clipped	1	—	—	—	—	17.84	0.0002
Crust intact/trampled	1	—	—	—	—	8.11	0.0072
Interaction	1	—	—	—	—	1.00	ns

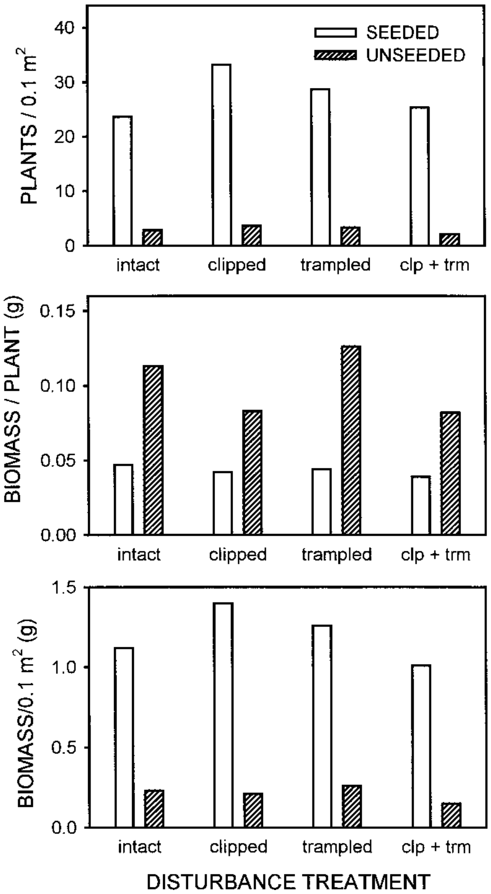

Figure 1—Plant number per 0.1 m^2 area, dry biomass per plant, and total dry biomass per 0.1 m^2 area for the large plot 1998 harvest. Disturbance treatments: intact (no disturbance), clipped (shrubs clipped at ground level), trampled (cryptobiotic crust trampled) and clp + trm (shrubs clipped in combination with crust trampled). Seeding treatments: seeds broadcast sown at 100 per 0.1 m^2 and no added seeds. See table 3 for significance tests.

Disturbance treatments had a slight but significant effect on cheatgrass success on the large plots in 1997 to 1998, and the effects were similar in seeded and unseeded plots (table 3). Plants were 30 percent larger overall where shrubs were left intact (table 3, nearly significant), but mild disturbance (either clipping or trampling but not both) resulted in a ca. 30 percent increase in recruitment and a ca. 20 percent increase in biomass per 0.1 m^2 (table 3, significant shrub treatment by crust treatment interactions; fig. 1). The severe disturbance treatment (shrubs clipped and crust trampled) did not show this beneficial effect, with numbers similar to those on intact plots and total biomass lower than any other treatment (fig. 1).

The 1998 to 1999 season was less favorable for cheatgrass at Camelback, with little late winter moisture (table 1). Biomass per 0.1 m^2 in the large plot study averaged only 0.262 g overall, little more than one-fifth of the value on seeded plots the previous year. In intact plots, biomass production was three times greater in 1998 than in 1999. Under this weather scenario, disturbance had a clear negative effect on biomass production, with the effects of both shrub clipping and crust trampling significant (table 2; fig. 2). Biomass production in the severe disturbance treatment was decreased by a factor of three relative to the intact plots.

The 1999 to 2000 season was categorically unfavorable for cheatgrass at Camelback, due to unusually dry conditions (table 1). Recruitment was minimal and no plants survived to reproduction, regardless of treatment, in either the large plot study or the small plot study described below.

Small Plot Study

Analysis of the 1999 harvest data for the small plot study showed that the shrub versus open treatment, the intact versus disturbed treatment, and the manipulation treatment main effects were all significant for plant number and total biomass per plot, but the intact versus removal treatment had no significant effect on plant size (table 4).

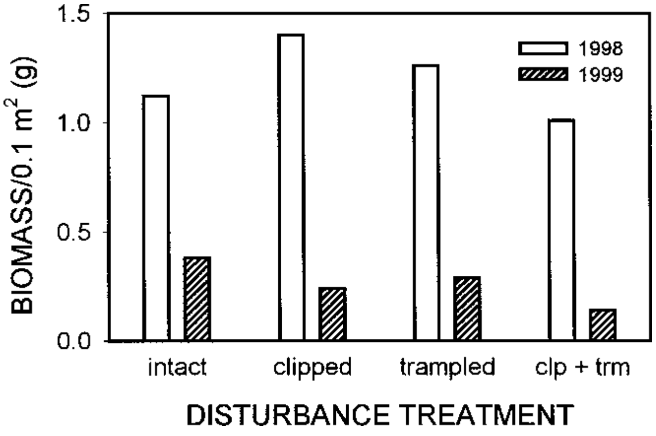

Figure 2—Total dry biomass per 0.1 m^2 area for the large plot 1998 and 1999 harvests. Disturbance treatments: intact (no disturbance), clipped (shrubs clipped at ground level), trampled (cryptobiotic crust trampled), and clp + trm (shrubs clipped in combination with crust trampled). See table 3 for significance tests.

Patterns for control plots were generally similar to patterns from the overall analysis, although sometimes not significant.

For plant number per plot, control and overall values were similar in shrub clumps and openings (fig. 3). Plant number was generally negatively impacted by disturbance, a result similar to the large plot study result from the same harvest year. This negative impact was greater in openings, resulting in a significant shrub clump versus opening intact versus removal interaction (table 4; fig. 3).

Biomass per plant was more than twice as high overall in shrub clumps as in openings, and this difference was even greater when intact control treatments were compared (table 4; fig. 4). The removal treatment had no significant effect on plant biomass overall in either shrub clumps or openings.

As a result of the interplay of the above two variables, biomass per 0.1 m^2 plot was significantly higher in shrub clumps than openings and significantly higher in intact plots than in removal plots overall (table 4; fig. 5). Total biomass was less impacted by disturbance in shrub clumps than in openings, resulting in a significant interaction for this variable. Control plots followed the same trends.

Only two manipulations significantly impacted plant number per plot, and these impacts were only sometimes evident. Shrub simulation had no effect on recruitment in intact shrub clumps, but had a large positive effect when shrubs were removed (fig. 3). Shrub simulation had no effect on recruitment in openings. Shade negatively impacted recruitment in openings but not in shrub clumps.

Biomass per plant was positively affected by supplemental water in shrub clumps, whether shrubs were intact or removed (fig. 4). Supplemental water had no effect on biomass per plant in openings. Conversely, added nitrogen increased and sucrose decreased biomass per plant in openings, but had no effect in shrub clumps. Shrub simulation (water + nitrogen + shade) had no effect in intact shrub clumps but a large positive effect when shrubs were removed. It had a significant positive effect on biomass per plant in openings whether or not crust was removed.

No manipulation treatment resulted in significantly increased biomass per plot relative to the control when shrubs were intact. With shrubs removed, shrub simulation had a large positive effect, while the positive effect of supplemental water alone was nearly significant (fig. 4). In openings, shrub simulation increased total biomass significantly over the control only when the crust was intact, although a similar but nonsignificant trend was evident in the removal treatment.

Seeds (florets) made up 29 to 48 percent of total dry mass, with a mean of 43 percent. Seed investment was significantly higher in shrub clumps than in openings and in intact versus removal treatments, although the differences in investment were not large (table 4; fig. 5). In control treatments, seed investment was higher in intact shrub clumps than in the other three treatments, and there was no significant manipulation effect with shrubs intact, although sucrose addition tended to reduce reproductive investment. With shrubs removed, added nitrogen decreased reproductive investment. In openings, which showed nitrogen limitation on plant biomass, added nitrogen had a null or positive effect on reproductive investment, while nitrogen depletion through sucrose addition resulted in a sharp decrease.

As mentioned above, the harvest for the 1999 to 2000 year in the small plot study was zero, regardless of position, disturbance treatment, or manipulation. There were, therefore, no significant treatment effects or interactions for any dependent variable.

Table 4—Analysis of variance for the 1999 harvest of the small plot factorial experiment. Data (except for seed fraction) were log transformed to increase homogeneity of variance prior to analysis. The block effect was not significant for any dependent variable; therefore, block and block interactions were pooled as the error term. Error degrees of freedom = 165.

		Number of plants		Plant biomass biomass		Total plot biomass		Seed fraction	
	d.f.	F	P	F	P	F	P	F	P
Shrub versus open	1	20.01	0.0001	237.2	0.0001	97.96	0.0001	4.77	0.0307
Intact versus removal	1	20.63	0.0001	0.67	ns	11.28	0.0010	4.41	0.0373
Manipulation	5	2.82	0.0178	18.88	0.0001	8.77	0.0001	9.03	0.0001
Shrub/open x intact/rem	1	19.07	0.0001	0.52	ns	10.61	0.0014	3.02	ns
Shrub/open x manip.	5	1.22	ns	8.09	0.0001	1.14	ns	7.70	0.0001
Intact/remove x manip.	5	2.09	ns	0.81	ns	1.93	ns	0.64	ns
Sh/op x int/rmv x manip.	5	0.66	ns	1.62	ns	1.22	ns	2.66	0.0427

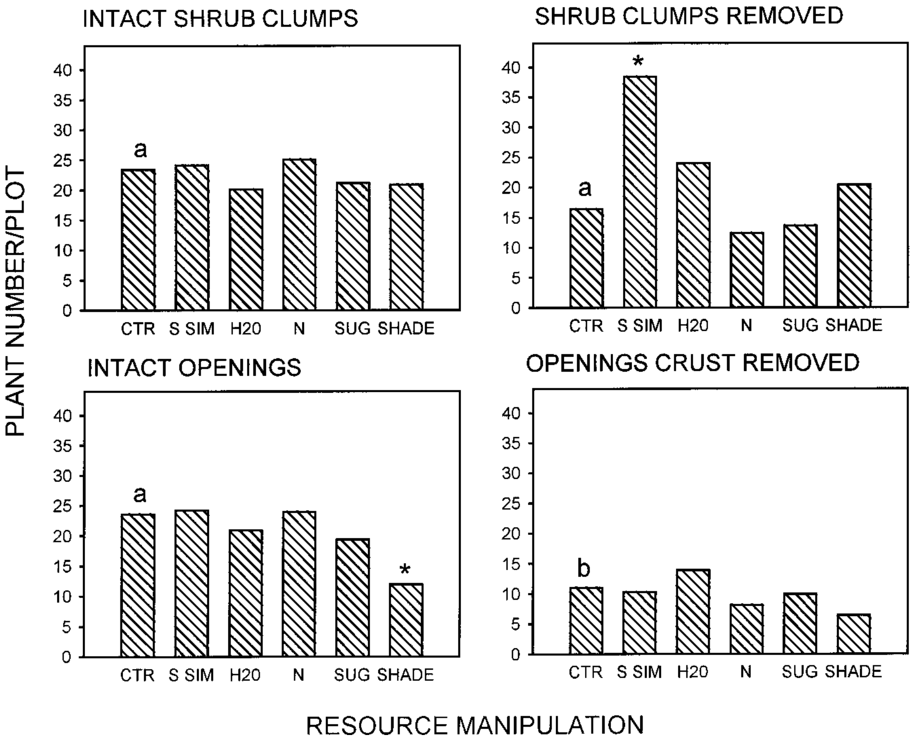

Figure 3—Plant number per 0.1 m^2 plot for each treatment combination in the small plot 1999 harvest. Control treatments with means not significantly different at the $p < 0.05$ level have columns headed by the same letter. Manipulation treatments that are significantly different from the control manipulation treatment within a shrub/open intact/removal treatment combination have columns headed by asterisks (*, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$; o, $p < 0.10$, marginally significant; CTR, control; S SIM, shrub simulation; H20, supplemental water; N, supplemental nitrogen; SUG, sucrose addition to reduce available nitrogen; SHADE, plots shaded).

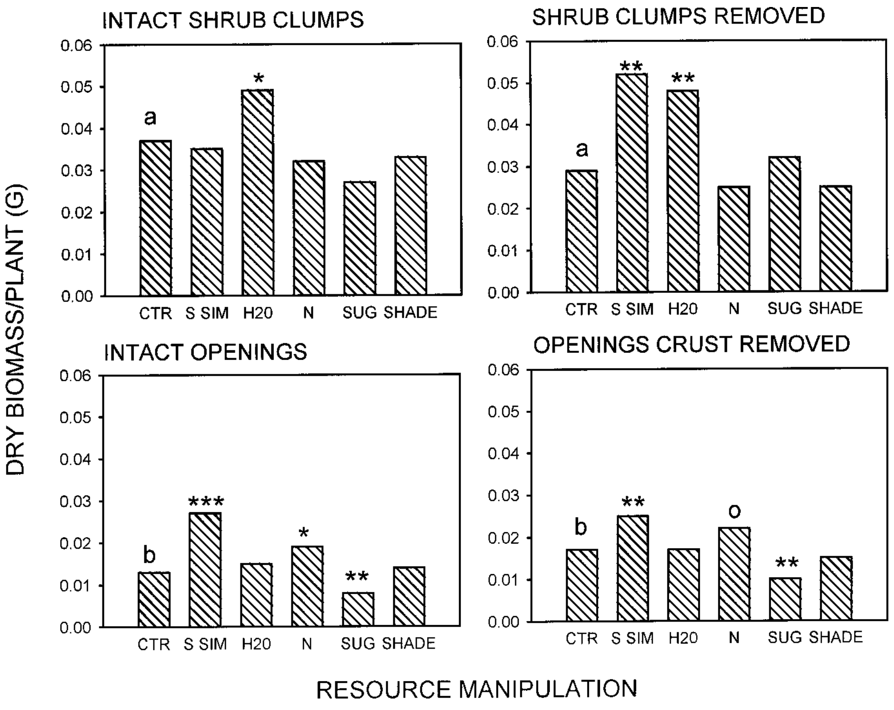

Figure 4—Dry biomass per plant for each treatment combination in the small plot 1999 harvest. Control treatments with means not significantly different at the $p < 0.05$ level have columns headed by the same letter. Manipulation treatments that are significantly different from the control manipulation treatment within a shrub/open intact/removal treatment combination have columns headed by asterisks (*, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$; o, $p < 0.10$, marginally significant; CTR, control; S SIM, shrub simulation; H20, supplemental water; N, supplemental nitrogen; SUG, sucrose addition to reduce available nitrogen; SHADE, plots shaded).

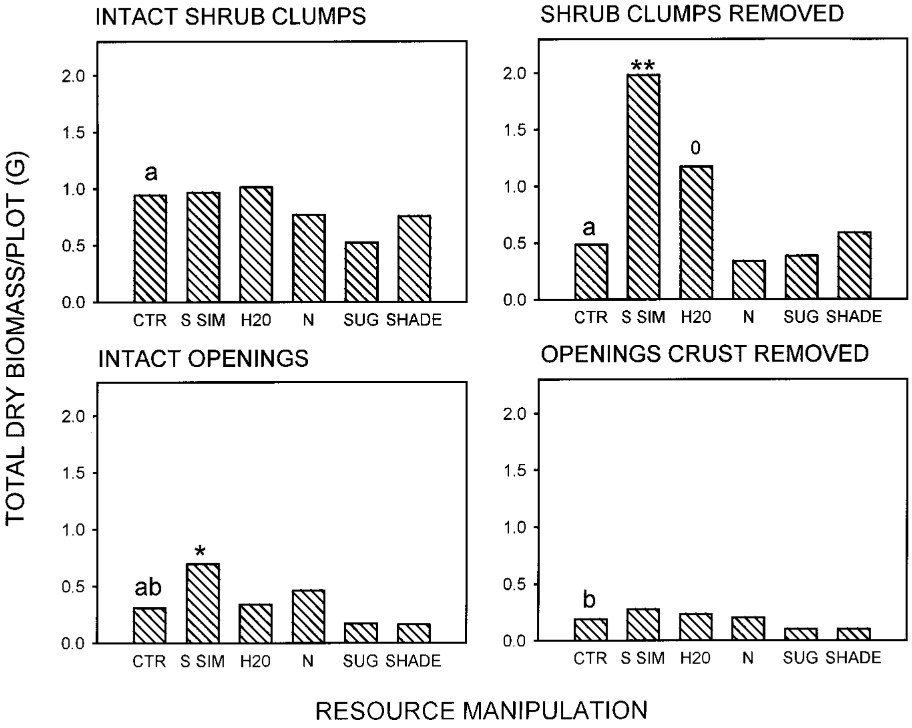

Figure 5—Total dry biomass per 0.1 m^2 plot for each treatment combination in the small plot 1999 harvest. Control treatments with means not significantly different at the $p < 0.05$ level have columns headed by the same letter. Manipulation treatments that are significantly different from the control manipulation treatment within a shrub/open intact/removal treatment combination have columns headed by asterisks (*, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$; o, $p < 0.10$, marginally significant; CTR, control; S SIM, shrub simulation; H20, supplemental water; N, supplemental nitrogen; SUG, sucrose addition to reduce available nitrogen; SHADE, plots shaded).

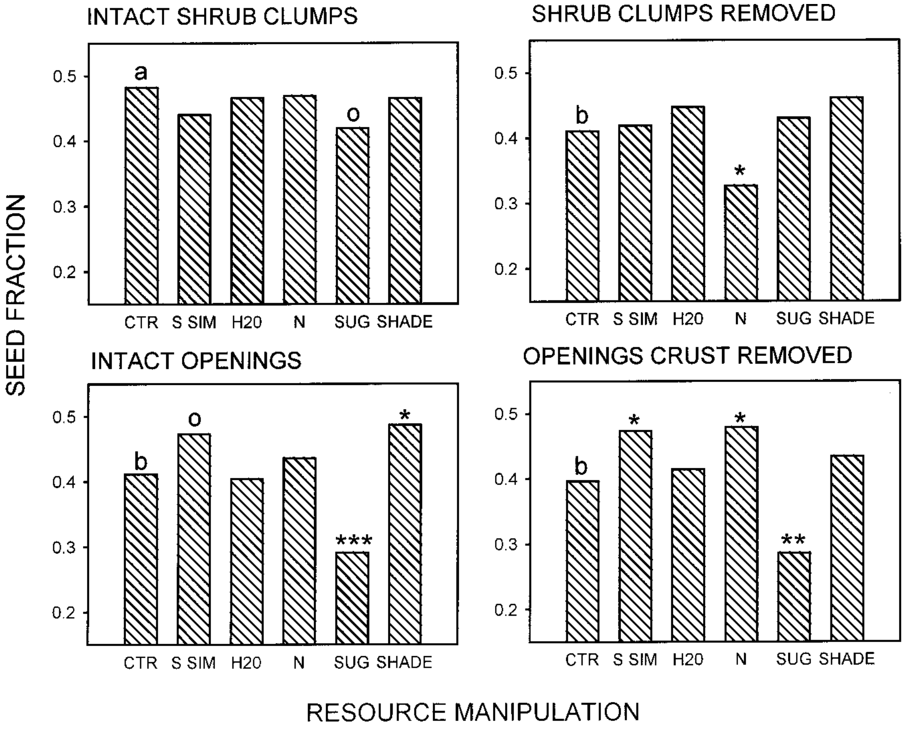

Figure 6—Fraction of dry mass invested in seeds (florets) for each of 24 treatment combinations in the small plot 1999 harvest. Control treatments with means not significantly different at the $p < 0.05$ level have columns headed by the same letter. Manipulation treatments that are significantly different from the control manipulation treatment within a shrub/open intact/removal treatment combination have columns headed by asterisks (*, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$; o, $p < 0.10$, marginally significant; CTR, control; S SIM, shrub simulation; H20, supplemental water; N, supplemental nitrogen; SUG, sucrose addition to reduce available nitrogen; SHADE, plots shaded).

Discussion

There appears to be little intrinsic resistance to cheatgrass invasion at the Camelback study site, in spite of its aridity, heavy soils, and high salinity. Seed supply or propagule pressure is the principal extrinsic factor mediating invasion rate. Resource availability determines the rate of recruitment from arriving propagules, and also regulates plant size and, therefore, seed production per plant. The degree of availability of "excess" resources to support cheatgrass recruitment and growth is related to effective precipitation and fluctuates from year to year (Davis and others 2000). The probable reasons that cheatgrass has not yet extensively invaded this plant community in Dugway Valley are at least twofold. First, dispersal into the area is minimized because human traffic is generally excluded or at least closely regulated, and herbivores that could transport seeds rarely enter this community type. Second, invasibility is greatly reduced in perhaps a majority of years by resource limitation related to the low and sporadic precipitation.

Recruitment from arriving propagules varied from 0 to 28 percent in our study. If we use 0.003 g as the average mass of a single cheatgrass propagule (Meyer, unpublished data), we can estimate seed production per plant from total biomass and seed investment values. In the 1997 to 1998 large plot study, plants in seeded plots averaged 0.050 g and produced an estimated seven seeds. At a return on seed for the following year of 24 percent (from 1998 to 1999 small plot study), those seven seeds would produce 1.7 plants, less than a doubling of the population. If we assume that in 1998 to 1999 recruitment was similar on intact large and small plots, namely 24 percent, then an individual plant on intact large plots would have averaged 0.016 g and would have produced 2.3 seeds. Given an optimistic return on seed for the following year of 25 percent, those seeds would produce on average 0.6 plants. Under this scenario, the population would experience no net growth across these three relatively favorable years.

In fact, the return on seed for 1999 to 2000 was much less than 25 percent; it was effectively zero. If all the seeds in the seed bank germinated but failed to survive, that would put the cheatgrass population at zero until the immigration of more seeds. An unknown fraction of the seeds produced in 1999 may have survived in the seed bank, although seed bank carryover is positively related to cheatgrass litter cover and, therefore, probably minimal at this site (Beckstead 2001). But even if, say, half of the seeds survived, the population would still be declining sharply, because recruitment from remaining seeds is not likely to exceed 25 to 30 percent, even in the most favorable year. This means that it would take a very unusual series of favorable water years to cause an exponential increase in cheatgrass biomass at this site.

Cheatgrass plants that occurred in intact shrub clumps in the 1999 small plot study were three times the size of those in openings and produced even more than three times as many seeds because of their higher reproductive investment. Even with an artificially equal initial distribution of propagules in the large plots and a shrub cover of 22 percent, almost as many seeds were produced in shrub clumps as in openings. Supplemental water increased this size advantage in shrub clumps. These facts may explain why plants in the unseeded plots in 1998 were twice as big as those in the seeded plots. Though we have no quantitative data to support this observation, it was clear that most of the plants in the unseeded plots were in shrub clumps. This would represent the natural invasion pattern. Shrub clumps are the foci of invasion because of their greater resource availability and the resulting increase in seed production per plant. Because 1998 was a more favorable water year than 1999 and because cheatgrass plants in shrub clumps respond more to additional water, the differential size advantage in shrub clumps would have been even greater in 1998. The shrubs apparently act as nurse plants for cheatgrass, ameliorating growing conditions for this understory species in an otherwise harsh environment, an effect commonly observed in warm desert ecosystems (Franco and Nobel 1989). The shrub clumps act as "fertile islands" surrounded by less productive openings (Garner and Steinberger 1989).

The impact of disturbance in opening the Camelback site to cheatgrass invasion was disappointingly small. In the most favorable water year, moderate disturbance (either trampling or clipping but not both) increased recruitment by 30 percent, and it increased biomass production and, therefore, seed production by 20 percent, but more severe disturbance (both trampling and clipping) had a null or negative effect. In a less favorable year, disturbance of any kind had a negative effect on cheatgrass biomass production. Disturbance is, therefore, not necessary for cheatgrass invasion at the Camelback site, but may speed the invasion process in favorable water years. This could have impact, because favorable water years are the only years when there can be net cheatgrass population growth at this site.

Because of low cheatgrass biomass and seed production even in favorable years, it may be hard to see how openings at Camelback could ever support closed stands of cheatgrass (Beckstead 2000). This would limit disturbance from fire, because the fuel would remain discontinuous even in high water years. But cheatgrass dominance results in a redistribution of organic matter and fertility from the subsurface to the surface (Meyer and Garvin, unpublished data). Heavy cheatgrass production in shrub clumps over a period of unusually wet years could result in a gradual encroachment and eventual coalescing of litter across the openings, resulting in less N limitation and more favorable soil physical characteristics for cheatgrass production. We have seen this process occurring in heavily invaded shadscale communities in adjacent, less xeric, Skull Valley. Once this happens, cheatgrass can thrive in the openings, the fuel can become continuous, and the vegetation can carry fire.

The shrub simulation treatment with shrubs removed dramatically increased cheatgrass recruitment and biomass production. This treatment may mimic what happens after a shadscale plant dies. The soil and microsite characteristics that make shrub clumps more favorable persist and, in the case of fertility, may even be enhanced in the years after shrub death, making dead shrub clumps highly favorable microsites for cheatgrass. This effect became important on a landscape scale in the early 1980s, when the same series of high water years that speeded cheatgrass invasion also resulted in widespread shadscale stand loss (Nelson and others 1990). Stand loss itself does not result in local extinction, because shadscale is able to recruit from a persistent seed bank (Meyer and others 1998). But the concomitant increase in cheatgrass biomass production within these communities greatly increases the probability of recurring fire and rapid conversion to cheatgrass domination.

This scenario was not played out in Dugway Valley as it was in many other eastern Great Basin desert valleys, principally because of its greater aridity and seed limitation. The probability that cheatgrass will eventually take over and displace shadscale communities in Dugway Valley depends on weather patterns as well as on seed availability. The best hope for protecting the salt desert shrub communities in Dugway Valley, therefore, lies in reducing the probability of propagule arrival by restricting entry and by eradicating adjacent populations, as well as limiting levels of anthropogenic disturbance.

Acknowledgments

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Sand Sagebrush Response to Fall and Spring Prescribed Burns

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Abstract—Sand sagebrush (*Artemisia filifolia*) is a dominant shrub on sandy soils throughout the Great Plains and Southwest. Sand sagebrush is reported to reduce wind erosion and provides valuable forage and cover to numerous wildlife species. However, the fire ecology of sand sagebrush is not well understood. Our objectives were to evaluate fire-induced mortality, occurrence of resprouting, and changes in sand sagebrush canopy structure and total non-structural carbohydrates (TNC) following fall and spring prescribed burns. We selected twelve 4-ha plots on sand sagebrush-dominated sites in high-seral sand sagebrush-mixed prairie near Woodward, OK. Four plots were burned during fall, four were burned during spring, and four served as controls. Soil temperature and soil water content were monitored. About 93 percent of burned shrubs resprouted and TNC was similar across burning treatments. Canopy volume in May was reduced 87 and 99 percent by fall and spring burns, respectively. Fall burning had no effect on soil water content and elevated soil temperature only during April and May. Spring-burned plots had greater soil water content and higher soil temperatures than control plots in May.

Introduction

Sand sagebrush (*Artemisia filifolia*) is a dominant climax shrub on sandy soils from South Dakota through northern Mexico and eastern Nevada through western Oklahoma. Sand sagebrush has high potential for reducing wind erosion (Hagen and Lyles 1988) and provides valuable forage for numerous wildlife species and occasionally livestock. The shrubs also provide important nesting and protective cover for lesser prairie chickens (*Tympanuchus pallidicinctus*) and other upland game birds (Cannon and Knopf 1981). However, the ecological impact of burning sand sagebrush is not well documented. Sand sagebrush has been classified as both a sprouter (Wright and Bailey 1982) and a non-sprouter capable of recolonizing disturbed sites with abundant seedlings (Sosebee 1983; Wright 1972; Wright and Bailey 1980). Numerical data are lacking to support either hypothesis. Our objectives were to evaluate the effects of fall and spring prescribed burns on (1) fire-induced mortality and occurrence of resprouting in sand sagebrush, (2) canopy structure, (3) total non-structural carbohydrate (TNC) trends, (4) soil water content, and (5) soil temperature.

Methods and Materials

Study Area

The study was located on the Hal and Fern Cooper Wildlife Management Area, 15 km northwest of Woodward, OK (36° 34' N, 99° 32' W, elevation 640 m). The area consists of sandhills in a high seral stage of the sand sagebrush-mixed prairie vegetation type. The climate is continental with 602 mm average annual precipitation, 70 percent of which occurs during the April to September growing season. The study was conducted on deep sand ecological sites. Soils were Pratt loamy fine sands (mixed, mesic, Psammentic Haplustalfs) with no limiting layers of clay in the top 150 cm. The woody plant community is strongly dominated by sand sagebrush, with lesser amounts of Chickasaw plum (*Prunus angustifolia*). Dominant grasses include little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*), sand bluestem (*Andropogon hallii*), and sand lovegrass (*Eragrostis trichodes*). Western ragweed (*Ambrosia psilostachya*), sand lily (*Mentzelia nuda*), and annual buckwheat (*Eriogonum annuum*) were prominent forbs at the time of the study.

Methods

We selected twelve 4-ha plots on sand sagebrush-dominated sites. Twenty shrubs in each plot were marked with rebar stakes, and canopy height, area, and volume were measured in November. Four plots were burned during fall (16 November 1999), four were burned during spring (17 April 2000), and four served as controls. Resprouting and canopy structure of marked plants were reevaluated in May 2000. Roots located below the bud zone were collected from five shrubs per burn treatment each month. Total nonstructural carbohydrates were measured colorimetrically (absorbance at 612 nm) with an anthrone reagent (Murphy 1958) and glucose as a standard. Soil water was determined gravimetrically from five soil cores taken monthly to 15- and 30-cm depths at each plot. Five mid-day soil temperature readings were recorded monthly from each plot at 7.5 and 22.5 cm below the soil surface.

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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Differences in TNC, resprouting, and canopy structure among burn treatments were determined with t-tests. Soil water content and soil temperature were analyzed with analysis of variance. The model contained terms for burn treatment, sampling depth, month (as a repeated measures effect), and their interactions. Where differences occurred, means were separated by the least significant difference. Unless otherwise noted, an alpha level of 0.05 was used for all hypothesis testing.

Results

Fire-induced mortality was less than 10 percent for fall and spring burns (table 1). Sand sagebrush on fall-burned plots began resprouting in March, a full month after bud break on non-burned shrubs. Shrubs in spring-burned plots initiated resprouting in May. However, TNC concentration was similar among burn treatments except during January (fig. 1). The primary effect of fire on sand sagebrush was the alteration of canopy structure (table 1). Fall burns reduced shrub height by nearly 50 percent, and canopy area and volume by more than 75 percent. The same shrub canopy measures were reduced more than 90 percent by spring burns.

Soil water content and soil temperature were similar among burn treatments from December through March. Soil water was unaffected by sampling depth, but soil temperature was 2.3 °C warmer at 7.5 cm than at 22.5 cm. Spring-burned plots had greater soil water content across sampling depths than fall-burned or control plots in May (table 2). Fall burning increased soil temperature by about 17 percent in April and May. Spring burns increased soil temperature by 16 percent in May.

Discussion

Sand sagebrush resprouts profusely following fall and spring burns, seemingly without any negative effects on carbohydrate reserves. Applying prescribed fire to sand sagebrush communities does not appear to be a viable option for reducing shrub density, unless delayed mortality occurs due to additional stresses, such as infestation by insects. Prescribed fire may be a useful tool for reducing sand sagebrush canopy height and volume and potentially making resources, such as light and water, available to more desirable grasses and forbs. Higher spring soil temperature can be expected on burned sites if non-burned sites are shaded by the plant canopy or sufficiently covered with mulch. We believe soil temperatures were likely similar over the winter because the lack of insulating plant material on burned sites allowed solar heat captured during the day to escape more readily at night. Similarly, increased evaporation rates on unprotected soils of burned sites may negate gains in soil water content from reduced canopy interception. Differences in soil water content occurred when the

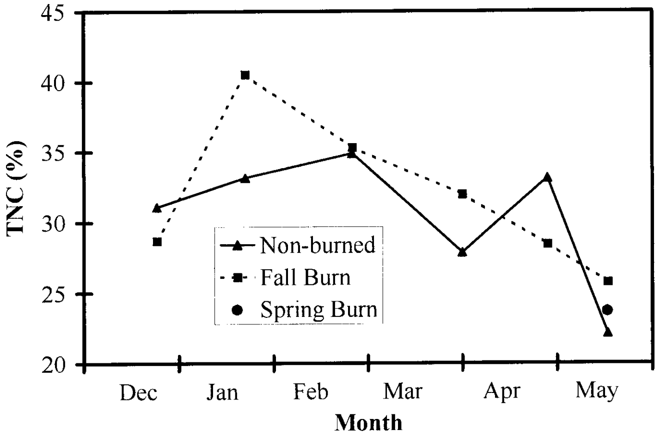

Figure 1—Monthly percent total nonstructural carbohydrates of sand sagebrush roots from non-burned, fall-burned, and spring-burned shrubs.

Table 1—Percentage of sand sagebrush plants resprouting in May after fall and spring burns and percent reduction in canopy structure.

Burn season	Resprouting	Canopy height	Canopy area	Canopy volume
	Percent	- - - - - - - - - - -	*Percent reduction*	- - - - - - - - -
Fall	94 a[1]	49 a	76 a	87 a
Spring	92 a	90 b	95 b	99 b

[1]Means followed by different letters within columns are different at alpha = 0.05.

Table 2—May soil water and soil temperature in non-burned, fall-burned, and spring-burned plots.

		Soil temperature (°C)	
Burn treatment	Soil water (percent)	7.5 cm depth	22.5 cm depth
Control	2.2 a [1]	22.6 a	16.4 a
Fall	2.0 a	27.2 b	18.5 b
Spring	3.1 b	25.9 b	19.3 b

[1]Means followed by different letters within columns are different at alpha = 0.05.

dominant plants began active seasonal growth. We suggest the reduced soil water content on fall-burned and non-burned sites was a reflection of their higher live plant cover.

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Managing Saltcedar After a Summer Wildfire in the Texas Rolling Plains

Russell Fox
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Mike Davin

Abstract—Saltcedar (*Tamarix* spp) has invaded nearly one million acres of riparian ecosystems in the southwestern U.S., displacing many native species. The objectives of this study were to estimate saltcedar mortality to summer wildfire, summer wildfire followed by rollerchopping, and dormant season treatment with 25 percent triclopyr to regrowth following a summer wildfire at Lake Meredith National Recreation Area. In July 1998, more than 100 acres of saltcedar-infested riparian area were burned. In February and March of 1999, regrowth of 200 dormant saltcedar trees were treated with 25 percent triclopyr in JLB oil using the basal bark treatment method. Rollerchopping was conducted in June 1999. Trees that were sprayed had multiple stems and were an average of 4 feet tall. Saltcedar mortality following the summer wildfire was 60.6 percent. Rollerchopping burned areas resulted in 85.1 percent mortality. Saltcedar mortality was 89.9 percent following the February herbicide treatment and 94.5 percent following treatment in March. Preliminary results indicate that dormant season individual plant treatment with 25 percent triclopyr following burning is an effective method for managing saltcedar infestations. However, rollerchopping burned areas may be the most economical in large, alluvial flood plains.

Introduction

In Texas, six species of Tamarix are found: (1) *T. africana*; (2) *T. aphylla*; (3) *T. chinensis*; (4) *T. gallica*; (5) *T. parviflora*; and (6) *T. ramosissima* (Correll and Johnston 1970). Saltcedar was introduced into the eastern U.S. in the early 1800s, escaped cultivation by late that century, and became established throughout the U.S. (Duncan 1997). Escapes from cultivation were first reported in the 1870s and were rapidly spreading from one watershed to another (Brotherson and Field 1987). During these early years of introduction, saltcedar was planted to create windbreaks, provide shade, stabilize eroding stream banks, and grown as ornamentals (Neill 1985). Estimates in 1961 indicated that saltcedar infestations occupied more than 900,000 acres in the U.S. (Robinson 1965). Deloach (1991) estimated one million acres of prime bottomland have been infested with saltcedar and that very little understory vegetation is present. Consequently, restoring native vegetation in saltcedar-dominated riparian areas is an important concern in the southwestern U.S. Our objectives were to estimate saltcedar mortality to summer wildfire, summer wildfire followed by rollerchopping, and dormant season treatment with 25 percent triclopyr to regrowth following a summer wildfire at Lake Meredith National Recreation Area (LMNRA).

Methods

This study was conducted in 1999 in a saltcedar-dominated riparian area at LMNRA near Fritch, Texas. The site was burned by a wildfire in July 1998. Daily maximum temperatures exceeded 100 °F during the wildfire. Many saltcedar were completely consumed by the wildfire. Regrowth of surviving plants exceeded 6 ft at the conclusion of the 1998 growing season. Five randomly located 10 m x 10 m plots in adjacent nonburned areas were used as estimates of pre-fire saltcedar density. Five randomly located 10 m x 10 m plots were used to estimate saltcedar density in burned areas. Saltcedar mortality due to the wildfire was estimated as the difference between saltcedar density in the nonburned and burned areas. In June 1999, about 50 acres of burned saltcedar was rollerchopped. Five randomly located burned and rollerchopped 10 m x 10 m plots were used to estimate saltcedar mortality from the combination of burning and rollerchopping. Two dormant season applications of 25 percent triclopyr (Garlon 4) in JLB oil (vegetable oil carrier) were applied during February and March 1999. Herbicide treatments were applied as individual plant basal treatments to 100 fire-generated resprouts each month. Herbicide efficacy on saltcedar regrowth was evaluated 12 months after treatment. Mortality was defined as lack of green material or failure to produce buds 12 months after treatment.

Results

Burning resulted in 60.6 percent saltcedar mortality 12 months after the summer wildfire when comparing saltcedar density in burned areas to adjacent nonburned areas. The combined effect of the summer wildfire and rollerchopping resulted in 85.1 percent saltcedar mortality as compared to the nonburned areas. Rollerchopping fire-induced regrowth uprooted many plants, and provided an excellent method for increasing saltcedar mortality following the summer wildfire. The moist, sandy, alluvial soils at LMNRA provided ideal conditions for uprooting the sprouting collar, and exposing root material to desiccation. Additionally, rollerchopping facilitated follow-up herbicide treatments by

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knocking down the standing dead trunks, increasing the accessibility of remaining resprouts. An added benefit of rollerchopping was soil disturbance, which encouraged the establishment of early seral species in the burned and rollerchopped areas. February and March basal stem treatments to post-fire saltcedar regrowth with 25 percent triclopyr in JLB oil resulted in 89.9 and 94.5 percent mortality, respectively, 12 months after treatment. Preliminary results indicate that dormant season individual plant treatment with 25 percent triclopyr following burning is an effective method for managing saltcedar infestations.

Conclusions

Fire effectively reduced saltcedar density. Rollerchopping standing dead and regrowth 11 months after burning further reduced saltcedar density, and stimulated forb growth. The application of 25 percent triclopyr in JLB oil during the dormant season effectively controlled saltcedar regrowth following burning. Preliminary results indicate combining fire, rollerchopping, and individual plant treatments with triclopyr is an effective approach for saltcedar management.

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Biodiversity Analysis of Vegetation on the Nevada Test Site

W. K. Ostler
D. J. Hansen

Abstract—The Nevada Test Site (NTS) located in south-central Nevada encompasses approximately 3,567 km^2 and straddles two major North American deserts, Mojave and Great Basin. Transitional areas between the two desert types have been created by gradients in elevation, precipitation, temperature, and soils. From 1996 to 1998, more than 1,500 ecological landform units were sampled at the NTS for numerous biotic and abiotic parameters. These data provide a basis for spatial evaluations of biodiversity over landscape scales at the NTS. Species diversity maps (species richness versus species abundance) have been produced. Differences in ecosystem diversity at the ecoregion, alliance, association, and ecological landform unit levels are presented. Spatial distribution maps of species presence and abundance provide evidence of where transition zones occur and the resulting impact on biodiversity. The influences of abiotic factors (elevation, soil, precipitation) and anthropogenic disturbance on biodiversity are assessed.

Introduction

The Nevada Test Site (NTS) is located in Nye County in south-central Nevada and encompasses 3,567 km^2 (1,375 mi^2). Three large valleys dominate the southern two-thirds of the NTS: Yucca, Frenchman, and Jackass Flats (fig. 1). Mountains, mesas, and hills enclose these valleys.

During years of high precipitation, surface water collects and forms shallow lakes in the closed basins of Yucca and Frenchman Flats. Jackass Flats is an open basin and drains to the southwest via Fortymile Wash. Mercury, Rock, Topopah, and Mid valleys are smaller basins and also have drainage outlets. Pahute Mesa and Timber and Shoshone mountains dominate the northern, northwestern, and west-central sections of the NTS. Elevation on the NTS ranges from less than 1,000 m (3,281 ft) above sea level in Frenchman Flat and Jackass Flats to about 2,340 m (7,677 ft) on Rainier Mesa. Elevations at the base of mountains on the NTS are an average of 975 m (3,200 ft) in the south, 1,370 m (4,496 ft) in the central region, and 1,600 m (5,250 ft) in the northern part of the NTS. Mountains range from 1,400 to 1,800 m (4,593 to 5,906 ft) in the south and 2,100 to 2,300 m (6,890 to 7,546 ft) in the north. Associated with these elevation increases is the northern boundary of the Mojave Desert and the southern boundary of the Great Basin Desert within a broad east-west corridor of transition (Beatley 1976).

The Nevada Test Site has a climate characteristic of high deserts with little precipitation, very hot summers, mild winters, and large diurnal temperature ranges. Monthly average temperatures on the NTS range from 7 °C (45 °F) in January to 32 °C (90 °F) in July (U.S. Department of Energy 1996a). The average annual precipitation on the NTS ranges from 15 cm (6 inches) at the lower elevations to 23 cm (9 inches) at the higher elevations. About 60 percent of this precipitation occurs from September through March. Winter precipitation frequently occurs as snow, which persists in northern Yucca Flat and to the north. Higher mountains commonly are snow covered much of the winter. Snow seldom persists for more than a few hours in the southern valleys.

Although the NTS was used for nuclear testing from 1951 to 1992 only about 7 percent of the site has been disturbed (U.S. Department of Energy 1996a). Despite drastic changes to localized areas due to nuclear testing, biological resources over much of the NTS remain relatively pristine and undisturbed. The abuses of overgrazing by livestock, land degradation due to uncontrolled recreational uses, industrial pollution, and other disturbances common to public lands have been minor or absent on the NTS. Protection of its biological resources has been strengthened by U.S. Department of Energy Policy 430.1 (U.S. Department of Energy 1996b), which mandated that land management practices incorporate ecosystem management principles. The U.S. Department of Energy is also working to preserve viable populations of native plants and animals as stated in its Resource Management Plan for the NTS (U.S. Department of Energy 1998).

Before resources can be effectively managed and preserved, they must first be identified and described. Vegetation classification and mapping are among the first steps in implementing ecosystem management on the NTS. Inventories and spatial mapping are useful tools to ensure that sensitive species and habitats including areas of high biodiversity are adequately described, located, and protected.

Methods

The description of the methods used in delineating Ecological Landform Units (ELU) and gathering field data that was used in this analysis was reported previously in early proceedings of the Shrub Research Consortium (Ostler and others 1999). Methods presented here describe how field data were analyzed to obtain species diversity values and distribution patterns.

A total of 1,508 ELUs were sampled on the NTS. At each ELU, we obtained a list of total species observed. From this

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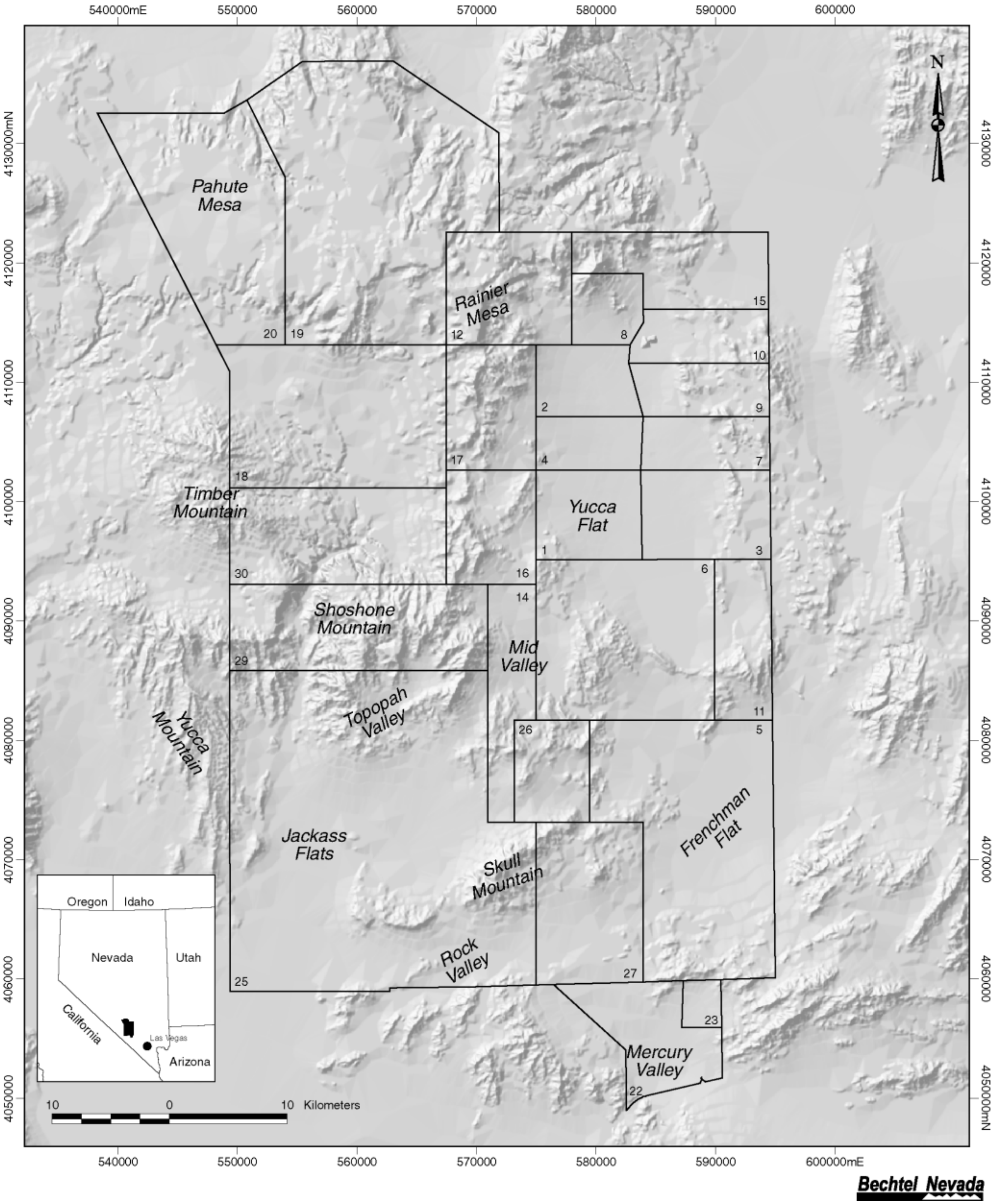

Figure 1—Major topographic features of the Nevada Test Site.

we calculated a species richness value for each ELU. We gathered relative abundance of woody species at each ELU along a 200-m transect. From that abundance data, we calculated species abundance using the Berger-Parker indices for each ELU (Berger and Parker 1970).

Based on our vegetation classification, 10 vegetation alliances and 20 associations were recognized as occurring on the NTS (Ostler and others 2000). Alliance and associations are described based on the standardized national classification system described by Grossman and others (1998). Species richness and species abundance were calculated for each association and alliance. Species richness was determined by recording all unique species in each ELU. Species richness for associations, alliances, and ecoregions were obtained by averaging of the species richness values for every ELU within that association, alliance, or ecoregion. Species abundance was obtained by averaging the species abundance values obtained for every ELU within that association, alliance, or ecoregion.

Two major ecoregions, Mojave Desert and Great Basin Desert, can be identified from the vegetation classification of the NTS. Between these two deserts is a broad transition zone that often includes a mixture of species from either major ecoregion. Beatley (1976) refers to this climatic zone as the "Transition Desert" and recognized several plant associations within this zone. We evaluated ecosystem diversity within these three major areas. Comparisons of species richness and species abundance were made for each ecoregion.

There are three alliances within the Mojave Desert, three within the transition zone, and four within the Great Basin Desert. In terms of total area, the Great Basin Desert occupies approximately 40 percent of the NTS, followed by the transition zone with 37 percent. The Mojave Desert occupies the southern 22 percent of the NTS. Sampling within each major zone was rather even with the average areas per ELU being 216 ha in the Mojave Desert, 221 ha in the Transition Zone, and 233 ha in the Great Basin Desert.

Results

Species diversity has been measured by numerous methods with each method having advantages and disadvantages. The management objective of the land manager often determines which measure of diversity should be used. Two major types of indices, species richness and species abundance (evenness), are generally recognized in ecological literature and these are discussed by Magurran (1988). In this paper, we report measures for both types of indices using two of the more commonly accepted techniques. Results of our analyses are reported at four different levels of scale, ELU, association, alliance, and ecoregion.

Analysis at Ecological Landform Unit Level

Species Richness—Species richness (or the number of species) of all species encountered within each ELU is shown in figure 2. Species richness varied tremendously across all ELUs ranging from a low of 1 to a high of 69. The mean species richness was 24.3 ± 10.9. The total number of species observed across all ELUs during this study was 466. This represents 67 percent of the total number of species (~694) that are listed as occurring on the NTS. Most of the species observed were forbs or grasses (~74 percent) while shrubs represented about 24 percent . The species richness for all of the perennial species is shown in figure 3. The pattern of distribution for perennial species is similar to that for all species.

Species Abundance—The values obtained for species abundance for the 1,508 ELUs using the Berger-Parker index ranged from a low of 1 to a high of 6.25 (fig. 4). Four ELUs had values of 6.25 while 11 ELUs had the second highest values, 5.56. On the other end of the scale, 11 ELUs had values of 1.00, meaning that a single species dominated these sites. However, it was not always the same species that was dominant. In those 11 ELUs with values of 1.00, seven different species dominated at least one of the ELUs. White burrobush (*Hymenoclea salsola*) dominated 3 ELUs while fourwing saltbush (*Atriplex canescens*) and black sagebrush (*Artemisia nova*) dominated in 2 ELUs. Basin big sagebrush (*Artemisia tridentata*), shadscale (*Atriplex confertifolia*), rubber rabbitbrush (*Ericameria nauseosa*), and blackbrush (*Coleogyne ramosissima*) dominated in 1 ELU each. Most of the ELUs (75 percent) had species abundance values under 3 while approximately 42 percent of the ELUs had species abundance values less than 2 (fig. 4).

Analysis at Plant Association Level

Species Richness—Of the 20 plant associations recognized on the NTS, species richness ranged from a low of 13.0 in the *Atriplex confertifolia-Kochia americana* shrubland to a high of 38.6 in the *Artemisia nova-Artemisia tridentata* shrubland (table 1). The range of richness values among ELUs within each association was very high. Those sites that had poor or harsh soils or that had been subject to previous disturbance such as in Yucca Flats tended to have low species richness. There also appears to be a positive relationship of species richness at the association level with elevation and precipitation.

Species Abundance—The Berger-Parker values for associations ranged from a low of 1.62 in the *Artemisia nova-Chrysothamnus viscidiflorus* shrubland to a high of 4.03 in the *Menodora spinescens-Ephedra nevadensis* shrubland. Values for all associations are reported in table 1. The species abundance of associations does show that transition associations tend to have higher species abundance than Mojave or Great Basin associations with the exception of the *Coleogyne ramosissima-Ephedra nevadensis* shrubland. Statistical analysis showed that there is no significant correlation between species richness and species abundance on an association level ($r^2 = 0.15$).

Analysis at Plant Alliance Level

Species Richness—Species richness values ranged from a low of 15.8 in the *Atriplex* spp. shrubland to a high of 33.7 in the *Pinus monophylla* / *Artemisia* spp. woodland alliance. Species richness values for all associations are reported in table 2. Those alliances that have less favorable soil conditions (*Lycium shockleyi-Lycium pallidum* shrubland alliance, *Atriple*x spp. shrubland alliance) or that have been

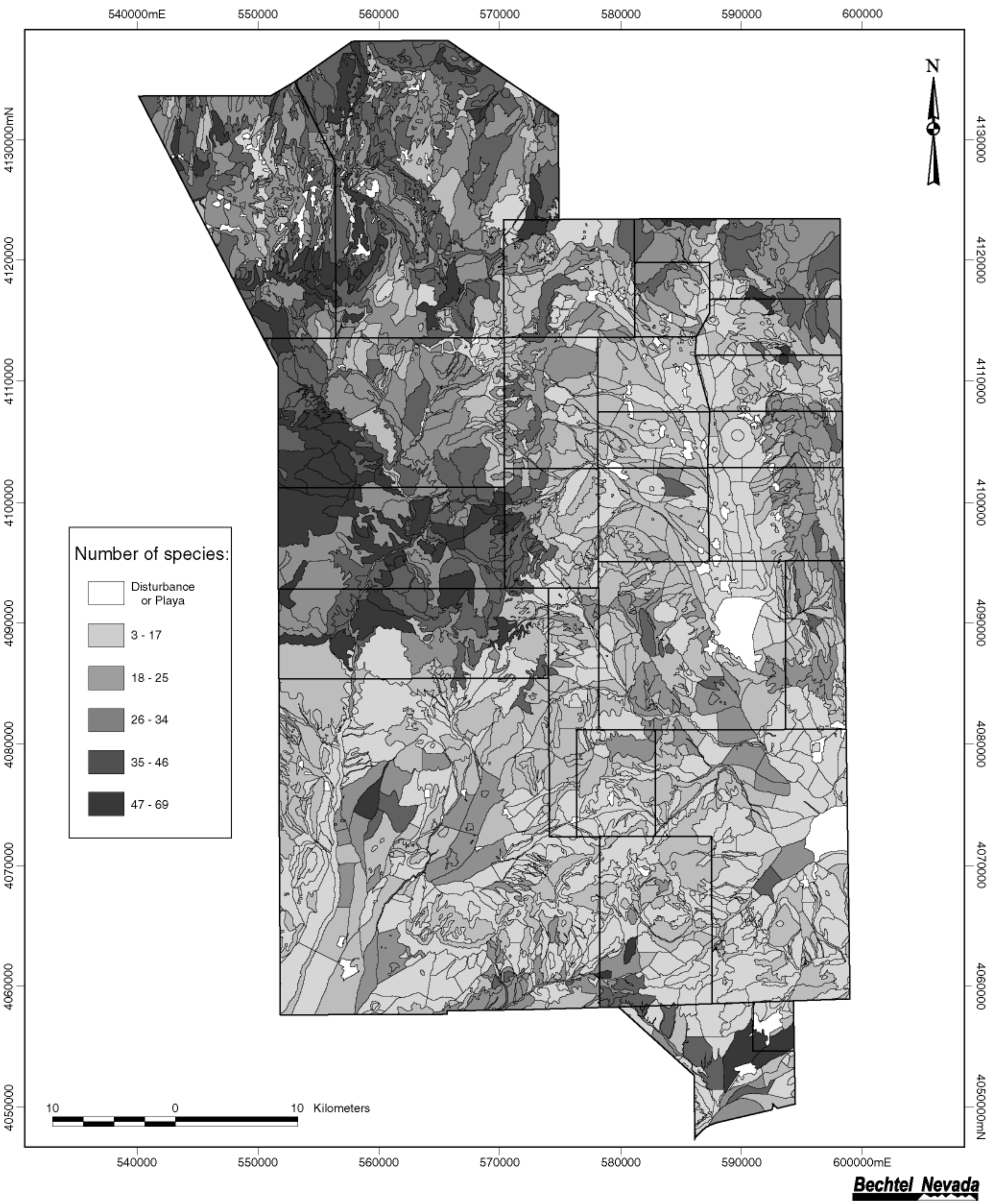

Figure 2—Species richness of all species for ELUs on the Nevada Test Site.

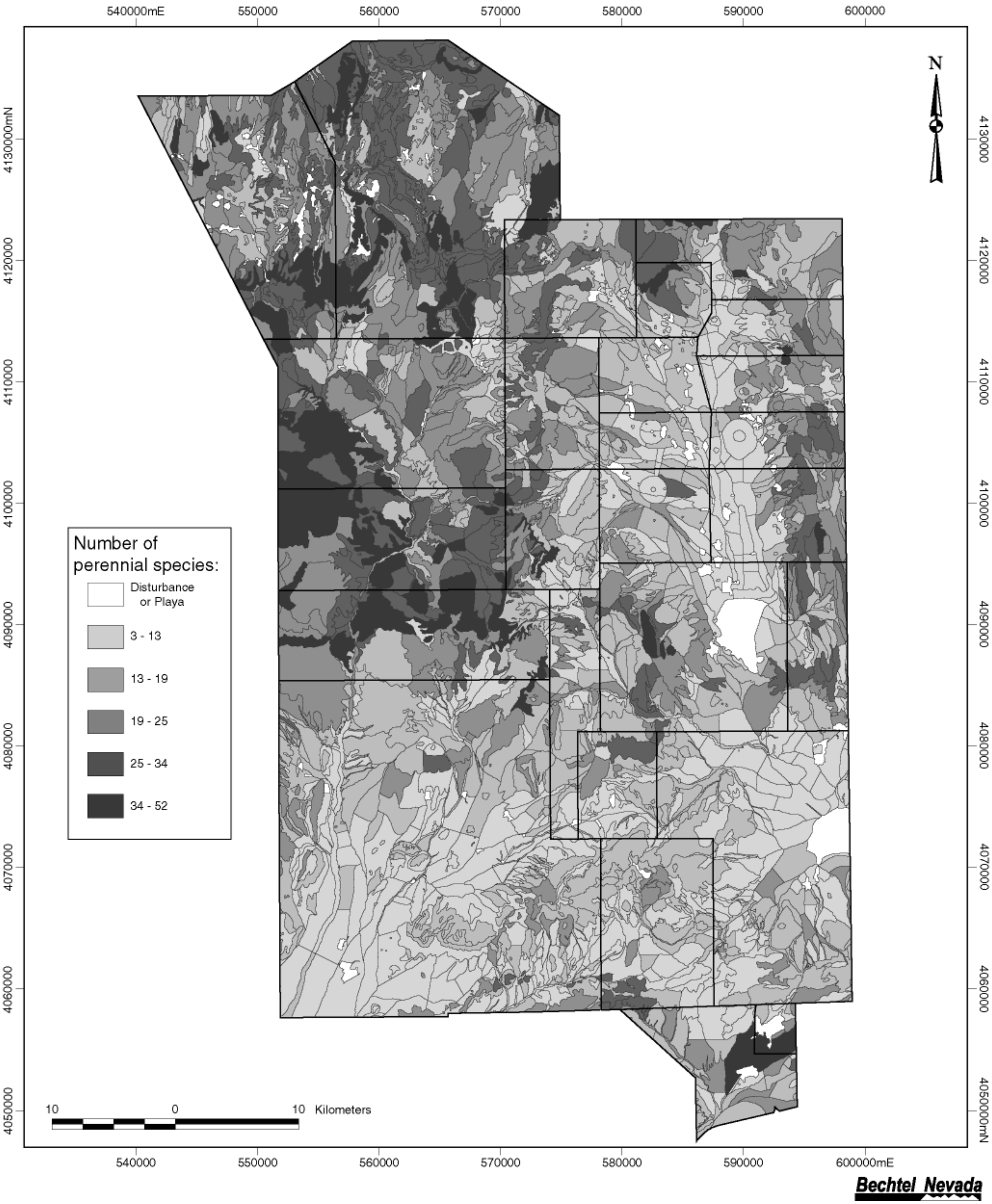

Figure 3—Species richness of perennial species for ELUs on the Nevada Test Site.

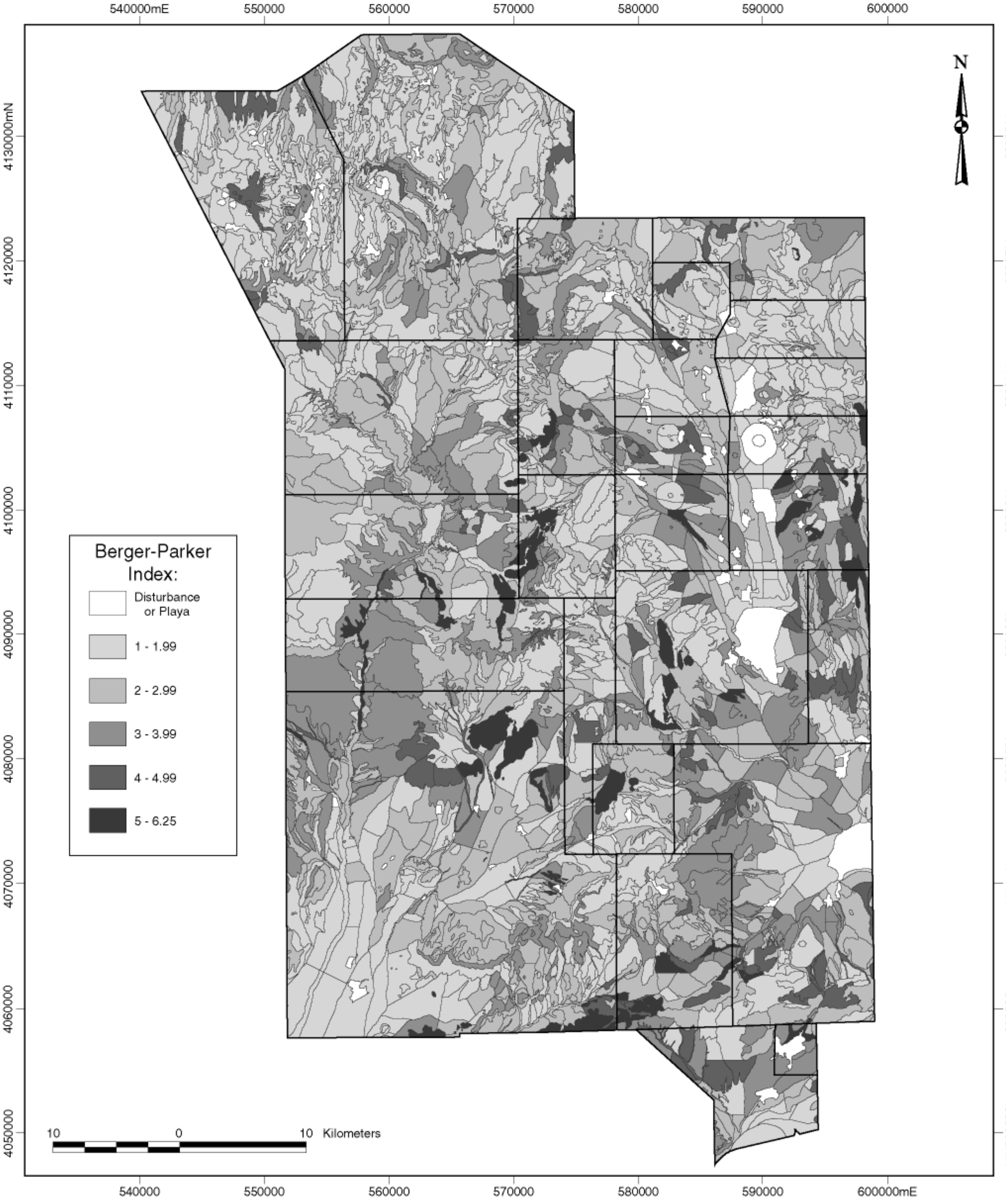

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Figure 4—Species abundance using the Berger-Parker index for ELUs on the Nevada Test Site.

Table 1—Species diversity for plant associations.

Shrubland associations	No. of ELUs	Species richness	Species abundance
Lycium shockleyi-Lycium pallidum	6	19.0	1.99
Larrea tridentata/Ambrosia dumosa	283	18.2	2.39
Atriplex confertifolia-Ambrosia dumosa	49	19.1	3.21
Lycium andersonii-Hymenoclea salsola	13	23.2	4.03
Hymenoclea salsola-Ephedra nevadensis	44	21.9	3.45
Menodora spinescens-Ephedra nevadensis	45	17.5	2.22
Krascheninnikovia lanata-Ephedra nevadensis	30	19.3	2.25
Eriogonum fasciculatum-Ephedra nevadensis	14	22.5	3.30
Ephedra nevadensis-Grayia spinosa	89	25.5	3.56
Coleogyne ramosissima-Ephedra nevadensis	323	21.2	2.03
Atriplex confertifolia-Kochia americana	19	13.9	1.80
Atriplex canescens-Krascheninnikovia lanata	38	16.7	1.91
Chrysothamnus viscidiflorus-Ephedra nevadensis	76	28.4	2.84
Ericameria nauseosa-Ephedra nevadensis	21	22.7	2.23
Ephedra viridis-Artemisia tridentata	20	36.0	3.24
Artemisia tridentata-Chrysothamnus viscidiflorus	139	29.9	1.82
Artemisia nova-Chrysothamnus viscidiflorus	103	32.3	1.62
Artemisia nova-Artemisia tridentata	30	38.6	2.85
Pinus monophylla/Artemisia nova[a]	78	34.3	2.84
Pinus monophylla/Artemisia tridentata[a]	58	33.3	1.95

[a] Woodland associations.

Table 2—Species diversity at the alliance level.

Alliances	Species richness	Species abundance
Lycium shockleyi-Lycium pallidum shrubland	19.0	1.99
Larrea tridentata/Ambrosia dumosa shrubland	18.2	2.39
Atriplex confertifolia-Ambrosia dumosa shrubland	19.1	3.21
Hymenoclea-Lycium shrubland	17.5	2.22
Ephedra nevadensis shrubland	23.2	3.37
Coleogyne ramosissima shrubland	21.2	2.03
Atriplex spp. shrubland	15.8	1.87
Chrysothamnus-Ericameria shrubland	27.2	2.71
Artemisia spp. shrubland	32.1	1.95
Pinus monophylla/Artemisia spp. woodland	33.7	2.33

disturbed routinely (*Hymenoclea-Lycium* shrubland alliance) tend to have both lower species richness and species abundance.

Species Abundance—The Berger-Parker values for alliances ranged from a low of 1.87 in the *Atriplex* spp. shrubland alliance to a high of 3.37 in the *Ephedra nevadensis* shrubland alliance. The *Ephedra nevadensis* shrubland alliance contains the top four associations in terms of species abundance. Values for all alliances are reported in table 2.

Analysis at Ecoregion Level

Species Richness—Species richness was greatest in the Great Basin Desert ecoregion. This ecoregion had a mean of 30.1 species compared to associations in the Transition Zone (mean of 21.9 species) and the Mojave Desert (mean of 18.9 species). Similar species diversity patterns were also observed for all combined perennial species on the NTS (for example, Great Basin Desert: 22.8 species per ELU, Transition Zone: 17.5 species per ELU, and Mojave Desert: 13.6 species per ELU).

Species Abundance—the Berger-Parker index showed that unlike species richness the Mojave Desert ecoregion had the highest species abundance with an average value of 2.67. This was followed by the Transition Zone with a value of 2.45 and the Great Basin Desert with a value of 2.15.

Analysis of Individual Species

An advantage of having data in a GIS format is that it allows us the flexibility to spatially display any or all of the data. We can display the distribution of a single species on the NTS. Not only is the presence of the species noted in each ELU, but we can display the relative abundance of the species in each ELU of occurrence (fig. 5). This also allows spatial analysis of congeneric species and other associated species and can help identify those environmental parameters that separate the distribution of those species. For example, figure 6 shows the distribution of the three species

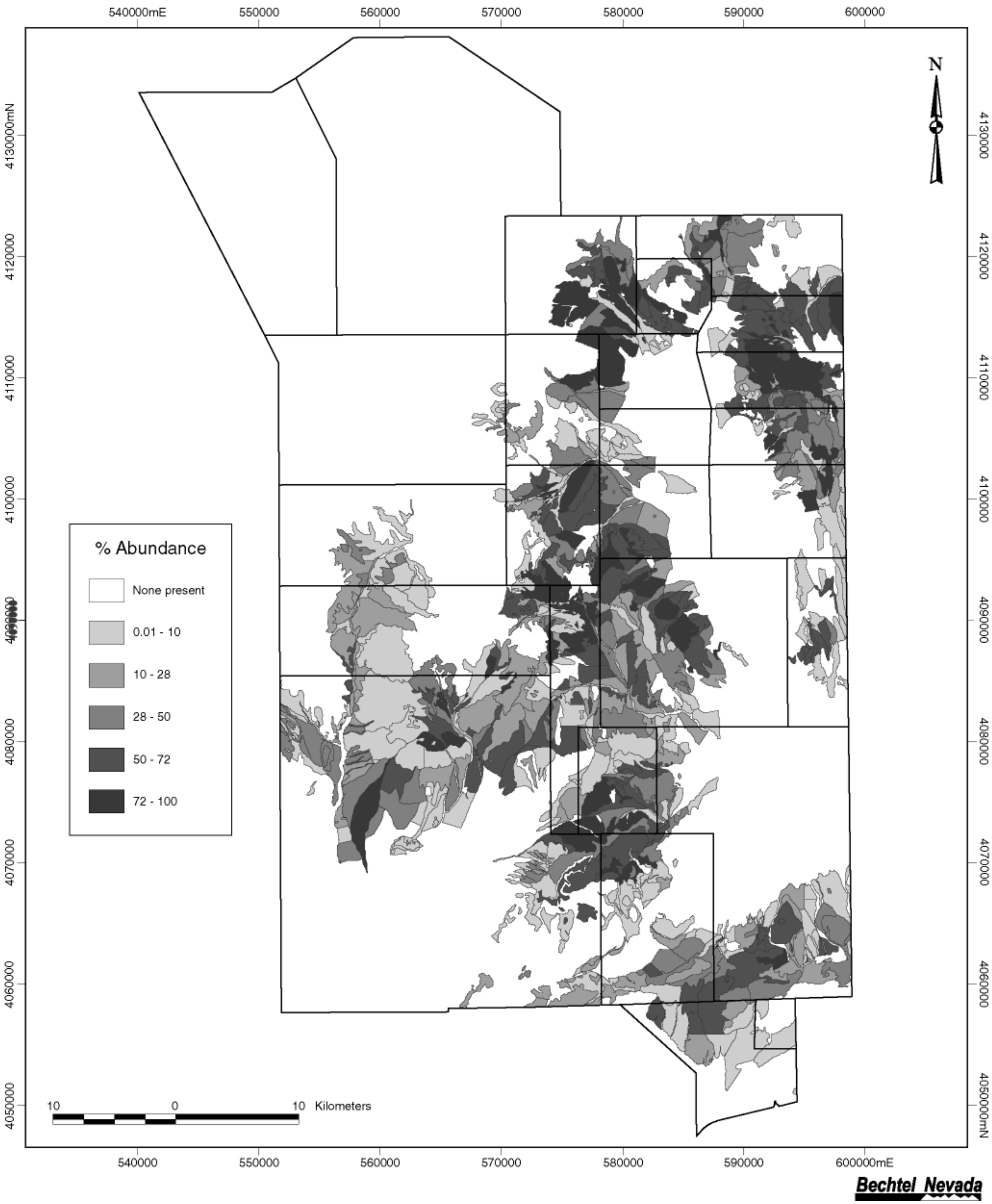

Figure 5—The distribution and relative abundance of blackbrush on the Nevada Test Site.

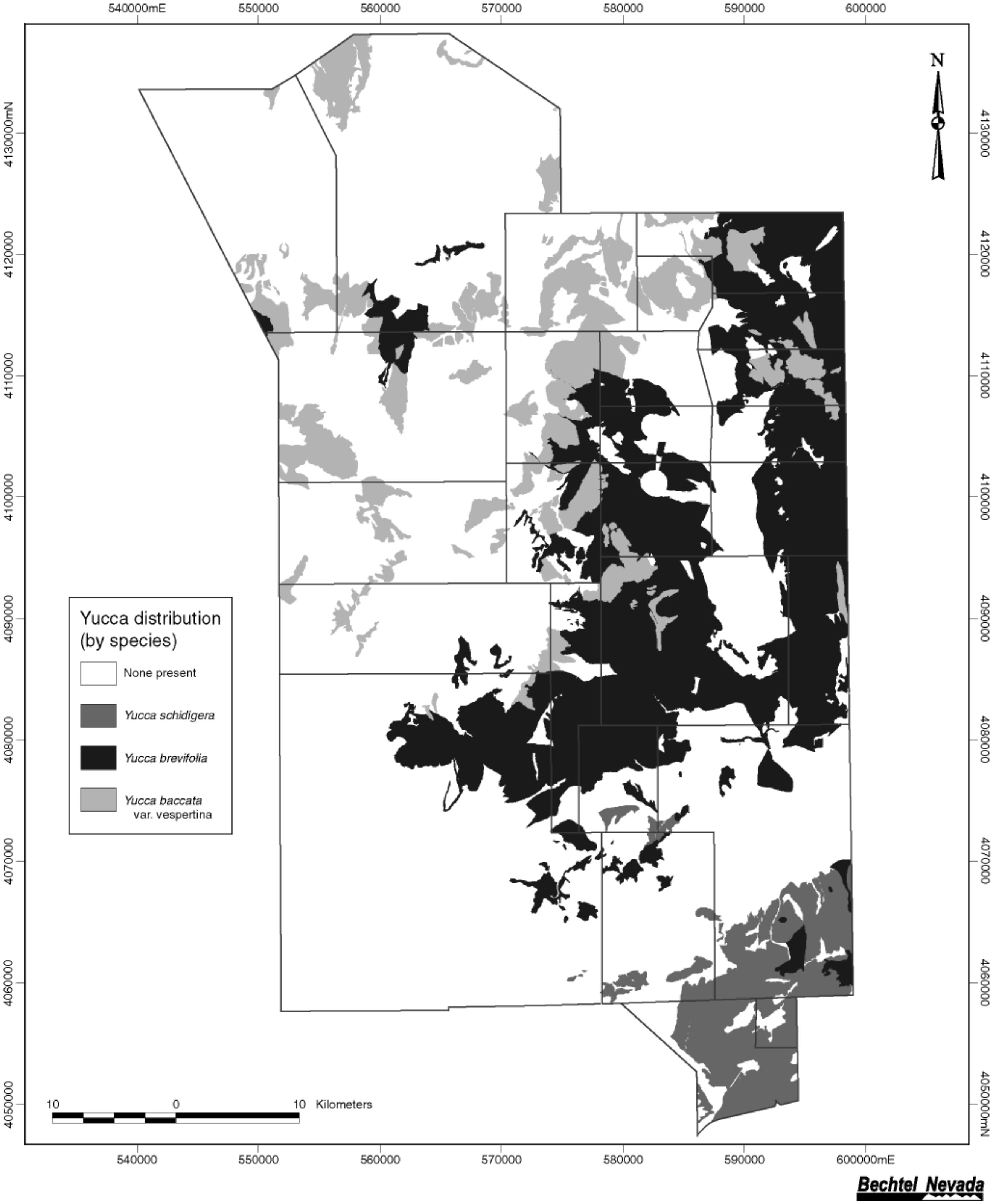

Figure 6—The distribution of three species of yuccas on the Nevada Test Site.

of yucca on the NTS. Mojave yucca (*Yucca schidigera*) is a Mojave Desert species and only occurs in the lower and hotter portions of the NTS. Joshua tree (*Yucca brevifolia*) is a transitional species and occurs in the central portions of the NTS while banana yucca (*Yucca bacata*) prefers the higher elevations and areas of greater precipitation that are characteristic of the Great Basin portions of the NTS.

Modality of Woody Species

A total of 117 woody species were encountered on the transects from which relative abundance values were obtained. Each of these species was evaluated for modality, in other words, the association that each species reached its maximum relative abundance. Three associations, *Pinus monophylla/Artemisia tridentata* woodland (16), *Menodora spinescens-Ephedra nevadensis* shrubland (12) and *Atriplex confertifolia-Ambrosia dumosa* shrubland (11), had a large number of modal species (table 3). Other associations, *Lycium andersonii-Hymenoclea salsola* shrubland, *Lycium shockleyi-Lycium pallidum* shrubland, and *Artemisia tridentata-Chrysothamnus viscidiflorus* shrubland had very few, 1, 2, and 2, respectively. Four other associations had only three modal species. The average number of modal species appeared to be independent of the number of species that occurred within an association (compare species richness in table 1 and table 3).

Table 3—Woody species modality in each vegetation association.

Shrubland associations	No. of modal species
Lycium shockleyi-Lycium pallidum	2
Larrea tridentata/Ambrosia dumosa	3
Atriplex confertifolia-Ambrosia dumosa	11
Lycium andersonii-Hymenoclea salsola	1
Hymenoclea salsola-Ephedra nevadensis	7
Menodora spinescens-Ephedra nevadensis	12
Krascheninnikovia lanata-Ephedra nevadensis	4
Eriogonum fasciculatum-Ephedra nevadensis	3
Ephedra nevadensis-Grayia spinosa	4
Coleogyne ramosissima-Ephedra nevadensis	8
Atriplex confertifolia-Kochia americana	3
Atriplex canescens-Krascheninnikovia lanata	3
Chrysothamnus viscidiflorus-Ephedra nevadensis	6
Ericameria nauseosa-Ephedra nevadensis	6
Ephedra viridis-Artemisia tridentata	7
Artemisia tridentata-Chrysothamnus viscidiflorus	2
Artemisia nova-Chrysothamnus viscidiflorus	6
Artemisia nova-Artemisia tridentata	5
Pinus monophylla/Artemisia nova[a]	8
Pinus monophylla/Artemisia tridentata[a]	16

[a] Woodland associations.

Conclusions

Understanding what is meant by diversity of an area can be very difficult because there are many measures of diversity over different spatial and temporal scales. The two common measures of diversity, species richness and species abundance, are not necessarily correlated as shown in this study. When we compared diversity at an ecoregional scale, richness and abundance appear to be inversely related. Low species richness appears to be associated with poor soil conditions and disturbances. Species richness appears to be related to increased elevation and precipitation at the NTS with those associations and alliances in the Great Basin Desert having higher values. Species abundance does not show this pattern. Species abundance is often greater in transition associations (four of the top five are transitional associations) and alliances. There are large differences in species modality in vegetation associations; however, no regional patterns are discernable as to their distribution.

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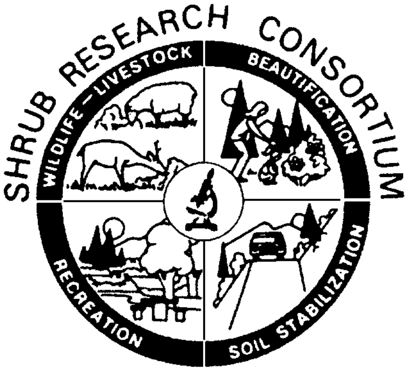

Ecophysiology

Determination of Plant Growth Rate and Growth Temperature Range From Measurement of Physiological Parameters

R. S. Criddle
B. N. Smith
L. D. Hansen
J. N. Church

Abstract—Many factors influence species range and diversity, but temperature and temperature variability are always major global determinants, irrespective of local constraints. On a global scale, the ranges of many taxa have been observed to increase and their diversity decrease with increasing latitude. On a local scale, gradients in species distribution are observable with increasing altitude. These gradients in species distribution have not previously been linked to physiology. In this communication, the gradients are proposed to be a consequence of the physical laws governing energy transduction, acting through natural selection in response to environmental temperature variability. Measurements of rates of energy production and its use in anabolic metabolism as a function of temperature show that respiratory rates and efficiency of green plants are closely adapted to diurnal temperature changes and mean temperatures of the native environment. Optimization of energy production and use by respiratory metabolism along global gradients in temperature and temperature variability is a genome x environment interaction, thus is a fundamental cause of the latitudinal/altitudinal gradients of species range and diversity.

Introduction

Gradients of species range and diversity with altitude and latitude are observed in some taxa of both endotherms and ectotherms (in other words, organisms, including plants, in which cellular temperature is determined by environmental temperature). In those taxa that exhibit an increase in species range and decrease in diversity with increasing latitude and altitude, an as yet unidentified fundamental mechanism linking geographical distribution, climate and physiology may exist (Gaston 1999; Pianka 1996). This paper develops a hypothesis that the physical laws governing energy transduction acting through natural selection in response to environmental variability, and on a global scale, specifically temperature variability is such a mechanism. Application of the laws of equilibrium and non-equilibrium thermodynamics and kinetics to the temperature dependence of respiratory metabolism in ectotherms leads to a prediction of range and diversity gradients in reasonable agreement with observations, and thus is proposed as a fundamental cause of these gradients. We show that under certain conditions species range is proportional to, and diversity is inversely related to, the magnitude of diurnal or short-term temperature changes.

Previous explanations or descriptions of species distributions have been based on observations that equatorial-lowland climates are more constant than climates at higher latitudes and altitudes (Dobzhanski 1950; Klopfer 1959; Fisher 1960; Saunders 1968; Rapoport 1975; Brown 1984; Stevens 1989; Hallam 1994; Hanski and Gyllenberg 1997) or on relations among species number, land area and niche size (Wilson 1943; Preston 1948; MacArthur and Wilson 1967; Stehli and others 1969; Levinton 1982; McIntosh 1985; Rosenzweig 1995). Differences in mutation rates in temperate versus tropical zones, faster selection due to increased physiological rates at higher temperatures, nonsaturation of habitats, non-equilibrium conditions, and temporal and latitudinal gradients of light intensity have been postulated to contribute to species diversity (Connell 1978; Hubbel 1979; Huston 1979; Rohde 1992, 1997). Water, soil conditions, day length, symbiotic mechanisms, and so forth, are all important determinants of the existence of a species at any site, but local-scale environmental properties cannot explain the global-scale patterns of species range and diversity. Temperature is the only global-scale abiotic factor that could determine the global-scale distributions observed for ectotherms.

Our hypothesis may be summarized as follows. Survival and reproduction of an individual requires the ability to acquire and use energy and nutrients within a given environment (Harshman and others 1999). Because this ability varies with temperature and temperature variability, a boundary will exist somewhere along the global-scale temperature gradient, and inversely correlated global scale of short-term temperature variability, beyond which an organism is unable to exist and another organism adapted to the prevailing range of temperature conditions will occupy the succeeding temperature niche. Theoretical considerations and experimental measurements show that metabolic rates are adapted to mean environmental temperature while energy use efficiency is adapted to temperature variability. Optimizing energy use (rate multiplied by efficiency) while maximizing probability of survival of extreme temperature

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In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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events thus requires that the temperature responses of energy metabolism be matched to both the mean temperature and the short-term or diurnal range of environmental temperature (Preston 1948). Ectotherm distribution emerges from the requirement for maintaining near constant intracellular ATP concentration and energy charge (phosphorylation potential, Wrigglesworth 1997) as conditions change.

A fundamental assumption of the paradigm developed in this paper is that the temperature range of adaptation is inversely related to mean growth rate defined as the rate of accumulation of energy in structural biomass. Thus, for organisms in which growth rate is important for survival or competitiveness, optimal adaptation requires adaptation to no broader range of temperatures than necessary, although this presents major risks to survival of the individual (Stiling 1999). The growth rate compromise between opposing needs to tolerate temperature extremes and to maximize energy use efficiency so as to compete for available resources is reflected in the rates and efficiency of ATP generation and use within a temperature regimen. The short-term (hours to days) variability of temperature and the absolute temperatures during the growth season thus determine the optimum energy strategy for many ectotherms. However, local and historical conditions (Rohde 1997) may override full expression of ecological consequences. Thus, for example, other reasons must be sought for the low diversity observed in some relatively constant temperature environments (for example, high latitude aquatic species) and in environments where scarcity of a necessary resource (for example, water) may play a more important role.

Because of the availability of plant experimental data and to avoid the complications introduced by animal behavior (for example, mobility), this paper is focused on plants. However, the principles apply directly to growth and distribution of all aerobic, ectothermic organisms and to homeotherms to the extent that their distributions are determined by the distribution of ectothermic symbionts, hosts, and food sources. The paper discusses first the response of energy metabolism to temperature, second, the respiratory variables that must be measured to characterize the metabolic response to temperature and temperature variability of an individual plant or species and the relationship of respiration to growth, third, the effect of temperature on growth rates as derived from measurements of temperature effects on respiration, and last, the predictions of the effects of temperature and temperature variability on species ranges and diversity.

Cellular Energy Metabolism Response to Temperature

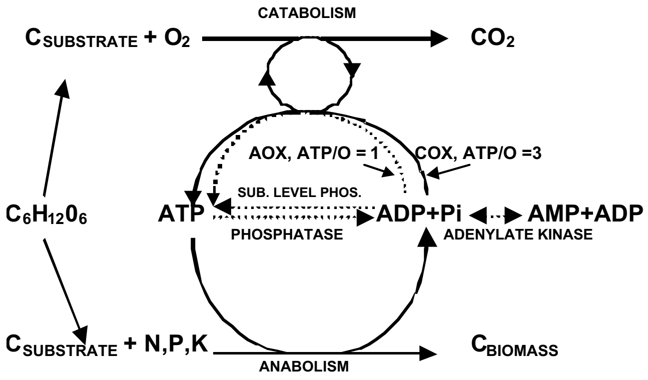

Figure 1—Coupled metabolic energy reactions in biomass production.

Figure 1 shows the reactions of respiratory metabolism. A fraction of substrate carbon is catabolized via oxidative pathways to form CO_2 and the energy thus obtained is used to synthesize ATP. Some ATP and the remainder of the substrate carbon are used for formation and maintenance of structural biomass. The phosphatase catalyzed reaction(s), the ADP disproportionation reaction(s), and alternative oxidase (or uncoupling proteins, Laloi and others 1997) pathway(s) shown in figure 1 are commonly not included in diagrams of respiratory energy metabolism as they are viewed as "futile" or wasteful reactions, not integral parts of properly functioning energy metabolism (Stryer 1988). However, the phosphatases and alternative oxidases must be included in proper representations of respiratory metabolism as they are absolutely necessary for controlling [ATP] and phosphorylation potential, particularly during changes in temperature or other reaction conditions. ADP disproportionation by adenylate kinase-type reactions with equilibrium constants near 1.0 is also necessary to buffer ATP concentration and maintain the proper [ATP]/[ADP] ratio (Stucki 1989). The requirement that the phosphorylation potential (in other words, the ratio [ATP]/[ADP] [Pi]), which is directly related to the free energy change for hydrolysis of ATP), must remain in a narrow range has been discussed extensively by Atkinson (1977), largely in terms of the energy charge.

Thus, equation 1 must obtain where n is the number of moles of ATP and t is time.

$$(dn/dt)_{synthesis} = (dn/dt)_{loss} \text{ and } (dn/dt)_{synthesis}/(dn/dt)_{loss} = 1 \qquad (1)$$

The static representations in figure 1 do not clearly convey the message that relative rates of parallel pathways of the ATP cycle, and therefore overall reaction stoichiometries between energy production and use, change continuously with reaction conditions (Stucki 1989; Gnaiger and Kemp 1990; Kemp and Guan 1997). The principles of energy coupling in biological systems elucidated by Stucki's (1989) studies of ATP metabolism in mammalian mitochondria at isothermal conditions also apply to intact ectotherms with variable temperature. Thus, the energy use efficiency of any coupled pair of reactions is defined by the ratio of Gibbs free energies $(-\Delta G_{\text{driving reaction}})/(\Delta G_{\text{driven reaction}})$ (Stucki 1989; Gnaiger and Kemp 1990; Kemp and Guan 1997). The efficiency is 100 percent when this ratio = 1, but the overall rate is zero because the system is at equilibrium. The greater the ratio above 1, the faster the rate, but the lower the efficiency because the excess energy from the driving reaction is lost from the system. Thus, there is an optimum value of the ratio at which the system can operate at the rate required to accomplish growth and reproduction within the time constraints of the environment while maximizing the efficiency to the range of environmental conditions.

Cellular growth rates can be expressed in terms of the relative rates of ATP synthesis and its anabolic use (Kemp 1996), equation 2.

$$(dn/dt)_{synthesis} = (dn_G/dt) + (dn_F/dt) \qquad (2)$$

(dn_G/dt) is the rate of synthesis of that portion of ATP used for biosynthesis reactions including maintenance, and (dn_F/dt) is the rate of synthesis of the portion of ATP used in futile reactions. The rates (dn_G/dt), (dn_F/dt), and $(dn/dt)_{synthesis}$ vary with temperature, including variability in the coupling of oxidative phosphorylation, in the coupling of ATP hydrolysis to energy requiring reactions, and in the ATP buffering reactions. Thus, the fraction of ATP used for biosynthesis varies with temperature. The second law of thermodynamics defines the upper limit of the efficiency of ATP use by requiring that $(dn_F/dt) > 0$. At the low limit of efficiency, ATP use in biosynthesis goes to zero, in other words, $(dn_F/dt) = (dn/dt)_{synthesis}$.

The driving force for evolutionary adaptation of energy metabolism in ectothermic organisms is optimization of the efficiency of ATP for biosynthesis within the limits of a niche defined by the environmental variables. This suggests that fitness for a thermal niche may be quantified by measurements of rates of ATP reactions as a function of temperature.

Respiratory CO_2 and Heat Production Are Measures of ATP Metabolism, Metabolic Efficiency, and Growth Rate

$(dn/dt)_{synthesis}$ and (dn_F/dt) and the temperature dependencies of these rates can be estimated from measurements of respiratory heat and CO_2 production rates. The rate of release of Gibbs energy (dG) in the coupled processes of catabolism and anabolism at constant pressure is described by

$$dG = dw + dQ - TdS \qquad (3)$$

where dw, the pdV work, is negligibly small. Under steady-state conditions, dG is proportional to $(dn/dt)_{synthesis}$, which in aerobic cells is proportional to CO_2 production rates (Kemp 1996). dQ, the rate of heat dissipation, is a measure of dn_F/dt. Thus, equation 3 shows that TdS closely approximates the rate of energy accumulated in structural biomass (in other words, growth rate). Since $TdS = (dG - dQ)$ therefore

$$\text{Growth rate} = k(dn_G/dt) = k\,[(dn/dt)_{synthesis} - (dn_F/dt)] \qquad (4)$$

where k is a proportionality constant. Equation 5, previously developed by Hansen and others (1994) is equivalent to equation 4.

$$R_{SG}\Delta H_B = -[R_{CO2}\,(1-\gamma_p/4)\,\Delta H_{O2}] - q \qquad (5)$$

R_{SG} is the specific growth rate (mol C s^{-1} g^{-1}) and ΔH_B is the enthalpy change for the reaction $C_{substrate} \rightarrow C_{biomass}$ (kJ mol C^{-1}). Therefore, $R_{SG}\Delta H_B$ is specific growth rate expressed as the rate of storage of chemical energy in structural biomass with units of kJ $s^{-1}g^{-1}$. R_{CO2} is the specific CO_2 production rate (mol $s^{-1}g^{-1}$), ΔH_{O2} is approximately constant with a value of –455 kJ mol^{-1} (Erickson 1987; Hansen and others 1997), γ_p is the mean chemical oxidation state of the substrate carbon, and q is the specific metabolic heat production rate (kJ s^{-1} g^{-1}).

Because ΔH_B is normally positive, it follows that q/R_{CO2} is a measure of efficiency, in other words,

$$q/R_{CO2} = K[(dn_F/dt) / (dn/dt)_{synthesis}] = K(1-\varepsilon_{ATP}) \qquad (6)$$

where K is a ratio of proportionality constants relating q to (dn_F/dt) and R_{CO2} to $(dn/dt)_{synthesis}$ and ε_{ATP} is efficiency of ATP use.

Experimental measurements on many plants (and insects, fish eggs, yeast, and so forth) show that the temperature dependence of q and the temperature dependence of R_{CO2}, and therefore the temperature dependencies of (dn_F/dt) and $(dn/dt)_{synthesis}$, differ within individuals, among individuals, within a species, and among species (Criddle and others 1994, 1996a, 1997; Anekonda and others 1996). Consequently, $(dn_F/dt)/(dn/dt)_{synthesis}$, and q/R_{CO2}, are functions of temperature.

Energy use efficiency can be extremely sensitive to small differences in temperature, emphasizing the importance of temperature in determining which organisms can survive, compete, and reproduce in a particular niche. The efficiency of ATP use, ε_{ATP}, is not directly measurable, but is related to the substrate carbon conversion efficiency, ε, which is also related to q/R_{CO2} (Hansen and others 1994).

Temperature Dependence of Growth Rates and Temperatures Allowing Growth

The temperatures at which experimentally determined temperature functions of q and $(1-\gamma_p/4)455R_{CO2}$ cross define the limits to the growth temperature range (equation 5). As examples, figure 2 shows plots of q and $455R_{CO2}$ and $R_{SG}\Delta H_B$ versus temperature for cultivars of tomato, as a representative warm climate plant, and cabbage, as a representative cool adapted species (Criddle and others 1997). The curves for q are approximately Arrhenius functions over the temperature range allowing growth. R_{CO2} increases exponentially only up to about 20 °C (tomato) and 16 °C (cabbage). At higher temperatures R_{CO2} decreases. Tomato has a larger temperature dependence for $455R_{CO2}$ than for q over much of the growth temperature range. The difference between $455R_{CO2}$ and q [and therefore between $(dn/dt)_{synthesis}$ and (dn_F/dt)] is positive only in the temperature range above 13–14 °C and below about 37 °C. For cabbage, the temperature dependencies of q and R_{CO2} are more similar, and $455R_{CO2} \geq q$ (in other words, $R_{SG}\Delta H_B$ is positive) only at temperatures below about 20 °C. Figure 2C shows that temperature ranges with positive values of $R_{SG}\Delta H_B$ correspond to the growth temperature ranges for these two cultivars.

Because the temperature dependence of q is typically greater than the temperature dependence of R_{CO2} in cold adapted plants (Criddle and others 1996a,b, 1997; Anekonda and others 1996; Hansen and others 1997; Earnshaw 1981) efficiency of cabbage growth decreases as temperature increases and a temperature is reached where $q > 455R_{CO2}$, in other words, the temperature at which the rate of energy production is exceeded by demands for ATP use is at the

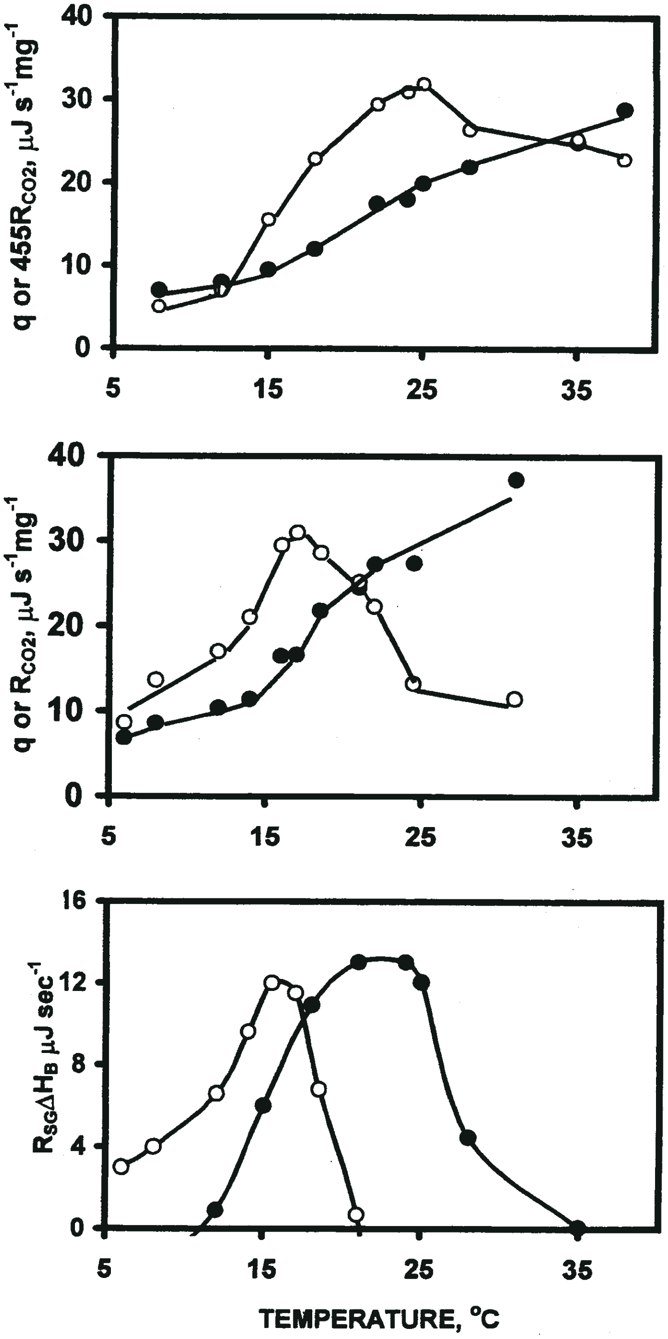

Figure 2—The temperature dependence of respiratory metabolism and growth rates of tomato and cabbage. Field observations show that the cabbage cultivar grows at low temperature, but growth ceases when the temperature is above about 20 °C. The tomato cultivar does not grow at temperatures below about 12 °C or above 35 °C. (A) Responses of $455R_{CO2}$ (open symbols) and q (solid symbols) values of tomato to changes in temperature. (B) Responses of the rate of CO_2 production (as $455R_{CO2}$) and heat rate (q) values of cabbage to changes in temperature. (C) Calculated values of the rates of deposition of respiratory energy in structural biomass ($R_{SG}\Delta H_B$) for tomato (solid symbols) and cabbage (open symbols) across their growth temperature ranges.

high temperature limits for these plants. At this temperature, the ATP/ADP ratio (and the phosphorylation potential) becomes too low to drive biosynthesis, and growth stops. At low temperature, growth rates of cold adapted plants will slow in spite of high efficiency because of the effect of temperature on metabolic rate.

In warm climate plants such as tomato where the temperature dependence of $q \leq$ the temperature dependence of R_{CO2}, efficiency decreases as temperature falls and the lower temperature limit to growth occurs at the temperature at which $[(1-\gamma_p/4)\ 455R_{CO2} - q]$ becomes zero (Criddle and others 1997). The high temperature decrease of tomato growth rate shown in figure 2C results from a rapid decrease in R_{CO2} that is not predicted by Arrhenius extrapolation of data collected at lower temperatures. Because the temperature coefficient of R_{CO2} is greater than that for q, the rate of ATP synthesis increases faster with increasing temperature than the rate of ATP loss, in other words, $d(dn/dt)_{synthesis}/dT$ becomes much greater than $d(dn_F/dt)dT$, and with increasing temperature, (dn_G/dt) approaches $(dn/dt)_{synthesis}$. Efficiency and metabolic rate both increase and growth rate increases. But, this can only continue to a maximum $(dn/dt)_{synthesis}/(dn_F/dt)$ (or $455R_{CO2}/q$) of about 1.4 (corresponding to an ε_{ATP} of about 0.75). Because a large ratio of [ATP]/[ADP] is incompatible with optimal economic growth (Stucki 1989; von Stockar and Marison 1993; Nath 1998; Ksenzhek and Volkov 1998) as the maximum value if this ratio is approached, the capacity of the ATP buffering enzyme systems is exceeded (Stucki 1989; Hoh and Cord-Ruwisch 1997), the ATP/ADP ratio becomes so large that the positive ΔG for ATP synthesis exceeds the negative ΔG from the oxidation reactions, ATP synthesis and correspondingly R_{CO2} is greatly reduced (as shown experimentally in fig. 2), energy use efficiency decreases to near zero, and growth stops.

The mean temperature and diurnal and short-term growth seasonal range of temperatures allowing growth, and therefore plant distribution, are thus explicitly determined by the kinetic laws of temperature dependence of chemical reactions and the thermodynamic laws governing energy coupled processes in changing environments. The functioning of these laws in plants is evident from measurements of q and R_{CO2} and their change with temperature in many species (Hansen and others 1994; Criddle and others 1994, 1996a,b, 1997; Anekonda and others 1996; Hansen and others 1997). If we assume an Arrhenius temperature dependence of q and R_{CO2}, the allowable growth temperature range (ΔT) can be calculated for various combinations of the temperature dependencies of q and R_{CO2}, as shown in figure 3. The temperature range over which $455R_{CO2}/q$ changes from 1 (zero efficiency) to 1.4 (maximum efficiency) is defined as ΔT. ΔT is plotted against the Arrhenius temperature coefficient for R_{CO2} (μ_{CO2}) for various fixed values of the temperature coefficient of q (μ_q). The region with μ_{CO2} from approximately 3 to 11 kK and ΔT from 5 to 37 °C includes essentially the entire physiological and environmental range. A similar set of curves could be drawn for $\mu_q > \mu_{CO2}$.

Figure 3 shows how the temperature dependencies of q and R_{CO2} (in other words, of (dn_F/dt) and $(dn/dT)_{synthesis}$,

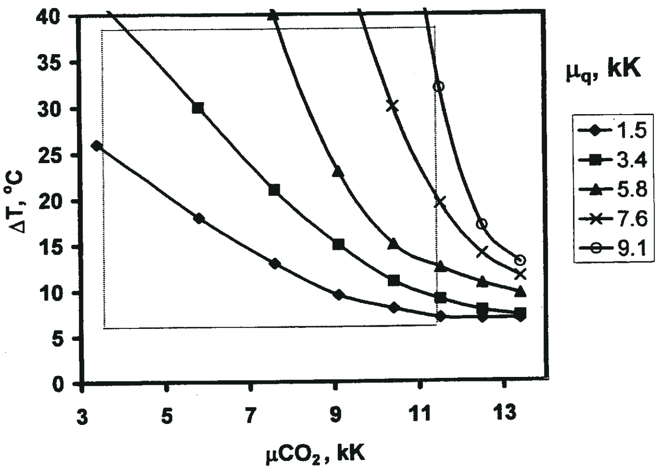

Figure 3—Dependence of the range of temperatures allowing growth (ΔT) on values of the Arrhenius temperature dependence of q and R_{CO2} (μ_q and μ_{CO2}). (A) Each curve represents ΔT dependence on μ_{CO2} at a different, constant μ_q. The μ_q values plotted are μ_q = 1.2 (open circles), μ_q = 1.5 (filled squares), μ_q = 2.0 (filled triangles), and μ_q = 2.5 (filled diamonds). The box insert includes the total range of experimentally observed combinations of μ_q and μ_{CO2}.

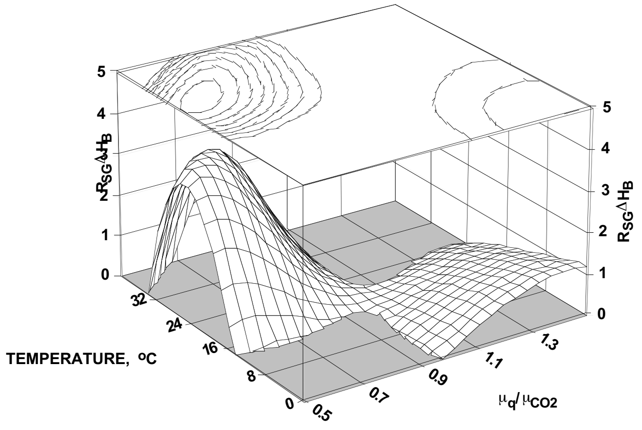

Figure 4—Growth rates for maize as a function of temperature and the ratio μ_{CO2}/μ_q calculated from data on maize cultivars.

respectively) determine fitness for a particular climate. If $\Delta T_{climate} > \Delta T$ ($\mu_{CO2} - \mu_q$) of the plant, the plant will not thrive if it spends too much time at the extreme temperatures where efficiency is zero. If $\Delta T_{climate} < \Delta T$ ($\mu_{CO2} - \mu_q$) of the plant, the plant will be less competitive than plants with $\Delta T(\mu_{CO2} - \mu_q)$ closer to $\Delta T_{climate}$. The minimum ΔT of about 5 °C is obtained only at large values of ($\mu_{CO2} - \mu_q$). The maximum and minimum values of ($\mu_{CO2} - \mu_q$) measured in our laboratories on ectotherms are about plus or minus 6 kK, (or a difference in Q_{10} values for R_{CO2} and q of about 2.0). When the absolute value of ($\mu_{CO2} - \mu q$) is less than about 0.8 kK, ΔT reaches 32 to 37 °C and growth is possible in extremely variable climates, but efficiency for converting photosynthate into structural biomass is very low.

Figure 4 shows a three-dimensional model of the relations among growth rate (as $R_{SG}\Delta H_B$), the ratio of temperature coefficients μ_q/μ_{CO2} (varied from 1:2 to 2:1), and temperature from 0 to 40 °C, derived from experimental data on maize (Taylor and others 1998, and unpublished data). High growth rates are obtained when the ratio μ_q/μ_{CO2} is either very large or very small. When $\mu_q >> \mu_{CO2}$, the growth temperature range is small and growth rate maxima occur at low temperatures. When $\mu_q \approx \mu_{CO2}$, growth temperature range is large, but growth rate is small across the entire range. (In the limit where $\mu_q = \mu_{CO2}$, the temperature range is infinite, but growth rate is zero.) When $\mu_{CO2} >> \mu_q$, the growth temperature range is again small, but growth rate maxima occur at high temperature. Growth rate reaches a maximum where $455R_{CO2}/q = 1.4$ and rapidly declines with further increase in temperature. The higher the ratio μ_{CO2}/μ_q, the lower the temperature at which the optimum is obtained. The projected contour map at the top of figure 4 allows visualization of the decrease of growth rate at temperatures above optimum.

Figure 4 shows that the penalty associated with an organism being adapted to a wider temperature range than required is a decreased growth rate. Plants adapted to a wide temperature range are capable of survival in a climate with little temperature variation, but to the extent that growth rate determines competitiveness, a widely adapted plant (a temperature generalist) will be out-competed by a narrowly adapted plant (a temperature specialist). However, plants adapted to too narrow a temperature range cannot tolerate the wide temperature range because much of the time they would be subjected to temperatures that disallow control of ATP metabolism.

An experimental test of the predicted inverse relation between environmental temperature range ΔT and growth rate has been done with 17 half-sib families of 15-year-old *Pinus ponderosa* planted at three or four sites with different latitudes and elevations (Church 2000). Plots of ΔT, the mean diurnal temperature variation during the growth season at each site versus height growth, show a linear decrease in height with increasing ΔT. Linear regression analysis of data for the 17 families gave an average regression coefficient (r^2) of 0.96 with a range from 0.88 to 0.99. Growth rate of these trees is not correlated with any other environmental variables except those co-correlated with ΔT.

A perfect adaptation of plants to temperature is not possible because climates vary from year to year. Thus, while individual plants are genetically limited in their response to temperature, a species evolves many genotypes with a range of responses. In addition, plants may alter their effective environmental growth temperatures simply by altering the time during the season when growth occurs. There is thus no "best" solution for adaptation of energy metabolism and growth rate to a location. Rather, plants with a range of properties exist both within and between species. However, the allowable ranges of energy metabolism and growth rate responses to temperature must change systematically with diurnal temperature range. Because of the covariance between diurnal temperature range ΔT and latitude/altitude, the relations among temperature, energy use efficiency, and growth rate are a fundamental mechanism that may explain the observed latitudinal and altitudinal gradients of species range and diversity.

The relation between climate and respiration has been further tested with three *Eucalyptus* species from different native climates with approximately the same mean temperature, 16.4 °C, but different temperature variation ΔT. Plots of $R_{SG}\Delta H_B$ versus temperature for individual trees of each species, grown in, and therefore acclimated to, a common environment, are presented in figure 5. Differences between species are much larger than intra-species variation and the patterns shown are representative of the species. Because these species grow throughout the year, annual temperature data describe the growth temperature range. The native environmental temperature ranges are similar to, and give the same ranking of ΔT as the temperature range of positive values of $R_{SG}\Delta H_{B,}$ which were calculated from measured q and R_{CO2} values (equation 5 with $\gamma = 0$). Acclimation of the trees to climate in the common growth environment is negligible because the temperature ranges allowing growth (positive $R_{SG}\Delta H_B$) are the same as the climatic temperature ranges at the different growth sites.

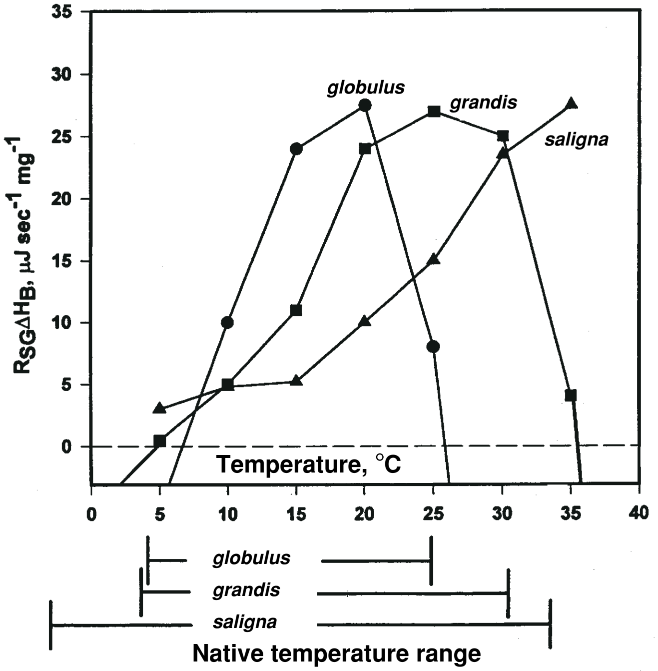

Figure 5—Growth rates of plants from three *Eucalyptus* species calculated as a function of temperature from q and R_{CO2} measurements and comparison with temperature ranges at the native growth sites of *E. Saligna* (Smith), *E. grandis* (W. Hill ex Maiden), and *E. globulus* (Labill. subsp. maidenii {F. Muell} Kirkpatr., commonly known as *E. Maidenii*) (Boland and others 1984). The trees tested were seedlings grown hydroponically in a common, controlled environment chamber. Measurements of q and R_{CO2} were made at several temperatures on small, expanding leaf tissues, followed by calculation of growth rates, $R_{SG}\Delta H_B$, by equation 8 with $\gamma = 0$ (Hansen and others1994). Lines at the lower portion of the figure connect the mean high temperature of the warmest month and the mean low of the coldest month at each site.

Predicted Magnitudes of Gradients of Species Range and Diversity

The principles developed above predict that range or niche size for growth of individual populations and species must increase with the magnitude of temperature fluctuations (ΔT) (equation 8)

$$A_T / N_T = c\,(\Delta T) \qquad (8)$$

where A_T is total area, N_T is total number of species, and A_T/N_T is the average species area. c is a proportionality coefficient. ΔT is related to latitude and altitude, in other words, $\Delta T = c'$ f(latitude, altitude). Through mid-range temperate latitudes and altitudes, the relation between ΔT and latitude or altitude is approximately linear so that in this range, species area, latitude/altitude, and ΔT are nearly linearly related.

Consider the effects of this relation on species areas in the northern hemisphere from 12° to 45° north latitude. The approximate mean temperature fluctuation (ΔT) at 45° latitude is about 3 times that at 12° latitude. Thus, the niche size increases (and number of thermal niches decreases) about threefold from 12 to 45°. However, if areas at the two latitudes are not constant, then the effect of area on species numbers also enters in.

An exponential relation exists between species number (N) and area (A), in other words, $N = kA^z$. z values from 0.1 to 0.6 have been reported (Rosenzweig 1998). For example, Hanski and Gyllenberg (1997) showed (for moth species) that plots of ln N versus ln A (of islands in an archipelago) yielded a line with slope, (or z value) near 0.4. Using this value and returning to our example, we find that the land area of the continents increases about 1.5 fold from 12° to 45° north latitude. The species area relation predicts N should be $(1.5)^{0.4} = 1.2$ fold higher at 45°, a trend in species diversity opposite that observed. However, combination of the species area relation with equation 8 and the effects of latitude on species range yields equation 9,

$$N^{[(1/z)-1)} = c''\,\Delta T \qquad (9)$$

where c" is again a constant. Comparison of species numbers at 12 °C and 45 °C north latitude using the combined temperature and area gradient effects indicates a decrease in number of species per unit area by a factor of 2.08. Species diversity should thus decrease about twofold from 12° to 45° north latitude, which agrees reasonably well with relative values noted for species diversities at these latitudes (Rohde 1997).

The concept that temperature dependence of cellular energy production by respiration contributes to the gradient of species diversity thus predicts the correct direction and allows an *a priori* estimation of the magnitude of the temperature-linked portion of the gradient of species diversity with latitude and altitude. It should be noted that there is no clear test of this number available in the literature. All studies to date examined limited areas where local climatic and geographical factors play important determinant roles in range and species numbers. Because ΔT is a function of latitude/altitude, the apparent value of the exponent, z, in species area curves will not be constant, but will increase with increasing latitude and altitude. This probably accounts for much of the observed variation between studies in values of z (Rosenzweig 1998).

Because optimization of metabolic properties with temperature within species must follow the same rules as for species, gradients of responses to temperature must exist within species. This intra-species variability helps ensure species survival during climate changes or influxes of competitors and provides the opportunity for farmers and plant scientists to select the best genotypes for optimal growth at a given site. These principles provide a unifying rationale for improving production by matching cultivars to environment. This paper has focused on plants, but the principles are applicable to ectothermic animals. Also, questions of ectotherm responses to climate change can be framed in more quantitative terms with an understanding of the underlying causes.

Summary

We conclude that the temperature responses of cellular energy metabolism are a fundamental determinant of latitudinal/altitudinal gradients of species range and diversity. To maximize the probability of growth, reproduction, and survival, organisms have been selected to optimize their ability to obtain and use energy throughout the range of ambient temperatures. Matching energy metabolism to climatic temperature is accomplished by variable engagement of "futile" reactions that are necessary to maintain efficient energy coupling with changing temperatures. Ectotherms growing in climates with a narrow temperature range can evolve high energy use efficiencies and enhance their ability to compete for resources, but in doing so they risk being damaged or killed by temperature excursions outside the normal range. Ectotherm adaptation to broad temperature ranges enhances survival during extreme temperature excursions, but at the cost of lower growth rates. Energy efficiency and survival requirements lead to species variability along latitudinal and elevational gradients of temperature range and diversity.

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Responses of Plant Growth and Metabolism to Environmental Variables Predicted From Laboratory Measurements

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Abstract—The Arrhenius activation energies, and therefore temperature coefficients, for rates of catabolic production of ATP and for anabolic use of ATP differ. Because the intracellular concentration of ATP and the phosphorylation potential must be controlled within a narrow range for cell survival, a mechanism must exist to balance these rates during temperature variation in ectotherms. We hypothesize that much of this control is accomplished via engagement of temperature-dependent reactions that waste ATP or the potential to make ATP in "futile" cycles and that energy-wasting metabolic cycles are essential for maintaining acceptable phosphorylation potentials across a temperature range. We further postulate that the mitochondrial alternative oxidase (AOX) activity is one important mechanism for "wasting" potential to make ATP and thus for controlling the phosphorylation potential in plants as temperature or other reaction conditions vary. Because of differences in temperature coefficients, the ratio of AOX to COX activities varies with temperature, resulting in a temperature-dependent change in coupling oxidation to phosphorylation. Matching the changes in substrate carbon conversion efficiency to environmental temperature patterns allows plants to maintain constant phosphorylation potentials. Thus, an apparent paradox exists that survival of all organisms in changing conditions depends on an energy loss via "futile cycles."

The Need for Futile Cycles

The biological function of apparently "futile" reactions has long been a subject of speculation. What is the purpose of the ubiquitous reactions that lose energy by cyclic production and breakdown of reaction intermediates or via reactions that result in energy loss by short-circuiting the formation of ATP? The answer to this question is known only for futile reactions employed in specialized thermogenic tissues. "Futile" reactions must contribute positively to fitness in non-thermogenic tissues or they would have been eliminated by natural selection. This study examines the hypothesis that an uncoupled energy loss is required to maintain [ATP] and phosphorylation potential nearly constant in varying cellular conditions and is therefore particularly important for survival of ectotherms in variable temperature environments.

The overall reaction for aerobic growth of plants may be written as in equation 1.

$$C_{substrate} + x(\text{compounds and ions of N, P, K, etc.}) + yO_2 \rightarrow \varepsilon\ C_{structural\ biomass} + (1\text{-}\varepsilon)CO_2 \tag{1}$$

Reaction 1 is the sum of two reactions, the catabolic reaction (2)

$$C_{substrate} + yO_2 + nADP + nPi + aNAD^+ \rightarrow CO_2 + nATP + aNADH + aH^+ \tag{2}$$

And the anabolic reaction 3.

$$C_{substrate} + x(\text{compounds and ions of N, P, K, etc.}) + mATP + bNADH + bH^+ \rightarrow C_{structural\ biomass} + mADP + mPi + bNAD^+ \tag{3}$$

Reactions 2 and 3 occur in the condition-dependent ratio $(1\text{-}\ \varepsilon)/\varepsilon$ where ε is the substrate carbon conversion efficiency. Reactions 2 and 3 are energy-coupled through cyclic production and hydrolysis of ATP and redox cycling of NADH. Because the rates of reactions 2 and 3 have different dependencies on temperature and other conditions, the coefficients n and m, and a and b, are generally not equal for the two reactions. Principles of nonequilibrium thermodynamics applied to the energy-coupled system of reactions 1–3 lead to the conclusion that reaction 2 must always produce ATP and NADH at rates equal to or in excess of their rates of use in the biosynthetic reactions of reaction 3 (in other words, $n \geq m$ and $a \geq b$). If ATP is synthesized faster than it is used for biosynthesis, the excess can be disposed of by hydrolytic reactions, but if ATP is synthesized slower than it is used, the phosphorylation potential, or free energy change for hydrolysis of ATP (ΔG_P, Equation 4), falls and cell death ensues. Therefore, the excess ATP and NADH is cycled through condition-dependent uncoupled hydrolysis and oxidation reactions in order to maintain the phosphorylation potential and [ATP] approximately constant.

$$\Delta G_p = -RT\ln\ [ATP]/[ADP][Pi] \approx \text{constant} \tag{4}$$

The rate of synthesis of ATP is also controlled by condition-dependent reactions that cause a loss of the potential to form ATP, in other words, reactions mediated by uncouplers and through such pathways as the alternative oxidase. The engagement of these less efficient alternate pathways of oxidation to control [ATP] and phosphorylation potential

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varies with reaction conditions. This variation is independent of the rate of reaction 3 because reactions 2 and 3 are not closely coupled. The overall result is a condition-dependent energy loss and a variable efficiency of energy coupling between catabolic and anabolic processes (Wrigglesworth 1997).

The requirement demonstrated above for engagement of less efficient pathways in plants to maintain phosphorylation potentials under variable reaction conditions is also apparent from fundamental thermodynamic considerations. The second law of thermodynamics requires that mass and energy flow through the system (described by equation 1) must be accompanied by an entropy increase, in other words, processes such as growth require a transfer of energy from the system to the surroundings. This is measurable as heat loss to the environment (Jou and Llebot 1990). When the reactions occur at steady state, the entropy (heat) loss to the surroundings is minimized (Prigogine 1980). Any displacement from steady state, in other words, varied reaction conditions, results in an increased energy loss to the environment. Various workers (Jou and Llebot 1990, p. 51) have confirmed that these concepts apply to growth of cells under near steady state conditions and have used measurements of heat dissipated as an indication of the increase in entropy during variable growth conditions. We propose that the concepts also apply to rapidly growing plant tissues with adequate substrate supplies. Thus, variation in reaction conditions that perturb steady-state growth (or further displace a growing system from steady state) results in an experimentally measurable increase in heat loss and an overall decrease in energy use efficiency during growth. Several sources infer (but do not rigorously prove for biological systems) that the larger and more frequent the variations perturbing steady-state growth, the greater the energy loss from the system (Zotin 1990; Lewis and Randall 1961, unpublished observations by the authors).

Futile Reactions in Plant Metabolism

Thermodynamic arguments clearly require variable efficiency and increased heat loss with variable growth conditions. However, the mechanisms by which energy is lost and mechanisms by which the energy loss and changing efficiency are matched to environmental conditions to ensure optimal growth and survival are not defined by the thermodynamic arguments. The mechanisms may be derived from analysis of the effects of changing conditions on enzyme activities involved in intracellular ATP energy cycles.

The ATP cycle for aerobic cellular energy metabolism may be presented in the form of two half-cycles, the catabolic formation of ATP and the anabolic hydrolysis and use of ATP (Kemp 1996) (fig. 1).

The concentrations of adenine nucleotides in cells is low (a few mM) and the rate of turnover of ATP is high (up to 1 g ATP per g rapidly expanding plant tissue per day). Thus, rates of the two halves of the cycle in figure 1 must remain carefully balanced to maintain [ATP] constant and the phosphorylation potential in the narrow range required for cell viability (Kemp 1996). However, variation in reaction conditions cause changes in the relative rates of all the reactions involved in ATP synthesis and breakdown. Because all cells experience changing reaction conditions during growth, all must have mechanisms to control the rates of synthesis and breakdown of ATP and the phosphorylation potentials. Such controls have frequently been discussed in terms of energy charge, with emphasis on regulation by adenylate binding to glycolytic enzymes (Atkinson 1977). However, simple feedback inhibition/activation by intermediates in energy metabolism alters rates, but not stoichiometry, and does not facilitate the thermodynamically required changes in stoichiometry and efficiency required during changes in reaction conditions. Multiple, parallel reactions with different effects on energy coupling as shown in figure 1 provide control of phosphorylation potential by altering the energy coupling efficiency.

Homeotherms, which experience relatively small changes in reaction conditions, contain enzymes or enzyme systems such as phosphatases and uncoupling proteins to control phosphorylation potentials during changing reaction conditions (Stucki 1989; Nath 1998). Ectotherms face a major additional problem in maintaining phosphorylation potentials during temperature change and require these enzymes plus enzymes that can adjust metabolic responses to the large temperature change. This becomes particularly evident from observations that the Arrhenius activation energies, and therefore the temperature dependencies of the rates of ATP synthesis and its anabolic use, are not the same (Criddle and others 1997; Taylor and others 1998; Smith and others 1999). Therefore, in the absence of a regulatory mechanism the relative rates of catabolic formation of ATP and its use in anabolic reactions would change continuously with changing temperature and [ATP] would vary with temperature. Ectotherm survival thus requires mechanisms to facilitate varying catabolic/anabolic stoichiometries, control phosphorylation potential and optimize energy use efficiency over a broad temperature range.

Some enzyme reactions that can function to control phosphorylation potential or alter the stoichiometries of oxidative phosphorylation and anabolic use of ATP for production of biomass are shown in figure 1 (reactions indicated with

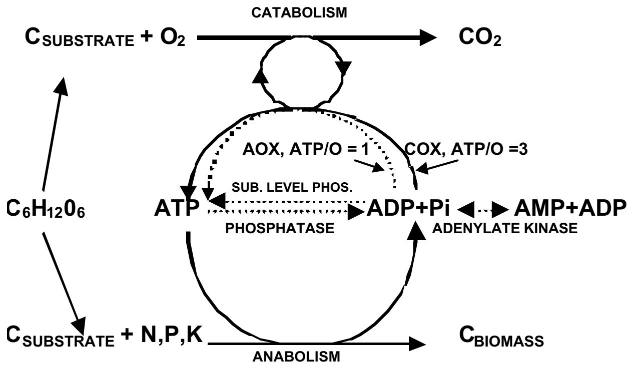

Figure 1—ATP cycle for plant respiration and biomass synthesis.

dashed arrows). For example, variation in relative amounts of substrate level phosphorylation can alter the ratios of substrate level to oxidative phosphorylation and affect overall reaction stoichiometries and energy use efficiency. The adenylate kinase reaction plays a critical role in buffering phosphorylation potentials against small changes in reaction conditions or intermediate concentrations (Stucki 1989). Phosphatases can alter energy-coupling stoichiometries via a classical "futile cycle" hydrolysis of ATP without accomplishing biochemical work. Uncouplers or uncoupling proteins can also cause a "futile" energy loss. However, this group of reactions probably plays a relatively limited role in balancing the overall condition-dependent production and use of ATP during metabolism of healthy, aerobic plant cells.

In contrast, because it is often present with high and variable activity in plant cells, the mitochondrial alternative oxidase (AOX) can have large effects on the efficiency of coupling energy metabolism to biomass production. Substrate oxidation via COX yields a maximum of 3 ATP mol^{-1} O_2. The alternative oxidase enzyme has no phosphorylation site and oxidation via the AOX pathway yields a maximum of 1 ATP mol^{-1} O_2. Oxidative energy that could have been used to synthesize two additional ATP is lost as heat. The AOX catalyzed reaction thus causes a "futile" energy loss. Consequently the number of moles of substrate required to produce one mole of ATP depends on the AOX/COX ratio (Lance and others 1985). Because the temperature coefficients of AOX and COX are not the same (McCaig and Hill 1977; Smakman and others 1982; Purvis 1985; Mc Nultly and Cummins 1987), this ratio changes with temperature (and probably with other reaction conditions). Figure 1 illustrates how changing this ratio changes the substrate carbon conversion efficiency, ε (in other words, the fraction of substrate carbon incorporated into structural biomass).

Thus, we hypothesize that the "futile" waste of the potential to produce ATP and the futile hydrolysis of ATP are the mechanisms by which phosphorylation potentials are controlled in plants growing in a variable temperature environment. We further propose that a primary reaction for adjusting the efficiency of ATP synthesis and maintaining the near constant phosphorylation potential in plants is the mitochondrial alternative oxidase. The relative temperature coefficients of the AOX and COX reactions determine the rate of change in efficiency with temperature and thereby the fitness of a plant for growth in a particular temperature environment. Matching a plant to environmental temperature is achieved by balancing the temperature coefficients of ATP synthesis, ATP use in anabolic reactions and ATP (or the potential to make ATP) wasted so that energy use efficiency is optimized over the time-temperature distribution during the growth season.

A quantitative test of these hypotheses is possible by comparison of data from direct calorespirometric measurements of substrate carbon conversion efficiencies of many different plants (Criddle and others 1997; Taylor and others 1998; Smith and others 1999) with measurements by Gonzalez-Meler and others (1999) of AOX and COX reaction rates of soybean and mung bean at 14 and 28 °C.

Demonstration of Futile Cycle Function From Changes in Substrate Carbon Conversion Efficiency With Temperature

Substrate carbon conversion efficiencies of plants can be calculated from direct calorimetric measurements of rate of heat loss (q) and either the CO_2 production rate (R_{CO2}) or the rate of O_2 consumption (R_{O2}) for rapidly growing plant tissues. The ratio of heat loss per mole CO_2 produced (or O_2 consumed) is a direct, and intuitive, measure of efficiency. The more heat lost per C-mole respired to CO_2, the less efficient the transfer of respiratory energy into anabolic products. The relation between q/R_{CO2} and ε is shown in equation 5 (Hansen and others 1994)

$$q/R_{CO2} = -(1-\gamma_p/4)\ \Delta H_{O2} - [\varepsilon/(1-\varepsilon)]\Delta H_B \tag{5}$$

where γ_p is the chemical oxidation state of the stored photosynthetic products used as substrate for biomass production, ΔH_{O2} = -455 kJ mole^{-1}, and ΔH_B is the enthalpy of incorporation of C into biomass, as kJ mole^{-1} C. As q/R_{CO2} increases, ε decreases (so long as the chemical nature of the photosynthetic substrate and biomass remain constant).

Simultaneous measurement of q and R_{CO2} on rapidly growing seedling tissues of cold climate plants, such as maize cultivars adapted for cultivation in the northeastern U.S. and eastern Canada, show increasing q/R_{CO2} as temperature increases (Criddle and others 1997; Taylor and others 1998) (table 1). Thus, ε for these plants decreases with increasing temperature. For example, an increase in

Table 1—Measured changes in q/R_{CO2} with temperature and calculated substrate carbon conversion efficiency.

	q/R_{CO2}, kJ mol^{-1}		ε, percent[a]	
	14 °C	**28 °C**	**14 °C**	**28 °C**
Maize cultivar[b]				
G17 (cool climate)	250	425	67	56
814 (warm climate)	400	295	44	60
T10 (cool climate)	225	425	70	23
Tom Thumb (warm)	444	338	10	54
Other species	q/R_{CO2}			
Cool climate	**14 °C**	**28 °C**		
Eucalyptus globulus	245	>700		
Cabbage	310	>800		
Strawberry	320	500		
Cheat Grass	328	455		
Warm climate				
Eucalyptus grandis	414	347		
Tomato	425	375		
Lily	305	255		
Rice (*Italico livorno*)	404	345		

[a] Calculations of ε with equation 5 used measured values of q and R_{CO2} and the assumption that ΔH_B = 100 kJ mol^{-1} C incorporated into plant biomass, with carbohydrate as the substrate carbon source, in other words, $\gamma_p = 0$.

[b] Data from (Taylor and others 1998).

temperature from 14 to 28 °C caused an increase in q/R_{CO2} from about 250 to 425 kJ mol^{-1} in the cold-climate adapted Pioneer Seed maize cultivar G-17. This corresponds to a decrease in ε from 67 to 56 percent. In contrast, there is a decrease in q/R_{CO2} from about 400 to 295 kJ mol^{-1} when temperature is increased from 14 to 28 °C for the warmer climate adapted Pioneer Seed maize cultivar 814. This corresponds to an increase in efficiency of seedlings from about 44 to 60 percent over this range (table 1). Values for additional maize cultivars and other species are included in table 1 to show that changes in q/R_{CO2} and ε for maize represent common trends for warm and cool climate plants (Smith and others 1999; Criddle and Hansen 1999). Thus, simple experimental measurements on plant tissues quantify values of ε and show that ε changes systematically with temperature in a pattern specific to growth temperature conditions.

Warm climate cultivars commonly increased while ε of the cooler climate cultivars decreased with increasing temperatures in the range studied (table 1). Since thermodynamic considerations require that efficiency must change with temperature, it is not unexpected that each species or cultivar is adapted to have higher efficiency in the temperature range to which it is adapted. Note that the designation of warm and cool climates refers to temperatures experienced during the growth season and not necessarily to annual average temperatures at a site. The four maize cultivars of this study and most of the additional examples were grown in common conditions with paired comparison plants, so the observed efficiency differences are genetically defined responses to environmental temperature, not a consequence of differences in acclimation during growth.

Evidence That the “Futile” AOX Reaction Supplies a Temperature-Dependent Change in Substrate Carbon Conversion Efficiency

Gonzalez-Meler and others (1999) measured the activities of AOX and COX in mung bean and soybean at two temperatures. They showed (a) simultaneous and continuous engagement of AOX and COX pathways in both mung bean and soybean (see also Hoefnagel and others 1995; Guy and others 1989; Ribas-Carbo and others 1995), (b) relatively high activities of both AOX and COX at 14 °C and 28 °C, and (c) large differences in the temperature dependencies of AOX and COX and therefore different substrate carbon conversion efficiencies at the two temperatures. Thus, the thermodynamic requirement for a changing efficiency with changing reaction temperatures can be satisfied in part by the presence of the parallel AOX and COX pathways. The remaining questions are: can the futile reaction catalyzed by AOX (a) provide both a mechanism for the thermodynamically required and experimentally observed changes in efficiency as temperature changes, and (b) provide a means for quantitatively matching the efficiency change to requirements of a specific environment.

The studies of Gonzalez-Meler and others (1999) partially answer these questions. With AOX and COX activity data at only two temperatures, it is not possible to calculate meaningful temperature coefficients, particularly when the high temperature (28 °C) may be above the optimum temperature for growth of one or both species. However, the limited available data do show large, species-dependent differences in ratios of activities at the two temperatures.

To consider changes in substrate carbon conversion efficiencies specifically due to the effects of temperature on activities of AOX and COX, we assume that plants with no AOX activity operate with a substrate carbon conversion efficiency near 0.7 (Stucki 1989), and that short-term, bidirectional, day-to-day changes in temperature affect the AOX/COX ratio predominantly by differences in responses to temperature rather than by other mechanisms (however, see discussion below). Increasing the temperature from 14 to 28 °C increased the AOX/COX ratio for soybean but decreased the ratio for mung bean. Table 2 shows that soybean ε increases from about 0.57 to 0.61 as temperature is increased between these two values, while ε for mung bean decreases from 0.64 at 14 °C to 0.61 at 28 °C. Thus, substrate carbon conversion efficiency changes with temperature in opposite directions for mung bean and soybean. ATP production efficiency of soybean increased at

Table 2—Calculated substrate carbon conversion efficiencies (ε) and growth rates for soybean and mung bean.

	Soybean				Mung bean			
T °C	ε[a]	ε/(1-ε)	R_{O2}[b]	Growth rate as (R_{O2} X ε/(1-ε))	ε	ε/(1-ε)	R_{O2}	Growth rate as (R_{O2} X ε/(1-ε))
1X AOX								
14	0.57	1.35	6.2	8.4	0.64	1.74	10.6	18.5
28	0.61	1.56	25.5	39.8	0.61	1.56	32.9	51.3
2X AOX[c]								
14	0.45	0.82	9.4	7.7	0.60	1.51	13.4	19.9
28	0.50	1.00	42.5	42.5	0.56	1.30	44.5	57.7

[a] Values of ε were calculated from AOX and COX activities at 14 °C and 28 °C reported by Gonzalez-Meler and others (1999). The calculations assume (a) a maximum substrate carbon conversion efficiency of 0.7 for both species when total respiration is via COX, (b) production of 3 ATP per O_2 via the COX pathway and 1 ATP per O_2 via the AOX pathway, and (c) that substrate carbon conversion efficiency is proportional to the total amount of ATP produced per mole O_2 for plants containing both AOX and COX.

[b] R_{O2} is total oxidation rate via AOX plus COX.

[c] Values of ε in the presence of 2 x AOX are based on the reported near doubling of AOX activity with little change in COX activity following cold acclimation of mung bean and soybean (Gonzalez-Meler and others 1999).

the higher temperature while efficiency was higher for mung bean at the lower temperature. The similarities of results in tables 1 and 2 show that a significant change in efficiency with temperature for both warm and cold climate plants could be accounted for by the presence of AOX and the ratios of the temperature dependencies of AOX and COX.

Engagement of AOX Benefits Plants Growing in Stress Conditions

An important consequence of temperature adaptation of energy metabolism based on futile cycle mechanisms becomes apparent when the effect of AOX activity on growth rate is considered. Growth rate is determined by the product of the respiration rate (R_{CO2}, or R_{O2} assuming the respiratory quotient = 1) multiplied by [$\varepsilon/(1-\varepsilon)$] (19). In the studies of Gonzalez-Meler and others (1999) cold acclimation of mung bean and soybean seedlings increased total oxidase rate of both plants by increasing AOX about two-fold with little change in COX activity. When AOX increases, the overall oxidase rate is higher, substrate carbon conversion efficiency is lower, but R_{CO2} multiplied by $\varepsilon/(1-\varepsilon)$ is little changed. Doubling AOX activity at 28 °C, soybean changes growth rate only from 39.8 to 42.5 $\mathrm{Cmol^{-1}\ s^{-1}\ mg^{-1}}$ and mung bean from 51.3 to 57.7 $\mathrm{Cmol^{-1}\ s^{-1}\ mg^{-1}}$ (table 2). Thus, growth rate at a given temperature is little affected by increasing (or decreasing) AOX because the changes in total respiration rate are closely offset by reciprocal changes in the efficiency of production of ATP per mole of O_2 respired. Irrespective of whether ε increases or decreases with temperature, growth rate is essentially self-regulating. AOX synthesis or activation thus provides a mechanism for increasing electron flow, without major effects on growth rate.

Mediation of the thermodynamically required changes in substrate carbon conversion efficiency with changing temperature via introduction of futile reactions such as AOX can have important benefits to cell survival. Engagement of AOX can help maintain rapid electron flow (though at lower efficiency) and plant viability when the COX pathway is blocked or stressed. The continued flow of electrons via AOX under temperature or other stress conditions that may otherwise shut down respiration is consistent with the previously proposed role of AOX in contributing to the protection of cells from harmful oxidative reactions and buildup of fermentation products when plants are stressed (Wagner and Krab 1995; Purvis and Shewfelt 1993).

Stresses, by definition, hinder plant growth. The common denominator linking all stresses is an effect on metabolism that decreases energy use efficiency with increasing stress. Any changes that differentially affect the rates of reactions involving ATP synthesis and use triggers changes in the requirement for futile cycling to maintain d[ATP]/dt = 0 and a near constant phosphorylation potential. Thus, AOX (or another reaction with similar effects) is required to "waste" increasing amounts of energy in the presence of increasing stress. In support of this conclusion, alternative oxidase has been shown to be induced by many stresses including low temperature, drought, some herbicides, hydrogen peroxide and some protein synthesis inhibitors. Increasing AOX in response to stress has correctly been discussed in context of the need to maintain electron flow as a defense mechanism, but the required role in changing energy coupling efficiencies to control phosphorylation potential and maintain viable cells has not been described.

The importance of AOX in providing means for response to stress is emphasized in studies by Parsons and others (1999). They demonstrated that, compared to control cells, tobacco cells lacking alternative oxidase were greatly restricted in their ability to adapt to phosphate-limited growth. The growth limitation was ameliorated by addition of an uncoupling agent that provided (in the context of this communication) the "futile," non-phosphorylating pathway necessary for adjustment of energy coupling stoichiometries and phosphorylation potentials when AOX was absent. We predict that the tobacco cells lacking AOX will also fail to tolerate changing temperature and many other stress conditions. We propose that these cells are similar to homeotherms that have more limited need for futile reactions because of smaller changes in growth conditions.

Summary

As immobile ectotherms, plants must adjust energy metabolism to nearly continuous variation in temperature. Thermodynamic arguments as well as experimental measurements show that this is accomplished via changing stoichiometries of energy-coupled reactions and changing energy use efficiencies. Adaptation of a plant to a particular environment includes selection for the temperature coefficients for ATP synthesis, for anabolic use of ATP, and for reactions wasting ATP or the potential to synthesize ATP that allow phosphorylation potentials to be maintained nearly constant over the required temperature range.

We have demonstrated that AOX activity can fill the essential role of altering both the rate and efficiency of respiratory metabolism in plant cells in response to temperature change. This is the mechanism by which AOX fulfills the additional roles (mostly protective) that have been ascribed to AOX (McCaig and Hill 1977; Parsons and others 1999). Thus, whatever other functions it accomplishes, a primary role of AOX is maintenance of the phosphorylation potential in the appropriate range for cell viability when temperature changes. Variable temperature requires all ectotherms to have enzymes with functions analogous to the plant alternative oxidase. Ectothermic animals that lack an alternative oxidase may satisfy this requirement by a combination of uncoupling factors and phosphatases, or analogous enzymes.

Alternative oxidase activity is adjusted by several factors in addition to temperature. Concentrations of α-ketoacid metabolites, disulfide reduction, oxidation state of quinones, allosteric regulation, gene expression and possibly other factors all fine-tune AOX activity (Buchanan and others 2000). Activity responses to some of these effectors may be slow while others act rapidly and may be difficult to distinguish from simple Arrhenius temperature effects on enzyme activity. Each could be expressed differentially as temperatures change. Thus, the presence of various activating mechanisms of AOX can cause activity changes with temperature to differ from those calculated simply on the basis of temperature coefficients for this discussion. However, all of these moderators of AOX activity must work against a background of nearly continuous, bi-directional temperature change with instantaneous effects on enzyme activity that change relative rates of AOX and COX activities, irrespective of enzyme level and activation state. No matter what the ultimate cause, AOX has a temperature dependence of activity that differs from the temperature dependence of COX and the pattern of response to temperature differs with species, cultivar, and genotype.

Unique consequences of altering respiration by variation in rates of AOX (or analogous "futile" reactions) are: (a) Changing the level of AOX activity alters electron flow, but the resulting changes in rates of electron flow and changes in efficiency are offsetting so that there is a self regulation of ATP availability for anabolism. Therefore, growth rates at a given temperature are little changed by alteration of AOX levels. (b) Via changes in AOX activity, plant respiration rate may be increased to counter stress effects, with an energy cost, but without altered growth rates or major regulatory changes in other aspects of plant metabolism. (c) Because adjustment of efficiency with temperature follows from the physical consequences of differences in temperature coefficients of AOX and COX, no complex biological regulatory system need be involved to meet the requirements of variable temperature. (d) Evolutionary adaptation of a plant to an environment by natural selection must include selection for the relative values of temperature coefficients of AOX and COX (in other words, efficiency change with temperature) that optimize growth within that environment.

Within photosynthesizing plant cells, chloroplasts also have an ATP cycle with different temperature coefficients for synthesis and use of ATP and must also maintain near constant phosphorylation potentials for proper function. Because there is no direct chemiosmotic link between chloroplasts and mitochondria, the chloroplasts require a separate class of futile cycle enzymes to maintain potentials when reaction conditions change. Differences in temperature coefficients between Calvin cycle and photorespiration activities (Mohr and Schopfer 1995) suggest that the "waste" of ATP by photorespiration may be an important key to maintaining phosphorylation potentials in chloroplasts during variation in temperature. The necessary waste of ATP in both mitochondria and chloroplasts suggests that the many unsuccessful attempts to improve crop productivity by reduction of "wasteful" reactions such as AOX and photorespiration can only achieve success for crops grown in a narrow temperature range.

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Effects of Salinity and Temperature on Respiratory Metabolism of *Salicornia utahensis* From a Great Basin Playa

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Abstract—Plants that live in the desert playas of the Great Basin must simultaneously tolerate very high concentrations of salt and high temperature. This study characterizes the respiratory metabolism of one species growing in this environment. An isothermal calorimetric method was used to measure the dark metabolic heat rate (q) and CO_2 production rate (R_{CO2}) of stem tissue from *Salicornia utahensis* grown in the greenhouse or in constant temperature growth chambers at six different concentrations of NaCl solutions ranging from 0 to 1.0 M. Metabolic rates were measured at eight temperatures from 5 to 40 °C. Temperature and salt dependencies of q and R_{CO2} were used to model response of both growth and substrate carbon conversion efficiency. Salt and temperature stresses are not additive, but rather oppose one another, in other words, the higher the salt, the higher the temperature the plants will tolerate and vice versa. The maximum temperature tolerated is an approximately linear function of salt concentration, being about 20 °C at 0 M salt and about 32 °C at 1 M. Concentration of the endogenous osmoticant glycinebetaine increased with salt and temperature but only to about 20 °C and 900 mM NaCl.

There are many indicators of stress responses of plants such as chlorophyll fluorescence, heat shock proteins, and osmoticant molecules. Each of these tells something about the way a plant responds to a stress. Ultimately in order to understand plant survival and growth, we must know how the particular stress affects the energy metabolism (Smith and others 2000). This study measured the effects of salt (NaCl) and temperature on the biomass accumulation and respiratory metabolism of a desert halophyte, *Salicornia utahensis* Tidestr. This species is adapted to growth and survival in wet, salty soils and a cold desert climate.

Growth of halophytes is stimulated by some level of salinity (Flowers and others 1986), however growth of most species is inhibited by too high salt concentrations, in other words, greater than about 0.5 M NaCl, the concentration of salt in seawater (Ungar 1991). Previous studies on growth of desert species (*Atriplex griffithii, Halopyrum mucronatum, Haloxylon recurvum,* and *Sueda fruticosa*) from Pakistan showed that low salinities promoted growth (Khan and others 1998). Increasing salt to 425 mM promoted growth of *Cressa cretica* but growth in 850 mM salt was not significantly different from controls grown without added salt (Khan and Aziz 1998). Growth of halophytes from the Great Basin in Western North America (*Salicornia rubra, Salicornia utahensis, Suaeda torreyana, Allenrolfea occidentalis*) shows a similar pattern of promotion at moderate salinities (400 to 600 mM NaCl) and a decline with further increases in salinity (Khan and others 2000).

Halophytes usually absorb a considerable amount of salt to maintain osmotic balance with their highly saline medium. The most salt tolerant species have high internal salt concentrations, suggesting that the ability of the cells to tolerate high salt concentrations is at least as important to survival as the ability to restrict accumulation of salt (Flowers and others 1977). However, the enzymes of halophytes, unlike those of salt tolerant bacteria, are inhibited by high salt concentrations suggesting that cytoplasmic enzymes are protected from salt either by sequestration of salt in cell walls and vacuoles (Weber and others 1977) or by protective solutes such as glycinebetaine, proline, polyols, or cyclitols (Flowers and others 1977).

Seed germination of *Triglochin maritima* from the Great Basin was most inhibited by exposure to high salinities at suboptimal thermoperiods (Khan and Ungar 1999). For halophytes *Salicornia rubra, S. utahensis, Distichlis spicata,* and *Allenrolfea occidentalis* growing in the field showed the highest metabolism, respiration, efficiency, and growth during May and June and lowest during the hot, dry month of August (Harris and others, in press). By contrast, *Salicornia europaea* from a salt marsh in Ohio germinated better following rain events in June than earlier in the year (Egan and Ungar 1999).

Except for the fact that *S. utahensis* is a common plant in the Great Basin desert with cold winters, hot summers, and large diurnal temperature changes (commonly 20 to 30 °C), little is known about the temperature tolerance of this species. During the period of high summer temperatures, which is also the time of least rainfall, water evaporates from the shallow playas, increasing salt concentration in the soil. It was thus of interest to examine the combined effects of temperature and salt. In their saline environment,

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halophytes are normally exposed to multiple stresses. In addition to salt and temperature stresses, there is often a low osmotic potential of water and a low partial pressure of oxygen due to standing water or a high water table (Ungar 1991). Presumably the imposition of one kind of stress reduces tolerance to other simultaneous stresses, a hypothesis looked at in this study. This study examines the interaction of both low and high salt and temperature stresses. Predicted biomass accumulation and characteristics of energy metabolism are used as indicators of stress response.

Aerobic respiration has two aspects: catabolism and anabolism. In catabolism, organic substrates are oxidized to produce CO_2. Part of the energy produced by oxidation is used to convert ADP and inorganic phosphate to ATP, the rest is lost as heat.

$$\text{substrate} + O_2 + \text{ADP} + P_i \rightarrow CO_2 + H_2O + \text{ATP} + \text{heat} \quad (1)$$

ATP produced in catabolism is transient, but is used for cellular work, including anabolism as shown below:

$$\text{substrate} + \text{ATP} \rightarrow \text{growth} + \text{ADP} + P_i + \text{heat} \quad (2)$$

In anabolism, heat and new plant tissue are produced and ATP is hydrolyzed back to ADP and phosphate. A calorimeter measures the rate of heat loss (q) from both catabolism and anabolism. The rate of CO_2 production (R_{CO2}) measures the rate of catabolism. With carbohydrate as the specific substrate, predicted growth rate of structural biomass or rate of anabolism (R_{SG}) is thus related to the difference in two measured variables as in equation 3,

$$R_{SG}\Delta H_B = 455R_{CO2} - q \quad (3)$$

where ΔH_B is the enthalpy change for the formation of biomass from photosynthate and Thornton's constant (-455 ± 15 kJ mol^{-1} of O_2) is incorporated to calculate the rate of energy generated by catabolism. Thus, growth rate in terms of energy is proportional to the difference between the measured values of R_{CO2} and q. The temperature dependencies of R_{CO2} and q are different (Hansen and others 1994). The difference between $455R_{CO2}$ and q therefore changes with temperature and this difference can be used to predict growth rate changes with temperature (Criddle and others 1997).

Predicted specific growth rate may also be expressed as a function of the substrate carbon conversion efficiency (ε) and respiration rate (R_{CO2}).

$$R_{SG} = R_{CO2}[\varepsilon/(1-\varepsilon)] \quad (4)$$

Combining equations 3 and 4 to eliminate R_{SG} gives equation 5,

$$[\varepsilon/(1-\varepsilon)]\Delta H_B = -q/R_{CO2} - (1-\gamma_P/4)455 \quad (5)$$

which relates the ratio of q/R_{CO2} to ε. Values of q/R_{CO2} measured as a function of temperature can thus provide information on substrate carbon conversion efficiency (ε) and the oxidation state of the substrate carbon, in other words, γ_P (Hansen and others 1994).

The purpose of this work is to examine how an extreme halophyte adapts its respiratory metabolism to temperature and salinity conditions common in its native habitat. In this study, calorimetry was used to determine the high and low stress temperatures and salinities for *Salicornia utahensis* grown in controlled conditions. When the metabolic heat rate exceeds energy made available through catabolism of carbohydrate, the plant is considered to be stressed (Smith and others 2000).

Materials and Methods

Seeds of *Salicornia utahensis* Tidestr. were collected during the fall of 1995 from salt playas 1–2 km east of Goshen, Utah. Seeds were separated from the inflorescence, surface sterilized using the fungicide Captan, and stored at 4 °C. Seeds were germinated in 36 cm^2 pots filled with sand and placed in trays of distilled water to sprout. Once sprouted, salt was introduced into the trays and increased by 200 mM every 2 days until desired salinity was reached. Ten pots each were grown at 0, 200, 400, 600, 800, and 1,000 mM NaCl. A half-strength Hoagland solution was used to supply nutrients. Pots were subirrigated and the water level adjusted daily to correct for evaporation. Salt solutions were completely replaced once a week to avoid buildup of salinity in the pots. Plants were grown in a greenhouse at a daytime mean temperature of 25 °C and a mean nighttime temperature of 15 °C. Metabolic heat rates (q) and respiration rates (R_{CO2}) and fresh and dry weights of plant shoots were measured 60 days after the highest salt concentration was reached.

Another set of plants was sprouted as above but grown at six different salinities in each of four controlled environmental chambers maintained at 10, 20, and 30 °C with a 12-hour photoperiod (200 μmol m^{-2} s^{-1}, 400–700 nm). Plants were harvested after about 5 months.

Plants were cut just below the cotyledon and about 100 mg fresh wt. of tissue was placed in each of three ampules of a microcalorimeter (Hart Scientific model 7707 or Calorimetry Sciences Corporation model 4100). After 15 to 20 minutes thermal equilibration at the desired temperature, the metabolic heat rate (q) was measured for another 15 to 20 minutes. The ampules were removed from the calorimeter and a small vial filled with 40 μl of 0.4 M NaOH placed in the calorimeter ampule with the tissue. Again a 15–20 minute thermal equilibration was necessary, followed by measurement of the sum of the heat rate from metabolism and CO_2 reaction with the NaOH (–108.5 kJ $mole^{-1}$) for 15–20 minutes. After the NaOH was removed, the heat rate (q) is measured again as before (Hansen and others 1994; Criddle and others 1997). The difference in the measurements with and without NaOH solution gives the rate of CO_2 evolution (R_{CO2}) by the plant tissue. The tissue was then run at another temperature. Measurements were made on each sample at 9 temperatures: 5, 10, 15, 20, 25, 30, 35, 40, and 45 °C.

For glycinebetaine measurements, the method of Gorham (1984) was followed. Plant material (0.5 g) was boiled in 10 ml of water for 2 hours at 100 °C in a dry heat bath. Samples were diluted with a 50 mM potassium dihydrogen phosphate buffer adjusted to pH 4.6. This was the carrier buffer that was also used in the HPLC system. The sample was cooled and filtered using a 0.45 μm membrane filter (Gelman, Ann Arbor, MI), and then used directly to measure glycinebetaine with a Hewlett Packard 1050 modular 3D HPLC (Boise, ID) with quaternary pump, online degasser, autosampler, and a diode array detector with a stainless steel flow cell (6-mm path length, 8 μl volume). Separations were performed on a 250 x 4 mm i.d. stainless steel column

Table 1—Endogenous levels of glycinebetaine in seedlings of *Salicornia utahensis* grown in different NaCl concentrations in the greenhouse.

NaCl concentrations, mM	g glycinebetaine/kg dry wt.
0	28.5
300	48.8
600	45.6
900	44.4
1,200	37.0
1,500	47.6

Table 2—Endogenous levels of glycinebetaine in seedlings of *Salicornia utahensis* grown at different temperatures in growth chambers in different NaCl concentrations.

Growth temperature	Salinity mM NaCl	Glycinebetaine g/kg dry weight
10 °C	0	34.4
	300	32.3
	900	46.3
	1,500	35.7
20 °C	0	14.9
	300	57.1
	900	59.4
	1,500	37.7
30 °C	0	ND
	300	54.2
	900	died
	1,500	died

packed with 10 μm Nucleoside 100-10SA (Phenomenex, Torrance, CA). Flow rate was 1.2 ml min^{-1}. Glycinebetaine standards were run at 1, 10, and 100 mmol l^{-1}.

Results and Discussion

Glycinebetaine concentrations (table 1) increased from 28.5 g glycinebetaine per kg dry wt. of plant tissue for *Salicornia utahensis* grown in zero salt to 48.8 g/kg for plants grown in the greenhouse in 300 mM NaCl. Increases in salinity above 300 mM had essentially no effect on the glycinebetaine concentration within the plant tissue. Temperatures at which the plants were grown (table 2) did affect glycinebetaine concentration. Compared with plants grown in zero salt at 20 °C, plants grown without salt at 10 °C had more than twice the concentration of glycinebetaine. Perhaps the glycinebetaine was not functioning as an osmoticant in this case. Unlike some reports in the literature (Khan and others 1998), there was not a linear increase in glycinebetaine with salt exposure. Other osmoticants exist (Flowers and others 1977) and may be operative as well here. Weber and others (1977) did show that salt tolerance in *Salicornia utahensis* was based on exclusion of salt from the photosynthetic cells and on the ability of the succulent stem to function even though sections were dead owing to high salt concentration. It may be that glycinebetaine operates at relatively low concentrations of NaCl but that active accumulation of salt into certain tissues occurs with higher concentrations of external salt and possibly at higher temperatures.

Figure 1 is a plot of the metabolic heat rate as a function of salt concentration at the various temperatures. The data show the heat rate generally increases with increasing

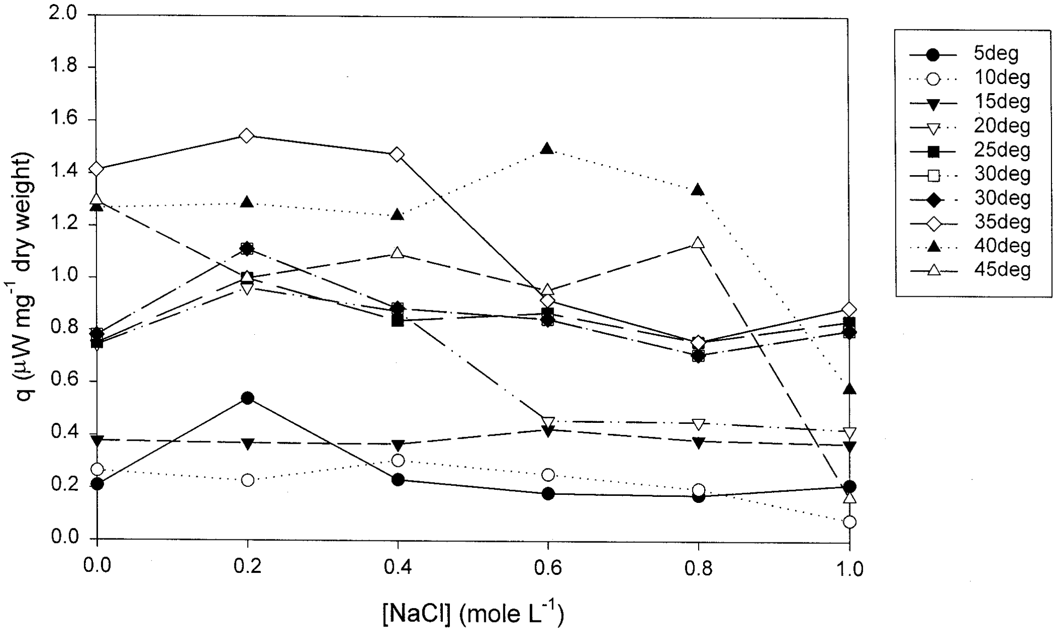

Figure 1—Plot of dark metabolic heat rate q versus the NaCl concentration in which the plants were grown. Each line presents the measurements made at the indicated temperature.

temperature up to 35 to 40 °C after which it decreases markedly. Metabolic heat rate generally decreases with increasing salt, the effect becoming more pronounced with increasing temperature.

Figure 2 is a plot of the respiratory CO_2 rate (R_{CO2}) as a function of salt concentration at the various temperatures. R_{CO2} increases with temperature at low temperatures, goes through a maximum at intermediate temperatures, then decreases at higher temperatures. Salt has little effect on R_{CO2} except at very low (≤5 °C) and very high (>35 °C) temperatures where R_{CO2} increases sharply.

Predicted growth of *S. utahensis* seedlings generally increased with salt concentrations (fig. 3), with high temperatures showing the largest effect of increasing salt.

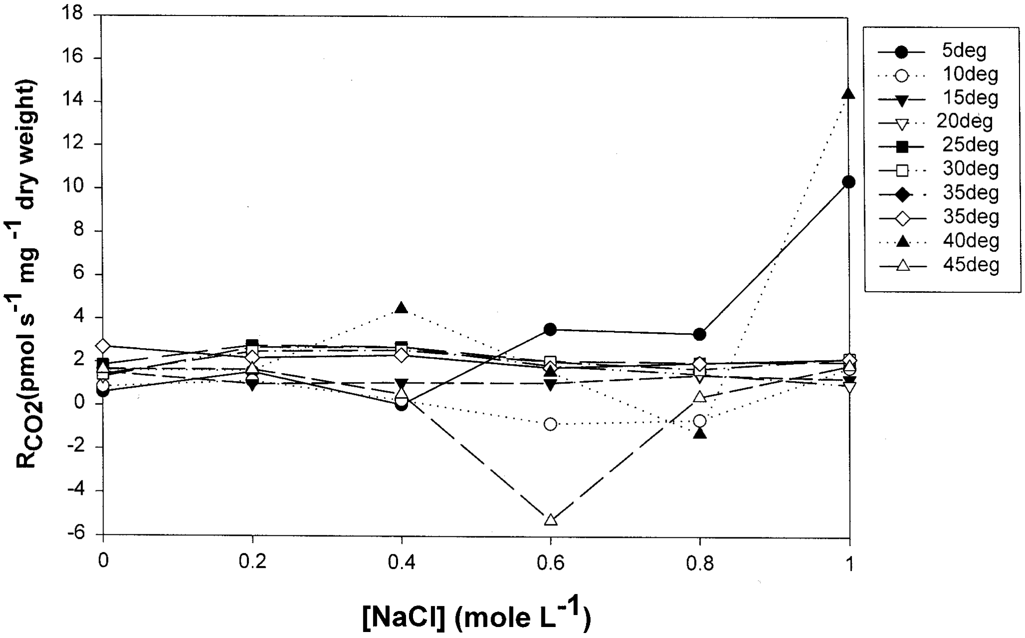

Figure 2—Plot of dark metabolic CO_2 rate versus the NaCl concentration in which the plants were grown. Each line presents the measurements made at the indicated temperature.

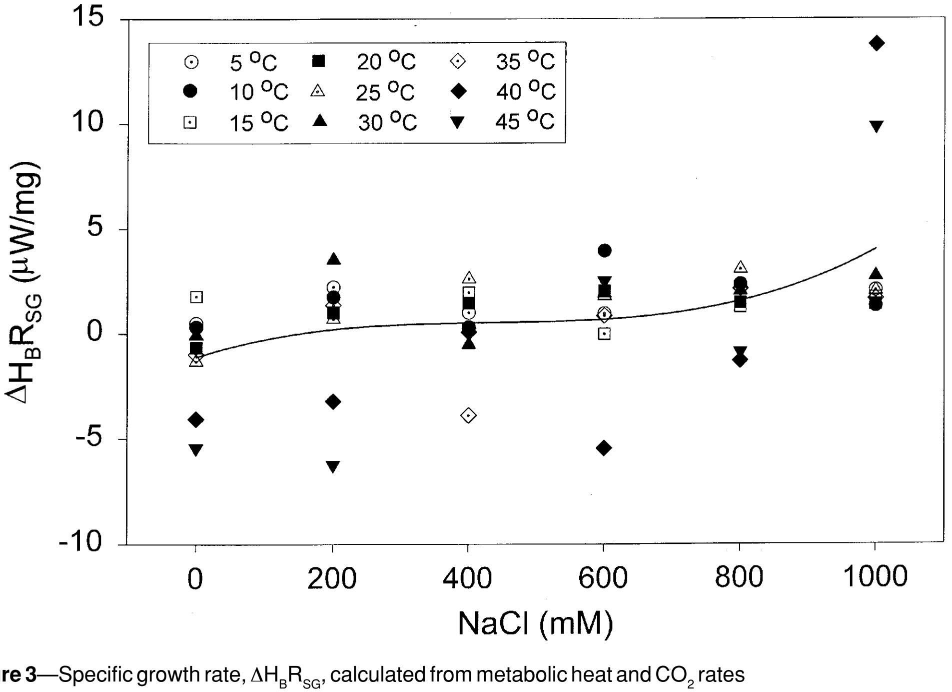

Figure 3—Specific growth rate, $\Delta H_B R_{SG}$, calculated from metabolic heat and CO_2 rates as a function of the salt concentration in the growth medium.

Plotting the same data another way (fig. 4), averaging the growth for all salt concentrations at each temperature predicts a decrease in growth with increasing temperature. The two data points at 1,000 mM NaCl at 40 and 45 °C are anomalous in both figures 3 and 4. These two points at high values of $\Delta H_B R_{SG}$ do not indicate high growth rates, instead these values are a result of the imposed stress and indicate the production of catabolic products other than CO_2.

Figure 5 is a contour plot of the specific growth rate, $\Delta H_B R_{SG}$, calculated from metabolic heat and CO_2 rates as a function of the measurement temperature and salt concentration in the growth medium. The synergism between these

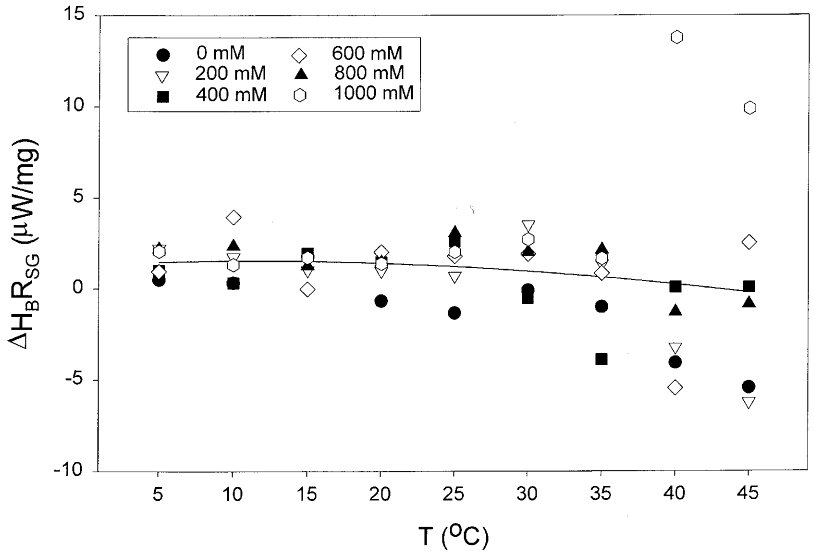

Figure 4—Specific growth rate, $\Delta H_B R_{SG}$, calculated from metabolic heat and CO_2 rates as a function of the measurement temperature.

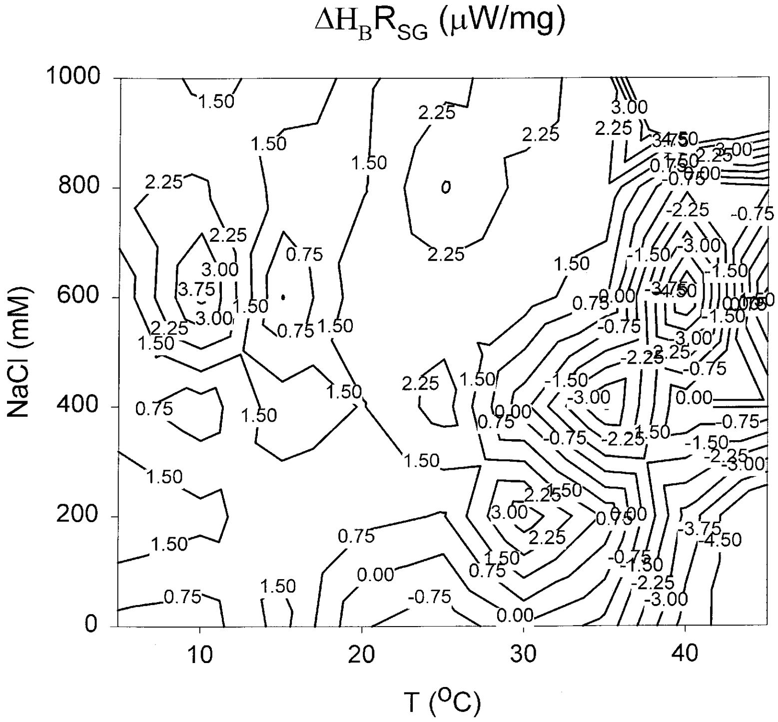

Figure 5—Contour plot of the specific growth rate, $\Delta H_B R_{SG}$, calculated from metabolic heat and CO_2 rates as a function of the measurement temperature and salt concentration in the growth medium.

two environmental variables can be deduced from this plot. Contrary to our intuitive assumption that high temperature and high salt would be more stressful than either stress alone, the results show that the two together are less stressful than either high salt or high temperature alone. This is shown by the approximately linear diagonal of maximum tolerable temperatures that runs from about 20 °C at 0 salt to about 30 °C at 1,000 mM salt on the contour plot. Note that $R_{SG}\Delta H_B$ tends toward negative values to the right of this diagonal.

The major conclusion of this paper agrees with the natural history of *S. utahensis*. In the Great Basin, precipitation occurs primarily during early spring (April-May) and late fall (October-November) when temperatures are typically around 5 °C at night and 20 to 25 °C during the day. Thus, the salt in the playas is most dilute during periods with these temperatures. In the summer, when daytime air temperatures range up to about 45 °C, is also when the salt is most concentrated. The data collected in this study show that *Salicornia utahensis* respiratory metabolism is well adapted to these conditions, that is, to lower salt concentrations at low temperatures and higher salt concentrations at higher temperatures. The details of how the species has accomplished the feat of adapting to the sum of two apparently deleterious stresses are certainly not clear as yet.

Halophytes are normally "includers" (in other words, they are generally in equilibrium with the salt in solution in the root environment), and thus there is probably little or no extra energy cost for operating in a variable, high-salt environment. Tertiary structures of proteins and membranes must however be appropriate for the environment.

In summary, the methods employed in this study have contributed to the understanding of the phenomenon of salt stress by providing information on the synergism between salt and temperature.

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Respiratory and Physiological Characteristics in Subpopulations of Great Basin Cheatgrass

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Bruce N. Smith

Abstract—Cheatgrass (*Bromus tectorum* L.) is a dominant weed that has increased the frequency of wildfire in the Great Basin since its introduction approximately 106 years ago. Characteristics of respiratory metabolism were examined in eleven subpopulations from different habitats. Seeds from each subpopulation were germinated (4mm radicle) and metabolic heat rates (q) and respiration rates (R_{CO2}) determined calorimetrically at 5 °C intervals from 5 to 30 °C or from 5 to 45 °C. From the experimental data, growth rates and ratios of q/R_{CO2} (a measure of efficiency) were calculated. In general, growth rate increases from a low temperature limit of 3 to 7 °C to an upper temperature limit between 27 to 31 °C. Beyond these limits growth ceases. These limits differ among subpopulations, and are related to the native microclimate.

Introduction

Since its Eurasian origins—introduced from the eastern Mediterranean area of Europe into the United States—cheatgrass (*Bromus tectorum* L.) has become one of the most troublesome weeds in the western United States (Upadhyaya and others 1986). Furthermore, cheatgrass—more than any other plant—has transformed the vegetative landscape in the Great Basin and Columbia Basin areas since its introduction approximately 106 years ago (Upadhyaya and others 1986; Klemmedson and Smith 1964). Despite a few advantageous characteristics, such as being high-quality forage in the early spring for grazing animals, and the fact that its dense root growth and expansive top growth prevent erosion, the disadvantages of cheatgrass—in relation to the environment and other native perennial plants—far outweigh the advantages (Morrow and Stahlman 1984).

Cheatgrass appears to have an extraordinary ability to adapt to a variety of microclimates. Some studies suggest that cheatgrass grows well, even under low-nitrogen situations (Klemmedson and Smith 1964). Additional studies suggest that, though water is a limiting factor in the growth of cheatgrass, its ability to thrive under relatively low-water conditions is superior to perennial grasses. If moisture levels allow seed production, the germination rate of stressed seed is unchanged relative to seed produced under normal conditions (Richardson and others 1989). As early as 1955, striking phenotypic variation was observed in cheatgrass (Klemmedson and Smith 1964). Moreover, a few studies conducted during the 1990s provide evidence for not only phenotypic variation (Meyer and Allen 1999), but also genetic variation within populations (Hemming and others 1999), and more robustly between populations (Novak and others 1991, 1993; Novak and Mack 1993; Mack and Pyke 1983, 1984). According to Novak and Mack (1993) genetic differentiation is greater between populations because cheatgrass has very high levels of inbreeding, which reduces the chance for recombination of the genome. Nevertheless, cheatgrass appears to be capable of adapting to a variety of climates and can do so even with low levels of water, relative to other native species.

Throughout the western United States, cheatgrass has invaded crop plants such as winter wheat (*Triticum aestivum* L.) and alfalfa (*Medicago sativa* L.) (Morrow and Stahlman 1984). A number of factors have contributed to this invasion—both in crop plants and undeveloped habitats. Wild fires and soil-nutrient depletion have been suggested, yet overall it becomes apparent that no matter how cheatgrass initially gained a foothold in the western United States, its ability to adapt and take over native habitats has increased. As Nasri and Doescher (1995) point out in their study of Idaho fescue, increased competition from cheatgrass depleted soil moisture available for the fescue and consequently reduced Idaho fescue's growth substantially. Further validating this claim, Evans and Young (1984) argue that cheatgrass was one of three alien grasses that established, dominated, and revolutionized plant succession in the sagebrush grasslands in the western United States. Even during the 1960s Klemmedson and Smith (1964) observed that cheatgrass' physiological responses were much quicker than their native perennial grass counterparts.

Fire, growth periods, and its physiological characteristics give cheatgrass a competitive advantage. The caryopes of cheatgrass are essentially fireproof and as it ends its growth cycle the extremely high flammability of the grass permits fires to start and spread with unusual rapidity. Cheatgrass seeds are protected while other perennial grass seeds are made impotent. Cheatgrass has added to the fire cycle: over a century ago, fire-return intervals on the sagebrush-steppe in Idaho's Snake River Plains fluctuated anywhere from 35 to 100 years. Now, because cheatgrass creates a more continuous fuelbed, the fire-return interval is very

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In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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short—anywhere from 2 to 4 years (Whisenant 1990). Furthermore, native plants, such as sagebrush do not have a quick capability to regenerate after a fire has devoured native habitats. Fire enhances the establishment of cheatgrass: while everything else is trying to regenerate—slowly—cheatgrass is back the next spring taking over the decimated lands. Since its growth season includes germination in the fall after autumn rains (Beckstead and others 1995), overwintering in the vegetative stage, and completing growth in the early spring, cheatgrass gets first track on available water and nutrients in the soil. Additionally, following rapid germination in the fall, cheatgrass quickly establishes an extensive fibrous root system that continues to grow through the winter (Thill and others 1984). Finally, even under drought conditions cheatgrass will mature sufficient seed to ensure plants for the following year (Klemmedson and Smith 1964).

From its Eurasian origins cheatgrass has adapted to the Great Basin remarkably quickly. If the restoration of native ecosystems is a primary goal, cheatgrass is one of the primary culprits in impoverishing native ecosystems of their natural species (Billings 1990; D'Antonio and Vitousek 1992); therefore, the physiology of cheatgrass must be understood. This study reflects an effort to understand the respiratory physiology of cheatgrass and its adaptation to the Great Basin.

In this study, the respiratory characteristics of cheatgrass subpopulations are determined by calorimetric techniques and analyzed with a model of plant growth first introduced nearly a decade ago (Criddle and others 1991, 1994, 1996, 1997; Criddle and Hansen 1999; Hansen and others 1994, 1997, 1998a, 1998b; Smith and others 1999, 2000). Since growth rates are functions of energy metabolism, calorimetry is necessary to understand plant metabolic physiology (Hansen and others 1994). Plant metabolic calorimetry might be defined as the thermodynamic study of physiological processes.

Materials and Methods

Caryopes from eleven subpopulations of cheatgrass in the Great Basin were used in this study. Nine of the eleven subpopulations came from Utah; the other two originate in Colorado and Nevada (table 1). The United States Department of Agriculture, Forest Service Shrub Sciences Laboratory, at Provo, Utah, provided the caryopes for this analysis. The caryopes were greenhouse-grown progeny of a number of maternal lines. The original seeds were collected in 1995 and this study conducted on seeds produced in 1998 and 1999. Seeds from each subpopulation were placed on petri dishes, dampened with distilled water, and germinated at 20 °C. Germinated seedlings' respiratory characteristics were measured when 2 to 5 days old.

Data were collected with calorimeters: Calorimetry Sciences Corporation model 4100 and Hart Scientific model 7707. R_{CO2} and q were determined at temperatures from 5 to 45 °C. These determinations came from (a) placing 80 to 150 mg (15 to 30 seeds) of germinated caryopes into 1-ml calorimeter ampules; (b) setting a desired temperature and waiting approximately 20 minutes for a steady-state heat rate; (c) placing a 40 μl vial of 0.4M NaOH in the ampule and again waiting for a steady-state heat rate, which now includes both metabolic heat and heat from the reaction of carbon dioxide and sodium hydroxide to produce carbonate; (d) removing the vial of NaOH and again waiting for a steady-state; and (e) repeating the process at another temperature. Measurements were done in the order of 20, 15, 10, and 5 °C on one sample and at 25, 30, 35, 40, and 45°C on another. Data were analyzed by averaging the heat rates directly measured in steps b and d, to obtain the metabolic heat rate q, subtracting this from the heat rate measured in step c, and dividing this difference by the enthalpy change for the reaction, –108.5 kJ mol^{-1}, which gives $R_{CO2.}$ The ratio of q/ R_{CO2} was calculated from average values of q and R_{CO2} obtained in approximately 5 replicates.

Table 1—Eleven subpopulations of cheatgrass (*Bromus tectorum* L.) in the Great Basin: classified by sites of origin.

Subpopulation	County	State	Altitude
St. George	Washington	Utah	850 m
Green River	Emery	Utah	1,280 m
Whiterocks	Tooele	Utah	1,450 m
Ephraim	Sanpete	Utah	1,740 m
Hobble Creek	Utah	Utah	1,800 m
Potosi	Clark	Nevada	1,850 m
Castle Rock	Douglas	Colorado	1,980 m
Salina	Sevier	Utah	2,040 m
Strawberry	Wasatch	Utah	2,400 m
Fairview	Sanpete	Utah	2,770 m
Nebo Summit	Utah	Utah	2,850 m

Thermodynamic Model

Growth rates were calculated from equation 1

$$R_{SG}\Delta H_B = 455R_{CO2} - q \qquad (1)$$

where R_{SG} is the specific growth rate in moles of carbon per gram of tissue per second, and ΔH_B is the enthalpy change for formation of structural biomass from substrate in kilojoules per mole of carbon. The constant, 455 kJ mol^{-1} CO_2, comes from Thornton's rule by assuming carbohydrate is the substrate. Note that under conditions where q is greater than $455R_{CO2}$, $R_{SG}\Delta H_B$ will be negative, indicating conditions of no growth.

Results

After replicating the experiment several times on each subpopulation and thereby providing mean data from about 100 caryopes per temperature, the data were analyzed for distinct differences in the physiological responses to temperature. Figures 1, 2 and 3 show plots of metabolism of subpopulations that, in general, are indicative of the response of other subpopulations to temperature. Figure 4 shows q/R_{CO2} averaged over the subpopulations as a function of temperature. Figure 5 depicts the calculated growth rate as a function of temperature averaged over the 11 subpopulations. Table 2 provides Arrhenius slopes for q and R_{CO2} (Criddle and Hansen 1999).

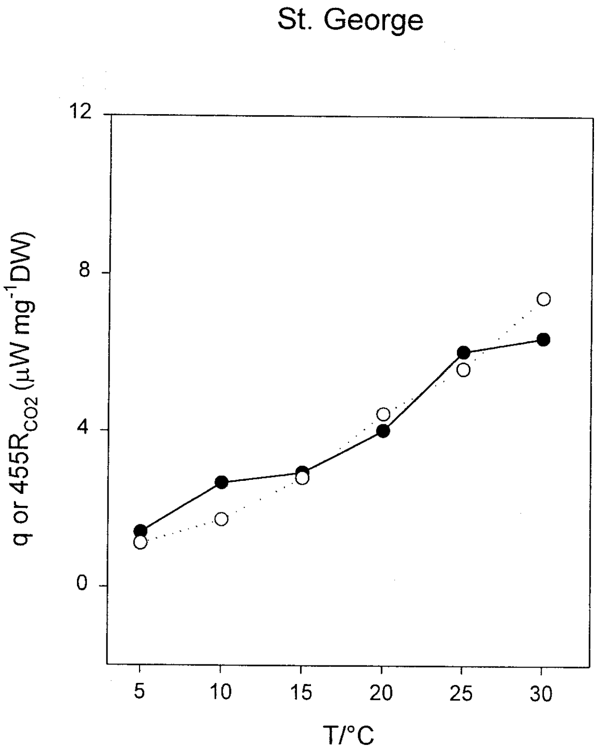

Figure 1—Metabolic heat rate (open circle) and R_{CO2} production rate (closed circle) as function of temperature for the St. George subpopulation.

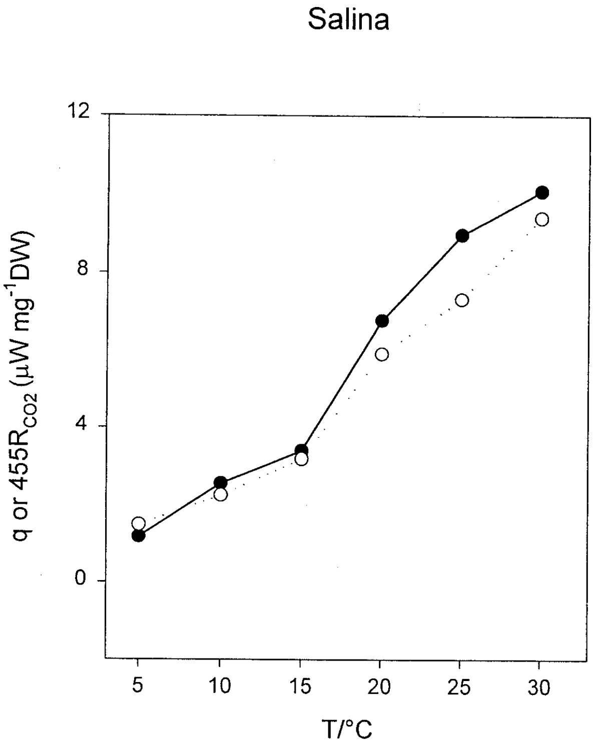

Figure 3— Metabolic heat rate (open circle) and R_{CO2} production rate (closed circle) as function of temperature for the Salina subpopulation.

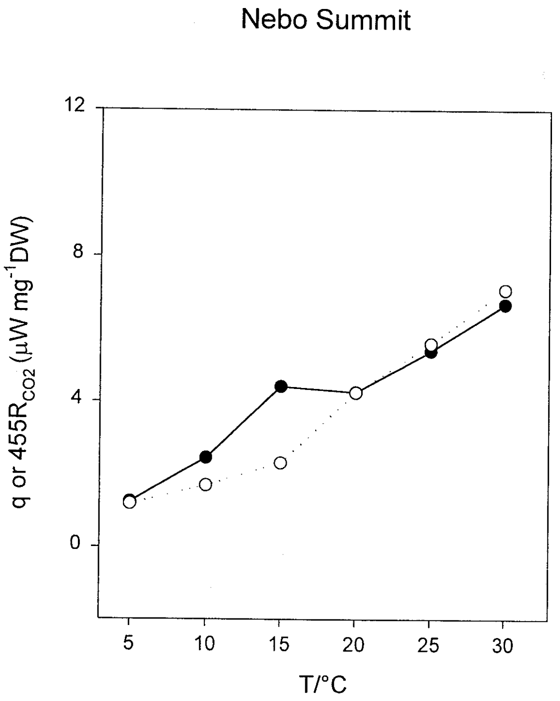

Figure 2—Metabolic heat rate (open circle) and R_{CO2} production rate (closed circle) as function of temperature for the Nebo Summit subpopulation.

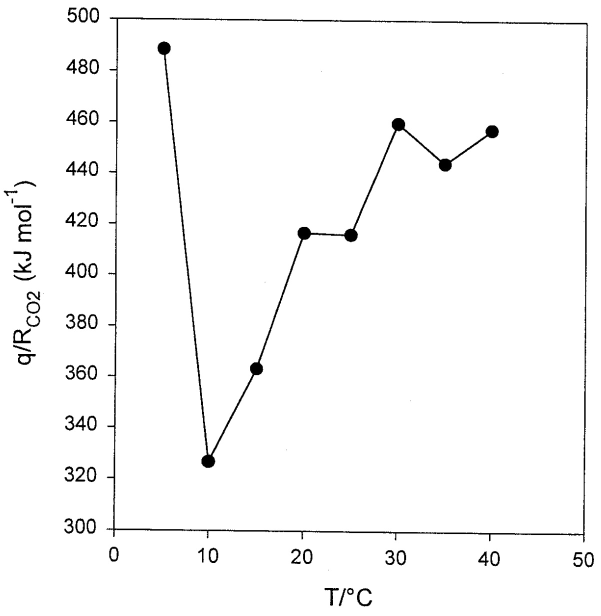

Figure 4—Averaged q/R_{CO2} ratios for eleven subpopulations of cheatgrass as functions of temperature. This ratio demonstrates, in general, the efficiency of cheatgrass throughout the Great Basin in converting substrate into biomass. Lower values translate into greater efficiency.

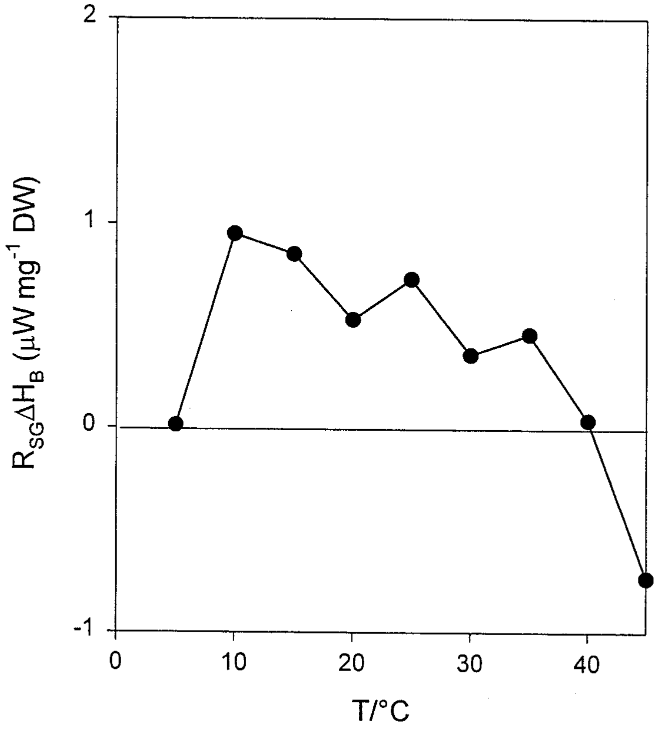

Figure 5—Calculated growth rate as a function of temperature averaged across eleven subpopulations. Depicts, in general, both low and high extreme temperature limits to growth.

Discussion

In this study, it has become apparent that although the subpopulations are different from one another in terms of temperature response (table 2), there are also some general conclusions. Cheatgrass barely grows at 5 °C (fig. 5), and is very inefficient in doing so (fig. 4). Furthermore, the optimum growth temperature is between 10 and 20 °C. Moreover, cheatgrass' growth rate is apparently a bi-phasic function, that is, at lower temperatures cheatgrass has a different physiological response or combination of responses, than at higher temperatures (figs. 1-3; table 2). Cheatgrass stops growing between 30 and 40 °C.

Another interesting finding is that, at very low temperatures (in other words around 5 °C) cheatgrass appears to waste a lot of energy in burning lipid as an energy substrate for growth as shown by the value of q/R_{CO2} greater than 455 at 5 °C (figure 4). Carbohydrate is a free fuel, in terms of energy expended, to an autotrophe; whereas lipid costs a substantial amount of energy to produce energy that could theoretically be used to produce more biomass. The drop in q/R_{CO2} from 5 to 10 °C indicates a switch to carbohydrate by 10 °C.

Cheatgrass has adapted (or adapts) to grow at temperatures extant when water is available. For example, St. George (fig. 1) cheatgrass is adapted to grow at some of the lowest temperatures relative to the other subpopulations. Thus, instead of growing in April, May, and June, the St. George growth temperatures loosely correlate with environmental temperatures in February, March, and April when rainfall occurs at this site, where by May available water is reduced by 65 percent. This means then, in general, that subpopulations, which experience the hottest climates, are adapted to the coldest temperatures. Therefore, we see that cheatgrass' respiratory metabolism is closely aligned with its environment.

Now, though we have said that cheatgrass has adapted to its specific environment, individuals cannot adapt to transplanted environments—we must remember that cheatgrass was only introduced approximately 106 years ago, and in many areas less. Nevertheless, cheatgrass grouped-progeny (stands) appear to have the capability to adapt rapidly to microclimates. The response to climate is clearly not a short-term acclimation or even acclimation of first or second-generation progeny or the subpopulation differences observed would not be present in the greenhouse-grown seed used in this study. A full analysis of temperatures at each site during the growth season for cheatgrass is expected to show that the Arrhenius slopes for each population are correlated with site temperature and temperature variability.

Table 2—Arrhenius slopes μq and μ_{CO2} that represent physiological responses to temperature, along with temperature range. Differences between slopes are related to the different microclimates at the site of origin.

Subpopulations	μq, kK^{-1}	ΔT	μ_{CO2}, kK^{-1}	ΔT	μq, kK^{-1}	ΔT	μ_{CO2}, kK^{-1}	ΔT
St. George	7.5	5 to 20 °C	10.1	5 to 10 °C	5.0	25 to 30 °C	5.3	15 to 20 °C
Green River	6.4	5 to 30 °C	17.0	5 to 10 °C	–0.8	35 to 40 °C	4.7	15 to 30 °C
Whiterocks	7.0	5 to 10 °C	13.1	5 to 15 °C	14.1	15 to 20 °C	–1.2	20 to 25 °C
Ephraim	7.2	5 to 15 °C	3.1	5 to 15 °C	4.6	20 to 30 °C	4.4	20 to 30 °C
Hobble Creek	7.8	5 to 15 °C	7.4	5 to 20 °C	4.3	20 to 30 °C	0.7	25 to 30 °C
Potosi	7.8	5 to 15 °C	6.6	5 to 20 °C	4.3	20 to 30 °C	3.0	25 to 30 °C
Castle Rock	7.4	5 to 20 °C	22.4	5 to 10 °C	3.5	25 to 35 °C	3.6	15 to 35 °C
Salina	6.1	5 to 15 °C	8.9	5 to 20 °C	4.1	20 to 30 °C	2.1	25 to 30 °C
Strawberry	7.2	5 to 30 °C	2.0	5 to 10 °C	–1.4	35 to 40 °C	6.4	15 to 30 °C
Fairview	5.4	5 to 30 °C	10.2	5 to 10 °C	0.3	35 to 40 °C	3.1	15 to 25 °C
Nebo Summit	5.3	5 to 15 °C	10.0	5 to 15 °C	4.5	20 to 30 °C	4.0	20 to 30 °C

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Temperature-Dependent Respiration-Growth Relations in Ancestral Maize Cultivars

Bruce N. Smith
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Rebekka L. Stone
Angela R. Jones
Lee D. Hansen

Abstract—Shoots from 4- to 6-day old seedlings of seven ancestral or old cultivars of *Zea mays* L. were placed in a calorimeter. Dark metabolic heat rate (q) and CO_2 production rate (R_{CO2}) were measured at nine temperatures (5, 10, 15, 20, 25, 30, 35, 40, and 45 °C). Temperature dependencies of q and R_{CO2} were used to model response of both growth and substrate carbon conversion efficiency. Responses at 5 °C were similar, but differences were noted at warmer temperatures. Upper temperature limits for growth were: Minipopcorn (26 °C), Black popcorn (30 °C), Black Mexican Sweet (31 °C), Pula Janku (32 °C), Santo Domingo White (32 °C), Loncho (39 °C), and Santa Ana Blue (45 °C). This study of seedling metabolism reveals climatic adaptation among cultivars that may prove beneficial to maize production across the globe.

Maize (*Zea mays* L.) is an important crop originating in the Americas, now grown for both biomass and grain production in a variety of climatic conditions around the world. Because small differences in climatic temperature significantly affect maize growth, increased production could result from a better understanding of the effects of temperature on metabolism and growth (Bandolini and others 2000; Greaves 1996; Miedema 1982; Singletary and others 1994).

All life depends on photosynthesis, however despite much effort to correlate photosynthesis with growth rates, no meaningful results have been obtained, only correlations (Nelson 1988). Respiratory rates of plants have frequently been empirically correlated with growth rates (Amthor 1989; Hay and Walker 1989; Loomis and Amthor 1999; Thornley and Cannell 2000), and a recent model allows predictions of growth rates from metabolic rate measurements. This model and rapid methods for measurement allow definition of responses to subtle changes in environmental factors, including temperature (Hansen and others 1994).

In an earlier study of maize (Taylor and others 1998), seed was purchased from commercial sources for nine cultivars of both flint and dent varieties, and five newer cultivars were supplied by Pioneer Hi-bred International. Metabolic heat rates and CO_2 rates were measured at just two temperatures, and these values were used to model the temperature dependences of both growth and substrate carbon conversion efficiency (Taylor and others 1998). Some cultivars were found to grow better at low temperatures, while others were better at higher temperatures.

For this study we obtained ancestral or old cultivars of maize and made metabolic measurements at nine temperatures (from 5 to 45 °C at 5 °C intervals) so that the curves presented are measured rather than calculated.

Respiration has two aspects: catabolism and anabolism. In catabolism organic substrates are oxidized to produce CO_2. Part of the energy produced by oxidation is used to convert ADP and inorganic phosphate to ATP, the rest is lost as heat.

$$\text{substrate} + O_2 \rightarrow CO_2 + H_2O + \text{ATP} + \text{heat} \qquad (1)$$

ATP produced in catabolism is transient, but is used for cellular work, including anabolism as shown below:

$$\text{substrate} + \text{ATP} \rightarrow \text{growth} + \text{heat} \qquad (2)$$

In anabolism, heat and new plant tissue are produced. A calorimeter measures the rate of heat loss from both catabolism and anabolism (q). The rate of CO_2 production measures the rate of catabolism (R_{CO2}).

Materials and Methods

The specific predicted growth rate of structural biomass or rate of anabolism (R_{SG}) is related to the two measured variables as in equation (3).

$$R_{SG}\Delta H_B = 455R_{CO2} - q \qquad (3)$$

where ΔH_B is the enthalpy change for the formation of biomass from photosynthate and Thornton's constant (–455 ± 15 kJ mol^{-1} of O_2) is incorporated.

Seven ancestral or older cultivars of *Zea mays* L. were obtained (table 1). (After considerable searching in library and web sites, we conclude that the experts disagree as to which cultivars resemble old or ancestral types). Seeds were germinated at room temperature and about 100 mg fresh weight of shoot tissue from 4- to 6-day old seedlings was placed in each of three ampules of the calorimeter (Hart Scientific model 7707 or Calorimetry Sciences Corporation MCDSC model 4100). After 15 to 20 minutes thermal equilibration at the desired temperature, the metabolic

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Table 1—Maize seedlings were grown from seven ancestral cultivars. Metabolic heat rate and CO_2 rate were measured every 5 °C from 5 to 45 °C. Low and high stress temperatures are indicated as well as the temperature for optimal growth.

	Temperature response		
Cultivar	**Low stress**	**Optimal**	**High stress**
Minipopcorn	<5	20	26
Black popcorn	<5	20	30
Black Mexican sweet	<5	25	31
Pula Janku	<5	20	32
Santo Domingo white	<5	20	32
Loncho	<5	25	39
Santa Ana Blue	<5	25	45

heat rate (q) was measured for another 15 to 20 minutes. The ampules were removed from the calorimeter and a small vial filled with 40 µl of 0.4 M NaOH was placed in the calorimeter ampule with the tissue. Again a 15 to 20 minute thermal equilibration was necessary, followed by measurement of the respiration rate (R_{CO2}) for 15 to 20 minutes. As the CO_2 and NaOH react in solution, additional heat is produced (–108.5 kJ mol^{-1} is the heat of reaction for carbonate formation), giving the rate of CO_2 evolution (R_{CO2}) by the plant tissue. Next the NaOH is removed and the heat rate (q) is measured as before (Hansen and others 1994; Criddle and Hansen 1999). The tissue was then run at another temperature. Measurements were made on each sample at 9 temperatures: 5, 10, 15, 20, 25, 30, 35, 40, and 45 °C. Three samples were used in each of the sequences: 15, 10, and 5 °C; 20, 25, and 30 °C; and 35, 40, and 45 °C.

Results and Discussion

For Minipopcorn (fig. 1), the calculated rate of energy production from catabolism ($455R_{CO2}$) exceeded heat loss (q) at 5 through 26 °C, while at higher temperatures heat loss exceeded calculated energy available from oxidation of carbohydrate. Above 35 °C, heat rate declined with increasing temperature, indicating possible tissue damage. Thus, growth ($R_{SG}\Delta H_B$) was predicted to occur only at temperatures below about 26 °C. By contrast, the data on Black Popcorn indicated growth would continue up to about 30 °C (fig. 2), but not at higher temperatures. The calculated

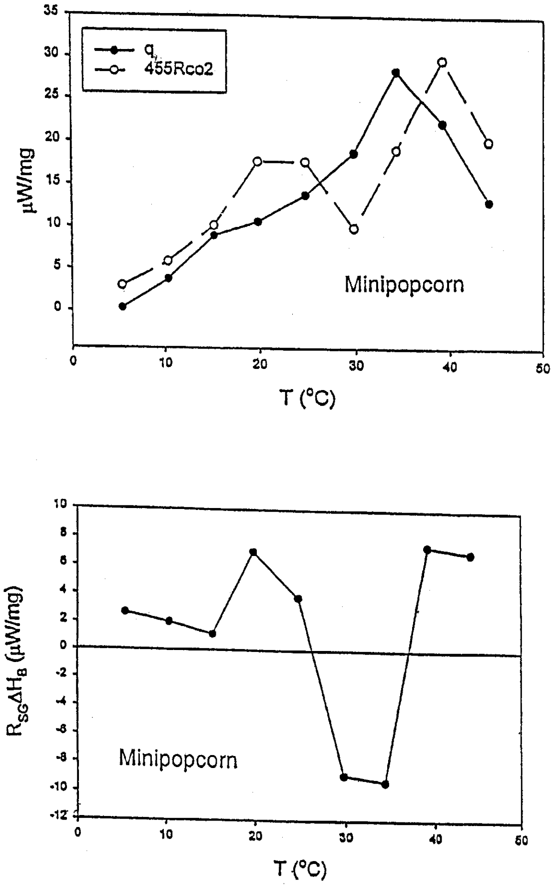

Figure 1—(A) Metabolic heat rate (q) and respiration rate ($455R_{CO2}$) for the Minipopcorn cultivar of *Zea mays* L. was measured as µW per mg dry wt. at 5 degree intervals from 5 to 45 °C. (B) Predicted specific growth rate ($R_{SG}\Delta H_B$) was calculated from the metabolic measurements in (A) according to equation 3.

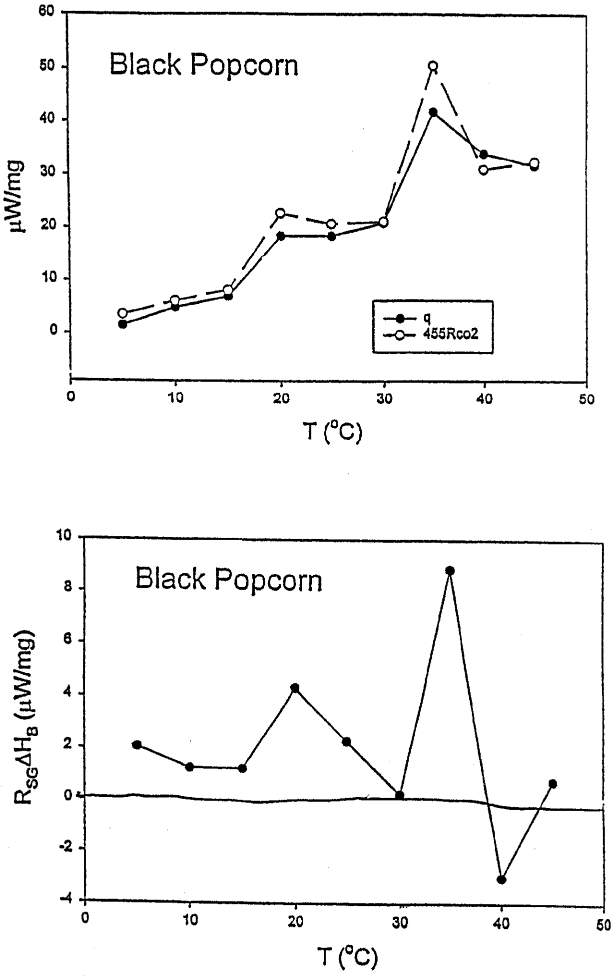

Figure 2—As in figure 1 but for the Black Popcorn cultivar.

growth rate of Black Mexican Sweet (fig. 3) had a temperature response a bit higher, to 31 °C. Pulu Janku (fig. 4) and Santo Domingo White (fig. 5) had very similar responses (to 32 °C). Loncho (fig. 6) was predicted to grow at temperatures below about 39 °C, while Santa Ana Blue (fig. 7) did well in warmer temperatures and would grow up to a temperature of about 45 °C.

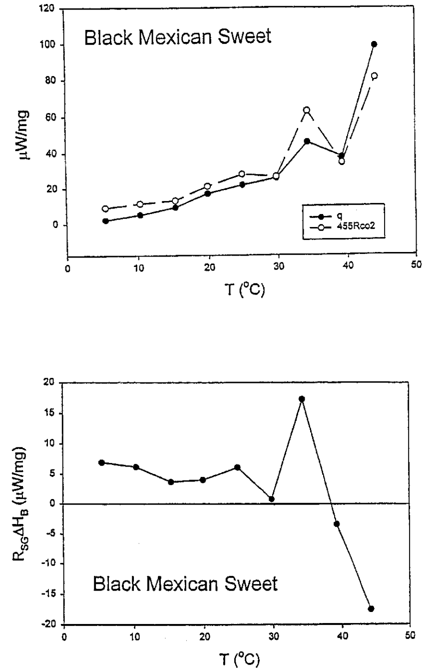

Figure 3—As in figure 1 but for the Black Mexican Sweet cultivar.

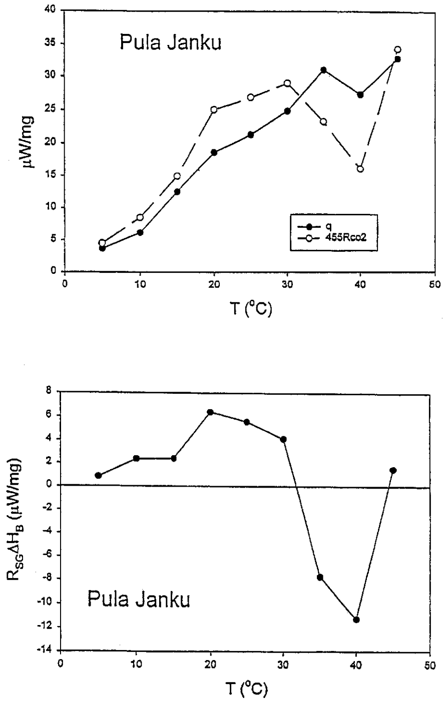

Figure 4—As in figure 1 but for the Pula Janku cultivar.

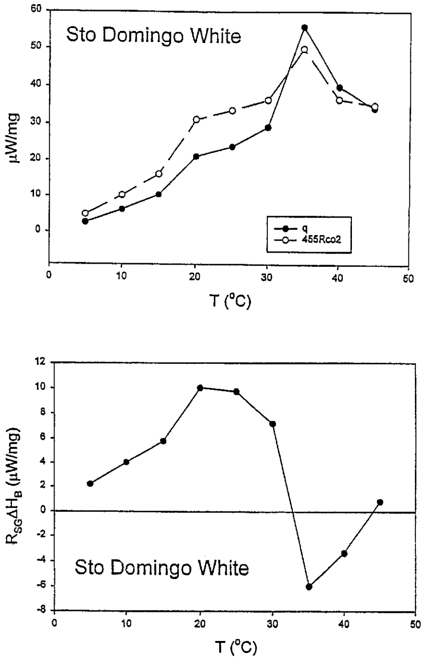

Figure 5—As in figure 1 but for the Santo Domingo White cultivar.

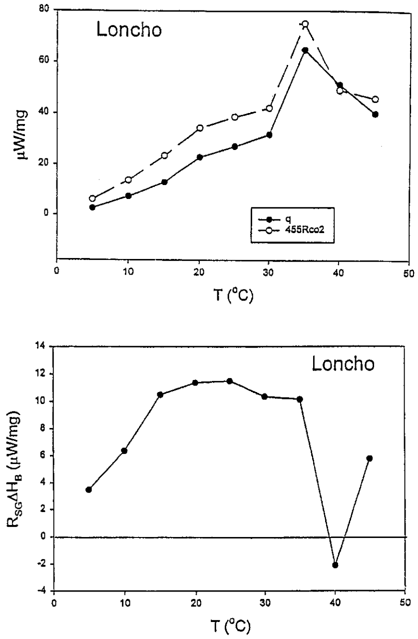

Figure 6—As in figure 1 but for the Loncho cultivar.

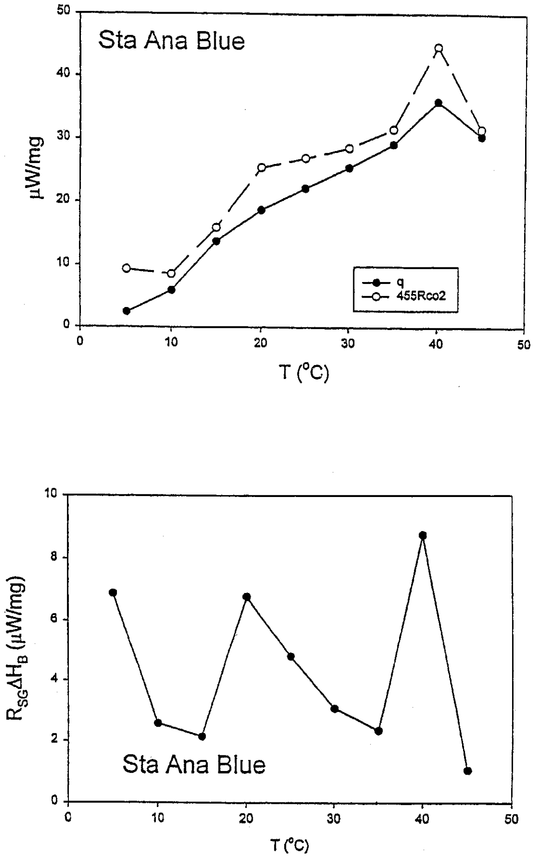

Figure 7—As in figure 1 but for the Santa Ana Blue cultivar.

Although no common cultivars were used in this and a previous study (Taylor and others 1998), the results show many similarities. Data obtained from metabolic measurements at nine temperatures is more definitive, and in essential agreement with the curves calculated from data at two temperatures, for example, Taylor and others 1998.

Different responses to temperature by cultivars (table 1) probably represents adaptation to different climates. All of the cultivars, except perhaps Black Mexican Sweet, exhibit a maximum in the calculated growth rate near 20 °C. Growth rates tend to decline at both higher and lower temperatures. The anomalous point at 5 °C for Santa Ana Blue is probably caused by tissue damage from chilling sensitivity in this cultivar.

Conclusions

- We studied older corn cultivars, however the experts disagree as to which cultivars resemble “old” or “ancestral” varieties. Metabolic measurements made in this and a previous study (Taylor and others 1998) indicate that the 21 cultivars examined have many similarities, and perhaps a common origin.
- Some cultivars are adapted to warm climates. Others are adapted to cooler climates.
- Data obtained from measurements at nine temperatures agrees with that obtained from modelling data at two temperatures, for example, Taylor and others 1998.
- With climatic information and calorimetric measurements, it is possible to quickly select the best cultivar for growth in a given location.

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Calorimetric Studies of Cryptogamic Crust Metabolism in Response to Temperature, Water Vapor, and Liquid Water

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Lee D. Hansen
Richard S. Criddle
Rosemary L. Pendleton

Abstract—Cryptogamic crusts are communities composed of lichens, cyanobacteria, algae, mosses, and fungi. These integrated soil crusts are susceptible to disturbance, but if intact, appear to play a role in providing nutrients, especially nitrogen, to higher plants. It is not known how or under what conditions desert crusts can grow. Crust samples from localities on the Colorado Plateau and the Great Basin were brought to the laboratory and exposed to atmospheres of different humidity and different levels of liquid water. Both metabolic heat rate (q) and carbon dioxide evolution rate (R_{CO2}) were measured in microcalorimeters at temperatures from 10 to 35 °C. While exposure to water vapor alone had little effect, addition of liquid water caused a marked increase in metabolic rate and a switch from anaerobic to aerobic metabolism.

Cryptogamic soil crusts cover as much as 40 to 60 percent of desert surfaces in the Intermountain Western U.S.A. (Evans and Johansen 1999). These microbiotic crusts are a mixture of lichens, mosses, cyanobacteria, and green algae that retain soil moisture, fix nitrogen, and protect the desert ecosystem by preceding vascular plant growth and preventing erosion (Brotherson and Rushforth 1983). Grazing by cattle is most destructive in spring and summer months, but even in the winter there is a 50 percent reduction in crusted area compared to a control plot (Memmott and others 1998). Crusts are vulnerable to destruction by roaming cattle and hikers (Anderson and others 1982). Crusts play an important role in nitrogen fixation (Evans and Belnap 1999). They may also be important for making other essential elements available to higher plants (Harper and Pendleton 1993).

Aerobic respiration has two aspects: catabolism and anabolism. In catabolism, organic substrates are oxidized to produce CO_2 and energy. Part of the energy produced by oxidation is used to convert ADP and inorganic phosphate to ATP, the rest is lost as heat.

$$\text{substrate} + O_2 + \text{ADP} + P_i \rightarrow CO_2 + H_2O + \text{ATP} + \text{heat} \quad (1)$$

ATP produced in catabolism is transient, but is used for cellular work, including anabolism as shown below:

$$\text{substrate} + \text{ATP} \rightarrow \text{growth} + \text{ADP} + P_i + \text{heat} \quad (2)$$

In anabolism, heat and new plant tissue are produced and ATP is hydrolyzed back to ADP and phosphate. A calorimeter measures the rate of heat loss (q) from both catabolism and anabolism. The rate of CO_2 production (R_{CO2}) measures the rate of catabolism. With carbohydrate as the specific substrate, predicted growth rate of structural biomass or rate of anabolism (R_{SG}) is related to three measurable variables and one constant as in equation 3.

$$R_{SG}\Delta H_B = 455R_{CO2} - q \quad (3)$$

ΔH_B is the enthalpy change for the formation of biomass from photosynthate and Thornton's constant (455 ± 15 kJ mol^{-1} of O_2) is incorporated to calculate the rate of energy generated by catabolism. Thus, growth rate in terms of energy (in other words, $R_{SG}\Delta H_B$) is proportional to the difference between the measured values of R_{CO2} and q. The temperature dependencies of R_{CO2} and q are different (Taylor and others 1998). The difference between $455R_{CO2}$ and q therefore changes with temperature and this difference can be used to predict growth rate changes with temperature (Criddle and others 1997).

Predicted specific growth rate may also be expressed as a function of the substrate carbon conversion efficiency (ε) and respiration rate (R_{CO2}).

$$R_{SG} = R_{CO2}[\varepsilon/(1-\varepsilon)] \quad (4)$$

Combining equations 3 and 4 to eliminate R_{SG} gives equation 5

$$q/R_{CO2} = (1-\gamma_P/4)455 - [\varepsilon/(1-\varepsilon)]\Delta H_B \quad (5)$$

which relates the ratio of q/R_{CO2} to ε. Values of q/R_{CO2} measured as a function of temperature can thus provide information on substrate carbon conversion efficiency (ε) and the oxidation state of the substrate carbon, γ_P (Hansen and others 1994).

Anaerobic respiration by definition does not involve oxygen uptake and conserves much less of the available energy

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than does aerobic catabolism. For this reason, most organisms use oxidative metabolism whenever possible. Anaerobic respiration is immediately recognizable from measurements of q and R_{CO2} because it produces CO_2 but little or no heat compared to aerobic respiration.

In this study, calorimetry was used to determine the high and low stress temperatures for desert crust under controlled conditions. When the metabolic heat rate exceeds energy made available through catabolism of carbohydrate, the plant is considered to be stressed (Smith and others 2000).

Given their importance, more needs to be learned about recovery of disturbed crusts (Belnap 1993). Our research explores conditions of temperature and moisture for optimal growth of microbiotic crust communities. Such information could help land managers protect the crusts during critical growth periods. In addition, the findings could help establish better inoculation techniques.

Materials and Methods

Samples were collected near Nephi, Utah, during the fall and winter of 1999. The cryptogams grew in a sagebrush community occasionally grazed by cattle. The collected crusts were approximately 2 cm thick and 15 cm in diameter. They were collected in petri dishes so the integrity of the crust could be maintained. No moisture was added at the time of collection. Samples were subdivided into two sets, one to measure the effects of humidity and the other to measure the effects of different amounts of liquid water.

Saturated salt solutions were used to adjust the relative humidity of the air surrounding crust samples in sealed jars to 31, 52, 79, and 100 percent, followed by 30 days of equilibration. A sample with no water or solution added to the jar was labeled 0 percent humidity and used as a control. The amount of water taken up was measured by weighing the crust before and after the equilibration period. In a separate experiment, different amounts of distilled water were added to the crust samples two hours preceding the calorimetric measurements. Following this preparation, the samples were cut off at the base of the mat and excess soil removed. Approximately 500 mg of visually equivalent crust was added to each calorimeter ampule. Measurements of metabolic heat rate and the rate of carbon dioxide evolution were taken in the isothermal mode in a Calorimetry Sciences Corp. Model 4100 calorimeter at 10, 15, 20, 25, and 30 °C.

Results and Discussion

Increasing relative humidity up to 100 percent had no effect on crusts. Heat rates (q) ranged from +0.068 to –0.045 and CO_2 rates from 0.614 to 0.031. The ratio of q/R_{CO2} ranged from +50 to –50 kJ $mole^{-1}$ with an average near zero. These data demonstrate that anaerobic respiration is the only important process in crusts exposed to water vapor. However, addition of even small amounts of liquid water switches the q/R_{CO2} ratio to values around 400 kJ $mole^{-1}$, very typical of aerobic respiration (Criddle and others 1997; Hansen and others 1994). Liquid water thus promotes growth of the crust (fig. 1). This probably relates to the central role of blue-green algae in metabolism of the desert crust community. Lange and others (1988) have shown that lichens with green algal photobionts respond to water vapor, while lichens with blue-green photobionts respond only to liquid water. Microtopography of crust growth may orient the community to maximize water retention (George and others 2000). The filamentous blue-green algae have a gelatinous coating which, in the absence of liquid water, may prevent oxygen uptake and carbon dioxide production, and thus inhibit oxidative catabolism (Lange and others 1998).

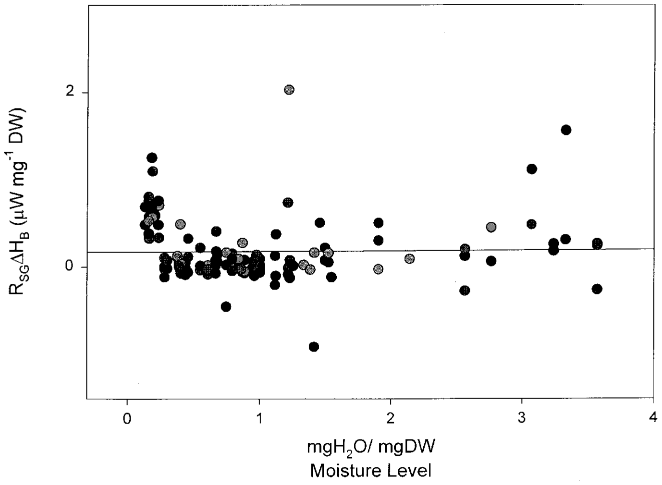

Figure 1—Cryptogamic crust predicted growth rate, $R_{SG}\Delta H_B$ (μW/mg dry weight), in response to addition of liquid water (mg H_2O/ mg dry weight).

Cryptogamic crusts with added liquid water had a slight, but not significant, decrease in metabolic efficiency with increasing temperatures (fig. 2). Thus rather than growing at a certain season of the year, cryptogamic crusts may show an opportunistic growth response to a significant rainfall event at any temperature from 10 to 35 °C.

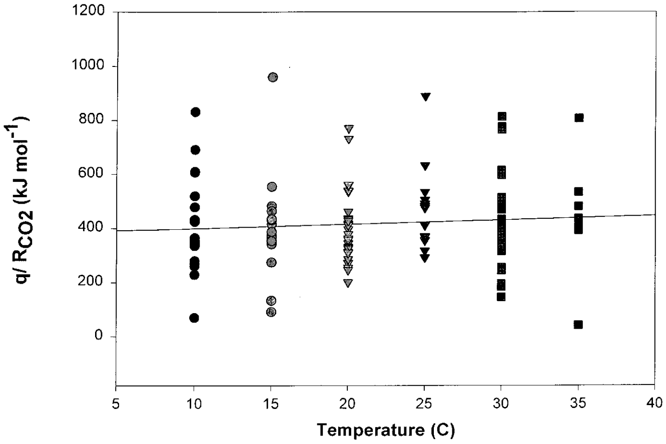

Figure 2—Cryptogamic crust metabolic efficiency of carbon conversion, q/R_{CO2} (kJ mol^{-1}), in response to temperature, °C.

Conclusions

- Changing the relative humidity of the air does not affect metabolism.
- Liquid water is a necessity for cryptogamic crusts to grow.
- Temperature seems to have no effect on either carbon conversion efficiency or growth rates.
- Growth of cryptogamic crusts is regulated by availability of liquid water rather than by temperature.

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Microcalorimetric Studies on Metabolic and Germination Response to Temperature for Three Populations of Winterfat (*Eurotia lanata*)

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Abstract–*Eurotia lanata* (Pursh) Moq. (winterfat) is a boreal cold-desert subshrub, seldom more than 2 feet tall, that thrives in dry climates at cool temperatures. Diaspore collections from Matador, Saskatchewan, Canada; Pine Bluffs, Wyoming; and Sterling, Colorado, were cleaned and placed on moistened filter paper in petri dishes maintained at 0, 5, 10, 15, and 20 °C to study germination. Seeds germinated at all temperatures but seedlings were not acclimated to cold by germination temperature. At radicle emergence (ca. 3 mm), seeds were placed in calorimeter ampules. Heat-rate (q) was measured at a given temperature, then a vial containing NaOH solution was added to measure the rate of CO_2 evolution (R_{CO2}) for the same tissue at the same temperature. This procedure was repeated for each of the populations at temperatures ranging from –10 to +20 °C. Metabolic efficiency and predicted specific growth rates were calculated from these measurements. Optimum temperature for germination, metabolism, and early seedling growth was about 10 °C. Stress was noted near 20 and –5 °C. Acclimation during germination had no effect. Differences between the three populations correlated with altitude rather than latitude.

Winterfat is a small cold-desert subshrub that thrives in dry climates at cool temperatures. Stems, leaves, and dispersal units called diaspores are covered with a dense mix of short and long white hairs that aid in water retention (Booth and Haferkamp 1995). Foliage and fruit are retained throughout the winter. Winterfat is excellent forage for both wildlife and domestic cattle and is a good source of protein and vitamin A. In North America, winterfat is found from Canada to Mexico, and from Manitoba to British Columbia and the Dakotas and Nebraska west to the Great Basin. The genus consists of only two species, one from North America, the other from the cold deserts of Asia (Mozingo 1987).

Populations within a species (accessions) are adapted to the particular microclimate of their origin and usually do not grow well when moved to a slightly different location. The purpose of this work is to examine how plants adapt their respiratory metabolism to match the temperature of their native climate. In this study, calorimetry was used to determine the temperature response and high and low stress temperatures of winterfat diaspores collected from three locations. When metabolic heat loss exceeds energy made available through catabolism of carbohydrate, the plant is considered to be stressed (Smith and others 2000).

Aerobic respiration has two aspects: catabolism and anabolism. In catabolism, organic substrates are oxidized to produce CO_2. Part of the energy produced by oxidation is used to convert ADP and inorganic phosphate to ATP, the rest is lost as heat.

$$\text{substrate} + O_2 + \text{ADP} + P_i \rightarrow CO_2 + H_2O + \text{ATP} + \text{heat} \quad (1)$$

ATP produced in catabolism is transient, but is used for cellular work, including anabolism as shown below:

$$\text{substrate} + \text{ATP} \rightarrow \text{growth} + \text{ADP} + P_i + \text{heat} \quad (2)$$

In anabolism, heat and new plant tissue are produced and ATP is hydrolyzed back to ADP and phosphate. A calorimeter measures the rate of heat loss (q) from both catabolism and anabolism. The rate of CO_2 production (R_{CO2}) measures the rate of catabolism. With carbohydrate as the specific substrate, predicted growth rate of structural biomass or rate of anabolism (R_{SG}) is related to the two measured variables as in equation 3.

$$R_{SG}\Delta H_B = 455R_{CO2} - q \quad (3)$$

where ΔH_B is the enthalpy change for the formation of biomass from photosynthate and Thornton's constant (–455 ± 15 kJ mol^{-1} of O_2) is incorporated to calculate the rate of energy generated by catabolism. Thus, growth rate in terms of energy is proportional to the difference between the measured values of R_{CO2} and q. The temperature dependencies of R_{CO2} and q are different (Hansen and others 1994). The difference between $455R_{CO2}$ and q therefore changes with temperature and this difference can be used to predict growth rate changes with temperature (Criddle and others 1997).

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Table 1—Sources and habitats for winterfat seeds (after Bai and others 1999).

Site	Location	Community	Seed weight g/100 seeds
Pine Bluffs, Wyoming, U.S.A.	41°10'N, 104°09'W elevation 1554 m	mixed prairie	0.18
Sterling, Colorado, U.S.A.	40°37'N, 103°13'W elevation 1181 m	shortgrass prairie	0.23
Matador, Saskatchewan, Canada	50°42'N, 107°43'W elevation 685 m	mixed prairie	0.25

Predicted specific growth rate may also be expressed as a function of the substrate carbon conversion efficiency (ε) and respiration rate (R_{CO2}).

$$R_{SG} = R_{CO2}\,[\varepsilon/(1-\varepsilon)] \qquad (4)$$

Combining equations 3 and 4 to eliminate R_{SG} gives equation 5

$$(\varepsilon/1-\varepsilon)\Delta H_B = -q/R_{CO2} - (1-\gamma_P/4)455 \qquad (5)$$

which relates the ratio of q/R_{CO2} to ε. Values of q/R_{CO2} measured as a function of temperature can thus provide information on substrate carbon conversion efficiency (ε) and the oxidation state of the substrate carbon, γ_P (Hansen and others 1994).

Winterfat diaspores collected from three locations were compared at several temperatures using calorimetry.

Materials and Methods

Diaspores from *Eurotia lanata* (Pursh) Moq. (winterfat) were collected from Matador, Saskatchewan, Canada; Pine Bluffs, Wyoming; and Sterling, Colorado (table 1; Bai and others 1999). The diaspore was first removed from the seed to decrease fungal growth during germination (Booth and Haferkamp 1995). The threshed seeds were soaked in a tween solution (10 percent) for 10 minutes, then in dilute sodium hypochlorite (1 percent) for 45 minutes. Then the seeds were placed on moistened filter paper in petri dishes kept in beakers partially submerged in coolant baths maintained at 0, 5, 10, 15, and 20 °C to study acclimation effects on germination and metabolism.

At the time of radicle emergence (to about 3 mm), seeds (about 100 mg fresh weight) were placed in each of three ampules of a microcalorimeter (Hart Scientific model 7707 or Calorimetry Sciences Corporation MCDSC model 4100). After 15 to 20 minutes thermal equilibration at the desired temperature, the metabolic heat rate (q) was measured for another 15 to 20 minutes. The ampules were removed from the calorimeter and a small vial filled with 40 µl of 0.4 M NaOH placed in the calorimeter ampule with the tissue. Again a 15 to 20 minute thermal equilibration was necessary, followed by measurement of the sum of the heat from metabolism and CO_2 reaction with the NaOH for 15 to 20 minutes. After the NaOH is removed the heat rate (q) is measured again as before (Hansen and others 1994; Criddle and others 1997). The reaction of CO_2 with the NaOH solution to form carbonate produces –108.5 kJ mol^{-1}. Dividing the difference in the measurements with and without NaOH solution present gives the rate of CO_2 evolution (R_{CO2}) by the plant tissue. The tissue was then run at another temperature. Measurements were made on each sample at 7 temperatures: 20, 15, 10, 5, 0, –5, and –10 °C.

Results and Discussion

Acclimating germinating seeds at various temperatures had no effect on germination or metabolism. Seeds germinated as rapidly at 0 °C as they did at 20 °C with essentially 100 percent germination at all temperatures in agreement with previous work (Bai and others 1998a). Also seeds germinated at a given temperature, say 5 °C, showed no different metabolic response at 5 °C than did seeds germinated at 15 °C (Bai and others 1998b). Desiccation and cold hardiness are often linked in winterfat (Hou and others 1999).

Since growth in terms of energy can occur only when catabolic energy generation rate ($455R_{CO2}$) exceeds total heat loss (q), metabolic data (fig. 1) for the winterfat population from Pinebluffs, Wyoming, indicated cold stress near 0 °C and heat stress at about 18 °C. Please note that a smaller ratio of q/R_{CO2} indicates greater efficiency (fig. 2) with values greater than 455 µW mg^{-1} dry wt. representing

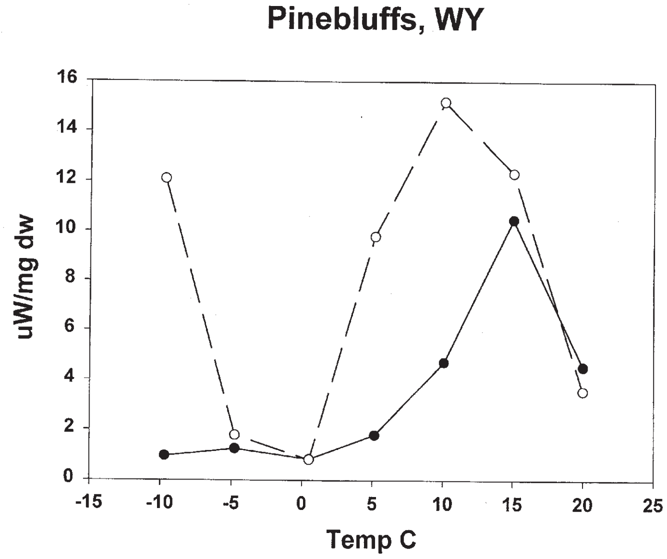

Figure 1—Winterfat seedlings from Pinebluffs, Wyoming, U.S.A.; metabolic heat rate (q), (●), and respiration rate ($455R_{CO2}$), (o), as µW per mg dry wt. versus temperature measured at 5 °C intervals.

a shift to another substrate (for example, lipid) or physical damage. Negative points in figure 3 occur because the substrate was assumed to be carbohydrate. Relative specific growth rates (R_{SG}) less than zero occur then this assumption is invalid.

Winterfat seedlings from Sterling, Colorado, (fig. 4) were cold-stressed at about –8 °C and heat stressed at about 16 °C with good efficiency (fig. 2) and growth (fig. 3) predicted between those temperatures.

Seedlings from Matador, Saskatchewan, Canada, (fig. 5) were cold-stressed at about –6 °C and heat stressed at about 19 °C with maximum efficiency (fig. 2) and growth (fig. 3) between 8 and 12 °C.

Seed weights decreased (Bai and others 1999) with increasing elevation (table 1). The highest elevation site probably has the shortest growing season. However, once daytime temperatures are above freezing, rapid growth can occur. Note that the Pinebluffs' population (figs. 1, 2, and 5)

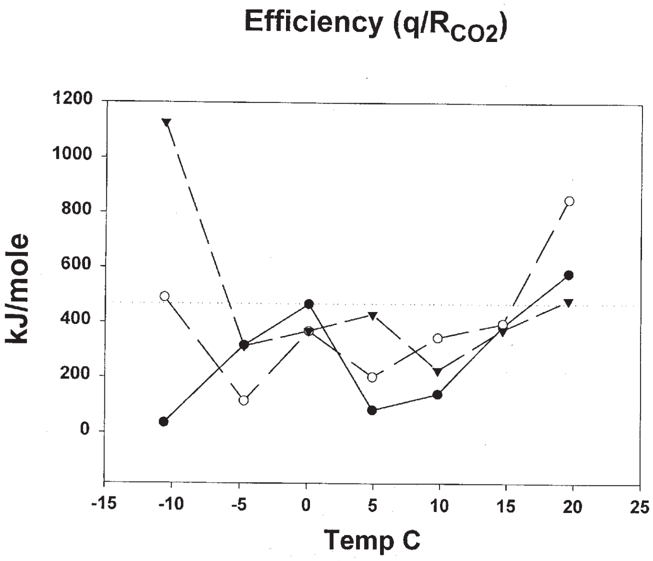

Figure 2—Comparison of the metabolic efficiency (q/R_{CO2} in kJ/mole) of the three populations versus temperature. Pinebluffs (●), Sterling (o), and Matador (▼). Note: smaller numbers mean greater efficiency.

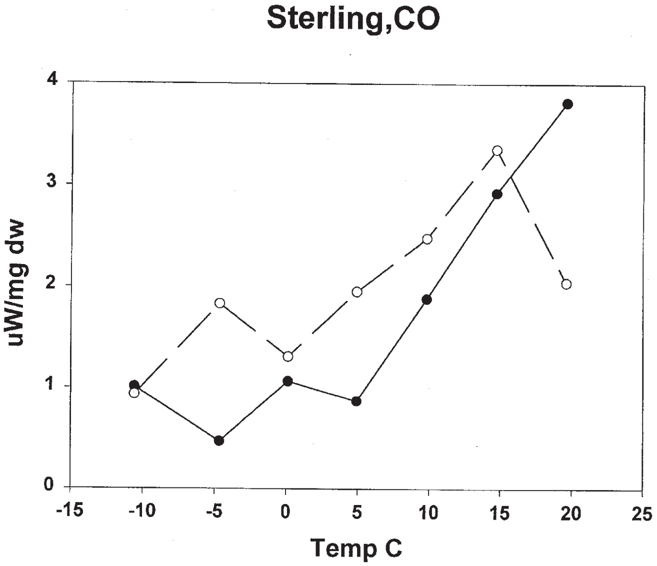

Figure 4—Winterfat seedlings from Sterling, Colorado, U.S.A., as in figure 1.

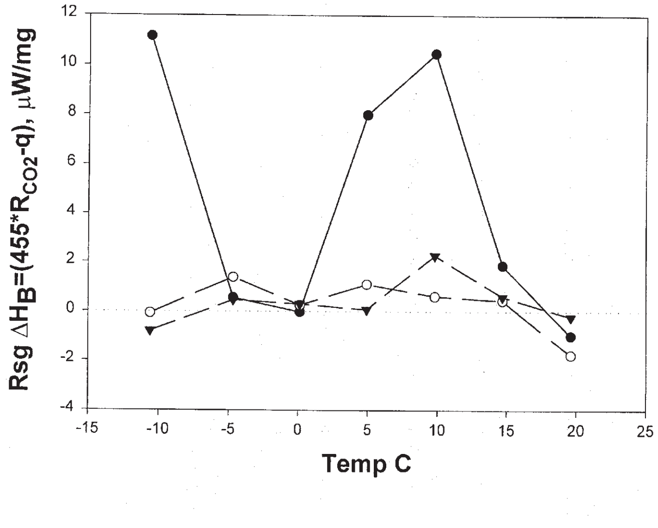

Figure 3—Comparison of the predicted growth rate ($R_{SG}\Delta H_B$ in $\mu W/mg$) of the three populations versus temperature. Pinebluffs (●), Sterling (o), and Matador (▼). $R_{SG}\Delta H_B$ values lower than zero indicate temperatures where no growth occurs.

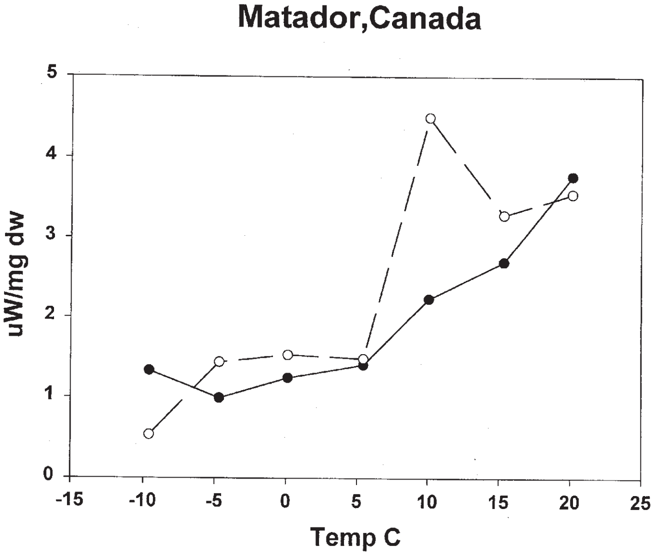

Figure 5—Winterfat seedlings from Matador, Saskatchewan, Canada, as in figure 1.

has a more narrow temperature range for growth, but efficiency of carbon conversion and growth rate exceeds those of both of the other populations. Metabolic data presented here indicate that these three closely related populations are differently adapted to temperature at their respective sites. We plan to expand this study to include winterfat populations across a broader range of environments. This may allow us to determine if the differences noted here among seedling populations also persist for mature plants grown *in situ* or in common gardens.

Conclusions

- Optimum temperature for metabolism and early seedling growth for three populations of winterfat is about 10 °C. Stress is noted below –5 and above +20 °C.
- Metabolic differences among the three populations studied were correlated with altitude rather than latitude, and probably reflect adaptation to different thermal environments.
- Winterfat seeds imbibe water, germinate, and grow at very cool temperatures—even 0 °C. Acclimation had no effect. Thus seeds germinated at 5 °C did no better at that temperature than did seeds germinated at 20 °C.

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Composition of Vegetable Oil From Seeds of Native Halophytes

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Abstract—Of the world's land area, about 7 percent is salt affected. Irrigated land is more susceptible to salinity and it is estimated that over 1/3 of the irrigated soils are becoming saline. Certain plants (halophytes) grow well on high saline soils. One approach would be to grow halophytes on high saline soils and harvest their seeds. The oil in the seeds would be extracted for cooking oil. The amount of unsaturated fatty acids is a measure of the quality of cooking oil. High-unsaturated fatty acid content is considered a factor in preventing heart diseases. Seeds of seven halophytic shrubs were extracted and the oil was analyzed for fatty acids using gas chromatography and mass spectrometry. The average unsaturation for the fatty acids in the seed oil was 84 percent, which is a favorable percent. The major saturated fatty acid was Hexadecanoic acid. There were several dominant unsaturated fatty acids namely: 9,12-Octadecadienoic acid, 13-Octadecenoic acid, 11-Eicosenoic acid, 9,12,15, Octadecatrienoic acid, and 9-Octadecenoic acid. It appears that these halophytes have potential for reclaiming and utilizing saline soil.

Introduction

Approximately 7 percent of the world's land area is salt affected (Dudal and Purnell 1986). The Great Basin area of the Western United States has no river that drains the water to the sea. The water drains into inland lakes such as Great Salt Lake or evaporates in the valleys. Many salt playa accumulate in the Great Basin area. The inland salt playas are harsh environments for living organisms (Goodin and others 1990). The high salt content of the soil limits the plant communities to mainly halophytic plants. This includes salt tolerant shrubs and annuals. The salinity of the soil ranges from 29 dS/m (2 percent NaCl) to 145 dS/m (9 percent). The salinity of the soil in the bottom of the salt pans can be as high as 15 percent salt. At the same time desert conditions exist during the hot summer months. Precipitation is about 66 mm (2.6 inches) per year. The water table varies from 1 m to 3.3 m below the surface (Khan and Ungar 1995).

Dregne and others (1991) suggested that about 74 million hectares of land are salt affected due to human causes. For use in the agricultural area, salt tolerant agriculture plants have been selected to grow on the saline soils. There has been some success but the selected agriculture plants cannot tolerate very high saline conditions. Another approach to this problem is to grow plants that are adapted to saline soils such as halophytes and then find an economic value for the halophytes (Khan and others 1990). One possibility would be animal forage or fuel (presto logs). The economic return of these products is low. A more valuable economic product would be cooking oil. Cooking oil is a basic food need throughout the world. The seeds of halophytes contain oil that could potentially be extracted for human use.

The composition of cooking oils has an impact on health. Dietary studies (Hu 1997; Lang 1997) support the concept that diets that are high in saturated fats result in greater risk to heart diseases. In contrast, foods that are high in polyunsaturated fatty acids are considered much more healthy. Animal fats are high in saturated fatty acids whereas plant fats are normally high in unsaturated fatty acids. A saturated fatty acid such as stearic acid has no double bonds in the hydrocarbon chain. With unsaturated fatty acids such as oleic acid, there is one double bond in the hydrocarbon chain. Linoleic has two double bonds and alpha linolenic acid has three double bonds in the hydrocarbon chain.

The purpose of this investigation was to analyze the oil from several native halophytes to determine their fatty acid content and quality.

Methods

Seeds of native halophytes were collected from salt playa and salt marsh areas in Utah Valley and Rush Valley in north-central Utah. The seeds were separated from the vegetative plant parts and cleaned. The seeds were ground with a Wiley mill and extracted three times with methanol and chloroform (1:2 v/v). The percent oil in the seeds was determined by weight.

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The fatty acids in the oil extract were methylated with Alltech meth prep 1 ((trifluoromethylphenyl) trimethylammonium hydroxide). The methylated fatty acids were separated by gas chromatography and identified by GC mass spectrometry.

Results

The following salt tolerant plants were analyzed for total oil content in their seeds and the fatty acids in the seed oil.

Allenrolfea occidentialis (Wats) Kuntze

One of the most salt tolerant plants in the Great Basin area. It has a fleshy stem with reduced leaves. The oil content of the seeds was 14 percent. The fatty acid composition was: 88.33 percent unsaturated and 11.67 percent saturated.

Unsaturated fatty acids	**Percent of fraction**
7-Hexadecenoic acid, methyl ester	0.30
9-Hexadecenoic acid, methyl ester	0.29
9-Octadecenoic acid, methyl ester	24.69
11-Eicosenoic acid, methyl ester	11.89
13-Docosenoic acid, methyl ester	15.13
9,12-Octadecadienoic acid, methyl ester	16.78
10,13-Octadecadienoic acid, methyl ester	23.57
9,12,15, Octadecatrienoic acid, methyl ester	7.36

Saturated fatty acids	**Percent of fraction**
Hexadecanoic acid, methyl ester	45.79
Heptadecanoic acid, methyl ester	2.06
Octadecanoic acid, methyl ester	19.93
Eicosanoic acid, methyl ester	10.92
Docosanoic acid, methyl ester	9.98
Teracosanoic acid, methyl ester	9.56
Pentadecanoic acid, methyl ester	0.68
Oxiraneundecanoic acid, 3 pentyl methyl ester	0.99

Atriplex heterosperma Bunge

This is a two-seeded Atriplex that grows in saline areas. The oil content of the seeds was 15.8 percent. The fatty acid composition was: 84.73 percent unsaturated and 15.27 percent saturated.

Unsaturated fatty acids	**Percent of fraction**
9-Hexadecenoic acid, methyl ester	0.61
11-Eicosenoic acid, methyl ester	7.01
13-Docosenoic acid, methyl ester	15.13
13-Octadecenoic acid, methyl ester	75.06
15-Tetracosenoic acid, methyl ester	1.02
6,9-Octadecadienoic acid, methyl ester	0.28
9,12,15, Octadecatrienoic acid, methyl ester	0.89

Saturated fatty acids	**Percent of fraction**
Nonanedioic acid dimethyl ester	2.87
Hexadecanoic acid, methyl ester	69.95
Octadecanoic acid, methyl ester	14.65
Eicosanoic acid, methyl ester	11.32
Teracosanoic acid, methyl ester	1.21

Atriplex rosea L.

This Atriplex grows in disturbed areas and is wide spread in the world. The oil content of the seeds was 12.9 percent. The fatty acid composition was: 82.79 percent unsaturated and 17.21 percent saturated.

Unsaturated fatty acids	**Percent of fraction**
9-Hexadecenoic acid, methyl ester	0.31
9-Octadecenoic acid, methyl ester	5.58
13-Octadecenoic acid, methyl ester	40.50
11-Eicosenoic acid, methyl ester	12.36
13-Docosenoic acid, methyl ester	13.89
15-Tetracosenoic acid, methyl ester	0.35
6.9-Octadecadienoic acid, methyl ester	0.15
7,10-Octadecadienoic acid, methyl ester	0.13
8,11-Octadecadienoic acid, methyl ester	1.21
9,12-Octadecadienoic acid, methyl ester	0.37
9,12,15, Octadecatrienoic acid, methyl ester	25.15

Saturated fatty acids	**Percent of fraction**
Hexadecanoic acid, methyl ester	51.47
Hexadecanoic acid, 14-methyl ester	1.31
Heneicosanoic acid, methyl ester	1.14
Octadioic acid, methyl ester	3.93
Nonanedioic acid, methyl ester	2.11
Octadecanoic acid, methyl ester	11.54
Eicosanoic acid, methyl ester	10.21
Docosanoic acid, methyl ester	3.85
Teracosanoic acid, methyl ester	3.14
15-Teracosanoic acid, methyl ester	5.46
Tricosanoic acid, methyl ester	0.83
Pentadecanoic acid, methyl ester	0.60
Oxiraneundecanoic acid, 3 pentyl methyl ester	1.65
Oxiraneundecanoic acid, 3 octyl methyl ester	2.76

Halogeton glomeratus (Bieb.) C. A. Mey

This plant is a native of Asia and grows well on alkaline soil. It contains oxalates that can be toxic to livestock if eaten in excess. The oil content of the seeds was 24.7 percent. The fatty acid composition was: 84.38 percent unsaturated and 15.62 percent saturated.

Unsaturated fatty acids	**Percent of fraction**
9-Hexadecenoic acid, methyl ester	0.48
Hexadecenoic acid, 14-methyl ester	0.16
13-Octadecenoic acid, methyl ester	66.54
11-Eicosenoic acid, methyl ester	2.44
13-Docosenoic acid, methyl ester	1.27
15-Tetracosenoic acid, methyl ester	0.32
6.9-Octadecadienoic acid, methyl ester	0.15
9,10-Octadecadienoic acid, methyl ester	0.24
7,10-Octadecadienoic acid, methyl ester	0.67
9,11-Octadecadienoic acid, methyl ester	0.28
9,12-Octadecadienoic acid, methyl ester	20.04
9,12,15, Octadecatrienoic acid, methyl ester	7.41

Saturated fatty acids	**Percent of fraction**
Hexadecanoic acid, methyl ester	77.10
Hexacosanoic acid, methyl ester	1.01
Octadecanoic acid, methyl ester	11.56
Eicosanoic acid, methyl ester	4.55

Docosanoic acid, methyl ester	3.01
Teracosanoic acid, methyl ester	2.51
Tricosanoic acid, methyl ester	0.26

Kochia scoparia (L.) Schrader

An annual plant that grows on saline soils and can be grazed by livestock. The oil content of the seeds was 9.7 percent. The fatty acid composition was: 80.79 percent unsaturated and 19.21 percent saturated.

Unsaturated fatty acids	**Percent of fraction**
9-Hexadecenoic acid, methyl ester	4.43
11-Eicosenoic acid, methyl ester	2.30
13-Docosenoic acid, methyl ester	2.59
15-Tetracosenoic acid, methyl ester	0.83
2,4-Hexadiecendioic acid, methyl ester	0.33
9,12-Octadecadienoic acid, methyl ester	89.52

Saturated fatty acids	**Percent of fraction**
Hexadecanoic acid, methyl ester	68.00
Heptadecosanoic acid, methyl ester	0.61
Hexacosanoic acid, methyl ester	0.88
Octadecanoic acid, methyl ester	16.68
Eicosanoic acid, methyl ester	4.61
Docosanoic acid, methyl ester	3.64
Teracosanoic acid, methyl ester	5.58

Sarcobatus vermiculatus (Hook.) Torr.

A perennial shrub that grows well on saline or alkaline flood plains. It is moderately poisonous to livestock if eaten in large amounts. The oil content of the seeds was 17.5 percent. The fatty acid composition was: 78.86 percent unsaturated and 21.14 percent saturated.

Unsaturated fatty acids	**Percent of fraction**
9-Hexadecenoic acid, methyl ester	0.45
11-Eicosenoic acid, methyl ester	1.22
13-Docosenoic acid, methyl ester	1.26
15-Tetracosenoic acid, methyl ester	0.28
7,10-Octadecadienoic acid, methyl ester	0.34
9,12 Octadecadienoic acid, methyl ester	96.16
Octadecatrienoic acid, methyl ester	0.29

Saturated fatty acids	**Percent of fraction**
Hexadecanoic acid, methyl ester	64.30
Heptadecosanoic acid, methyl ester	1.79
Hexacosanoic acid, methyl ester	1.54
Heneicosanoic acid, methyl ester	2.07
Octadecanoic acid, methyl ester	5.82
Tetradecanoic acid, methyl ester	13.15
Eicosanoic acid, methyl ester	4.96
Docosanoic acid, methyl ester	3.56
Tetracosanoic acid, methyl ester	1.23
Tricosanoic acid, methyl ester	1.49

Suaeda torreyana Wats

A shrubby plant that is commonly associated with salt desert shrub communities. It produces black and brown seeds that have different properties towards salinity. The oil content of the seeds was 25.25 percent. The fatty acid composition was: 89.58 percent unsaturated and 10.42 percent saturated.

Unsaturated fatty acids	**Percent of fraction**
9-Hexadecenoic acid, methyl ester	0.39
Hexadecenoic acid, 14-methyl ester	6.94
7-Hexadecenoic acid, 14-methyl ester	0.38
Nonanedioic acid, methyl ester	0.51
11-Eicosenoic acid, methyl ester	1.12
13-Docosenoic acid, methyl ester	2.40
15-Tetracosenoic acid, methyl ester	0.17
7,10-Octadecadienoic acid, methyl ester	0.95
9,12-Octadecadienoic acid, methyl ester	86.21
9,12,15, Octadecatrienoic acid, methyl ester	0.93

Saturated fatty acids	**Percent of fraction**
Hexadecanoic acid, methyl ester	58.27
Hexacosanoic acid, methyl ester	0.73
Heneicosanoic acid, methyl ester	1.86
Octadecanoic acid, methyl ester	19.70
Tetradecanoic acid, methyl ester	0.95
Eicosanoic acid, methyl ester	6.11
Docosanoic acid, methyl ester	6.24
Tetracosanoic acid, methyl ester	6.14

The percent unsaturation for the oil from the seeds of the halophytes ranges from 78.8 percent to 89.5 percent with an average of 84.2 percent.

Certain fatty acids tended to represent the major concentration. In the saturated fatty acids fraction of the halophytic seed oil, hexadecanoic acid was the major fatty acid in all cases. The average percent of the fraction was 62 percent.

In the unsaturated fatty acids, there was more diversity with 9,12-Octadecadienoic acid being the most common, followed by 13-Octadecenoic acid, 11-Eicosenoic acid, 9,12,15, Octadecatrienoic acid, and 9-Octadecenoic acid. The total number of fatty acids detected for *Allenrolfea occidentialis* was 31 even though the concentration of most of the individual fatty acids were very low.

Discussion

The seeds of the halophytes analyzed had an oil content ranging from 9.7 percent in *Kochia* to 25.5 percent in *Sueada*. The actual yield per hectare for these halophyes has not been determined. In the case of the *Salicornia europaea,* field studies in Mexico, Egypt, and United Arab Emirates indicated a production of 20 tons of plant material per hectare (Goodin and others 1990). The oilseed yield was 2 ton per hectare. Based on 15 percent oil content, the oil yield would be 600 lbs of cooking oil per hectare (Goodin and others 1990).

The quality of the cooking oil is of importance and is related to the percent unsaturation. High unsaturation is considered more healthy. Animal fat (lard) is 59 percent unsaturated and butter is 32 percent unsaturated. Plant fats are higher in unsaturated fatty acids such as soybean (84.6 percent), olive oil (85.8 percent), safflower oil (91.l percent) and canola oil (92.8 percent) (USDA handbook 8-4). The percent unsaturated from the seed oil of the halophytes was favorable with the average being 84 percent. The seed oil of *Sueada torreyana* had an unsaturation of 89.6 percent, which is very close to canola oil. These results would suggest that the oil from the halophyte seeds is of high quality.

Future questions that need to be answered include conditions for establishment of stands of halophytes, level of production, and yield of seeds.

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Carbon Transport by Symbiotic Fungi in Fourwing Saltbush, *Atriplex canescens* (Pursh) Nutt.

Jerry R. Barrow

Abstract—Mycorrhizal fungi enhance the nutrition and survival of host plants in native ecosystems. Arid rangelands severely challenge plants because of chronic nutrient and water stress. Fourwing saltbush, *Atriplex canescens* (Pursh) Nutt., a dominant and important shrub of western arid rangelands, generally considered to be non-mycorrhizal, is more extensively colonized by dark septate (DS) fungal endophytes than by traditional mycorrhizal fungi. Roots of fourwing saltbush colonized by DS fungi were stained with sudan IV and analyzed with differential interference microscopy that revealed extensive internal colonization by vacuolated hyaline hyphae that is not evident using conventional fungus staining methods. Fungal vacuoles accumulated substantial quantities of lipids in the sieve elements and cortex when roots were physiologically active. The widespread colonization of fourwing saltbush by DS fungi and their extensive accumulation of lipids suggests that these fungi transport and manage carbon in arid ecosystems. Their potential role in ecosystems stability is discussed.

Mycorrhizal fungi form specific internal interfaces by which they exchange resources with their host. Their hyphae extend from the root into soil enhancing the uptake and transport of mineral nutrients. They perform varied and significant ecological functions in native ecosystems such as enhanced nutrition, water relations and survival of host plants. They regulate key processes that impact soil, vegetation structure, and stability. Recent evidence suggests that external hyphae also link plants together within a community, forming a common mycorrhizal network by which plants may share carbon and mineral nutrients. The transport and sharing of essential resources such as carbon and mineral nutrients could significantly affect the structure and stability of native plant communities (Ayling and others 1997; Brandes and others 1998; Duan and others 1996; Graves and others 1997; Simard and others 1997).

The mycorrhizal status of desert plants is not clearly defined, but their survival in water and nutrient stressed arid ecosystems is likely enhanced by mycorrhizal or other symbiotic fungi. Chenopodiacious shrubs, common in many arid ecosystems, are generally considered to be non-mycorrhizal (Aguilera and others 1998). Fourwing saltbush, *Atriplex canescens* (Pursh) Nutt., is an ubiquitous and ecologically important shrub in arid southwestern U.S.A. rangelands. Its roots are more extensively colonized by dark septate endophytic fungi (DS) than by traditional mycorrhizal fungi (Barrow and others 1997). DS fungi are widespread root colonizers in many stressed ecosystems. These fungi form nondestructive interfaces with roots and species include recognized pathogens, saprophytes, soil and rhizosphere inhabiting fungi (Jumpponen and Trappe 1998). It has been suggested that they may establish beneficial associations with specific plants under stressed conditions that are unfavorable for traditional mycorrhizal fungi (Kohn and Stasovski 1990). DS fungi are typically recognized as stained or pigmented (melanized) hyphae and microsclerotia in roots prepared and stained with conventional fungal staining and microscopic methods. Their ubiquitous presence in stressed ecosystems strongly suggests an important but presently unresolved ecological function (Jumpponen and Trappe 1998).

Fungal associations with plants range from parasitic to mutually beneficial. This relationship is based upon the costs expended or benefits received by each partner (Smith and Smith 1996). Mycorrhizal fungi form nondestructive interfaces with plant roots and supply mineral nutrients in exchange for organic carbon constituting a mutually beneficial relationship. Mycorrhizal fungi vary in their strategy for accessing and utilizing carbon (Smith and Read 1998). The internal mycelia of obligate arbuscular mycorrhizae (AM) fungi can only assimilate photosynthetically derived glucose from the host, from which they synthesize lipids, and transfer them to the external mycelia. The external mycellia are incapable of assimilating glucose or other forms of organic carbon (Sachar-Hill and others 1995; Pfeffer and others 1999). The external hyphae of ectomycorrhizal fungi are able to hydrolyze and utilize complex external polysaccharides (Smith and Read 1998). Ericoid mycorrhizal fungi degrade cellulose, pectin, and lignin (Cairney and Burke 1998) and wood rotting orchid mycorrhizal fungi can degrade lignin and other complex soil organic matter and transfer simple sugars to the heterotrophic protocorm for growth and differentiation of a shoot and root system (Peterson and others 1998).

Barrow and Aaltonen (2001) analyzed roots of *A. canescens* colonized by DS fungi with differential interference microscopy (DIC). They observed extensive nondestructive colonization of the cortex and vascular cylinder with hyaline hyphae that are not visible with conventional staining and microscopy. Staining of physiologically active roots with sudan IV revealed substantial accumulation of lipids in fungal vacuoles that further enhanced fungal visibility and suggested that carbon management and transport may be a significant ecological function of DS fungi. The objective of this study was to analyze *A. canescens* roots colonized by DS fungi at different levels of physiological activity and to

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determine if lipid accumulation is affected by seasonal influence.

Materials and Methods

Roots were sampled from a native population of *A. canescens* near the headquarters of the USDA Agricultural Research Service's Jornada Experimental Range in southern New Mexico from winter, early to late spring, summer, until late fall of 1999. They were prepared and cleared using modified methods developed by Bevege (1969), Brundrett and others (1983), Kormanik and others (1980), and Phillips and Hayman (1970) for *A. canescens* roots. They were stained with sudan IV and analyzed with DIC microscopy using the method developed by Barrow and Aaltonen (2001).

Results

The expression of DS fungal colonization in *A. canescens* roots was highly variable and was affected by the conditions of the plant or soil at the time of sampling. Typical DS fungal structures, pigmented (melanized) septate hyphae, and microsclerotia, were most frequently observed within the cortex of physiologically inactive roots sampled during the winter or during extended drought. In the spring, fall, and following precipitation events when roots were physiologically active, melanized fungal structures decreased and a corresponding increase in unique vacuolated hyaline hyphae were observed. Hyaline hyphae were more frequently associated with metabolically active roots and were considered active stages of DS fungi. Hyaline hyphae form an extensive inter- and intracellular network within the cortex and sieve elements. In the cortex, hyphae were larger, 2 to 5 µm diameter, and had distinctly visible walls. Within the sieve elements, they were smaller in diameter, 1 to 2 µm, and their walls were less visible. Staining with sudan IV positively stained lipids in fungal vacuoles further enhancing the visibility of internal colonization of DS fungi.

Lipid accumulation in fungal vacuoles was highly variable and was also influenced by physiological activity of the roots. Lipids began to accumulate in spherical fungal vacuoles in hyphae growing in the cortex and in the vascular cylinder in early spring before any growth response was observed and continued until new leaves were established, at which time lipids were not observed in fungal vacuoles. Lipid accumulation was again observed in fungal vacuoles in response to intense, short duration precipitation events that increased soil moisture in late summer then they decreased as soil moisture decreased. In late fall, as mean temperatures dropped, fungal vacuoles again accumulated substantial lipids in the cortex. The vacuoles were elongated and more abundant than the smaller, more spherical vacuoles observed in the spring.

Discussion

Dark septate fungal endophytes are not only the dominant colonizers of native plant roots in arid southwestern rangelands (Barrow and others 1997), but they are wide spread in other stressed ecosystems (Jumpponen and Trappe 1998). The staining of colonized roots with sudan IV and analysis with DIC (Barrow and Aaltonen 2001) revealed extensive internal colonization by hyaline hyphae that are not evident using conventional fungus staining methods. Dark septate fungi are highly polymorphic and produce hyaline internal structures from external pigmented septate hyphae (Barrow and Aaltonen 2001; Haselwandter and Read 1982; Newsham 1999). They form unique nondestructive internal interfaces with cortical cells and sieve elements. Their cumulation of substantial quantities of lipids in response to physiological activity suggests that they have a significant ecological role in the transport and management of carbon.

The small diameter hyaline hyphae that nondestructively colonize the sieve elements are virtually indistinguishable with DIC microscopy because they lack chitin and melanin and are very thin walled. These characteristics would increase their permeability and facilitate resource exchange with the host (Barrow and Aaltonen 2001; Cousin 1996; Money and others 1998). The accumulation of lipids in fungal vacuoles within the sieve elements (carbon transport cells) suggests that the fungus is accessing host photosynthate and converting it to fungal lipids. The amount of lipids within hyaline hyphae in both the vascular cylinder and the cortex suggests that they are being transported by the fungus, but the direction of carbon transport is not clear. Both pathogenic and symbiotic fungi access photosynthetic carbon from their hosts. DS fungi accumulate substantial quantities of lipids without any deleterious effects on the host suggesting that they manage carbon for the benefit of the host.

Mycorrhizal fungi not only enhance nutrient and water uptake in exchange for carbon, but they also contribute other significant ecological factors that enhance the stability and survival of native plant communities. They increase total chlorophyll and carotenoid content of host plants, accelerate net photosynthesis, increase total carbohydrate accumulation in the roots, and carbon flow into the soil contents (Graves and others 1997). Soil organic carbon and nitrogen pools were found to be 13 percent greater under tall fescue pastures with high fungal endophyte colonization compared with soil pools under low colonized pastures (Franzluebbers and others 1999). Plants likewise exude substantial quantities of carbon as simple sugars, organic acids, and polysaccharides in the rhizosphere (Isobe and Tsuboki 1998) into the soil that favorably modifies the microenvironment of the rhizosphere, improving soil properties and enhancing plant stability (Grayston and others 1997; Perry and others 1992). Mucigels or polysaccharides have high water binding capacity (Chenu and Roberson 1996), maintain hydraulic continuity between the root and soil (Read and others 1999), and enhance nutrient diffusion and uptake in dry soils (Sutherland 1998). Organic acids change pH and enhance mineralization and nutrient uptake (Jones 1998). Soil polysaccharides are polymers of simple sugars, which are released by hydrolysis and provide an energy source for soil microflora involved in mineralization (Bianciotto and others 1996). Soil carbon enhances soil aggregation and stability, water-holding capacity, and serves as an energy reserve for plants and microbes.

It is proposed that DS fungi stimulate photosynthesis, convert host photosynthate to lipids, transport it to the soil where it insulates plant roots allowing them to survive and function in harsh dry soil. The dynamic and variable response of lipid accumulation by DS fungi as it was influenced by physiological activity of the host suggested the potential of bidirectional transport of carbon between the host and the soil. In the spring, before any new growth was evident and when photosynthetic activity was low, substantial lipid transport and accumulation was observed in hyphae in the cortical cells and in the sieve elements. It is suggested that the fungi were accessing carbon from soil reserves and supplying the plant energy rich carbon for the synthesis of new leaves, similar to the mechanism used by orchid mycorrhizal fungi, which degrade complex external carbohydrates and supply the host with simple sugars for the production of roots and shoots (Peterson and others 1998). After new leaves were established and the host was presumed to be photosynthetically active, lipid accumulation ceased. A pathogenic association would suggest that the fungi would extract more carbon from the host when it was photosynthetically active. It is suggested that DS fungi receive carbon from the host to meet its physiological and growth requirements and transport substantial quantities to the soil to recharge soil supplies essential for water retention, mineralization, and nutrient uptake. During periods of stress, they may reverse the flow of carbon to supply the host sufficient energy rich carbon for growth and survival.

The widespread colonization of native grasses and shrubs by DS fungi in arid rangelands, their nondestructive interface with sieve elements, and accumulation of substantial quantities of lipids during periods of peak physiological activity in the host suggest that these fungi manage and recycle carbon for the survival and stability of plant communities. Future studies must focus on the direction of carbon flow, the nature of carbon profiles that are established in the soil, and how they relate to ecosystem stability.

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Nitrogen-Fixing Nodule Characterization and Morphology of Four Species in the Northern Intermountain Region

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Abstract—*Purshia tridentata* (antelope bitterbrush), C*eanothus velutinus* (snowbrush), *Ceanothus sanguenius* (redstem ceanothus), and *Shepherdia canadensis* (buffaloberry) are native shrubs of the Northern Intermountain Region that are generally characterized as nitrogen-fixing species. These species occupy a range of habitats from steppe to alpine environments. Nodulation of these species is initiated through root infection by *Frankia* species and the resulting nodules are described as coralloid. Nodulation is not necessarily confirmation that nitrogen-fixation is taking place in the nodular and root tissue of the shrub. Nodule formation, abundance, and functionality on individual plants is strongly influenced by soil moisture, soil nutrient balance, and age and health of the individual shrub, thus the character of nitrogen-fixation as an ecological process across a shrub population, and through time, may be tremendously varied. We determined the degree of nodulation and the nodule morphological characteristics on plants between stands and sites to be consistent.

Introduction

Non-legume nitrogen-fixing shrubs are frequently among the first colonizers on disturbed forest and range sites especially when nitrogen availability is one of the principal limiting factors. Non-leguminous shrubs and trees that fix atmospheric nitrogen for plant use are known as actinorhizal plants and the roots of these plants form a symbiotic relationship with an actinomycete in the genus *Frankia*. Actinorhizal plants are found almost everywhere in the world and most species, as far as is presently known, are found in temperate climate regimes.

The potential to incorporate actinorhizal plants in the design of vegetative covers for severely disturbed areas is great and often a significant means of stimulating and stabilizing nutrient cycling on these sites. In this paper we have documented the nitrogen-fixing nodular structures on each of four native woody shrub species found in the Northern Intermountain Region. This study is part of a large research effort examining soil nutrient regimes that will promote native vegetative development on severely disturbed sites. Initially, we assumed that each species has distinct nodule morphology. Our study focused on characterization of nodule morphology but included nodule occurrence within a stand, nodule placement on individual roots and root types, and the mode of nodule attachment to roots. The character of nodules that occur on these wild plants will be used as a means for comparison to nodule development on experimentally grown plants being researched for reclamation of severely disturbed landscapes.

Nodule Form and Function in Wild Nitrogen-Fixing Plants—Knowledge of Northern Intermountain Region actinorhizal plants in the wild is limited. The majority of research has been made on agricultural and horticultural nitrogen fixation and nitrogen fixation under controlled conditions. Relatively few research efforts to this point have addressed native nitrogen-fixing plants in the wild and the role they can play in reclamation vegetation cover in severely disturbed landscapes in the Northern Intermountain Region. Genera receiving the most research are *Alnus*, *Ceanothus*, and *Purshia* in that order. In the United States there are over a 100 actinorhizal native species and several naturalized species considered to be noxious weeds (Paschke 1997). The genus with the greatest number of actinorhizal species is *Ceanothus*. This genus has more than 30 actinorhizal species. *Ceanothus* and *Purshia* are the most prevalent actinorhizal shrub genera in the Northern Intermountain Region. In the Northern Intermountain Region of North America there are several nitrogen-fixing woody species (table 1) that are important as wildlife cover, livestock and wildlife browse, and considered pioneers in ecological succession.

The site of nitrogen fixation is in nodules on plant roots (fig. 1). Morphologically, nodules in actinorhizal species are modified lateral roots. The nodulation originates in the pericycle of the root (Strand and Laetsch 1977; Berry and Sunell 1990). *Frankia* infections are known to initially take place by intracellular penetration in which the bacteria enters a deformed host root hair and by an intercellular host cell penetration that is capable of infecting multiple sites in mature root cortical tissues. The type(s) of infection depends on the host plant species (Berry and Sunell 1990). Vascular tissue is central in the nodule and the bacterial organisms are found in the cells of the nodule cortex. This is different from the structure of legume nodules that are more tumor-like in which vascular tissue surrounds the nitrogen-fixing organism (Baker and Schwintzer 1990). The stele in nodules is not invaded by the *Frankia* bacteria and there are no root hairs, root cap (Nelson and Schuttler 1984), or root epidermis (Strand and Laetsch 1977).

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Table 1—Pacific Northwest native nitrogen-fixing shrubs and trees of forests and rangelands.

			Environments			
Family	**Genus**	**Species**	**Moist forest**	**Dry forest**	**Subalpine**	**Steppe**
Elaeagnaceae	*Shepherdia*	*canadensis*	+			
		argentia	+			
	Elaeagnus	*commutata*				+
Myricaceae	*Myrica*	*californica*	+			
		gale	+			
Betulaceae	*Alnus*	*rubra*	+			
		incana	+			
		rhombifolia	+			
		sitchensis	+			
Rhamnaceae	*Ceanothus*	*velutinus*	+	+	+	
		sanguineus	+	+		
		cuneatus		+		
		integerrimus	+			
		prostratus		+		
Rosaceae	*Cercocarpus*	*ledifolius*		+		+
		montanus		+		+
	Dryas	*drummondii*			+	
		integrifolia			+	
					+	
	Purshia	*tridentata*		+		+

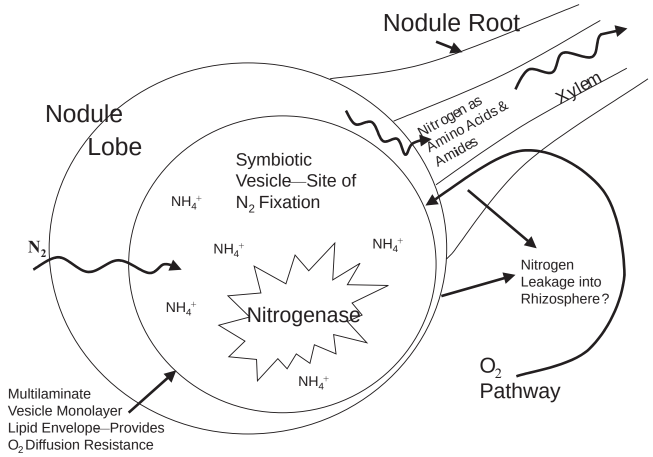

Figure 1—Generalized process of nitrogen-fixation (adapted from Huss-Danell 1990; Silvester and others 1990; Smith and others 1999).

Atmospheric nitrogen is reduced by a bacterial nitrogenase enzyme system provided by the *Frankia* species. Nitrogenase catalyzes the dinitrogen reduction reaction to form the ammonium ion (Huss-Danell 1990). Ammonium is a form of nitrogen able to be used by plants (Sprent and Sprent 1990) and can give them a survival advantage in nitrogen limited environments (Wollum and Youngberg 1969; Postgate 1982; Righetti and others 1986; Sprent 1993; Walker 1993; Kohls and others 1994; Paschke 1997).

The enzymatic reduction of atmospheric nitrogen is relatively slow and very expensive in terms of ATP provided by the host plant (Huss-Danell 1990; Sprent 1993). Because large amounts of ATP energy are consumed for metabolic activities and nitrogen fixation, the nodules require increased amounts of oxygen energy derived from plant respiration. At the same time the need for oxygen is increased, nitrogenase has to be protected from oxygen exposure because the enzyme is lethally sensitive to it (fig. 1). The host cell wall and plasmalemma surround the bacteria and are thought to afford it the needed protection (Silvester and others 1990).

Frankia induced nodules have been described in almost all actinorhizal species as coralloid clusters and consist of multiple dichotomously branching lobes (Krebill and Muir 1974; Wood and others 1989). Their colors range from light tan to dark brown (Krebill and Muir 1974) and almost whitish (Nelson 1983).

Various authors have determined that *Frankia* nodules are perennial (Strand and Laetsch 1977; Nelson and Schuttler 1984). A nodule cluster may arise from a single infection site and may be effective for several years in the field (Schwintzer and Tjepkema 1996). The nodules, as does the whole plant in temperate regions, become dormant in the winter (Huss-Danell 1990). Kummerow and others (1978) determined the age of some *Ceanothus* species nodules to be 6 to 8 years old. Nelson (1983) observed *Cowania stansburiana* nodules to be on roots that were distinctly larger than roots of a comparable age. He postulated that this root enlargement was perhaps hormonally mediated and contributed to longevity of nodules as well as more secure nodule attachment and provided for the larger volume of needed vascular translocation.

Only the distal portion of nodules (about 10 to 20 percent of live weight) is known to be fixing nitrogen (Kummerow and others1978). The tips of nodules are much lighter than the rest of the nodule. The number of nodules clusters on each plant is inversely correlated to the mass of the nodules (Sangina and others 1996). There appear to be large differences in the numbers of nodules between *Cowania* and *Purshia* species and the nodule clusters are often larger on field plants that have fewer numbers of nodules (Nelson 1983).

Nodulation and nodule activity generally thrive when the whole plant thrives and are affected by pH, temperature, and available moisture. Optimal pH range is 6.5 to 8.0 and below 5 nodules become inactive (Alexander 1977). Burggraaf and Shipton (1982) found some *Frankia* isolates to grow well on media at pH 6.5 to 7.0 but can extend their range from 4.6 to 8.0. Generally, actinomycetes temperature range for optimal growth is 29 to 37 °C. There is little growth below 5 °C and none at 39 °C (Alexander 1977). When soil temperature at 20 cm is increased above 10 °C (Dalton and Zobel 1977) nodule growth and activity begins. Under strongly aerobic conditions, *Frankia* require temperatures of around 25 to 30 °C (Stowers 1987). Youngberg and Wollum (1976) feel the optimal temperature for nodule activity is 23 °C.

Nitrogenase is severely depressed under even slight soil/water deficit (Abdel Wahab and Abd-Alla 1995). Righetti and others (1986) found evidence that nodules slough off in dry years. In excessive water they fail to thrive because when O_2 is lacking they cannot metabolize (Alexander 1977).

Righetti and Munns (1981) thought nitrogen additions inhibited nodulation and nodule activity. However, nitrogen levels in the soil were not thought to be the reason for lack of nodules or nodule nitrogen fixation activity (Righetti and others 1986). When nitrogen is supplied to plants the roots form more callus than plant roots grown in nitrogen deficient soil. Callus is incapable of fixing nitrogen.

Nodulation does not necessarily mean nitrogen fixation is taking place and some nodules exist but never fix nitrogen (Kohls and others 1994). Nitrogenase activity is one means by which researchers have been able to measure nitrogen fixation. Several methods of measuring nitrogenase activity have been available for the past 40 years and of these methods, acetylene reduction assay has been determined to be the most sensitive and the least expensive (Sprent 1979). Estimates of nitrogen addition by *Ceanothus* species systems are more a function of the *Frankia* species than the host species (Nelson and Lopez 1989). Nitrogen fixation rates are also thought to vary with plant species and *Frankia* combination, plant and nodule age, growth conditions in the field, time of day, season of the year, method of measurement, and how the rates are expressed (Huss-Danell 1990).

Seasonal patterns of nodule lobe growth and nitrogenase activity have been studied to some extent and are found to vary throughout the growing season. In central Oregon, nodule growth and activity in *Purshia tridentata* begins mid-May at the time the soil temperature at 20 cm below the surface rises above 10 °C. The greatest nodule activity appears to be in late June, and in July. In late July and August, activity declines with higher air temperatures and increased water stress (Dalton and Zobel 1977). The nitrogenase enzyme system is greatly affected by water stress and depletion of carbohydrates derived from photosynthesis is often effected by stomatal closure (Dalton and Zobel 1977).

Dalton and Zobel (1977) also found diurnal and seasonal diurnal patterns in nitrogen-fixation activity. Rates of acetylene reduction were low at predawn and late in the afternoon. Activity was greatest in the mid day. The declines in nodule activity were greater from June to August than were the mid day nitrogenase reduction rates.

The Role of Nitrogen-Fixing Woody Plants in Revegetation—*Purshia tridentata* is a dominant in several distinct climax forest and steppe vegetation types of the Northern Intermountain Region. Because of its prevalence in some areas, it may also occur as an early seral species on xeric soils. *Purshia tridentata* will commonly colonize recently burned *Pseudotsuga menziesii* sites and dominate the shrub layer until shaded out by other shrubs or development of an overstory tree layer. *Purshia* species can pioneer on semiarid foothills, plains, and mountain slopes and nodulation within the first 20 to 30 cm of root depth might be important for vegetation establishment in nitrogen deficient pioneer situations (Righetti and others 1986). Field observations show moisture is the limiting factor in nodule formation (Kummerow and others 1978). When nitrogen in the system is limiting and other factors are plentiful, nitrogen-fixing symbioses can have a significant role. Once nitrogen is no longer limiting, nitrogen fixers are not as competitive and other species take over in succession (Sprent 1993). Sprent (1993) postulated removal of nitrogen limitations could encourage more rapid cycling of all nutrients and lead to possible losses due to leaching and addition of nitrates to groundwater (Sprent 1993).

Both *Ceanothus velutinus and Ceanothus sanguineus* are most prevalent during the early vegetation stages of disturbed forest sites where the overstory layer has been removed and the site subjected to fire. *Ceanothus* species are also very often present following stand-replacing wildfire events. Because of surface and soil depletion by fire and other soil disturbances, these sites are generally considered deficient if not devoid of available soil nitrogen. Youngberg and Wollum (1976) estimated that *Ceanothus velutinus* brings nitrogen concentrations up to pre-burn levels in just 7 years.

Shepherdia canadensis is most prevalent in more advanced successional stages of disturbed forest vegetation and is present, but not dominant, in old-growth forests. In early succession, *Shepherdia* will maintain itself as part of the seral vegetation.

Nitrogen-fixing plants are able to survive in environments unfavorable to other plants and, therefore, build up organic matter. Woody nitrogen fixers, in addition to adding to nitrogen accumulation in the soil in the form of dead leaf and root tissue, can affect other species' successful colonization by providing shade, moist microsites, seed capture, and soil stabilization. In fact, nitrogen fixation may not be the most important contribution. Actinorhizal species such as *Alnus rubra* when planted with *Pseudotsuga menziesii* tend to suppress fungal root diseases and increase wood production in the conifer (Dawson 1990). Nitrogen fixers can sustain themselves in otherwise limiting environments and by the mere fact of their presence, pave the way for later successional species (Walker 1993). Pioneer succession plants add to soil organic matter. *Ceanothus velutinus* is one of the species that increases soil organic matter. Organic matter is the primary storage medium for soil N and the relatively decay resistant nature of humidified organic matter means that chemically bound organic nitrogen will be released fairly slowly (Hibbs and Cromack 1990). Soil pH can be reduced, which will minimize nitrogen and ammonia losses due to volatization (Alexander 1977) but can increase the loss of cations by encouraging their release from soil and subsequent loss by leaching (Paschke and others 1989).

The role of nitrogen fixers in revegetation has only been postulated based on inference that nitrogen fixers put nitrogen back into their environments (Munshower 1993). Nitrogen-fixing plants can also become a trapping mechanism for nitrogen and in turn, release it slowly into its soil environment. Dawson (1993) estimated tropical systems to be some of the most important nitrogen-fixing systems on the earth but estimates of their contribution to global nitrogen fixation may be underestimated because accurate data from these areas are lacking. Burns and Hardy (1975) estimate $4,100 \times 10^6$ ha in forests and woodlands to be responsible for fixing 10 kg nitrogen per hectare per year. This amounts to 28 percent of terrestrial ecosystems' contribution of nitrogen fixed every year.

Others working with actinorhizal nitrogen fixers have obtained specific results that vary from 0.057 kg N ha^{-1} yr^{-1} in *Purshia tridentata* (Dalton and Zobel 1977), 80 kg N ha^{-1} yr^{-1} for *Ceanothus velutinus* (Cromack and others 1979), 24–50 kg N ha^{-1} yr^{-1} in *Ceanothus sanguineus* (Binkley and Husted 1983), 42–100 kg N ha^{-1} yr^{-1} for Ceanothus in the Pacific Northwest (Binkley and others 1982), 101 kg N ha^{-1} yr^{-1} (McNabb and Cromack 1983), and 50–200 kg N ha^{-1} yr^{-1} for *Alnus rubra* (Hart and others 1997).

Most woody tree and shrub actinorhizal plants are shade intolerant early colonizers of disturbed sites. *Ceanothus velutinus* is considered to compete negatively with *Pseudotsuga menziesii* in regeneration of severely disturbed sites (Dawson 1990). On the other hand, Binkley and others (1982) argue that *Ceanothus velutinus* competes for water, light, and nutrients early on in the stand regeneration but over time, nitrogen accretion is enough to compensate for nitrogen losses generated by the disturbance. They feel the species is critical in regeneration of secondary successional sites.

Actinorhizal plants can also benefit from associations with other plant species. In *Alnus rubra* stands, for instance, associated species such as *Thuja plicata* offer wind protection and controlled spacing, resulting in increased tree diameter and straighter stems (Dawson 1990).

Materials and Methods

The incidence and morphology of nitrogen-fixing nodules were examined on the shrubs *Purshia tridentata, Ceanothus velutinus, Ceanothus sanguineus,* and *Shepherdia canadensis.* These species are native to the Northern Intermountain Region and are being studied for their utility in reclamation vegetation covers.

Sample Populations—Three areas in Washington and Idaho were chosen for collection of plant materials for all four species.

Two populations of *Purshia tridentata* were sampled on the Spokane Indian Reservation, Stevens County, east-central Washington. Both sites are near the abandoned uranium Midnite Mine for which native vegetation covers are being studied. The soil of both sites is sandy gravel glacial till and both belong to the *Pinus ponderosa/Purshia tridentata* habitat type.

Three populations of *Shepherdia canadensis* plants were sampled. Two of the sites are on the Spokane Indian Reservation. Both sites had been logged and prescribed burned within the last 5 years and represent the *Pseudotsuga menziesii/Calamagrostis rubescens* and the *Pseudotsuga menziesii/Symphoricarpos albus* habitat types. The third population is from a gravely soil, *Pseudotsuga menziesii/Symphoricarpos albus* habitat type that was also recently logged and burned. This site is south of Thrapp Mountain, Twisp Ranger District, Wenatchee National Forest, Okanogan County in north-central Washington.

Ceanothus velutinus was taken from the same Okanogan site. A second population of *Ceanothus velutinus* was sampled from disturbed sites in a *Tsuga heterophylla/Clintonia uniflora* habitat type of the St. Joe National Forest, Potlatch Ranger District, Idaho. All soils of these sites were a gravely sand.

Ceanothus sanguineus was located the same area as the first *Shepherdia* and second *Shepherdia* sites.

Sample Collection and Analysis—Fifteen cubic decimeters soil (65 cm diameter by 45 cm deep) with root material were carefully removed from around the root crown of each shrub. On every plant, all nodule distances from the crown were noted. The number of nodules and their root attachments were recorded. Crown height and dry weights, and root length and dry weights were determined. Nodules were carefully examined, photographed, and dry weights taken. Averages of data from plants in each species were computed for comparison between species.

Results and Discussion

Species Characteristics in the Northern Intermountain Region—*Purshia tridentata* in the Northern Intermountain Region is often a species with winter persistent leaves and found in low elevations with coarse textured, well-drained soils. It is considered a late successional species but can be an early colonizer on disturbed sites of more moist habitat types. It is found on warm, dry sites in steppe and forest zones. *Purshia* quickly develops a large, single, deep taproot that appears to be an adaptation to survive in water stressed habitats.

Ceanothus velutinus is an early seral evergreen species found on *Pseudotsuga menziesii* to warm *Abies lasiocarpa* habitat types. This species is best adapted to dry forest conditions and grows on hillsides and is commonly found on coarse textured soils. This forest shrub is not shade tolerant and is limited in its successional role to early states of vegetation development following fire and other kinds of severe soil disturbances on cold and drought-prone sites. This species is considered to have a deep taproot; however, in our samples, none of the plants formed a distinct taproot. The upper portion of the root beneath the caudex was a single large diameter root that divided within a depth of 15 to 20 cm into small diameter, lateral, spreading roots.

Ceanothus sanguineus in the Northern Intermountain Region is a deciduous forest shrub in the *Pseudotsuga menziesii* to warm *Abies lasiocarpa* sites. It is a seral species with low-moderate shade tolerance, grows on dry rocky hillsides, and is fire adapted. The caudex develops into a large structure that resembles the start of a taproot but no distinct taproot was evident in any of the plants we sampled. Primary branching produces fairly large lateral branches. These lateral branches became a diffuse root system within a short distance from the plant. It is more drought and cold tolerant than *Ceanothus velutinus* and overlaps *Ceanothus velutinus* in range and habitat characteristics (Hibbs and Cromack 1990).

Shepherdia canadensis is a deciduous forest shrub found on moist, cool sites with fine to sandy, gravely, rocky soils. It is found on *Pseudotsuga menziesii* to warm *Abies lasiocarpa* sites. It is shade and fire tolerant. This species has no distinct taproot and branching of the main lateral roots is evident immediately below the crown.

Species Nodule Characteristics—In our *Purshia* study areas, only 50 percent of the *Purshia* plants examined were nodulated. The nodules were predominantly small masses of 8 mm in diameter with an average weight of.0.081 grams (table 2). Single lobed nodule development was scarce and the nodules were usually found on fine lateral roots at least 15 cm but no deeper than 25 cm below the crown of the plant. No nodules were observed directly attached to the primary root. The nodules were irregularly lobed globular clusters and were very fragile, easily breaking apart from their attachments to one another and associated roots to which they were attached (fig. 2). There was a strong tendency for the clusters to form a spherical shape.

Ceanothus velutinus nodules were irregularly shaped lobed masses. Seventy percent of the plants excavated had nodules at one site and 60 percent at the other site had nodules. The nodules were large (33 mm diameter and dry weight of 1.191 g), and relatively sturdy. Most of the nodules were found at an average depth of 20 cm below the crown and attached directly to the main root. A distinguishing characteristic of these nodule clusters was the long lobe roots. The average nodule lobe root length was 5 mm (fig. 3) compared to 3.5 mm and less in the other species we examined.

Ceanothus sanguineus nodules were generally large and irregularly shaped masses. In comparison to *Purshia* and *Shepherdia*, the nodules were large in size, averaging 24 mm diameter, and heaviest in dry weight. Nodules in this *Ceanothus* species were the least fragile of the four plant species examined. The nodule lobes were thick, short, and firmly attached to one another (fig. 4). Most of these nodules were found on fine roots within 5 to 30 cm of the caudex.

Shepherdia nodules, in contrast to *Purshia*, were 80 percent attached immediately below the root crown and nodule masses varied substantially in size from small to large. Clusters of nodules in this species were also attached to young, fine roots. *Shepherdia* nodules had a tendency to branch in one plane only and produce fan-shaped masses (fig. 5) even when nodules' growth were not restricted by rocks in close proximity. This species often had numerous strings of single lobed nodules along roots.

General Observations—There was a greater tendency for larger nodule masses to form rather than single lobed structures. With each species, we found that as the root

Table 2—Characteristics of plants and attached nodule clusters in field-collected samples.

Character		*Purshia tridentata*	*Ceanothus velutinus*	*Ceanothus sanguineus*	*Shepherdia canadensis*
Plant and stem dry weight (g)	mean	111	209	125	187
	range	114–259	14–612	62–180	63–416
Plant age (yr)	mean	7	11	5	6
	range	2–5	7–18	3–8	3–9
Percentage of plants with nodules		50	65	100	100
Sites of nodule attachment		10% lateral off secondary root, 85% lateral off primary, 5% tap root	100% primary root, some lateral	100% lateral root off primary root	100% lateral root off primary root
Number of nodule clusters in sample	mean	8	many	19	13
	range	1–26	3 to many	4–59	3–37
Diameter of clusters (mm)	mean	8	33	24	19
	range	1–14	10–55	10–47	3–27
Tendency to form clusters nodules		90% intermediate clusters form	100% very large clusters form	90% small clusters form	20% intermediate, 80% small single lobed
Nodule dry weight (g)	mean	0.081	1.191	0.142	0.096
	range	0.012–0.218	0.212–2.547	0.017–0.644	0.01–0.0259

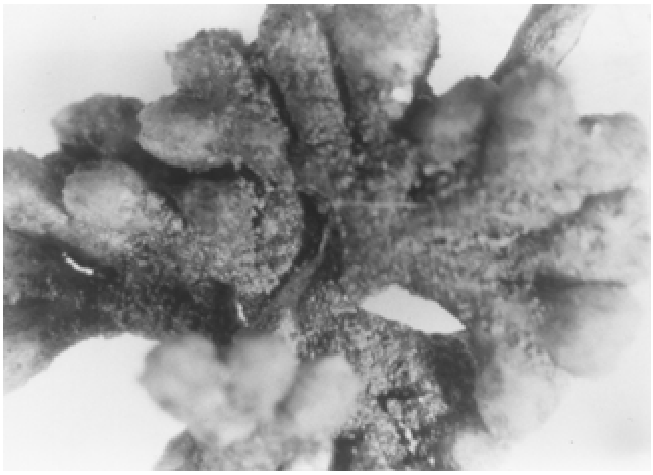

Figure 2—*Purshia tridentata*—Irregular globular clusters of fragile individual lobes.

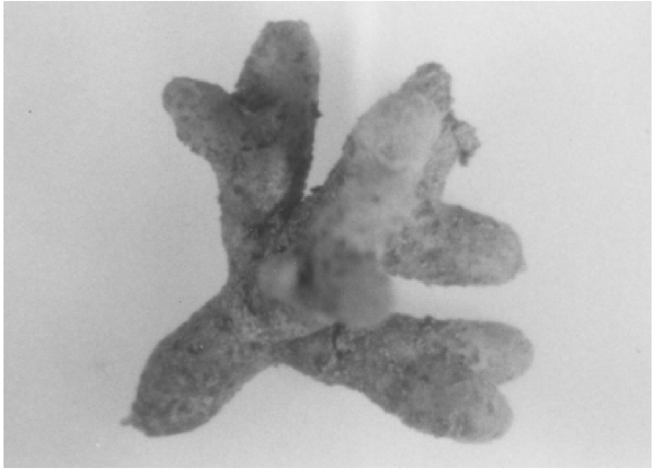

Figure 4—*Ceanothus sanguineus*—Plump, strong nodule lobes.

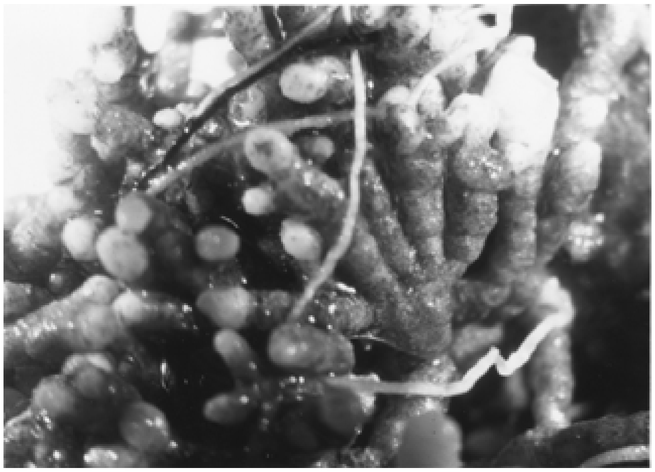

Figure 3—*Ceanothus velutinus*—Long lobe roots averaging 5 mm.

Figure 5—*Shepherdia canadensis*—Nodule clusters form in one plane and result in fan shaped clusters.

diameter increased, there was a greater prevalence of senesced nodule masses. The most viable nodular masses were strongly associated with younger and smaller roots.

Nodules were generally found within the first 10 to 30 cm below the root crown of the plants examined. Nodules also tended to be present on lateral roots off secondary roots.

Each of the actinorhizal species examined in this study had nodules with physical features that were distinct for the host plant. Distinguishing external morphological features set them apart from one another based on size and form of nodule mass, cluster weight, fragility of nodule tissue, and nodule root characteristics.

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Total Available Carbohydrates in Serviceberry After Late Summer and Fall Burning

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Abstract—Total available carbohydrate (TAC) storage and depletion was measured in late summer and fall burned and unburned serviceberry (*Amelanchier alnifolia*). The purpose of the study was to assess the influence of late season prescribed fire on the vigor of serviceberry, a key browse species on white-tailed deer (*Odecoileus virginianus ochrourus*) winter range in northeastern Washington. All plants displayed similar TAC cycles through the first growing season following treatment. TAC levels in stems were highest prior to bud activity and declined during the early stages of growth (March, April, May). The low levels of stem TAC coincided with periods of maximum stem growth. Roots had the highest TAC concentrations prior to dormancy, then declined as stem elongation progressed to mid-season. After maximum stem elongation, root TAC levels increased significantly through the remaining growing season. Late summer burned plants displayed immediate new growth following treatment and advanced phenology during the first growing season in contrast to fall burned and control plants. The first year growth of fall burned shrubs was delayed until after control plants had initiated stem elongation. Neither burn treatment had major impacts on carbohydrate storage nor vigor of shrub growth.

Introduction

Serviceberry (*Amelanchier alnifolia*) is a preferred winter browse for white-tailed deer on many habitat types of northeastern Washington and adjacent Idaho. The shrub is common in late stages of forest vegetation succession in the Northern Intermountain Region but is most abundant in the early stages of vegetation development following fire. Serviceberry is a prolific resprouter following fire (Leege and others 1971; Miller 1976). Most of the prescribed burning to enhance deer winter habitat in northeastern Washington is conducted during the fall season. The time of burn varies according to fuel and weather conditions, but commonly burns are conducted prior to onset of winter dormancy in many of the browse species of the area. Concern was raised about the potential influence of late summer and early fall burning on browse recovery if browse species were burned while still in active growth at the time of the burn. A key physiological function in woody plants is the storage of available carbohydrates produced by photosynthesis in excess of plant maintenance (Chapin and Shaver 1990; Coyne and others 1995). This function provides an essential source of energy for plant survival during dormancy and production of plant tissue during early spring growth when carbohydrate utilization exceeds photosynthetic production. Interruption of the normal storage cycle of reserves in the later stages of growth would potentially impact the survival, vigor, and vitality of plants. Indication of such impact should be apparent during the first growing season following treatment.

The objective of this study was to determine the trends in depletion and storage of total available carbohydrates within various parts of serviceberry shrubs during the first growing season following canopy removal by late summer and fall burning.

Methods

Study Area

The study area is located on the Little Pend Orielle Wildlife Recreation Area in Stevens County, northeastern Washington. The area is controlled and managed by the Washington State Game Department by permission of the United States Fish and Wildlife Service of the Department of the Interior who retains ownership. Location is 18.5 km east-southeast of Colville, Washington. Annual precipitation averages 40 cm. Snow provided approximately 32 percent of this moisture. Snow can be expected by November and commonly remains on the ground from December through February. White-tailed deer (*Odecoileus virginianus ochrourus*) occupy the area from mid-November to mid-March. Average daily winter temperatures during this time range from 20 to 35 °F. Summers are warm, and sunny with regularly occurring light rainfall throughout the summer. The elevational range of the area is 730 to 775 m. Soil characters are strongly influenced by glacial till composition overlain by erosionally deposited fines. The Douglas-fir/mallow ninebark (*Pseudotsuga menziesii*/*Physocapus malvaceus*) plant association represents more than 70 percent of the area's vegetation (Williams and others 1990). Serviceberry averages less than 9 percent canopy cover throughout the study area. While not the most abundant browse species of the winter range, this species is designated a key management species because of its low abundance and high browse preference to white-tailed deer.

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Field Methods

Thirty-six shrubs were selected for early August and mid-October burn treatments. Twenty-five additional shrubs were selected as control plants. Early August represents a physiologically active mature shrub having achieved maximum stem elongation and supporting maximum leaf area. Mid-October represents a fully dormant, leafless mature shrub condition. Pre-burn characteristics of the shrubs are shown in table 1. The biomass of each shrub was calculated using regression equations relating biomass to individual stem diameter at ground level length, and total canopy volume of the plant. Total canopy volume was calculated using the formula for a cylinder where the maximum diameter and the average height of the canopy are used as dimension variables.

Each shrub was burned individually in the treatments. Additional fuel was inserted into the canopy of each shrub in order to achieve a complete canopy removal burn. This fuel consisted of twenty 2 cm x 2 cm x 120 cm 200 g mill strips or 8 kg of air dry straw.

The control shrubs served as the base for comparison to plants in the burn treatments. Four stems of each control plant were labeled with small metal tags for repeated observation to characterize phenology and growth. Length measurements in mm were made from bud scars at the base of the current year twig to the tip of the true-terminal bud.

Laboratory Methods

Burned and control plants were excavated during the first growing season following treatment. Sampling was conducted according to the specific phenological stages of late winter dormancy, active growth, end of stem elongation, and total leaf senescence. Subsamples of small roots (less than 7 mm in diameter), large roots (greater than 7 mm in diameter), root crowns, current year stems, and second year wood were collected. Samples were placed in plastic bags, labeled, immediately frozen on dry ice, then transported to the laboratory and stored in a freezer until freeze-dried. The freeze-dried samples were ground in a Wiley mill through a 2 mm screen and stored in airtight jars at 68 °F until analyzed. Total available carbohydrates (TAC) will be the preferred term used throughout this paper to identify the nonstructural reserve component which can be readily metabolized by the plant (Weinmann 1947; McConnel and Garrison 1966). The TAC was extracted from the ground plant samples using 0.2N sulfuric acid as described by Smith and others (1964). This method hydrolyzes TAC to reducing sugars that can be measured quantitatively by the Shaffer-Somogyi copper-iodometric titration method outlined by Heizne and Murneek (1940). Data were subjected to analysis of variance and Duncan's new multiple range test within the GLM procedure of the Statistical Analysis System, 1979 Edition (Helwig and Council 1979). Significant differences between means are interpreted at the 0.05 level.

Results and Discussion

Phenological Development

Serviceberry plants typically remain dormant through the end of February. By early March, plants begin to enter the active bud stage. This progresses to nearly 100 percent expression of the active bud stage by end of April. At this time, a small percentage of the plants begin to enter the bud burst stage and express anthesis. By mid-May, all plants had entered the bud burst stage and show anthesis and the beginning of stem elongation. The maximum rate of stem elongation occurs from early-May to mid-June. Maximum leaf area generally is achieved by mid-June and will persist as a physiologically active leaf set until mid-July. After this point in time, insect depredation, water and heat stress, and fungal disease begin to cause varying degrees of leaf senescence. Maximum stem elongation is achieved by early August. Leaf senescence started in ernest at the end of August and is complete by early October. Leaf fall of senesced leaves may extend into mid-November.

The phenological development of the burn treatment plants was similar in timing and pattern to that of the control plants with some important exceptions. All plants burned in late summer regenerated a significant amount of new stem and leaf growth within 1 month of the treatment. The new leaf sets appeared vigorous and physiologically active later into October. Fall burned and control plants did not initiate new fall growth. In the first growing season following treatment, all late summer burn plants initiated growth well in advance of the fall burned and control plants. The late summer burned plants became bud active in late February with stem growth initiating by mid-March and

Table 1—Average total available carbohydrates (TAC) percentages across phenological stages for five plant parts of unburned control plants.

	Phenological stage			
Plant part	**Bud active**	**Anthesis**	**Maximum stem elongation**	**Entering winter dormancy**
Current year stem	***	11.7 a	8.9 b	8.5 c
Second year stem	9.2 d	8.1 e	8.1 e	8.3 e
Root crown	8.7 e	7.2 f	7.6 g	9.3 d
Large roots	9.5 d	9.4 d	9.3 d	9.9 e
Small roots	7.3 f	7.8 g	9.4 d	7.4 f

***Current year growth had not been initiated by this date.
Means followed by the same letter are not significantly different at the 5 percent level of probability.

rapid stem elongation by early-April. Anthesis did not occur in plants of either burn treatments. Both fall burned and control plants followed an identical phenological pattern.

TAC Levels

The TAC depletion and storage cycle in the control plants is shown in table 1. Generally, all stems were at high TAC levels at the beginning of the bud active stage. TAC levels in current and second year wood peaked at the time of anthesis, then began a sharp decline as stem elongation accelerated. TAC levels of these plant parts stabilized by the end of the stem elongation period. These peaks in stem TAC coincide with declining levels of TAC in roots, root crowns, and older stem portions suggesting that stored TAC in these plant parts is being translocated to new growth sites in the canopy. After anthesis, the TAC levels in roots and root crowns began to progressively increase through the remaining growth period. All below ground parts combined, had higher concentrations of TAC than the aerial portions of the plants after midseason.

Current year growth of burned plants was the only canopy portion available for comparison to the control plants. The seasonal trends in depletion and storage of TAC plants of both burn treatments were generally similar to the control plants (table 2). A significant reduction in current year stem TAC of all burned plants occurred after anthesis, leveling off at the end of stem elongation period. No significant differences were found in the TAC trends of all treatment plants. Small roots of late summer burn shrubs exhibited a continual decline with a significantly lower level of TAC by early October. Small roots of late summer burned plants began the season at higher TAC levels than plants in other treatments. Excavation of these roots indicated that they were actively growing at the time. Garrison (1971) stated that stored carbohydrates are not affected by top removal in many shrubs because small roots store the bulk of carbohydrates needed by the plant. Large root TAC remained fairly constant for the control and fall burned shrubs with a small upward trend after anthesis and maximum stem elongation. The late summer burned plants showed a statistically significant increase in TAC levels between the end of stem elongation and mid-October dormancy. Root crown TAC remained constant for all burned shrubs throughout the season.

Coyne (1969) felt maximum carbohydrate reserves are not attained until a plant completes its annual life cycle and that maximum plant vigor depends upon the level of TAC storage. Interruption of this cycle by burning in early August, prior to completion of serviceberry's growing cycle did not appear to reduce serviceberry vigor during the first growing season following treatment. Roots had the highest concentration of TAC prior to dormancy. Therefore, as long as the root component of the plant is not damaged by the late summer fire, the crown portion is not requisite to the plant survival. Coyne and others (1995) have suggested that fall growth may tap stored reserves of the plant and stress the plant to a point of low vigor, especially if repeated cropping of the new growth is taking place. The fall growth of late summer burned plants may potentially reduce TAC root levels to the point of affecting the subsequent year's canopy growth. Continual crown removal has been shown in other studies (George and McKell 1978) to affect root reserves and ultimately kill the plant. However, this was not evident in the trends of TAC following treatment nor growth of plants in this study.

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Table 2—Average total available carbohydrates (TAC) percentages across phenological stages for four plant parts of late summer and fall burned plants during the first growing season following treatment.

		Phenological stage			
Plant part	Burn treatment	Bud active	Anthesis/ stem elongation initiated	Maximum stem elongation	Entering winter dormancy
Current year stem	Late summer	12.3 a	10.2 b	8.1 c	7.4 c
	Fall	***	10.7 b	8.3 c	8.2 c
Root crown	Late summer	8.5 a	8.5 a	7.8 b	7.9 b
	Fall	8.2 c	8.2 c	8.8 d	8.6 d
Large roots	Late summer	7.9 a	7.8 a	7.1 b	9.5 c
	Fall	8.4 d	7.6 a	8.3 d	9.0 e
Small roots	Late summer	9.4 a	8.4 b	7.8 c	7.1 d
	Fall	7.3 d	8.0 c	7.4 d	8.5 b

***Current year growth had not initiated in this treatment by this date.

Within each plant part category, means shown in the 2 treatment rows followed by the same letter are not significantly different at the 5 percent level of probability.

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Long-Shoot/Short-Shoot Phenomenon in Woody Plants

Ronald E. Sosebee

Abstract—Shoot growth in shrubs is often overlooked as an important component of phenological development in woody plants. However, shoot growth dictates the pattern of growth of deciduous trees or shrubs, especially following defoliation or canopy damage. In general, woody shoots are divided into short- and long-shoots. Short-shoots, sometimes called "spurs," are reproductive shoots (in other words, spurs on an apple (*Malus pumila*) tree). The long-shoots, sometimes called "watersprouts," are vegetative shoots. From a management perspective, herbicidal control of shrubs (in other words, mesquite (*Prosopis glandulosa*)) with long-shoots is highly ineffective. All of the energy synthesized by the plant is translocated to the long-shoot and converted to structural materials; in other words, stem growth. Similarly, one could postulate that browsing during the long-shoot stage would not significantly impair shrub viability if the shrub was healthy and vigorous at the time of browsing. Likewise, pruning shrubs during long-shoot growth (in a lawn or garden) stimulates "wolf-like growth" of the shrub. In contrast, herbicidal control of shrubs during the short-shoot stage usually conveys a high degree of success. Likewise, pruning or defoliation during the short-shoot stage significantly reduces fruit production.

Long-Shoots/Short-Shoots

Shoot growth in woody plants is seldom considered in management decisions relating to grazing, browsing, chemical control, mowing, and so forth. Likewise, it is seldom considered an important component of phenological development in woody plants. Yet, the type of shoot growth, especially following defoliation or crown damage, dictates the growth pattern of a deciduous tree or shrub when they initiate spring growth, fruit production, or resprouting.

This paper is not intended to present new scientific results or as a literature review of research that has been conducted on the subject. Rather, it is an opportunity to describe long- and short-shoots and to present some management implications relating to long- and short-shoot growth patterns. For a basic understanding of long- and short-shoots (fig. 1), the reader is referred to Dahl and Hyder (1977) and Dahl (1995).

In general, shoot growth of woody plants is divided into long- or short-shoots. In woody plants, long-shoots are vegetative shoots and short-shoots are reproductive shoots. Long-shoots grow very rapidly (and remain vegetative) and are called watersprouts in some species. They are major energy sinks during rapid growth and internode expansion. In contrast, short-shoots are sometimes called "spurs" (as in apple (*Malus pumila*) trees) and are the shoots that bear

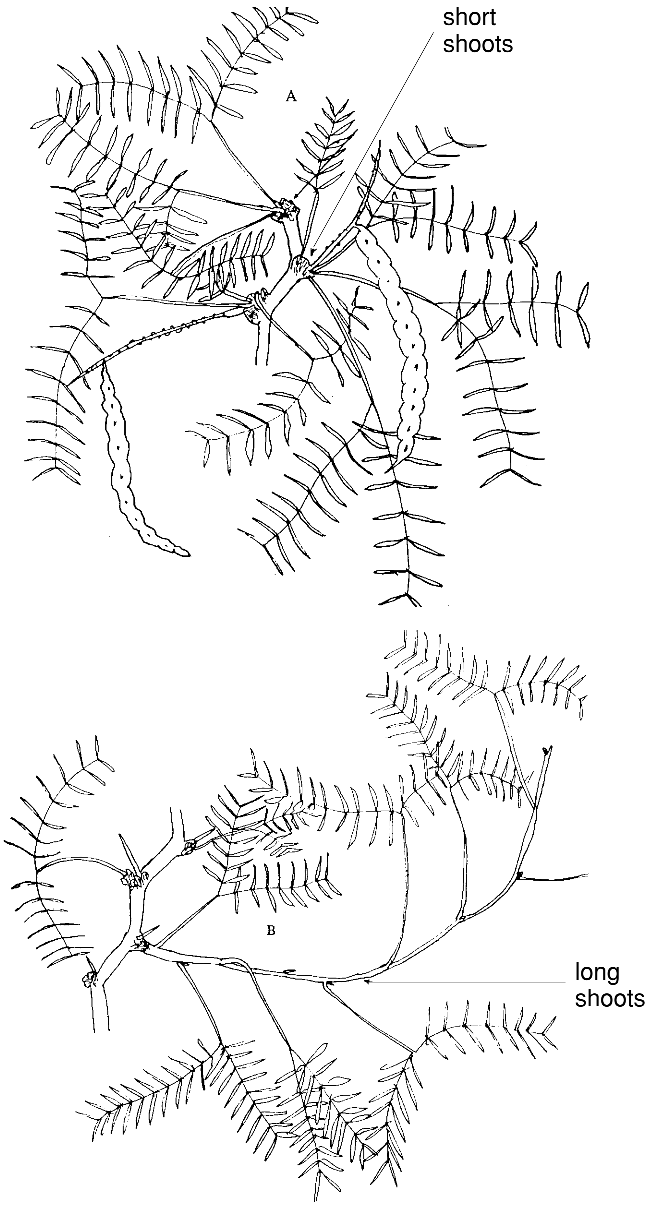

Figure 1—(A) Mesquite stem with predominantly short-shoots (note almost total absence of internode elongation); (B) mesquite branch with a long-shoot showing typical internode elongation. Source: Dahl 1995.

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fruit. Internodes are compressed and elongation is minimal. Therefore, they are reproductive rather than vegetative shoots. Since they are not rapidly expanding shoots, they are not major energy sinks.

From a management perspective, it is important that one recognize long- and short-shoot stages in plant development. Any form of defoliation, damage, or injury to the shoots of woody plants will stimulate long-shoot development. When long-shoots are rapidly growing, they require a great deal of energy that is synthesized by the plant to produce structural materials in the long-shoots (in other words, stem growth). Since these shoots are vegetative, shoot removal by grazing, browsing, or even mechanical mowing during the long-shoot stage would not be particularly detrimental to the tree or shrub if the tree or shrub was healthy and vigorous at the time of shoot damage or removal. Pruning shrubs in the long-shoot stage, by whatever means (even in a lawn setting), often stimulates "wolf-like growth" of the tree or shrub.

Foliar application of herbicides to resprouting woody plants in the long-shoot stage usually results in ineffective control. Since foliar-applied herbicides are generally translocated with the photosynthate (in other words, carbohydrate) stream, the herbicides would primarily be translocated to the shoots along with the carbohydrates for synthesis of structural material and not to the perennating organs and tissues that must be killed by the herbicide if chemical control is to be effective.

On the other hand, defoliation or injury to the shoots of woody plants in the short-shoot stage can be quite damaging to a tree or shrub. Damage or removal of the short-shoots of woody plants can significantly impair subsequent growth of a tree or shrub. Any removal or damage to a shoot during the short-shoot stage can significantly reduce fruit production and development of new buds from which the subsequent year's growth and fruit production will originate.

Since the shoots are not primary sinks for photosynthates during the short-shoot stage, the photosynthates (in other words, carbohydrates) are translocated to the perennating lateral buds (including basal buds) and storage tissues. Therefore, chemical control of trees and shrubs is usually quite successful when herbicides are foliar-applied during the short-shoot stage (assuming that all other physiological and environmental conditions are appropriate for control).

Interestingly enough, long- or short-shoot status of woody plants is not necessarily related to chronological age of the tree or shrub. For example, often one hears that control of resprouts should not be planned for 5 to 7 years post-resprouting, particularly in mesquite (*Prosopis glandulosa*). However, our research indicated that dormant mesquite shredded to ground level resprouted in the spring and produced short-shoots during the first year of resprouting (Beck and others 1975). Foliar-applied herbicidal control was equally as effective on the first-year resprouts (short-shoots) as it was on 7- and 14-year old resprouts.

Without damage or defoliation to the shoots of woody plants, trees and shrubs grow very methodically. The main stem (or bole) of trees and shrubs is the first order long-shoot. Stems branching off of the first order long-shoot (or lateral stems) are second order long-shoots. Lateral stems branching off of second order long-shoots are third order long-shoots, Usually as the order of long-shoots increase, fewer and less vigorous long-shoots are produced. By the time the trees and shrubs attain either fourth or fifth order long-shoots, they produce no lateral long-shoots, only short-shoots. These short-shoots bear no long-shoots.

In summary, recognition of long- or short-shoot growth is imperative in making woody plant management decisions. How woody plants respond to grazing, browsing, mowing, pruning, or herbicidal control depends upon whether they are in the long- or short-shoot stage. As resource managers, we should become cognizant of how trees and shrubs grow and incorporate that knowledge into our management plans.

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Aerial Biomass and Elemental Changes in *Atriplex canescens* and *A. acanthocarpa* as Affected by Salinity and Soil Water Availability

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J. Jesús Martínez-Hernández

Abstract—*Atriplex canescens* and *A. acanthocarpa* from the Chihuahuan Desert in México were subjected to different salinity and irrigation treatments in a greenhouse study. Plants were grown in pots containing soil and irrigated with NaCl solutions of 0, 50, and 100 mM at 40 and 80 percent available soil water. Aerial biomass of *A. canescens* declined as NaCl treatments increased. In contrast, the aerial biomass of *A. acanthocarpa* was not negatively affected by the salinity treatments, suggesting a high salt tolerance of this species. Aerial biomass of *A. acanthocarpa* was more reduced by the decrease in irrigation level than that of *A. canescens*. *A. acanthocarpa* had a much higher accumulation of Na in leaf tissues throughout the salinity gradient than *A. canescens*. Tissue concentration of K in both species was minimally affected by the salinity or irrigation treatments. Leaf N concentration increased in both species as plants were subjected to higher salinity treatments. The higher salt tolerance and higher Na absorption of *A. acanthocarpa* favor the use of this plant in reclamation of saline areas, while the low Na accumulation of *A. canescens* makes this species an attractive forage in saline rangelands.

Plants of the genus *Atriplex* are considered xero-halophytes for their ability to grow in dry and saline areas, which allows them to succeed in many disturbed environments (Osmond and others 1980). This characteristic makes *Atriplex* spp. suitable plants for reclamation of highly disturbed areas (Booth 1985). Some species of *Atriplex* are appreciated as forage for livestock and wildlife since their nutritive value is fairly high and their foliage is evergreen (Garza and Fulbright 1988). The high biomass productivity of *Atriplex* has motivated researchers to investigate the feasibility of cultivating some species under seawater irrigation (O'Leary and others 1985).

A. canescens is the most widely distributed *Atriplex* species in North America and its ecophysiological characteristics, forage potential and genetic diversity have been extensively studied (Glenn and others 1996; Cibils and others 1998). *A. acanthocarpa* is a native shrub to North America, has potential for revegetation in saline rangelands, and is considered a good forage for cattle and deer (Garza and Fulbright 1988). However, this species has received little attention from researchers and very little is known about its salt tolerance and ecophysiological characteristics.

It is important to study the salt tolerance characteristics of halophytes because it could help to understand the potential utilization value of these plants and their ecological adaptations. The present study was an attempt to evaluate the effect of salinity and soil water availability on aerial biomass and leaf concentration of Na, K, and N of *A. canescens* and *A. acanthocarpa*. We hypothesized that increasing salinity levels has a negative effect on aerial biomass production of both species. The second hypothesis was that elemental changes are related to the characteristics of salt tolerance of these species.

Materials and Methods

This study was conducted in a greenhouse located in the Unidad Regional Universitaria de Zonas Aridas, Universidad Autónoma Chapingo, Bermejillo, Durango, México, in 1988. Seeds of *Atriplex canescens* and *A. acanthocarpa* were collected from native populations near San Luis Potosí City and Viesca, Coahuila, respectively. In April, seeds of both species were soaked with distilled water, changing the water daily, during 4 days. Subsequently, seeds were sown in germinating trays filled with a mixture of river sand (60 percent) and soil (40 percent) and irrigated with water from local municipal supply. Seedlings emerged within 3 weeks, and 8 weeks after sowing, one plant of each species was transplanted to 36 pots of approximately 3.5 L volume.

Pots contained a clay loam soil with low electrical conductivity (2 dS m^{-1}) from Rancho El Cono, Salinas de Hidalgo, San Luis Potosí. After plant establishment, plants of both species were watered twice a week with solutions of 0, 50, and 100 mM NaCl and maintained gravimetrically to either 40 or 80 percent available soil water. These treatments were applied during 4 months. In October, the aerial part of the plants were harvested, oven-dried and weighed to measure

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dry matter production. The leaves were separated and ground to determine K and Na by flame emission with a Varian AA-1275 atomic absorption spectrophotometer. Total Kjeldahl N was determined in leaves as outlined by Bremner and Mulvaney (1982). The completely randomized design was used in this experiment. The data were subjected to analysis of variance, and mean separation tests at $P < 0.05$ (protected Fisher's LSD) were performed with a Statistical Analysis System (SAS) computer program.

Results

Aerial biomass of *A. canescens* declined as NaCl concentration in the irrigation solution increased (fig. 1). A decrease of 37 percent in dry weight was observed in plants as NaCl concentration increased from 0 to 100 mM. In contrast, *A. acanthocarpa* did not show significant changes in aerial biomass as a result of the salinity treatments (fig. 1). Aerial biomass of *A. acanthocarpa* declined 20 percent in plants irrigated at 40 percent available soil water compared to plants irrigated at 80 percent available soil water (fig. 2). On the other hand, the decrease in water availability did not produce significant changes in the aerial biomass of *A. canescenes* (fig. 2).

A low concentration of Na in leaves of both species was observed in plants irrigated with 0 mM NaCl solutions and increased in plants irrigated with 50 and 100 mM NaCl solutions (fig. 3). A proportion of 1:2.4:2.7 reflected the variation in leaf Na concentration of *A. canescens* irrigated with solutions of 0, 50, and 100 mM NaCl, respectively. In *A. acanthocarpa* the proportion of change was 1:2.1:2.3 (fig. 3). Although leaf Na concentration was similarly affected by salinity in both species, the Na concentration was much higher in *A. acanthocarpa* than in *A. canescens* regardless of the salinity level (fig. 3). The concentration of K was very similar in both species and it was not affected by the salinity treatments (fig. 4). Irrigation treatments did not exert a significant effect on leaf Na and K concentrations in any species.

Salinity and irrigation treatments interacted to determine the variation of N concentration in leaves of *A. canescens*. Plants irrigated at 40 percent available soil water had higher N concentration than plants irrigated at 80 percent available soil water when NaCl concentrations in the irrigation solution were 0 and 50 mM (fig. 5). However, plants irrigated with solutions of 100 mM NaCl did not show variations in N concentration due to changes in available soil water. Regardless of the irrigation treatments, there was a tendency to increase leaf N concentration as salinity levels increased (fig. 5). Leaf N concentration in *A. acanthocarpa* was higher in plants irrigated with solutions of 100 mM NaCl than in plants irrigated with solutions of 0 and 50 mM NaCl (fig. 6). Irrigation treatments did not produce significant changes in leaf N concentration of *A. acanthocarpa*.

Discussion

The decline observed in shoot growth of *A canescens* as salinity levels increased has been previously observed (Glenn and others 1994; Glenn and others 1996). The apparent high salt tolerance of *A. acanthocarpa* has not been previously reported but seems to be similar to that of *Atriplex amnicola*, a halophyte that shows growth reduction only when the salinity of the irrigation solution surpasses 100 mM (El-Haddad and O'Leary 1994). *A. acanthocarpa* seemed to be more tolerant to salinity but less tolerant to drought than *A. canescens*. In agreement with this, Wilkins and Klopateck (1984) found that *A. canescens* had higher drought tolerance than several other native shrubs in Arizona.

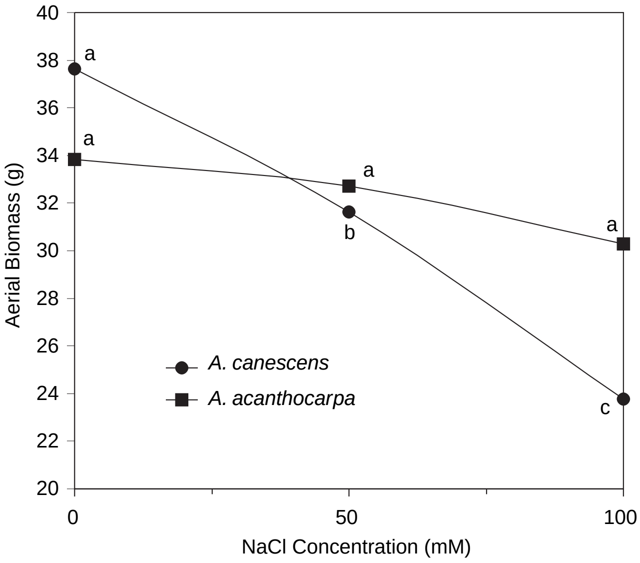

Figure 1—Aerial biomass (g) of *Atriplex canescens* and *Atriplex acanthocarpa* as affected by NaCl concentration in the irrigation solution (means with the same letter are not significantly different at $P > 0.05$).

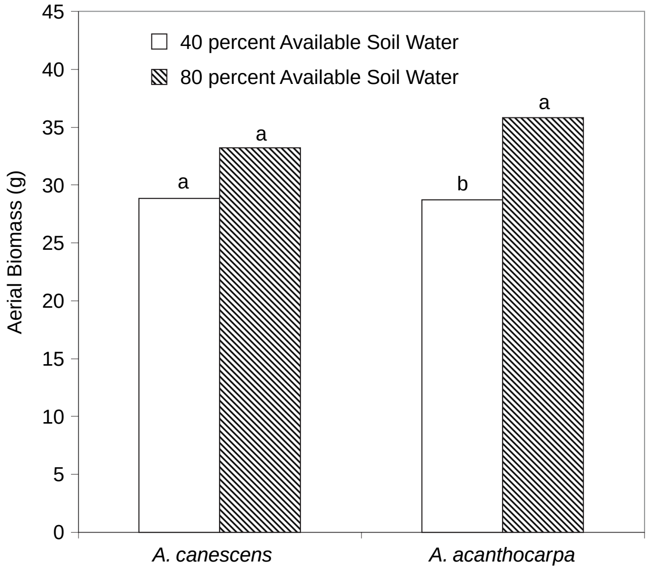

Figure 2—Aerial biomass (g) of *Atriplex canescens* and *Atriplex acanthocarpa* as affected by available soil water (means with the same letter are not significantly different at $P > 0.05$).

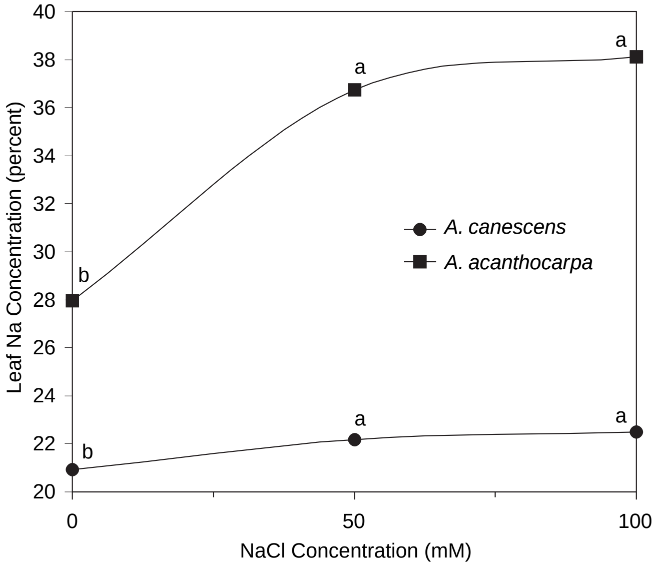

Figure 3—Leaf Na concentration (percent) of *Atriplex canescens* and *Atriplex acanthocarpa* as affected by NaCl concentration in the irrigation solution (means with the same letter are not significantly different at P > 0.05).

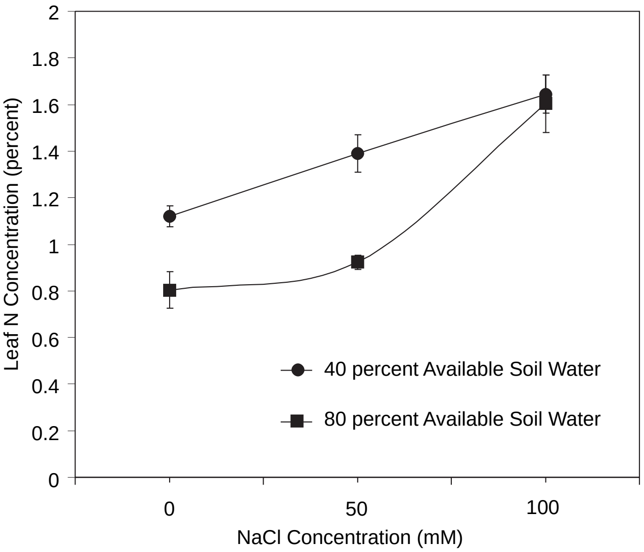

Figure 5—Leaf N concentration (percent) (± 1 SE) of *Atriplex canescens* as affected by NaCl concentration in the irrigation solution and soil water availability.

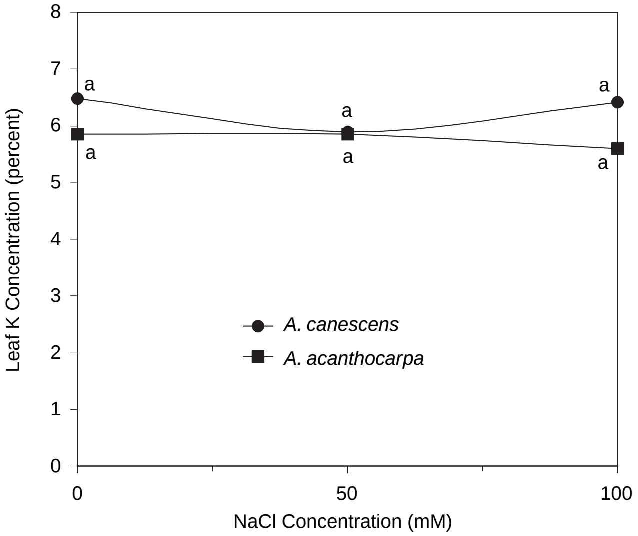

Figure 4—Leaf K concentration (percent) of *Atriplex canescens* and *Atriplex acanthocarpa* as affected by NaCl concentration in the irrigation solution (means with the same letter are not significantly different at P > 0.05).

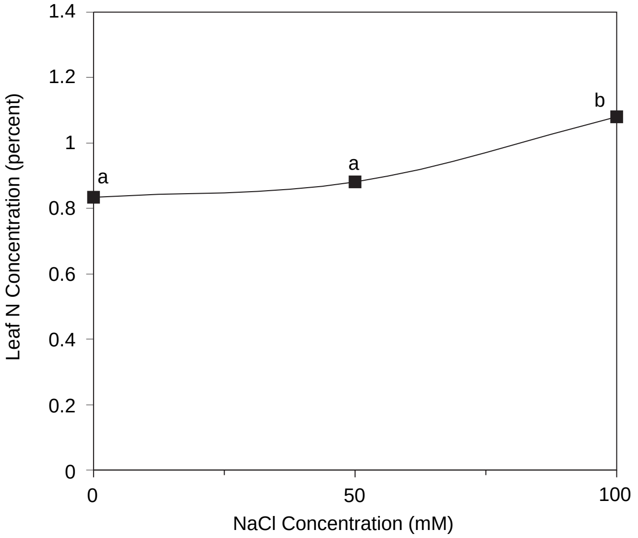

Figure 6—Leaf N concentration (percent) of *Atriplex acanthocarpa* as affected by NaCl concentration in the irrigation solution (means with the same letter are not significantly different at P > 0.05).

Na accumulation increased in *A. canescens* and *A. acanthocarpa* as plants faced increasing salinity levels. This response has been previously reported in *A. canescens* (Glenn and others 1996) and seems to be a typical response in halophytes. Presumably, Na accumulation contributes to decrease leaf osmotic potential in response to salinity increases in the root medium (El-Haddad and O'Leary 1994). However, Na levels in leaves of *A. canescens* were much lower than Na levels in leaves of *A. acanthocarpa* irrespective of the salinity treatments. These results agree with those of Garza and Fulbright (1988). Other studies have shown that under low salinity in the root medium *A. canescens* tends to have lower Na levels in leaves (Wallace and others 1973; Khalil and others 1986), but higher Na levels in roots (Wallace and others 1973) than other *Atriplex* species.

According to Glenn and others (1994) Na is the main cation involved in the osmotic adjustment of *A. canescens*. However, compared to other *Atriplex* species, *A. canescens* seems to exclude Na from the leaves, as many crop plants do to avoid Na damage to leaf tissues (Yeo and Flowers 1986). The low Na accumulation in leaves of *A. canescens* is considered a reason for its high forage value (Wallace and others 1973), but this feature might be also associated with characteristics of low salt tolerance (Glenn and others 1994, 1996). In agreement with this, results of this study showed that *A. canescens* had lower salt tolerance and lower leaf Na levels than *A. acanthocarpa*. The higher salt tolerance and Na uptake of *A. acanthocarpa* make this species a viable candidate for reclamation of disturbed saline areas.

Leaf K concentration in both species remained very stable and was not affected by salinity or irrigation treatments. K is an essential nutrient for plants and its absorption, even under salinity stress, must be maintained under acceptable levels for plant survival (Grattan and Grieve 1992). K and Na uptake by roots are competitive processes, but roots have higher affinity for K than for Na absorption. This characteristic is particularly important in saline soils where Na is much more available than K for plant uptake (Grattan and Grieve 1992).

Leaf N concentration tended to increase in both species as plants faced increasingly high salinity levels, although the effect was more clearly expressed in *A. canescens* than in *A. acanthocarpa*. This result could be partly a consequence of the reduction in aerial biomass caused by salinity stress. Pessarakli and others (1989) reported an increase of N concentration and a dramatic decrease in dry matter yield in salinized corn compared to control plants. Presumably, salinity reduced dry matter yield more than N absorption causing an increase in the concentration of N in leaves. A similar effect was found in red kidney beans subjected to salt and water stresses (Frota and Tucker 1978). In *A. canescens* the low irrigation level also caused increases in N concentration compared to the high irrigation level under low and intermediate salinity treatments. Apparently water stress caused similar effects than salt stress reducing aerial biomass more than N absorption.

Conclusions

Our results supported the hypothesis that increasing salinity levels causes a decline in aerial biomass but only for *A. canescens*. The salinity levels tested in this experiment were not clearly deleterious for *A. acanthocarpa*, which makes it a more salt tolerant species than *A. canescens*. On the other hand, *A. canescens* was more tolerant to drought than *A. acanthocarpa*. The higher salt tolerance of *A. acanthocarpa* corresponded with a high capacity to accumulate Na ions in its leaves compared to *A. canescens*. This supported our second hypothesis. N concentration increased as salinity stress increased in both species, but more evidently in *A. canescens*, perhaps because N absorption was less affected by salinity than plant growth.

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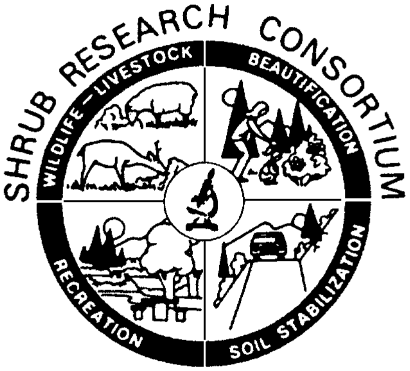

Community Ecology

Field Test of a New Australian Method of Rangeland Monitoring

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Neil West

Abstract—Managers need more efficient means of monitoring changes on the lands they manage. Accordingly, a new Australian approach was field tested and compared to the Daubenmire method of assessing plant cover, litter, and bare soil. The study area was a 2 mile wide by 30.15 mile long strip, mostly covered by salt desert shrub ecosystem types, centered along the SE boundary of the Eagle Bombing Range in NW Utah. Paired T analyses were used to see what differences in condition could be detected between Bureau of Land Management and U.S. Air Force lands occupying the same ecological sites. Because of low statistical power of the test, no statistically significant differences were detected between ownerships. We did however, find some numerical differences illustrating the strengths and shortcomings of the two approaches. The Australian technique was less time consuming but not more readily repeated than the Daubenmire technique. The Australian technique focuses on the importance of protecting soils against erosion. The Daubenmire technique allows collection of data for addressing biodiversity and weed invasion issues. Either or both methods can be done on the same locations, thus, the managers' objectives and budgetary considerations should guide choices of method(s) employed.

Introduction

Monitoring, while necessary for adaptive natural resource management, can become expensive and tedious. The monitoring process on rangelands has traditionally involved estimates of plant abundances in quadrats by species. Complete and accurate enumeration of abundance-weighted species composition in samples from plant communities requires practitioners who know the flora. Familiarity with the flora requires training followed by experience. Universities are training fewer people with lower levels of competence in field botany than was the case in the past. Agencies and other employers are offering fewer opportunities for young professionals to gain further experience in learning to identify plants. We, thus, need to explore additional ways to monitor rangelands that do not require as much investment in time to learn plant species as the traditional approach has entailed.

Methods

During the summer of 1997, we gathered field data for comparing a new Australian method (Tongway and Ludwig 1997) with a traditional approach (Daubenmire 1959) long used to enumerate vegetation cover in the Intermountain Region. Our study area was in northwestern Utah, along the southeastern boundary of the North Unit ("Eagle Bombing Range") of the Utah Test and Training Range in Box Elder and Tooele Counties, Utah. For a two mile wide by 30.15 mile long transect along this boundary, we compared characteristics of vegetation and soil surfaces for ecological site polygons (Creque and others 1999) that straddled the fence line separating the land managed by the U.S. Air Force (AF) from that controlled by the Bureau of Land Management (BLM). The fence at this boundary had been constructed in 1968 and differing management pursued thereafter. Prior to 1968, livestock, mostly sheep, had grazed the land under both current ownerships. Since livestock had been fenced out of the AF property for nearly 30 years, we expected to find higher (later seral) conditions on the AF side of the fence because of the greater opportunity for the vegetation to recover from livestock grazing impacts there.

Before we could evenhandedly sample the vegetation and soil surfaces characteristics under the two ownerships, we had to delineate polygons of relative high internal environmental homogeneity that could be expected to have the same potentials for vegetation and responses to management. In other words, the first step was to delineate ecological sites (Creque and others 1999). We did this in the field with conventional orthophotos (1:24,000 scale) taken between 1972 and 1978 (depending on the particular quadrangles involved). Polygons delineating individual examples of ecological sites were drawn on acetate overlays and questionable boundaries checked on the ground. We didn't distinguish polygons that were less than 5 ha in total size (the minimum mapping unit). We also didn't distinguish potential lobes of polygons less than 100 m in width. In other words, if there were small but nearly symmetrical inclusions of another possible ecological site within the polygon, these were ignored in the delineation. The width criterion meant that differing environments along bottoms of drainages or ridgelines were also ignored. Since we needed adequate area on both sides of the fence for reasonable sampling, we had to identify those polygons representing a given ecological site (ES) that straddled the fence and provided at least 5 ha area on each side. Each potentially sampled piece of land also had to extend at least 200 m along the same general slope in order for the Australian method (requiring a 100 m transect) to be accommodated with some buffer left for any disturbance created by fence building, fence maintenance, and changes in animal behavior next to the fence. We found

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23 such opportunities. Color-coded maps of the individual polygons, the ecological site represented, and of our plot locations can be found in Sharik (2000). These areas were linked to the Natural Resources Conservation Service (NRCS) soil survey (Trickler 1986) of the UTTR and later county soil surveys of the adjacent BLM land by the NRCS. This process led to the grouping of the 23 polygons meeting our criteria into 4 of the commonest ecological sites. Nine comparisons were made in the Desert Loam ES, five in the Desert Gravelly Loam ES, five in the Desert Flat ES, and four in the Alkali Flat ES. The sampled sites are all variants of the salt desert shrub ecosystem type (West 1983).

The next step was select points to sample within the AF and BLM portions of the large enough individual site polygons straddling the fence line. We examined the variation in photographic texture across the paired portions of the polygon on the orthophotos and chose a location where texture was both homogeneous and representative of the entire polygon. We then went to that location in the field. Both plot locations and polygon boundaries were entered into a geographic information system (Sharik 2000).

At each of the 46 transects (one per each side of the fence) a 100 m tape was laid out down the prevailing slope. Along these transects, two types of ground cover data were taken: by the traditional Daubenmire and the new Australian method.

The Daubenmire approach involved placement of twenty-five 20 x 50 cm micro-plots at random points along one side of the tape. Within the micro-plots, plant canopy cover estimates were made by species using the cover classes suggested by Daubenmire (1959).

Under the Australian method (Tongway and Ludwig 1997), line intercepts of basal cover of only the perennial plants were recorded. While Tongway and Ludwig (1997) recommend that these data be recorded by growth form category, we recorded live plant cover by species as well. Litter was not distinguished by what plant species it likely was derived from. This approach yields some other attributes besides basal cover. The amount of distance between patches of perennial plants is termed "fetch length." This is a proxy for bare ground ignoring any ephemeral plants. The number of patches intercepted was also recorded, as were the widths of plant bases that were intercepted.

In order to gain a sense of repeatability in applying the two methods, four pairs of transects (one representing each of the four ecological sites encountered) were read by both methods a second time the next day following the initial reading.

Statistical analysis of the data derived from the Australian method was by the paired T method (Subcommittee 1962). A T-test for the results derived from the Daubenmire method was not performed because these data were not spatially independent from those of the Australian method (the main focus of our investigation). Both types of data were recorded along the same transect lines. The power of these tests and sample numbers required to reach predefined statistical adequacies were calculated by the methods suggested in Chapter 11 and Appendix A of Elzinga and others (1998).

Range condition, derived only from the Daubenmire data, was scored by two methods. First, the Grazing Lands Technology Institute (1997) method was used with reference to the Utah Condition Guides (Natural Resources Conservation Service 1998). A second approach, based on degree of dominance by native plants, as suggested by Anderson (1991), was also employed. We also calculated the percent of the encountered flora that were considered invasive. For the listing of which species were considered weeds see Sharik (2000).

Results and Discussion

Using the traditional (Daubenmire) approach showed numerically higher average total cover by plants and less bare ground on the AF than BLM side of the fence (table 1). Shrub cover was slightly higher on the AF side, whereas canopy cover of perennial herbs was identical (table 1). Annual herb cover, bare soil, litter and soil cover by microphytes (lichens, mosses, and algae) was nearly the same on both sides of the fence (table 1).

Range conditions were apparently the same on both sides of the fence using the traditional NRCS method (table 1). The degree of invasion by exotics was slightly less on the AF side. Since the Index of Naturalness is 100 minus the percentage of invasion by exotics, the AF property sampled has a higher value for this property as well.

The new Australian method didn't yield total plant cover data. It focuses instead on the basal cover of perennials, whereas the traditional method assesses canopy cover by all plants present at the time of sampling. It should be pointed out that the leaves of most of the cool season herbs had already shattered when the data were taken in July and thus, had probably become greatly diminished from their earlier stature. Warm season herbs were still growing in July, however, and thus would have greater contributions to cover if measured later.

We intuitively expected the Australian method to be more repeatable than the traditional approach. This is because the Australian approach focuses on the intercepted basal cover of perennials. However, when there are numerous small-sized perennials, it proved difficult for the same intercepts to be encountered during the second reading. Thus, the eye adjustments required in the Daubenmire canopy cover method may compensate for the inexactitudes of line intercept approach. The Australian method presents data bearing on the fragmentation of perennial cover (Kuehl and others 2001), features not addressed by the traditional method. For instance, the mean fetch length was greater on the AF side of the fence (table 1). This means that there was more distance between clumps of individual perennial plants and their more durable litter there. In other words, more bare ground in larger patches occurred on the AF side. Mean patch width was greater on the BLM side (table 1). This suggests that perennial plants were, on average, larger there.

None of the differences discussed above were statistically significant at anywhere near conventional levels (table 1, fourth column). This was because statistical power was low (table 1, fifth column). In order to reach within 10 percent of the true mean with a 90 percent chance of not making a Type I error, we would have had to employ many more transects per polygon (table 1, sixth column). This would have greatly increased the cost of monitoring, especially for the traditional method. The Australian method is faster and focuses only on the perennial cover, thus statistical adequacy could

Table 1—Summary of overall results obtained by the two methods on the two sides of the fence. BLM = Bureau of Land Management, AF = Air Force, T = probability of a statistically significant difference with a chance of a type I error of one in ten. N = number of samples, that would have to have been obtained for a statistically significance (p = 0.10) to have been obtained.

	BLM	AF	Difference	T	Power	n
Daubenmire method (percent of ground covered)						
Shrub cover	14	16	2		0.135	370
Perennial herb cover	2	2	0		0.057	1,811
Annual herb cover	13	12	1		0.029	7,322
Microphytic crusts	43	42	1		0.028	47,550
Total plant cover	30	31	1		0.077	934
Litter	4	4	0		0.928	26
Bare ground	10	9	1		0.176	260
Total	112	113	1		0.026	80,091
Range condition	48	48	0		0.068	1,228
Degree of weed invasion	36	33	3			
Index of naturalness	64	67	3			
Australian method (per 100 m)						
Mean fetch length (cm)	580	910	321	0.309	0.156	304
Percentage in fetches	5.8	9.1	33			
Mean patch number	26	24	2	0.096	0.037	463
Mean total patch width (m)	4.3	3.4	0.9	0.612	0.116	463

be reached with fewer samples (table 1, sixth column). Another advantage of the Australian method is that it is based on a concept that allows scaling up to landscapes and provides means of connecting the data to estimates of soil erosion and nutrient conservation (Ludwig and others 2000).

Conclusions

Choice of methods to use in monitoring of rangelands should follow expression of what the land is being managed for, balanced against costs and reliability of the method employed. For instance, the Australian method assumes that protection of the soil against erosion is the number one land management issue. Tongway and Ludwig (1997) also assume that ephemeral vegetation and microphytes (mosses, lichens, algae) play no decisive role in protecting the soil. Contrary to what Tongway and Ludwig (1997) assert, choosing this focus on soil protection is not a value-free choice, but as much a moralistic decision as choice of any other condition objective.

The Australian method does not involve creating a full species list with any expression of their abundance for example, cover. Without practitioners trained to identify plant species, the best that can be done under the Australian approach is an enumeration of a modest set of life form categories for the perennials only. Thus, if differences in species level biodiversity within the entire plant community is something one desires to know, a more traditional approach must be employed. These kinds of data are required to calculate indices of similarity to reference states such as usually done by the Grazing Lands Technology Institute (1997) or using the Index of Naturalness (or degree of invasion that is its inverse) as suggested by Anderson (1991). Keeping these traditional approaches in play will require that universities keep introducing students to the topic of plant taxonomy and that employers give their new employees opportunities to improve upon those initial skills.

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Quantifying Plant Diversity in Zion National Park, Utah

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Abstract—The vegetation of Zion National Park (ZNP) is used to illustrate the use of various indices that describe aspects of botanical diversity. The simplest method reports the average number of vascular species per 0.01 ha (0.025 acre) macroplot. The MacArthur-Wilson index of diversity is given for each plant community of occurrence in the Park. Neither the number of species per macroplot nor the MacArthur-Wilson index show much variation among the plant communities of the Park. A third index shows the proportion of a community's major species that reach maximum regional abundance in that community. This index records large differences among communities and is indicative of the amount of genetic diversity inherent in a community. Such information will be of interest to evolutionists, plant breeders, and horticulturists. A fourth index quantifies the degree to which major species of a community are rare elsewhere in the region. This rarity index also shows large differences among the communities considered. Since rarity has unusual appeal to humans, this index identifies communities of particular interest to users and managers. Vegetational composition upon which all indices are based is reported for the 10 major communities of ZNP. Procedures for computing each index are given.

Most conservation efforts of the past have focused on individual species. Such activities have emphasized the life cycle, reproductive biology, and habitat requirements of individual species. Those studies have often resulted in greatly enlarged populations and improved habitat for species in danger of extinction. Nevertheless, conservationists have increasingly called for preservation of entire biotic communities and habitats associated with them (Owen and others 1998).

A large literature has developed around the general theme of preservation of individual species. Included are rigorous methods for quantifying genetic diversity of individuals and populations, for estimating population size, and for evaluating the likelihood of extinction in future time periods of variable length (Primack 1998). In contrast, little attention has been directed to procedures for quantifying the degree to which various natural communities are threatened, the likelihood that they harbor rare species or contain unique genotypes, or are the habitat of species vulnerable to extinction. Greater effort has been devoted to development of procedures for describing characteristics of individual plant communities (Whittaker 1975).

This paper represents an attempt to quantify various aspects of the biodiversity of the plant communities of Zion National Park (ZNP). Our analyses are based on a large vegetational sample drawn from throughout ZNP, an area that covers approximately 60,000 ha in southwestern Utah. Since the Park extends over an area of variable geology and diverse topography, plant communities adapted to very different microenvironments are represented in the sample.

Methods

Our sample is based on 0.01 ha macroplots placed at the intersection of a 1.61 km (1.0 mile) grid across the entire surface of ZNP. In all, 309 macroplots were thus sampled within the Park. Since essentially the entire area of concern has been covered by the United States land survey, we used U.S. Geological Survey, 7.5 min quadrangle, topographic maps to locate the site of each section corner in the field. Workers visited each corner and delimited a circular macroplot centered on the corner.

At each section corner (or as near that point as topography would permit), a macroplot was inventoried using procedures similar to those developed by workers at the Zurick-Montpellier School of Phytosociology (Braun-Blanquet 1932). At each plot, all vascular species rooted therein were recorded and foliage cover (projected crown) of each was visually estimated. Workers also recorded elevation, aspect, and slope at each plot. Geologic substrate at the site, seral state of the vegetation, and evidence of prior disturbing influences (such as domestic grazers, logging, abandoned roads or trails, wildfire, and so forth) on the plot were recorded. Finally, the worker made an estimate of composition of the living cover (percentage of the total contributed by lifeform groups such as trees, shrubs, perennial broadleaved-herbs or graminoids, annuals, or nonvascular species) and the abiotic surface (relative cover of bare soil, consolidated rock, rock pavement, boulders, or litter).

Since some of the plant communities of occurrence within ZNP are of very limited area there (for example, abandoned fields, riparian forests, and hanging gardens), we have arbitrarily selected sampling points in those community types that do not fall on section corners. All well-developed hanging gardens encountered that approached 0.01 ha in area were sampled. Within the abandoned fields and riparian

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community types, a stratified-random method was used to select additional macroplot locations when section corners within the type were few in number. Plant nomenclature follows Welsh and others (1993).

Since our study utilized concepts and indices not commonly employed among land managers, we have provided a list of terms and indices used as we prepared this manuscript. Words and terms are defined and procedures given for computing the four indices that we use (table 1).

Results

We have recognized 10 plant communities in ZNP (table 2). Criteria for recognition were those commonly used by land managers in the area. Most of the community types could be justifiably further subdivided, but such fragmentation quickly results in sample sizes that are too small to permit reliable statistical tests of differences

Table 1—Definitions of words or terms used to describe the various indices computed to characterize aspects of plant diversity of the several plant communities recognized in Zion National Park. Procedures for computing the four indices are also given.

Word or term	Definition or computational procedures
Modal species	Prevalent species that reach maximum regional commonness in the community in question (Curtis 1959).
Percentage presence	The percentage of all macroplots placed in each community type that included rooted individuals of species X.
Prevalent species	The commonest species in a particular community type selected in a number equal to the species density for that community. All species encountered in the full sample for a community are arranged in decreasing order of percentage presence. Prevalents are selected from the top of that list in a number equal to average species density for the community. The number is rounded up to the nearest whole number (Curtis 1959).
Species density	The average number of species occurring in the macroplots of any particular community type (Curtis 1959).
Index Computation	
Diversity	Diversity (D) = $1/\sum pi^2$ where p = the decimal proportion of the sum of percent of presence of all prevalent species in the community contributed by each prevalent species. D is an approximation of the number of species of equal commonness in the community (MacArthur and Wilson 1962).
Distinctiveness	Distinctiveness = $\frac{\text{no. modal prevalent species} \times 100}{\text{no. prevalent species}}$ (Curtis 1959)
Rarity	The number of occurrences of each community prevalent in the entire study (309 macroplots) is expressed as a decimal fraction of the total of plots observe (309). The reciprocal of each fraction is taken. These reciprocal values are summed across all prevalent species of any given community and their average value is obtained. That average is taken as the rarity index for that community.

Table 2—The 10 plant communities recognized in Zion National Park, the gross characteristics of their environments, the relative area of each within the Park, and sample size by community are presented here. Aspects of the soils associated with each community can be found in Mortensen and others (1977).

Community	Percent of Park area	Average elevation (m)	Predicted annual precipitation[a] (cm)	Percent of coverage of bare rock	No. macro-plots
Blackbrush (CORA)	1.7	1,261	~25.4	10.9	10
Abandoned fields	0.6	1,366	~25.4	0.1	6
Riparian	1.5	1,490	~25.4	12.6	19
Hanging gardens	Trace	1,505	~25.4	27.2	23
Sagebrush (ARTR)	2.4	1,510	~32.6	4.9	7
Juniper- pinyon (JUOS-PIMO)	46.5	1,700	~38.1	20.1	108
Rock crevice	19.1	1,770	~38.1	60.6	25
Mountain brush	13.9	1,946	~45.6	8.5	57
Ponderosa pine (PIPO)	8.3	1,970	~45.6	14.2	33
Douglas-fir-white fir (PSME-ABCO)	6.1	1,997	~50.8	9.3	21

[a] Based on a regression equation developed by Harper (1993) using data from stations of known elevation and precipitation in the general region of ZNP.

observed between subunits. We have elsewhere (Harper 1993) suggested habitat-type subdivisions for the major communities that are likely to be useful for management.

The communities recognized in the Park range in elevation from an average of 1,261 m (blackbrush or *Coleogyne ramosissima* community) to almost 2,000 m (Douglas-fir/white fir or *Pseudotsuga menziesii*/*Abies concolor* forests). Precipitation averages from about 25 cm per year in the blackbrush shrub deserts to over 50 cm per year in the mixed conifer forests (table 2). Since the Park covers an area of rugged, rapidly eroding terrain, most of the plant communities occur on very rocky sites. The rock crevice community, as recognized here, averaged over 60 percent of bare rock on constituent sites, and only four communities showed less than 10 percent bare rock (table 2).

The commonest communities in the Park were juniper-pinyon (46.5 percent of the surface area of the Park), rock crevice (19.1 percent of the Park), and mountain brush (13.9 percent). Five communities individually covered less than 3.0 percent of the area of the Park: uncommon communities arranged in order of increasing area included hanging gardens, abandoned fields, riparian, blackbrush, and sagebrush (table 2).

We summarize data for occurrence (percent presence in the macroplots of each community type) of all prevalent species in the 10 communities recognized in the Park in table 3. Although 929 plant taxa have been collected in ZNP [based on a checklist prepared by Kaye Thorne (1989) and collections made during the course of the field work for this report], only 514 taxa occurred in the macroplots inventoried

Table 3—Prevalent species performance in 10 plant communities of Zion National Park. The values reported are percentage occurrence in the 0.01 ha (0.025 acre) macroplots placed in each community. Values are underlined in communities where the species is prevalent and underlined and bold where the species are both prevalent and modal. See table 1 for definitions of the terms prevalent and modal. All results reported here are derived from a report by Harper (1993).

Species	CORA	Aband. fields	Riparian	Hang. garden	ARTR	JUOS PIMO	Rock. crev.	Mt. brush	PIPO	PSME ABCO
Woody										
Abies concolor			16	20			4	5		**52**
Acer grandidentatum			37	40		1		14	6	**43**
A. negundo			**63**	60			4	2		10
Amelanchier utahensis				40	14	**65**	56	49	64	62
Arctostaphylos patula			5	20		38	60	35	**61**	10
Arenaria macradenia			11			16		18	**24**	19
Artemisia tridentata	10		5		**100**	26		19	18	
Atriplex canescens		**33**			14	1				
Cercocarpus intricatus			5	20		5	**84**	7	21	24
Chrysothamnus nauseosus	20	17	16		**43**	13	16	16	12	5
Coleogyne ramosissima	**100**					5		2		
Ephedra nevadensis	**40**					9	4			
Fraxinus anomala			5	20		27	12	12		**29**
F. velutina			**32**							
Gutierrezia microcephala	**80**	50	21	20						
G. sarothrae					**71**	44	36	21	21	
Haplopappus scopulorum					14	19	4	12	15	**38**
Holodiscus dumosus			16	20			32	2	3	**33**
Juniperus osteosperma	60	33		20	14	**82**	12	19	18	
J. scopulorum			5	20		1		19	9	**24**
Lycium pallidum		**33**								
Mahonia repens			16	20		6		12	12	**38**
Opuntia macrorhiza	30		11		29	53	**56**	44	49	24
O. phaeacantha		17			**29**	2		5	3	
Pachystima myrsinites			11	60		12	4	23	24	**71**
Petrophytum caespitosum			5	**39**			28		3	10
Pinus edulis				20		**34**	4	12	15	19
P. monophylla	40		5			**53**		12		
P. ponderosa			5	20		2	56	11	**97**	29
Phlox austromontana			5		14	15	20	30	**39**	5
Populus fremontii			**32**							
Pseudotsuga menziesii			11	40			4	2	3	**48**
Psorothamnus fremontii	**30**				14	5				
Purshia tridentata			5	20		14	4	19	**30**	5
Quercus gambelii		17	37	60		34	24	75	67	**86**
Q. trubinella			5			30	**32**	16	12	
Symphoricarpos oreophilus			11			13	4	46	18	**52**
Tamarix ramosissima			**21**		14					
Yucca angustissima			5			17	20	14	**24**	10

(con.)

Table 3 (Con.)

Species	CORA	Aband. fields	Riparian	Hang. garden	ARTR	JUOS PIMO	Rock. crev.	Mt. brush	PIPO	PSME ABCO
Monocotyledonous herbs										
Agrostis stolonifera				**28**						
Aristida purpurea	10	**33**	5		14	11	24	2	9	
Bromus ciliatus		17	**37**	20				2		14
B. diandrus		17	**42**					2		
B. rubens	**80**	17				25	12	5	3	
B.tectorum	70	**100**	47		86	54	24	37	33	10
Calamagrostis scopulorum				**79**						
Calochortus flexuosus	**40**					2				
Carex curatorum				**28**						
C. rossii			5	20		13	48	26	42	**57**
Elymus elymoides	20		11		**57**	26	12	14	9	10
Hilaria jamesii	**60**	17			43	22	4	4		
Muhlenbergia thurberi				**33**			32			
Poa bigelovii	**30**					3		2		
P. fendleriana		17	47		14	69	84	74	**85**	71
P. pratensis			**21**			1		7	6	14
Sporobolus cryptandrus	20	**67**	21		29	11	12	26	12	5
Stipa hymenoides	**40**		21	20	29	32	16	19	9	5
Vulpia octoflora	**70**	17	16		43	35	44	14	24	5
Dicotyledonous Herbs										
Antennaria rosulata				**20**		1		2		
Apocynum androsaemifolium				**40**						
Aquilegia chrysantha				**50**						
A. formosa				**50**						
Arabis perennans	20		32			**57**	36	47	36	38
Arenaria fendleri							**64**	7	18	
Artemisia dracunculus		**33**			14	2		11	3	
A. ludoviciana		17	**42**	20		17	12	25	12	14
Aster glaucodes			5	**40**		2		2		
A. herperius				**72**						
Astragalus nuttallianus		**40**				4				
Castilleja scabrida							**60**			
Chaenactis douglasii						18	**36**	12	30	10
Cirsium arizonicum				**26**		3	8	7	9	
Comandra umbellatum						11	16	19	**24**	10
Cryptantha (unknown annual)	**50**				14	32	32	18	12	
C. confertiflora							**36**			
Descurainia pinnata	**40**				29	18		5		5
Dodecatheon pulchellum				**44**						
Draba asprella			16	20		4	32	11	15	**38**
D. verna	**50**		11		14	21	12	9	6	
Eriastrum eremicum	**30**					3				
E. spariflorum	10		5		**29**	7				
Erigeron canaani			5				**28**	4	9	24
E. divergens					**29**	8		5	9	
E. sionis	10					**29**	20	12		5
E. utahensis				**39**						
Eriogonum palmerianum	**50**					8		2		
E. racemosum	10		26	20		16	16	**33**	27	24
Erodium cicutarium	10	**50**			14					
Erysimum asperum			11			27	8	**32**	30	19
Eupatorium herbaceum			21	**40**				2		19
Euphorbia albomarginata	10	**67**	11	20	14	9	4		6	
Gilia inconspicua	**90**		11			49	16	25	12	
Heterotheca villosa		33	37	20	14	14	**64**	32	49	10
Heuchera rubescens			11				8	2		**29**
Lactuca serriola		**50**	16		14	3		4		
Lobelia cardinalis				**56**						
Machaeranthera canescens			5			11	8	**32**	15	5
Mimulus cardinalis			**72**							
Oenothera pallida	**33**					4				
Pectocarya setosa					**29**	1				

(con.)

Table 3 (Con.)

Species	CORA	Aband. fields	Riparian	Hang. garden	ARTR	JUOS PIMO	Rock. crev.	Mt. brush	PIPO	PSME ABCO
Penstemon humilis							**36**			
P. laevis							**40**			
P. rostriflorus			26			7	**28**	18	6	19
Phacelia heterophylla			26	20		8	12	**32**	9	19
Polygonum douglasii						7	12	28	**33**	14
Senecio multilobatus			16	20		36	40	46	**52**	33
S. spartioides			**37**		29	4		14	9	14
Smilacina stellata				**33**						
Solidago sparsiflora			26	**40**		1	28	21	18	19
Stellaria jamesiana			5					18	3	**29**
Sphaeralcea grossularifolia		**33**				5		2		
Stephanomeria tenuifolia			32	20		13	**48**	18	24	19
Streptanthus cordatus	10					**31**		4		10
Thelypodium laxiflorum			**21**			1		4		5
Tragopogon dubius		**67**						4	3	5
Vicia americana			5	20		10		28	12	**48**
Zauchneria latifolia			**26**			1	12	4	6	14
Nonseed plants										
Adiantum capillus-veneris				**89**						
Cystopteris fragilis			**21**	20				2		
Equisetum hyemale		17	**26**	20					3	
No. prevalent species	19	16	22	23	14	22	24	23	22	22
No. modal species	17	12	11	18	8	7	13	4	10	16
No. prevalents encountered	32	25	66	48	32	81	64	83	65	60

for this study. Furthermore, only 117 different species were recognized as prevalent species in the 10 communities of concern (table 3). These data emphasize that most species in the flora of ZNP are uncommon. Only seven species occurred in over 100 macroplots. In order of decreasing commonness, those species are *Poa fendleriana* (189 macroplots), *Amelanchier utahensis, Quercus gambelii, Bromus tectorum, Arabis perennans, Opuntia macrorhiza*, and *Juniperus osteosperma* (115 macroplots). All are native perennials with the exception of *Bromus tectorum,* which is both an annual and an alien to North America. Woody species are over-represented in this group of seven common species, since woody taxa account for only 19.6 percent of the species of occurrence in the full flora of the Park.

The data (table 3) show that only *Bromus tectorum* was a prevalent species in seven plant communities. Another five species were prevalents in six different plant communities. That group of broadly adapted, abundant species consisted of *Amelanchier utahensis, Opuntia macrorhiza, Quercus gambelii, Poa fendleriana*, and *Arabis perennans.*

The vast majority of prevalents (71 species) were so narrowly adapted that they were designated as prevalent species in a single community only. Such data further emphasize that most species are uncommon in any region.

Analysis shows that woody species are significantly more likely to be prevalent (39 of 117 prevalents) than one would expect by chance given the incidence of woodiness in the Park flora (19.6 percent of the 929 taxa). Wind pollinated taxa are also significantly more likely to be prevalents (39 of 117 prevalents) than expected by chance, since only 23.4 percent of the taxa in the flora were considered to be wind pollinated. Alien species were about equally represented in the Park flora (9.8 percent) and among the prevalents (9 taxa) listed in table 3.

In table 4, we present values for four different indices considered to reflect diversity or rarity characteristics inherent in each plant community considered. It is immediately clear that neither the average number of species per macroplot nor the MacArthur-Wilson diversity index show much difference among the 10 plant communities. By both indices, sagebrush and abandoned field communities have the lowest values observed for the 10 communities.

In contrast, both the distinctiveness index and especially the rarity index show large differences among the communities considered (table 4). The distinctiveness index indicates the percentage of prevalents species achieve maximum regional commonness in that community. Three communities show less than 40 percent of their prevalents reaching maximum regional abundance in that community (the mountain brush, ponderosa pine, and juniper-pinyon communities). Other communities such as hanging gardens, blackbrush, and abandoned fields have over 80 percent of their prevalents achieving maximum regional commonness in that community (table 4).

The rarity index shows low values for the juniper-pinyon, mountain brush, ponderosa pine, rock crevice, and Douglas-fir-white fir communities (table 4). Low rarity scores indicate that few of the prevalent species in a community are otherwise rare in the region. Three communities (hanging gardens, sagebrush, and abandoned fields) had very high values for the rarity index. High rarity values arise when many of the commonest species in the community are uncommon in all other communities in the region.

Table 4—Four indices reflective of phytodiversity or species rarity are presented here for the 10 major plant communities of Zion National Park.

	Indices			
Plant community	**Average no. species per macroplot**	**MacArthur-Wilson diversity**	**Distinctiveness**	**Rarity**
Blackbrush	19	17.4	81	14.4
Abandoned fields	16	14.8	82	29.3
Riparian	22	17.5	60	18.3
Hanging gardens	23	20.8	96	37.2
Sagebrush	14	12.8	53	31.8
Juniper-pinyon	22	19.5	39	4.0
Rock crevices	24	20.9	54	6.8
Mountain brush	23	18.2	17	4.4
Ponderosa pine	22	18.1	38	4.5
Douglas-fir-white fir	22	19.1	60	8.5

Discussion

The prevalent species concept as formulated by Curtis (1959) provides an objective method for identifying the important species of any particular community. Since there are usually more species encountered in large samples of any community than one can list and discuss within the space limitations of a published report, there is a definite need for an objective method for selecting a manageable number of species representative of any community type. By focusing on the commonest species, as the prevalent species concept does, one identifies those species from the regional flora that are best adapted to the unique environments associated with a particular community type. Our experience has demonstrated that one is often unable to identify any behavior characteristic that is statistically over- or under-represented in a given community type relative to the representation of that character in the regional flora, when every species encountered in the community sample is used for the test. However, when such tests are based upon prevalent species, various behavioral traits (such as plant longevity, pollinating agent, or lifeform-class) can be demonstrated to diverge significantly from their commonness in the regional flora. Apparently, species that survive only in rare microsites within a community or that represent chance introductions that will not long survive in the community weaken analyses based upon all species encountered in a sample.

The foregoing discussion illustrates the desirability of simultaneously studying the entire flora and the full vegetational complex of an area. Without a regional checklist of species occurring in a region, one cannot determine whether any particular plant characteristic is being selected for or against in a particular environmental complex. However, when both a regional checklist and prevalent species list exists for a particular community types in that region, it is possible to use Chi-square tests to determine whether a given plant character is over- or under-represented in a particular community. In ZNP, for example, the checklist shows that 236 of the 929 species in the Park are annuals or biennials. In the lowest elevation and driest plant community (blackbrush), 10 of 19 prevalent species are annuals. A Chi-square test suggests that the annual habit is significantly over-represented in the blackbrush community, given the incidence of annuals in the regional flora (SX^2 value = 10.4, $p < 0.01$). By contrast, annuals are significantly less common than one would expect by chance (none of the 22 prevalents are annuals) in the Douglas-fir-white fir community, the highest elevation community in ZNP (SX^2 value = 7.4, $p < 0.01$).

Although Curtis (1959) made no inferences about genetic variability and modal species, we suggest that modal species are likely to harbor more genetic diversity than non-modal species in the community of modality. We draw that inference from the fact that the origin of new mutations is directly proportional to the size of a population (Dobzhansky 1951). In addition, as Wright (1931) theorized, the rate of gene loss by “drift” from a population is inversely proportional to population size. Consequently, we suggest that genetic diversity should be greatest for a species where it is modal (regionally most common). Furthermore, those communities in which a large percentage of the prevalents are also modal (that is, community distinctiveness is high) are likely to harbor more genetic diversity (summed across all constituent species) than communities having low distinctiveness indices (see table 1 for definitions). Again, Curtis (1959) makes no connection between community distinctiveness and genetic diversity inherent in a community, but we suggest that such a correlation is likely.

The rarity index varies in magnitude according to the degree to which species common (prevalent) in one community are uncommon in other communities of the region. Since rarity is of unusual interest to many users of plant communities, managers would benefit from an index that objectively quantified the amount of rarity in communities. The rarity index of table 1 provides a means for ranking local communities in respect to the degree to which they harbor species that are elsewhere uncommon in the region. Since the index is based on prevalent species, it also identifies those communities in which regionally uncommon species maintain larger populations and are likely to generate and conserve genetic diversity important for their continued persistence in the region.

Finally, we acknowledge that the distinctiveness and the rarity indices are positively correlated, but their relationship is sufficiently diffuse that we recommend that both be used to describe plant communities. In respect to distinctiveness for example, the sagebrush community ranked seventh from the top, but by the rarity index, sagebrush communities rank second from the top. Both indices provide information useful to managers, and since their values sometimes differ markedly for the same community, we recommend that both be used to describe communities.

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Plant Diversity at Box-Death Hollow Wilderness Area, Garfield County, Utah

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Abstract—"The Box" is a canyon located in the western portion of Box-Death Hollow Wilderness Area, Garfield County, southern Utah. The objectives of this study included: (1) collect, identify and make a checklist of the species of vascular plants found in "The Box," (2) search for threatened and endangered species within the area, (3) provide an opportunity for high school students to develop research skills that contribute to the reservoir of scientific information. During a period of 2 years, students of the Provo High School Botany Club, the club advisor, and others collected and identified 304 species in 63 families. Twenty plant taxa collected during this study had not previously been reported for Garfield County, UT. Species-area relationships at this area are compared to selected locations in Utah.

"The Box" is a north-south trending canyon which begins in an aspen-fir forest near "Hells Backbone" road at an elevation of 2,450 m in the Box-Death Hollow Wilderness area, Garfield County, Utah. From this elevation the forest gradually slopes downward to the riparian community adjacent to Pine Creek. Pine Creek is a clear, fast flowing stream of moderate size. The stream flows through a canyon of sandstone walls that become progressively higher and closer together, forcing the stream-side trail to cross the creek over 40 times. It is impossible to hike through the 16 km canyon without doing some wading. The southern end of the canyon, at 2,040 m, opens to a relatively level pinyon-juniper-sagebrush community seven miles north of Escalante, Utah. The Pine Creek gaging station is located near the canyon mouth.

The rocks of the canyon are sedimentary and of Jurassic and Cretaceous age. The soils are derived primarily from sandstone. They include such soil type as the Mikim clay loam, Yarts sandy loam and Mepsum loamy fine sand (Stokes 1986).

The warmest month is July with an average temperature of 22.4EC. The coldest month is January with an average temperature of –2.4EC. The average annual precipitation for the period 1901 to 1996 totaled 25.5 cm at Escalante. An average of 77.2 cm of snow falls each year at Escalante (Pope and Brough 1986).

Under the direction of Janet Cooper, the Provo High School Botany Club initiated this study in the fall of 1993. During the following 2 years (1994 and 1995) five collection trips were taken at different times of the year to provide a reliable sample of the canyon's flora. Each collection trip emphasized a different section of the canyon, but on each trip, specimens of species previously unknown in the area were collected throughout the canyon. Plants collected were either immediately identified and pressed or collected in plastic bags and pressed as soon as the group arrived back at camp. Identification and classification followed "A Utah Flora" (Welsh and others 1993). "The Intermountain Flora" (Cronquist and others 1989) was used as a supplementary guide for plant identification.

This project provides the first thorough description of the vascular flora occurring in the study area. The checklist of 304 species in 63 families is included in this report as table 1. Twenty taxa on the list have not previously been reported for Garfield County (table 2). The six largest families include: Asteraceae (50 species), Poaceae (36 species), Rosaceae (16 species), Scrophulariaceae (16 species), Fabaceae (15 species), and Brassicaceae (15 species). Voucher specimens are deposited in the herbarium at Utah Valley State College.

The relative area and floristic richness of the Box Wilderness area is compared with the same characteristics for seven other locations in Utah (table 3). The relationship between species and land area is graphically shown in figure 1. The number of named plant taxa is somewhat linearly related to the logarithm (base 10) of area sampled. The regression of species on the area is statistically significant ($p < 0.05$), but the regression accounts for only slightly more than 50 percent of the variation observed. Nevertheless, the regression line does serve a useful function in that it shows locations that fall above (more species than expected for their area in this analysis) or below the regression line. Locations falling below the line may be poorly collected or have inherently low biodiversity. A reverse explanation could be offered for locations falling above the regression line.

Several points seem worthy of note in figure 1: (1) The Box Wilderness study area appears to be quite thoroughly collected, since it is not unusually complex ecologically in this suite of locations. (2) Two locations below the regression line (the Desert Experimental Range and Tooele County) are more arid than average for this set of locations and somewhat less topographically variable. (3) Zion National Park and Washington County fall far above the regression line: both are topographically complex and well collected.

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Table 1—Vascular plant checklist for “The Box”, Death Box Hollow Wilderness Area, Garfield County, UT. Sixty three families, 304 species. LB = plants collected in the lower part of “The Box” (elevation 2,040 to 2,200 m); MB = plants collected in the middle part of “The Box” (elevation 2,200 to 2,500 m); UB = plants collected in the upper part of “The Box” (elevation >2,500 m).

Botanical name	Location
Division Lycopodiophyta	
Family Selaginellaceae	
Selaginella mutica D. C. Eaton	LB
Division Equisetophyta	
Family Equisetaceae	
Equisetum arvense L.	LB, UB
Equisetum hyemale L.	UB
Equisetum laevigatum A. Br.	
Division Polypodiophyta	
Family Polypodiaceae	
Cystopteris fragilis (L.) Bernh.	MB
Division Pinophyta	
Family Cupressaceae	
Juniperus communis L.	UB,MB
Juniperus osteosperma (Torr.) Little	LB
Juniperus scopulorum Sarg.	LB
Ephedra viridis Cov.	LB
Family Pinaceae (pine)	
Picea pungens Engelm.	LB,MB
Pinus edulis Engelm.	LB, MB
Pinus ponderosa Lawson	LB,MB
Pseudotsuga menziesii (Mirbel) Franco	UB, MB
Division Magnoliophyta	
Class Magnoliopsida	
Family Aceraceae	
Acer glabrum Torr.	UB, MB
Acer negundo L.	MB
Family Amaranthaceae	
Amaranthus retroflexus L.	LB
Family Anacardiaceae	
Rhus aromatica Ait var. *trilobata* (Nutt.) Gray	LB
Family Apiaceae	
Angelica pinnata Wats.	UB
Conioselinum scopulorum (Gray) Coult & Rose	UB
Cymopterus lemmonii (Coult.& Rose) Dorn	LB
Cymopterus purpureus Wats.	LB
Ligusticum porteri Coult. & Rose	UB
Lomatium latilobum (Rydb.) Mathias	LB
Osmorhiza depauperata H. & A.	UB
Family Apocynaceae	
Apocynum androsaemifolium L.	LB
Family Asclepiadaceae	
Asclepias asperula (Decne.) Woodson	LB
Family Asteraceae	
Achillea millefolium L.	UB
Ambrosia acanthicarpa Hook.	
Antennaria neglecta Greene	LB
Antennaria parvifolia Nutt.	MB
Artemisia bigelovii Gray	LB
Artemisia campestris L.	LB
Artemisia carruthii Wood ex Carruth	LB
Artemisia frigida Willd.	LB
Artemisia ludoviciana Nutt.	UB
Artemisia tridentata var. *tridentata* Nutt.	LB
Aster ascendens Lindl.	MB
Aster chilensis Nees	UB
Aster foliaceus Lindl. in DC. var. *parryi* (D.C. Eaton) Gray	UB
Aster glaucodes Blake	UB
Aster occidentalis (Nutt.) T. & G.	LB
Bahia dissecta (Gray) Britt.	
Brickellia grandiflora (Hook.) Nutt.	
Brickellia microphylla (Nutt.) var. *scabra* Gray	LB
Chaetopappa ericoides (Torr.) Nesom	LB
Chrysothamnus linifolius Greene	LB
Chrysothamnus nauseosus (Pallas) Britt var. *arenarius* (L.C. Anderson)	LB
Chrysothamnus viscidiflorus (Hook.) Nutt.	UB
Cirsium neomexicanum var. *utahensis* (Petrak) Welsh	LB
Erigeron abajoensis Cronq.	UB
Erigeron awapensis Welsh	UB
Erigeron flagellaris Gray	LB
Erigeron pumilus Nutt.	LB
Gutierrezia sarothrae (Pursh) Britt. & Rusby	UB
Helenium hoopesii Gray	UB
Helianthella microcephala Gray	LB
Heterotheca villosa (Pursh) Shinn. var. *hispida* (Hook.) Harms	LB
Hymenopappus filifolius Hook. var. *cinereus* (Rydb.) Johnston	LB
Hymenoxys acaulis (Pursh) Parker var. *arizonica* (Greene) Parker	LB
Hymenoxys acaulis (Pursh) parker var. *nana* Welsh	LB
Hymenoxys richardsonii (Hook.) Cockerell	UB
Iva axillaris L.	UB
Machaeranthera bigelovii (Gray) Green	
Machaeranthera canescens (Pursh) Gray var. *canescens*	UB,LB
Machaeranthera grindelioides (Nutt.) Shinn.	LB
Psilostrophe sparsiflora (Gray) A. Nels.	LB
Senecio douglasii DC.	MB
Senecio eremophilus Richards.	UB
Senecio multilobatus T. & G.	UB
Senecio spartioides T. & G. var. *spartioides*	LB
Stephanomeria spinosa (Nutt.) Tomb	UB
Stephanomeria tenuifolia (Torr.) Hall	LB
Taraxacum officinale Weber ex Wiggers	UB
Tetradymia canescens DC.	UB
Townsendia incana Nutt.	LB
Tragopogon dubius Scop.	LB
Family Berberidaceae	
Mahonia repens (Lindl.) G. Don	MB
Family Betulaceae	
Betula occidentalis Hook.	UB
Family Boraginaceae	
Cryptantha confertiflora (Greene) Payson	LB
Cryptantha fulvocanescens (Wats.) Payson	LB
Cryptantha pterocarya (Torr.) Greene	LB
Lappula occidentalis (Wats.) Greene	LB
Lithospermum multiflorum Torr. ex A. Gray	UB,LB
Lithospermum ruderale Dougl. ex Lehm	LB
Mertensia arizonica Greene	MB
Family Brassicaceae	
Arabis demissa Greene	MB
Arabis holboellii Hornem. var. *pinetorum* (Tidestr.) Rollins	LB
Cardamine cordifolia Gray	UB
Chorispora tenella (Pallas) DC.	LB
Descurainia californica (Gray) Schulz	LB
Descurainia richardsonii (Sweet) Schulz var. *sonnei* (Robins.) C.L.Hitchc	LB
Draba sp.	UB
Lepidium montanum Nutt. var. *jonesii* (Rydb.) C.L. Hitchc.	LB
Lesquerella intermedia (Wats.) Heller	LB
Lesquerella ludoviciana (Nutt.) Wats.	MB
Lesquerella rectipes Woot. & Standl.	LB

(con.)

Table 1 (Con.)

Botanical name	Location
Physaria newberryi Gray	LB
Streptanthella longirostris (Wats.) Rydb	LB
Streptanthus cordatus Nutt. ex T. & G.	LB
Thlaspi montanum L. var. *montanum*	LB
Family Cactaceae	
Echinocereus triglochidiatus Engelm.	LB
Opuntia fragilis (Nutt.) Haw.	LB
Opuntia phaeacantha Engelm.	LB
Opuntia polyacantha Haw.	LB
Family Campanulaceae	
Campanula parryi Gray	LB
Campanula rotundifolia L.	LB
Family Capparaceae	
Cleome lutea Hook.	LB
Family Caprifoliaceae	
Lonicera involucrata (Richards.) Banks ex Sprengel	UB
Sambucus caerulea Raf.	LB
Sambucus racemosa L.	MB
Symphoricarpos oreophilus Gray	UB
Family Caryophyllaceae	
Arenaria fendleri Gray	LB
Arenaria macradenia Wats.	LB
Stellaria longipes Goldie var. *longipes*	UB
Family Chenopodiaceae	
Chenopodium fremontii Wats.	UB
Chenopodium graveolens var. *neomexicana* (Aellen) Aellens	LB
Chenopodium leptophyllum (Moq.) Wats.	LB
Monolepis nuttalliana (Schultes) Greene	LB
Salsola pestifer A. Nels.	LB
Family Cornaceae	
Cornus sericea L.	UB, MB
Family Elaeagnaceae	
Elaeagnus angustifolia L.	LB
Shepherdia canadensis (L.) Nutt.	UB
Shepherdia rotundifolia Parry	LB
Family Ericaceae	
Arctostaphylos patula Greene	LB
Family Euphorbiaceae	
Euphorbia brachycera Engelm. in Emory	MB
Euphorbia micromera Boiss.	LB
Family Fabaceae	
Astragalus argophyllus Nutt. ex T. & G.	LB
Astragalus ceramicus Sheldon	LB
Astragalus kentrophyta Gray	LB
Astragalus mollissimus Torr.	LB
Astragalus subcinereus Gray	LB
Astragalus utahensis (Torr.) T. & G.	LB
Dalea searlsiae (Gray) Barneby.	LB
Lotus utahensis Ottley	LB
Lupinus sericeus Pursh	LB
Medicago sativa L.	LB
Melilotus albus Desr. ex Lam.	LB
Melilotus officinalis (L.) Pallas	LB
Oxytropis deflexa (Pallas) DC. var. *sericea* T. & G.	UB
Thermopsis montana Nutt. in T. & G.	LB
Trifolium repens L.	UB
Family Fagaceae	
Quercus gambelii Nutt.	LB
Family Gentianaceae	
Swertia radiata (Kellogg) Kuntze	UB
Family Geraniaceae	
Geranium caespitosum James	LB, UB
Geranium richardsonii Fisch. and Trautv.	UB
Geranium viscosissimum Fisch. and Mey.	LB
Family Hydrophyllaceae	
Phacelia ivesiana Torr. in Ives var. *ivesiana*	LB
Family Lamiaceae	
Mentha arvensis L.	LB
Monardella odoratissima Benth	UB
Family Malvaceae	
Sidalcea candida Gray	UB
Sphaeralcea coccinea (Nutt.) Rydb	LB
Sphaeralcea parvifolia A. Nels.	LB
Family Monotropaceae (Indian-pipe)	
Pterospora andromeda Nutt.	UB
Family Nyctaginaceae	
Abronia fragrans Nutt. ex Hook	LB
Boerhaavia spicata var. *torreyana* Wats.	LB
Mirabilis linearis var. *decipiens* (Standley) Welsh	
Mirabilis linearis (Pursh) Heimerl var. *linearis*	LB
Mirabilis oxybaphoides (Gray) Gray in Torr	LB
Family Oleaceae	
Fraxinus anomala Torr. ex Wats.	LB
Family Onagraceae	
Epilobium angustifolium L.	UB
Epilobium halleanum Hausskn.	LB
Oenothera caespitosa var. *marginata* (Nutt.) Munz.	LB
Oenothera flava (A. Nels.) Garrett var. *flava*	UB
Oenothera pallida Lindl.	LB
Family Plantaginaceae	
Plantago patagonica Jacq.	LB
Family Polemoniaceae	
Gilia aggregata (Pursh) Sprengel	MB
Gilia congesta Hook. var. *frutescens* (Rydb.) Cronq.	LB
Leptodactylon pungens (Torr.) Nutt.	LB
Linanthastrum nuttallii (Gray) Ewan	LB
Linanthus bigelovii (Gray) Greene	
Phlox pulvinata (Wherry) Cronq.	LB
Phlox tumulosa Wherry	LB
Family Polygalaceae	
Polygala subspinosa Wats.	LB
Family Polygonaceae	
Eriogonum alatum Torr. in Sitgr.	LB
Eriogonum cernuum Nutt.	LB
Eriogonum palmerianum Reveal in Munz	LB
Eriogonum racemosum Nutt.	LB
Eriogonum subreniforme Wats.	LB
Rumex patentia L.	UB
Family Portulaceae	
Portulaca oleracea L.‘	LB
Family Primulaceae	
Androsace septentrionalis L.	UB
Primula parryi Gray	LB
Family Pyrolaceae	
Pyrola chlorantha Swartz	UB
Pyrola secunda L.	UB
Family Ranunculaceae	
Aconitum columbianum Nutt. in T. & G.	UB
Actaea rubra (Ait.) Willd.	UB
Clematis columbiana (Nutt.) T. & G.	UB
Clematis ligusticifolia Nutt.	LB
Ranunculus cymbalaria Pursh	UB
Ranunculus inamoenus Greene	UB
Ranunculus repens L.	UB
Thalictrum fendleri Englem. ex Gray	UB,MB
Family Rhamnaceae	
Ceanothus fendleri Gray	MB

(con.)

Table 1 (Con.)

Botanical name	Location
Family Rosaceae	
Amelanchier alnifolia (Nutt.) Nutt.	UB
Amelanchier utahensis Koehne	LB
Cercocarpus intricatus Wats.	LB
Fragaria virginiana Duchesne	UB
Geum macrophyllum Willd.	UB
Holodiscus dumosus (Nutt.) Heller	MB
Physocarpus alternans (Jones) J.T. Howell	MB
Potentilla concinna Richards	UB,MB
Potentilla crinita Gray	UB
Potentilla fruticosa L.	UB
Potentilla ovina Macoun	UB
Prunus virginiana L.	UB,MB
Purshia mexicana (D. Don) Welsh var. *stansburyana* (Torr.) Welsh	LB,MB
Purshia tridentata (Pursh) DC.	MB
Rosa woodsii Lindl.	LB
Rubus idaeus L.	MB
Family Salicaceae	
Populus angustifolia James	LB,MB
Populus balsamifera L. var. *trichocarpa* (T. & G.) Brayshaw	MB
Populus tremuloides Michx.	UB,MB
Salix bebbiana Sarg.	UB
Salix boothii Dorn	MB
Salix brachycarpa Nutt.	UB
Salix drummondiana Barratt in Hook.	MB
Salix exigua Nutt.	LB
Salix geyeriana Anderss.	UB
Family Santalaceae	
Comandra umbellata (L.) Nutt.	LB
Family Saxifragaceae	
Fendlerella utahensis (Wats.) Heller	LB
Heuchera parvifolia Nutt. in T. & G. var. *utahensis*	LB
Heuchera rubescens Torr. in Stansbury	MB UB
Ribes cereum Dougl.	UB,MB
Ribes inerme Rydb.	UB,MB
Saxifraga odontoloma Piper	UB,MB
Family Scrophulariaceae	
Castilleja flava Wats.	
Castilleja linariifolia Benth.	LB
Castilleja scabrida Eastw.	LB
Mimulus guttatus DC.	UB
Orthocarpus purpureo-albus Gray	LB
Penstemon barbatus (Cav.) Roth.	UB
Penstemon breviculus (Keck) Nisbet & R. Jackson	LB
Penstemon eatonii Gray	LB
Penstemon linarioides Gray	LB
Penstemon moffattii Eastw.	LB
Penstemon ophianthus Pennell	LB
Penstemon pachyphyllus var. *mucronatus* (N. Holmgren) Neese	LB
Penstemon strictus Benth.	LB
Penstemon utahensis Eastw.	LB
Veronica americana Schwein. ex Benth	LB
Veronica arvensis L.	UB
Family Urticaceae	
Urtica dioica L.	UB
Family Valerianaceae	
Valeriana edulis Nutt. ex T. & G.	UB
Family Violaceae	
Viola adunca J.E. Sm. ex Rees	UB
Viola nephrophylla Greene	UB
Family Viscaceae	
Arceothobium americanum Nutt. ex Engelm. in Gray	LB
Arceuthobium divaricatum Engelm.	LB,MB
Arceuthobium douglasii Engelm.	UB
Phoradendron juniperinum Gray	LB
Class Liliopsida	
Family Agavaceae	
Yucca harrimaniae Trel.	LB
Family Commelinaceae	
Tradescantia occidentalis (Britt.) Smyth	LB
Family Cyperaceae	
Carex aquatilis Wahl.	LB
Carex praegracilis W. Boot.	UB
Carex lanuginosa Michx.	UB
Carex microptera Mack.	UB,LB
Carex nebraskensis Dewey	LB
Carex rossii F. Boott	UB
Carex rostrata Stokes ex With.	LB
Eleocharis palustris (L.) R. & S.	LB
Family Iridaceae	
Sisyrinchium demissum Greene	LB
Family Juncaceae	
Juncus arcticus Willd.	LB, UB
Juncus ensifolius Wikstrom	UB
Family Liliaceae	
Allium cernuum Roth	LB
Fritillaria atropurpurea Nutt.	MB
Smilacina stellata (L.) Desf.	LB, MB
Family Orchidaceae	
Habenaria sparsiflora Wats.	MB
Family Poaceae	
Agropyron cristatum (L.) Gaertner var. *desertorum*	LB
Agrostis stolonifera L.	LB
Aristida purpurea Nutt.	LB
Bouteloua gracilis (H.B.K.) Lag. ex Steudel	LB
Bromus carinatus H. & A.	UB
Bromus ciliatus L.	UB
Bromus inermis Leysser	UB
Bromus tectorum L.	LB
Catabrosa aquatica (L.) Beauv.	UB
Elymus elymoides (Raf.) Swezey	UB
Elymus glaucus Buckley	UB
Elymus hispidus (Opiz) Meld.	UB
Elymus junceus Fisch.	LB
Elymus smithii (Rydb.) Gould	LB
Elymus trachycaulus (Link) Gould ex Shinn	UB
Festuca octoflora Walter	LB
Festuca ovina L.	LB
Hilaria jamesii (Torr.) Benth.	LB
Muhlenbergia andina (Nutt.) A. S. Hitchc.	
Muhlenbergia asperifolia (Nees & Mey.) Parodi	
Muhlenbergia richardsonis (Trin.) Rydb	UB
Muhlenbergia thurberi Rydb.	UB
Munroa squarrosa (Nutt.) Torr.	LB
Poa compressa L.	LB
Poa fendleriana (Steudel) Vasey	LB
Poa nervosa (Hook.) Vasey	UB
Poa palustris L.	UB
Poa pratensis L.	LB
Poa trivialis L.	UB
Schizachyrium scoparium (Michx.) Nash in Small	LB
Sporobolus cryptandrus (Torr.) Gray	LB
Sporobolus flexuosus (Thurber) Rydb.	LB
Stipa comata Trin. & Rupr.	LB
Stipa coronata Thurber	LB
Stipa hymenoides R. & S.	UB
Stipa lettermanii Vasey	UB

Table 2—Species collected in "The Box" that are new records for Garfield County, Utah.

Astragalus argophyllus var. *martinii*
Boerhaavia spicata var. *torreyana*
Campanula rotundifolia
Chrysothamnus nauseosus var. *arenarius*
Cryptantha pterocarya var. *pterocarya*
Elymus glaucus
Epilobium hallaenum
Geranium viscosissimum
Habenaria sparsiflora var. *laxiflora*
Hymenoxys acaulis var. *nana*
Linanthus biglovii
Lithospermum ruderale
Lomatium latilobum
Opuntia phaeacantha var. *phaeacantha*
Penstemon barbatus
Phlox tumulosa
Poa compressa
Poa nervosa
Populus balsamifera
Rumex patentia
Salix drummondiana
Veronica arvensis

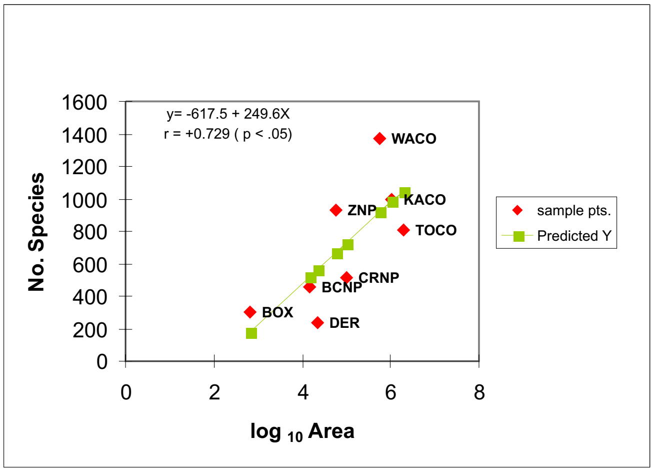

Figure 1—The relationship between area and plant diversity at eight locations in Utah. (BCNP = Bryce Canyon National Park; BOX = Box Wilderness study area; CRNP = Capitol Reef National Park; DER = Desert Experimental Range; KACO = Kane County; TOCO = Tooele County; WACO = Washington County).

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Table 3—Area and number of species and sub-specific taxa at each of several locations in Utah. The literature source for the information at each location is shown.

Location	Area	Number of Families	Number of Genera	Number of Species
	ha			
Box Wilderness[a]	648	63	175	304
Desert Experimental Range[b]	22,543	42	134	240
Bryce Canyon National Park[c]	15,092	73	232	458
Capitol Reef National Park[d]	97,937	74	280	512
Zion National Park[e]	59,926	94	402	929
Kane County[f]	1,075,828	92	399	998
Tooele County[f]	1,914,592	84	380	881
Washington County[f]	584,121	110	556	1,374

[a] This manuscript.
[b] Goodrich (1986).
[c] Spence and Buchanan (1993).
[d] Meyer (1982).
[e] Harper, Sanderson, and McArthur (2001).
[f] Albee, Schulz, and Goodrich (1988).

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Mountain Big Sagebrush Age Distribution and Relationships on the Northern Yellowstone Winter Range

Carl L. Wambolt
Trista L. Hoffman

Abstract—This study was conducted within the Gardiner Basin, an especially critical wintering area for native ungulates utilizing the Northern Yellowstone Winter Range. Mountain big sagebrush plants on 33 sites were classified as large (≥22 cm canopy cover), small (<22 cm canopy cover), or dead and then aged by counting growth rings. Large and small plants averaged 32 and 6 years old, respectively. Nearly half of the small plants were 5 years old, the result of optimal conditions for establishment in 1988, the year large wildfires burned much of Yellowstone National Park. Dead plants averaged 41 years of age. A bimodal peak in establishment of mountain big sagebrush corresponded with two large reductions in the Northern Yellowstone elk population.

Introduction

Big sagebrush (*Artemisia tridentata* Nutt.) grassland comprises the largest vegetation type in the Western United States (Colbert and Colbert 1983) dominating 60 million ha (Beetle 1960). Since the 1930s, control of sagebrush has been a primary objective of many land managers, with the intent of improving herbaceous production for livestock (Best 1972). However, big sagebrush is recognized as valuable forage and cover for many wild ungulates, (Kufeld and others 1973; Welch and Peterson 1981; Wambolt and McNeal 1987; Ngugi and others 1992; Wambolt 1996, 1998), birds, (Best 1972; Reynolds 1981; McAdoo and others 1989), and other wildlife (Mullican and Keller 1986). Ironically, some land managers are increasingly engaged in reducing big sagebrush, often for the stated purpose of benefiting wildlife.

There is much conjecture about the dynamics of big sagebrush production, including the relationship with age. Some believe that big sagebrush declines in production or vigor after a certain age (West and others 1984), but details and the interrelationships with environmental factors related to possible declines are unclear. Decadence, degradation, and senescence are terms commonly used in the literature (Roughton 1972; Evans and Young 1978; Sinclair 1984) and in management plans relating to big sagebrush (Anonymous 1979, 1982; Petroni 1991), but their relevance to big sagebrush is vague. Our objective was to obtain an understanding of the age distribution of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* [Rydb.] Beetle) over a range of environmental conditions on 33 sites on the Northern Yellowstone Winter Range (NYWR).

Methods

Study Area

The study was conducted in the Gardiner Basin of the NYWR adjacent to Yellowstone National Park (YNP) in southwestern Montana (fig. 1). Along the Yellowstone River annual precipitation averages 305 mm. The nearby benchlands receive 406 mm of precipitation. Half of the annual precipitation is in the form of snow and June is the wettest month. The Gardiner Basin is a natural winter range for ungulates due to the orographic effects on precipitation of mountain peaks up to 3,353 m (Wambolt 1996). Elk (*Cervus elaphus nelsoni*) and mule deer (*Odocoileus hemionus hemionus*) are the important ungulates on the study area.

Glacial scouring and deposition have been strong influences on the soils. Parent materials include granites and limestones deposited by glaciers as well as basalts and breccias. The soil regolith in the study area may range from a few cm in areas scoured by glaciers to over 1.5 m in depositional areas. Mollisols are the dominant soil order. Soil textures are most commonly loams and sandy loams (Wambolt and McNeal 1987).

Four sagebrush taxa, basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*), Wyoming big sagebrush (*A.t.* ssp. *wyomingensis* Beetle and Young), mountain big sagebrush, and black sagebrush (*A. nova* Nels.), occur sympatrically but with varying frequency. Mountain big sagebrush is the dominant on the majority of the area. Threadleaf rubber rabbitbrush (*Chrysothamnus nauseosus* ssp. *consimilis* [Green] Hall & Clem.), mountain low rabbitbrush (*C. viscidiflorus* ssp. *lanceolatus* [Nutt.] Hall & Clem.), narrowleaf low rabbitbrush (*C.v.* ssp. *viscidiflorus* var. *stenophyllus* [Hook] Nutt.), and gray horsebrush (*Tetradymia canescens* D.C.) occur throughout the sagebrush-dominated portions of the area.

Bluebunch wheatgrass (*Agropyron spicatum* [Pursh.] Scribn.) and Idaho fescue (*Festuca idahoensis* Elmer) are the principal grasses found as sagebrush understory. Other common grasses are prairie junegrass (*Koeleria macrantha* Ledeb.), needle-and-thread (*Stipa comata* Trin.& Rupr.), and Indian ricegrass (*Oryzopsis hymenoides* [R. & S.] Ricker).

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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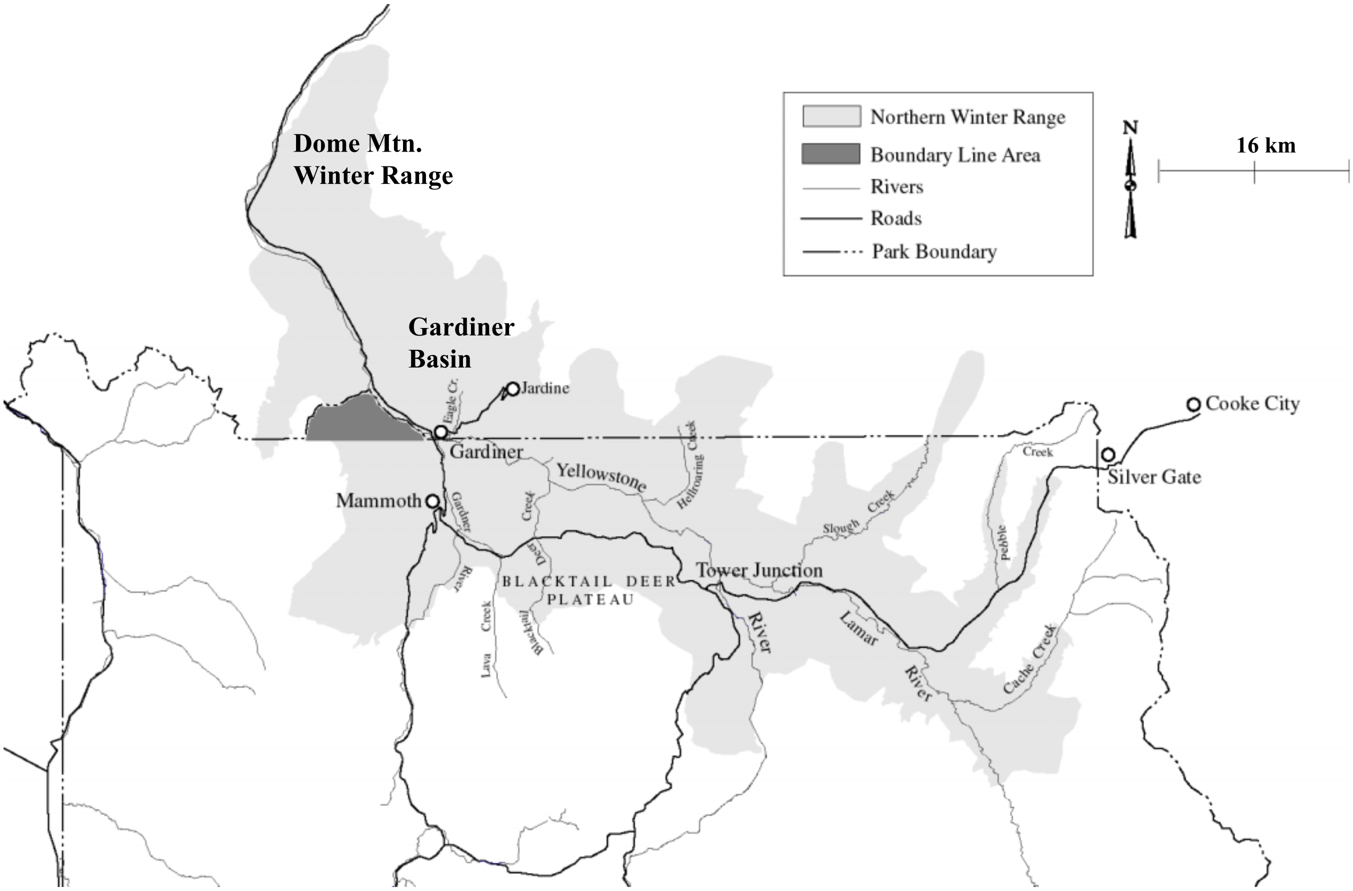

Figure 1—The Northern Yellowstone Winter Range. This study was conducted north of Yellowstone National Park in the Gardiner Basin. That area is especially important for wintering ungulates.

Sampling

Each study site was a stand of mountain big sagebrush that was relatively homogenous in characteristics such as slope, aspect, and elevation. Confirmation of the mountain big sagebrush subspecies was made in the lab using an ultraviolet light (Stevens and McArthur 1974). Each study site was at least 0.25 ha in size (40 x 60 m) and ranged up to 3 ha.

Measurements of plant parameters began near the end of June 1993. The majority of sagebrush growth for the year occurred before this time. Long shoots and leaves were fully elongated, and an annual growth ring was well established in the stem xylem. Therefore, measurable production increases by sagebrush plants were not expected over the remainder of the summer. The plant parameters recorded included browse form class, percent cover of live and dead sagebrush, density of large, small and dead plants, percent dead crown, age, and production of winter forage.

Browse form classes used were described by Wambolt and others (1994). Plants that receive repeated heavy browsing develop a dense canopy and a hedged appearance. Lightly browsed plants have a more open canopy with linear growth due to the annual extension of terminal leaders. Usually, all of the plants on a site exhibited nearly the same browse form class.

At each site, two line transects, 30 m long, were established with the slope to measure cover. The transects were parallel to one another and 10 m apart. Belt transects of 60 m^2 were established to obtain the other parameters by measuring 1 m on each side of the line transect. Measurements from the transects were pooled.

A plumb bob was used to determine live and dead cover to the nearest cm along the line transects. Live cover included any leaves, leaders, stems or seedheads that intercepted the line transect. Dead cover referred to the intercept of dead sagebrush branches elevated above the ground.

Plant density was determined by counting all sagebrush plants rooted within the belt transect. Plants were divided into large, small and dead categories. A large plant measured >22 cm across the widest portion of its crown. This minimum measurement was adapted from the sagebrush production models used (Wambolt and others 1994). Plants <22 cm were not considered to be significant contributors to site production, but were important as representatives of the younger age classes. Dead plants were separated from woody litter by the requirement of at least one main stem still rooted in place, and some portion of the stem remaining above the ground. An ocular estimate of the percentage of dead crown area was made for each large sagebrush. Estimates were made to the nearest 10 percent.

Production was defined after Wambolt and others (1994) as the amount of sagebrush forage available to wildlife during winter. Production measurements were made on 10 large plants per line transect. The 10 plants were those rooted closest to 3 m increments along the 30 m belt transect. Four measurements were recorded for each plant to model production. The major axis referred to the longest horizontal line between living plant tissue across the plant crown. The minor axis was a similar line perpendicular to the major axis. Two additional axes were measured perpendicular to one another and set at 45° angles to the intersection of the major and minor axes. The modeled forage production per plant was multiplied by the density of large plants to determine the mass of sagebrush forage available on a per ha basis.

Each of the 20 plants measured for production (10 plants x 2 transects) was cut at the base and transported to the lab for aging (total of 660 large plants). Twenty small immature plants (<22 cm across the widest portion of their crown) were collected in the same manner for aging at each of the 33 sites (total of 660 small plants). Twenty dead plants per site were also collected, but because dead plants were uncommon and often not found near the 3 m marks, these plants were collected by walking through the site and cutting the first 20 plants encountered. Often, dead stems were rotted or colonized by ants and had to be discarded, thus, on some sites, it was not possible to collect 20 specimens.

Annual growth rings were counted in cross-sections (Ferguson 1964; Taha 1972). Sagebrush cross-sections were sanded smooth and a fresh razor was used to take a thin veneer off the surface. This removed the surface pores that were filled with sawdust or impurities and clarified the annual growth rings. A light coating of vegetable oil was sometimes used to highlight rings before counting with a 10x hand lens under a full spectrum light.

Results and Discussion

The age distribution of large mountain big sagebrush is shown in figure 2. Ages of individual large plants ranged from 5 to 88 years with an average age of 32 years. Because no large plants were less than 5 years old, it appears that 5 years are required for a mountain big sagebrush plant to reach an age where it is large enough to have a crown >22 cm at the widest portion. Roughton (1972) excluded all plants less than 9 years old in his discussion of sagebrush age classes. When mountain big sagebrush is burned, recovery to pre-burn levels of forage production is a slow process and requires almost a decade for shrubs to attain any notable level of production (Roughton 1972). Further, frequent burning of sagebrush should be expected to reduce sagebrush forage production (Watts and Wambolt 1996).

The population of sagebrush in the study area is relatively young. The age classes with the largest number of individual plants were between 25 and 35 years old. When plants were grouped as stands (20 plants measured per stand), the average stand age (n = 33) ranged from 18 to 45 years with an average overall stand age of 32 years in 1993 (table 1). Therefore, the average stand age was identical to the average individual age. Only 12 percent of the individuals exceeded 50 years of age, and 5 percent were older than 60 years.

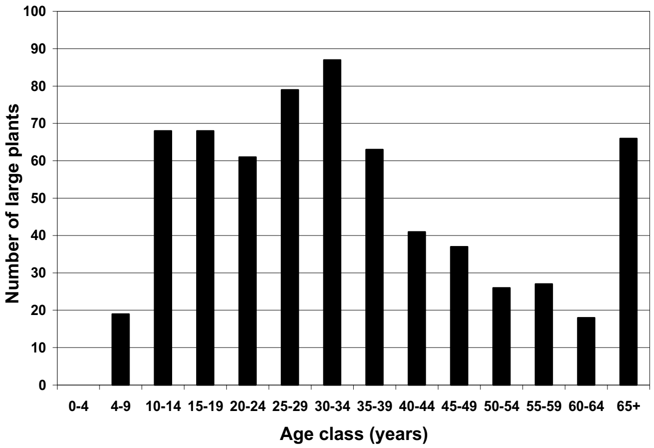

Figure 2—Age distribution of 660 large (>22 cm across widest portion of crown) mountain big sagebrush plants from 33 sites in 1993.

While big sagebrush have been reported to live as long as 200 years (Ferguson 1964), the oldest plant we recorded was a dead individual of 109 years. The oldest living plant was 88 years of age. In areas such as southwest Montana and southern Idaho where most sagebrush stands have been treated in various manners in attempts to improve livestock forage, the majority of mountain big sagebrush have been aged at 11 to 20 years with the next most common age class 21 to 30 years (Brown 1982). Although the length of time since the last disturbance (such as fire) was not discussed, Brown (1982) found only 3 percent of plants were older than 50 years. In Nevada, the average longevity of big sagebrush (subspecies not considered) was estimated at 30 to 40 years (Wallace and Romney 1972). The oldest big sagebrush plant (subspecies not considered) observed by Roughton (1972) in Colorado was 72 years old. On two sites, he found that 60 to 75 percent of shrubs were between 5 and 35 years of age (the 0 to 4 year age class was excluded). By excluding age classes below 9 years, he found that the majority of sagebrush on a third site was between 50 and 59 years old. He described this age structure as "decadent" even though thousands more

Table 1—Averages and ranges of plant characteristics for 33 mountain big sagebrush sites.

	Mean	Standard deviation	Maximum	Minimum
Percent live line cover	14.2	0.1	38.8	3.0
Percent dead line cover	5.5	0.0	15.0	0.1
Density large plants/m^2	0.9	0.3	1.5	0.4
Density small plants/m^2	1.0	1.0	4.0	0.1
Density dead plants/m^2	0.2	0.1	0.7	0.1
Winter forage (g/plant)	127.6	73.6	330.1	34.8
Percent deadcrown	22.5	7.2	43.2	11.1
Age large stand	32.2	6.4	45.0	18.0
Age small stand	6.1	0.5	25.0	1.0
Age dead stand	40.7	7.5	56.0	20.0

plants were observed between 1 and 9 years old than all the other age classes put together. This description seems misleading because thousands of young replacement plants were not considered. Although the sagebrush stands apparently had begun a cycle of self-rejuvenation as described by Lommasson (1948), stands were described by Roughton (1972) as if the young members were of no consequence.

In the Gardiner Basin of the NYWR, every site measured had young age classes well represented with the majority of plants less than 50 years old. Because none of the 33 sites have been drastically disturbed (as with fire, spraying, and so forth), this relatively young condition has maintained itself, with sagebrush plants establishing, maturing, dying and being replaced in a relatively short period of time (around 50 years) in the absence of human intervention as expected from a climax dominant. This indicates that burning or other disturbances are not necessary to maintain sagebrush stands in a productive state.

Dead mountain big sagebrush plants also provided evidence that mountain big sagebrush stands turn over relatively rapidly without intervention. The average age of dead plants was 40.7 years (table 1). This does not precisely establish the age at which mountain big sagebrush are likely to die because plants with rot were excluded from the sample. However, the estimate comes from 440 observations, which indicates that turnover by age 41 is not uncommon. Lommasson (1948) reported 40 years as the stand age at which old mountain big sagebrush plants begin to senesce, thereby breaking down and creating natural openings in which young plants may establish. Recruitment by seedlings in closed stands of mountain big sagebrush occurs only infrequently due to intraspecies competition (Meyer 1994). However, patterns of seedling establishment are not always clearly related to natural openings associated with aging stands. They may also be influenced by environmental factors such as soil moisture or seed production (Tyrrell and Crow 1994).

The year of establishment for small mountain big sagebrush individuals is shown in figure 3. Such small plants do not contribute notably to the production by mountain big sagebrush in the study area. Occasionally plants that were over 20 years old and still small were found in areas with adverse growing conditions such as very dry, shallow soils on exposed ridgetops.

Individual small mountain big sagebrush plants ranged from 1 to 25 years old. Nearly one-half of 660 small plants sampled were 5 years old (germinated in 1988) when sampled in 1993. This age dominated on all 33 sites. When small plants were grouped as stands (20 plants per stand), the average age (n = 33) ranged from 4 to 11 years with an overall average age of 6 years (table 1).

Crisp and Lange (1976) proposed a model for age structure of shrubs that under hypothetical natural conditions, mortality is highest in young and old individuals, with reduced mortality in mature, but relatively young plants. A sharp decline would occur early after germination, followed by a period of reduced mortality. Eventually, mortality rates would again increase after plants reached a critical age.

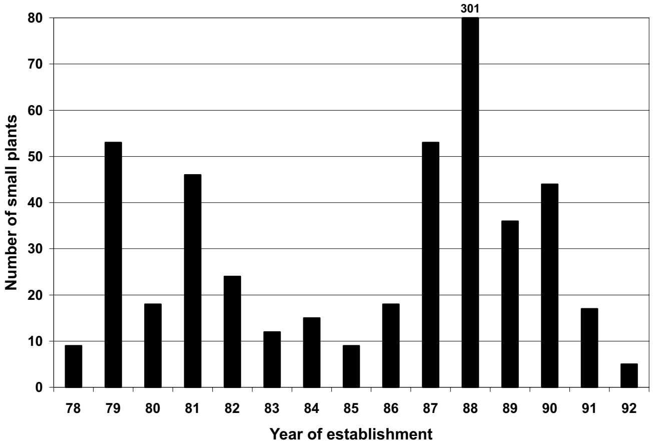

Figure 3—Year of establishment for 660 small (<22 cm across widest portion of crown) mountain big sagebrush plants from 33 sites.

The average stand establishment dates of large and small mountain big sagebrush plants are shown in figure 4. Data were collected from different populations and should not be combined to form a continuous age structure. The survivorship curve (fig. 4) from this study area is quite different from the hypothetical change described in Crisp and Lange (1976). Within the age distribution for large plants, several stands have average ages that date to the late 1940s and early 1950s. Stand ages do not pre-date the 1940s because, as a whole, mountain big sagebrush in this area were found to average 41 years (table 1). The stands at the older end of the curve are probably approaching the lifespan of mountain big sagebrush. This lifespan is influenced in part by the large ungulate populations that have been present since these plants germinated.

In the late 1950s and early 1960s, mountain big sagebrush establishment generally increased, reaching a peak in 1961 (fig. 4). This event was followed by a general decrease in recruitment by the late 1960s. This is inconsistent with the hypothesis that decreased mortality is observed in mature

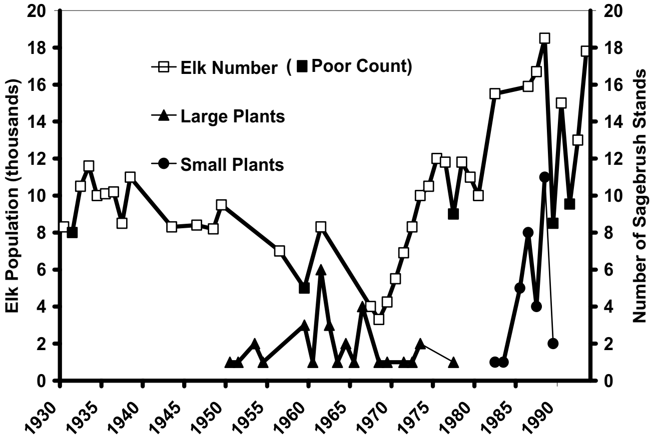

Figure 4—Large (>22 cm across widest portion of crown) and small (<22 cm) mountain big sagebrush stands average establishment date and elk winter counts on the Northern Yellowstone Winter Range.

but relatively young plants (Crisp and Lange 1976). Assuming that plants germinate and establish equally each year and that survival followed the hypothetical curve described by Crisp and Lange (1976), then many more site ages should have been observed in the late 1960s and early 1970s. However, by the 1970s, establishment of mountain big sagebrush is extremely low.

According to the hypothetical age distribution model (Crisp and Lange 1976), small mountain big sagebrush should have high mortality rates that perhaps slow as the plants get older and begin to mature. Because nearly half of the small plants measured were 5 years old, their distribution also contrasts with the hypothetical model. Establishment peaks dramatically in 1988. This type of establishment was not found during other years.

The bimodal curve of the age distribution of mountain big sagebrush corresponds to two distinct reduction events for the Yellowstone elk population (Tom Lemke, unpublished report, Montana Fish, Wildlife & Parks, Houston 1982). Removals of 6,365 animals in the winter of 1955 and 1956 (mostly from outside YNP) and of 5,135 (mostly from within YNP) in the winter of 1961 to 1962, primarily by shooting, cut the elk population approximately in half each year (Houston 1982). During the winter of 1988 and 1989, snow conditions, coupled with habitat loss from the large Yellowstone fires the previous summer, resulted in approximately a 40 percent loss of the herd (Tom Lemke, unpublished report, Montana Fish, Wildlife & Parks).

Declines in the elk herd that occurred during these two periods of sagebrush establishment may partially explain the difference between the curves in this study and the hypothetical curve. A reduction in herbivory and trampling may have increased establishment and survival of mountain big sagebrush, while declines occurred when elk populations were high.

Episodic germination due to other environmental conditions may also play a role in determining the age distribution observed in this study. Daubenmire (1975) found that in basin big sagebrush (*Artemisia tridentata Nutt* ssp. *tridentata)*, recruitment of seedlings may be delayed for years until favorable moisture conditions occur for germination and establishment. Humphrey (1984) found similar results, although big sagebrush subspecies was not considered. Microtopographic characteristics of the seedbed and precipitation timing are critical for germination of mountain big sagebrush (Booth and others 1990; Young and others 1990). Successful emergence of mountain big sagebrush seedlings may depend on the amount and timing of spring snowpack (Meyer 1994). In addition, weather conditions, especially early drought are the primary factors in causing seedling mortality (Meyer 1994), although seedlings may be able to withstand water shortages by early summer (Booth and others 1990).

Table 2—Precipitation extremes during the 15 year period between 1977 and 1992.

Month	Precipitation	15 year ranking
	mm	
1987		
July	910	Wettest
August	410	4th wettest
1988		
April	490	2nd wettest
May	920	Wettest
June	120	Driest
July	240	3rd driest
August	36	Driest

Temperature and precipitation records from the years 1977 to 1992 show unusual climatic conditions that may have contributed to the large number of plants that germinated in 1988 (table 2). The late summer of 1987 was one of the wettest in the 15 year interval. This moisture corresponded with a period of mountain big sagebrush flowering and seed production. An increase in water availability during late summer has been shown to increase the growth of reproductive tissues of big sagebrush (Evans and Black 1993). The spring of 1988 was also one of the wettest of the 15 years sampled, but was followed by a drought in the summer and fall. A moist spring would promote seed germination of many plant species, but a summer drought would likely hamper growth of competing plants. Mountain big sagebrush, which is drought tolerant relatively soon after emergence (Booth and others 1990), would likely have higher survival rates.

The age structure of large and small plants includes two major episodes of establishment. The event in the late 1950s and early 1960s may be accounted for in part by the dramatic declines in the elk population. Detailed climatic conditions for this period were not found. In 1988, unusual climatic conditions coupled with an approximately 40 percent reduction in the Yellowstone elk herd may have created an ideal situation for mountain big sagebrush establishment.

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Mountain Big Sagebrush Communities on the Bishop Conglomerate in the Eastern Uinta Mountains

Sherel Goodrich
Allen Huber

Abstract —The Bishop Conglomerate forms broad, gently sloping pediments that include a mantle or veneer of coarse gravel and some cobble over underlying formations. These pediments cover large areas at the margins of the Uinta Mountains. Mountain big sagebrush (*Artemisia tridentata* var. *pauciflora*) communities cover rather large areas at the outer edge or lower end of these pediment-plains. These communities are a conspicuous feature of the Diamond Mountain, Brush Creek Mountain, and Taylor Mountain areas toward the eastern end of the Uinta Mountains.

Consistency, frequency, crown cover, and other features of plants on these pediment-plains suggest an ecological unit in which biotic and abiotic components are important to classification.

Features of classification include geomorphology, geology, gradient, soils, vegetation, wildlife, and human values. Classification, capabilities, values, and management implications are discussed. Mountain big sagebrush communities are compared to Wyoming big sagebrush (*A. tridentata* var. *wyomingensis*) communities of pediments associated with the Green River. Importance of recognizing differences between communities of these two sagebrush taxa are emphasized.

Study Sites and Methods

Numerous studies have been established on plateaus of Bishop Conglomerate of the eastern Uinta Mountains on the Ashley National Forest. Some of these are listed in table 1. These and other studies referred to in the following discussion are on file at the Supervisor's Office of the Ashley National Forest, Vernal, Utah.

Studies at sites listed in table 1 include Rooted Nested Frequency and Line Intercept of crown cover of shrubs in which 500 ft of intercept per site was standard. Studies also include ground cover determination by a point method. Procedures for these study methods are described by USDA Forest Service (1993). Rooted Nested Frequency studies provide quadrat frequency as well as nested frequency of plant taxa by which diversity of plant communities can be evaluated. For this paper quadrat frequency rather than nested frequency is used to express diversity. Frequency studies at each site included 100 quadrats of 2.7 ft^2 (50 x 50 cm). The procedures outlined by USDA Forest Service (1993) for Line Intercept specifies including openings in crowns of individual shrubs as crown cover. Thus the measurements of crown cover referred to in this paper tend to overrate actual crown cover.

In addition to the above studies, line intercept of crown cover of shrubs has been measured at 36 other sites in this ecological unit. In addition production (air dry weight) by species has been measured at numerous sites of which data from 31 sites was reviewed for this paper. Production measurements were made by clipping and weighing green weight of annual growth by individual taxa. For the most part production measurements were taken from 30 plots of 0.98 ft square for each site. Dry weight was determined from dry weight tables or by comparing green weight with air dry weight after air-drying samples in paper bags. Study sites have a varied history of fire, herbicide applications, livestock grazing, and other management practices.

Comparisons with Wyoming big sagebrush/grass communities of pediments associated with the Green River are based on information provided for those communities by Goodrich and others (1999).

Plant nomenclature follows that of Welsh and others (1993). Authors of plant taxa are not listed in this paper. They can be found in Welsh and others (1993).

Abiotic and Biotic Features

The Bishop Conglomerate Formation varies from boulder-conglomerate to pebble-conglomerate. Deposition of the formation apparently began in Oligocene, or perhaps late Eocene. It mantles a smooth erosion surface and forms a pediplain (Winkler 1970). This formation is quite extensive on the south slope and on the north slope of the Uinta Mountains. Gradient of the plateau lands of this pediment is mostly less than 5 percent

At the eastern end of the south slope of the Uinta Mountains, lodgepole pine forests cover upper elevations of this pediment formation. At mid elevations of the formation, aspen is common and locally dominant. Toward the lower or southern edge of the formation, mountain big sagebrush-grass communities are extensive. These sagebrush communities that are below the aspen and lodgepole pine belts are the focus of this paper.

The study area is included in the Uinta Mountains Section of the National Hierarchical Framework of Ecological Units as discussed by McNab and Avers (1994). Consistent with that framework of ecological units, the study area is classified in this paper at the landtype level as a "Bishop Conglomerate Plateau/Mountain Big Sagebrush Ecological Unit." This name reflects abiotic and biotic components of the unit.

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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Table 1—Study sites with nested frequency data.

Study site name	Study no.	Comments
Taylor Mtn. Exclosure	31–4	Inside an exclosure with fence high enough to exclude wild ungulates as well as livestock. The exclosure was constructed in 1962. Data for this paper was taken in 1991.
Taylor Mtn.	31–4D	Outside the Taylor Mountain Exclosure with a history of cattle grazing since before establishment of the Ashley National Forest in 1908. Rest rotation grazing since 1960 with stocking rates at about 3.3 acres/AUM*.
Mud Spring	31–-35A	Grazing history same as for 31–4D.
Grasshopper	32–66	Cattle grazing since before establishment of the Ashley National Forest in 1908. Rest rotation and deferred rotation grazing since 1967 with permitted stocking rates at about 2.74 acres/AUM*
Counting Corral	32–67	Grazing history same as for 32–66.
Diamond 3	32–78	Grazing history same as for 32–66. This site was burned in 1993. Data was taken in 1995 only two years after burning.

*AUM or Animal Unit Month is considered here to be equivalent to the grazing of 1 mature cow with calf for one month.

Average annual precipitation for this ecological unit likely varies between 12 and 20 inches. Frost-free period is 40 to 80 days (Ashcroft and others 1992). Summer thundershowers are common. Snow depth near the end of winter varies from about 1 ft in rare or occasional winters to 2 to 3 ft in most winters. Snow commonly covers the ground from November through April and through much of May in some years.

Soils are generally Typic or Pachic Argiborolls, Cryoborolls, and Calciborolls. Calciborolls are likely more common toward the edges of the formation where the mantle of Bishop Conglomerate thins and contacts more calcareous substrates. Soils are generally fine, loamy mixed, fine mixed, or loamy-skeletal mixed.

Vascular plant communities are highly diverse with shrubs, graminoids, and forbs usually well represented (tables 2, 3, and 4). These communities generally support from 3 to 6 shrub species, 10 to 12 graminoid species, and 30 to 44 forb taxa. With a sample size of 100 quadrats of 2.7 ft^2 (50 x 50 cm) each,

Table 2—Percent quadrat frequency, average quadrat frequency (Ave. QF), and percent site consistency (percent con.) of plant taxa.

Plant taxa	Study sites							
	32–66	32–67	31–35A	32–78	31–4	31–4D	Average QF	Percent con.
Shrubs								
Artemisia tridentata pauciflora	41	44	12	3	29	35	27	100
Cercocarpus montanus						1	0	17
Chrysothamnus viscidiflorus	16	2	3	6	10	4	7	100
Eriogonum corymbosum						15	3	17
Mahonia repens					5		1	17
Purshia tridentata				4	47	27	13	50
Symphoricarpos oreophilus	1	8	4	2	10	5	5	100
Graminoids (Poaceae)								
Bouteloua gracilis						1	0	17
Bromus anomalus		1	1		1		1	50
Bromus tectorum						1	0	17
Danthonia intermedia		2					0	17
Elymus elymoides	50	66	51	53	25	41	48	100
Elymus lanceolatus	59	81	7	39	39	62	48	100
Elymus spicatus				7	44	1	9	50
Elymus trachycaulus			2				0	17
Festuca ovina	6	47	2	3	9	11	83	
Koeleria macrantha	34	1	7	2	6	6	9	100
Poa fendleriana	77	78	21	36	71	54	56	100
Poa pratensis	4	5	6	5		20	7	83
Poa secunda	49	62	28	66	6	1	35	100
Stipa comata	46	18	100	38	11	15	38	100
Stipa hymenoides					1		0	17
Stipa lettermanii	9	34	6	4	20	24	16	100
Stipa nelsonii	9	34	6	4	20	24	16	100

(con.)

Table 2 (Con.)

	Study sites							
Plant taxa	**32–66**	**32–67**	**31–35A**	**32–78**	**31–4**	**31–4D**	**Average QF**	**Percent con.**
Graminoids (Cyperaceae)								
Carex obtusata		5					1	17
Carex petasata			5				1	17
Carex rossii	44	70		34	1		25	67
Perennial forbs								
Achillea millefolium	1	6			1	2	2	67
Agoseris glauca	21	3	17	15			9	67
Antennaria microphylla	62	71	4	16	3	25	30	100
Arabis drummondii			3	6			2	33
Arabis holboellii	7			3			2	33
Arabis perennans			1				0	17
Arabis spp.		5			12	7	4	50
Arenaria congesta	94	88	81	85	1	54	67	100
Aster chilensis	1	24				3	5	50
Astragalus agrestis		3					1	17
Astragalus argophyllus	12	14		2			5	50
Astragalus convallarius	21	12	1		11	3	8	83
Astragalus spatulatus		4					1	17
Astragalus tenellus						2	0	17
Balsamorhiza hookeri	85	30	4	89	40	37	48	100
Castilleja leariifolia	3				17	8	4	50
Cirsium spp.						1	0	17
Comandra umbellata						2	0	17
Crepis acuminata					2	7	2	33
Cryptantha flavoculata						2	0	17
Cymopterus longipes					12		2	17
Delphinium nuttallianum			12	82	1		16	50
Erigeron eatonii	23		42	12	14		15	67
Erigeron flagellaris	12	57	1	33		21	21	83
Erigeron pumilis	7						1	17
Eriogonum umbellatum	1		15	2	26	28	12	83
Gilia aggregata				4	2	2	1	50
Heterotheca villosa		1	4				1	33
Hymenoxys acaulis		2				2	1	33
Lesquerella spp.						2	0	17
Lewisia pygmaea				4			1	17
Linum lewisii		1					0	17
Lithophragma glabra				63			11	17
Lithospermum ruderale					1	1	0	33
Lomatium spp.						9	2	17
Lomatium triternatum	27	2	48	6	11		16	83
Lupinus argenteus	94		77	19	3	35	38	83
Lychnis drummondii	3	1	7				2	50
Mertensia fusiformis	8	5	25	12	4	4	10	100
Penstemon humilis	12	8			5	19	7	67
Penstemon spp.						5	1	17
Petradoria pumila	19	26		8	20	29	17	83
Phlox hoodii		17					3	17
Phlox longifolia	2	39			11	25	13	67
Phlox multiflora	73	4	40	2	16	12	25	100
Potentilla gracilis	14	22	53			16	18	67
Ranunculus glabberrimus			7				1	17
Sedum lanceolatum					31	21	9	33
Senecio integerrimus			43	5	5	17	12	67
Senecio multilobatus					1	1	0	33
Stellaria jamesiana	30						5	17
Taraxacum officinale	3	49	41	3	1	14	19	100
Thlaspi montanum			40	13			9	33
Trifolium gymnocarpon	84	53	51	12	12	49	44	100
Viola nuttallii		4	2				1	33
Zigadenus paniculatus	1	6	20	4	2	8	7	100
Annual forbs								
Androsace septentrionalis				10		9	3	33
Chenopodium spp.			7				1	17
Collinsia parviflora			67	97		31	33	50
Collomia linearis			71	82		34	31	50
Draba nemorosa			10				2	17
Gayophytum spp.				53		1	9	33
Gymnosteris parvula				3			1	17
Lappula occidentalis					1		0	17
Lepidium densiflorum		3					1	17
Polygonum douglasii		2	49	64		58	29	67

Table 3—Vascular plant diversity and ground cover.

Site	Alpha	Beta	Crown cover of sagebrush	Ground cover
			Percent	*Percent*
32–66	11.66	40	16.4	95
32–67	11.64	44	15.1	87
32–78	11.20	46	0.2	65[a]
31–35A	10.91	45	5.0	87
31-4	5.98[b]	46	32.4[c]	95
31–4D	14.1	67	—	95
Average	11.35	48		92[d]

[a] At 1.5 growing seasons after fire. Not included in average.

[b] Inside a 30-year old exclosure. Not included in average.

[c] In addition to sagebrush cover, crown cover of bitterbrush was 37.9 percent. Total crown cover of these two shrubs was 70.3 percent.

[d] All sites included in this average have a long history of livestock grazing.

Table 4—Plant taxa with 100 percent site consistency at 6 sites on Bishop Conglomerate Plateau/Mountain big sagebrush ecological unit.

Taxon	Site consistency	Average quadrat* frequency
	n = 6	*n = 6*
Mountain big sagebrush	100	27
Yellowbrush	100	7
Mountain snowberry	100	5
Squirreltail	100	48
Thickspike wheatgrass	100	48
Muttongrass	100	56
Sandberg bluegrass	100	35
Needle-and-thread grass	100	38
Letterman needlegrass	100	16
Pussytoes	100	30
Ballhead sandwort	100	67
Hooker balsamroot	100	48
Bluebells	100	10
Many-flowered phlox	100	25
Dandelion	100	19
Hollyleaf clover	100	44
Death camas	100	7

*Quadrat size is 19.7 x 19.7 inches (50 x 50 cm).

average number of vascular plant taxa was 48 per site, and average number of taxa per quadrat was 11.35 (table 3).

Except for common dandelion (*Taraxacum officinale*) and perhaps Kentucky bluegrass (*Poa pratensis*), plants found at study plots across the ecological unit are mostly native to the area. Other introduced plants are of low consistency and of low frequency. An exception to native plant dominance is found in areas that have been seeded to smooth brome (*Bromus inermis*) and intermediate wheatgrass (*Elymus hispidus*).

Vascular plant production (table 5) is generally high enough to produce a ground cover of vegetation and litter that covers over 90 percent of the soil surface (table 6). With this extent of vascular plant and litter cover, cryptogrammic crusts appear to be of minor importance as ground cover.

Table 5—Production (lbs/acre air dry wt.) at various shrub cover.

	Percent shrub cover		
	0–10 (n = 17)	11–20 (n = 8)	>20 (n = 6)
Graminoids	637	193	167
Forbs	175	204	179
Shrubs	37	660	915
Total	847	1054	1261

Table 6—Percent of production at various shrub cover.

	Percent shrub cover		
	0–10 (n = 17)	11–20 (n = 8)	>20 (n = 6)
Graminoids	75	18	13
Forbs	21	19	14
Shrubs	4	63	73
Total	100	100	100

Vascular Plants and Community Dynamics

Plant communities are highly diverse with high numbers of vascular plants (table 2). Vascular plants of high site consistency and high quadrat frequency are considered here to be the most descriptive of the ecological unit. Those with higher values are listed in table 4, and some of these are included in the following discussion.

Mountain Big Sagebrush

Crown cover of mountain big sagebrush on this ecological unit has been found between 0 percent and 38 percent depending on fire and other processes and management actions. As mentioned above the method used to determine crown cover tends to over estimate crown cover. The data indicate crown cover of sagebrush rarely, if ever, exceeds an average of 40 percent on sites of over 0.75 acres. Following fire, herbicide application, and plowing and seeding, sagebrush cover has been decreased to 0 percent. Within 15 to 25 years mountain big sagebrush has returned to pretreatment crown cover at most sites. At a few sites this happened in as little as 10 years. At sites plowed and seeded to aggressive grasses such as smooth brome and intermediate wheatgrass, the return of sagebrush has been slower. In some of these cases, sagebrush has not returned to pretreatment status after 40 years. However, it is present and slowly increasing in most of these treatments.

Essentially all of the dynamics of sagebrush studied or observed on this landscape has been concurrent with a long history of livestock grazing. It appears that livestock grazing has accelerated return of sagebrush after fire and herbicide applications. It also appears livestock grazing can push crown cover of sagebrush beyond levels that would be found in absence of livestock grazing. However, as noted by Knight (1994) for Wyoming, presence of sagebrush should not be considered an artifact of livestock grazing. The conclusion of Johnson (1984) that the current distribution of sagebrush matches the distribution prior to settlement seems highly applicable to this ecological unit. Livestock grazing appears to have done little to move sagebrush beyond its presettlement distribution. It appears livestock grazing can increase sagebrush cover in areas were it existed prior to settlement. This is more likely for persistent, heavy use by livestock than for light or moderate use.

Snow mold and other features of winter can damage sagebrush (Nelson and Tiernan 1983; Sturges and Nelson 1986). Winter damage of sagebrush is evident on parts of this ecological unit. This is more conspicuous on concave and flat topography than on convex topography. At one study site (32-66), crown cover of sagebrush was decreased from 16 percent down to 5 percent in 7 years. At some other sites winter damage has limited sagebrush crown cover to less than 10 percent over as many as 4 decades (site 32-14). Other agents of injury to sagebrush include rodents that girdle the stems (Frischknecht and Baker 1972; Sturges 1983).

Regardless of agents of injury and mortality, including fire, herbicide applications, rodents, insects, and winter damage, mountain big sagebrush has persisted as a landscape dominant on the study area for several decades and probably thousands of years. Although livestock are likely to have increased crown cover of sagebrush on this area, the competitive ability of sagebrush indicates it was a strong component of these communities prior to introduction of Euro-American livestock.

With high ability to return after disturbance, sagebrush is clearly a major force in plant community dynamics. Other plant species generally respond or react to sagebrush. This is demonstrated in response of the understory to sagebrush reduction and recovery. As shown in tables 5 and 6, graminoid production is highly sensitive to crown cover of sagebrush. At 0 to 10 percent crown cover of sagebrush, graminoids produced an average of 637 lbs/acre (air dry weight) or 75 percent of annual herbage production. At 20 to 30 percent crown cover of sagebrush, graminoid production was decreased to an average of 167 lbs/acre or 13 percent of total production. Forbs respond similarly to grasses. However, the range of variation is narrower. At 0 to 10 percent crown cover, sagebrush contributed 4 of production. At 20-30 percent crown cover it increased to 73 percent of production.

The influence of high percent crown cover of shrubs is also indicated in alpha diversity as shown in table 3 for site 31-4. Crown cover of shrubs at that site far exceeded that of other sites, and alpha diversity was only about ½ as high as at other sites.

Regardless of high percent crown cover of sagebrush and its suppression of the understory, the understory of this area appears to have high capacity to increase rapidly after disturbances that decrease sagebrush. As many as 37 forbs, 12 graminoids, and 4 shrubs have been found on burned sites at 2 years postfire. Plant and litter cover have been found as high as 90 percent at 5 to 7 years following fire (study sites 32-70 and 32-78), and this was concurrent with livestock grazing.

Other Shrubs

Average number of shrub taxa at nested frequency study sites was four. Both yellowbrush (*Chrysothamnus viscidiflorus* var. *lanceolatus*) and mountain snowberry (*Symphoricarpos oreophilus*) had 100 percent site consistency, but these had rather low quadrat frequency values (table 2). Yellowbrush and mountain snowberry appear to play a minor part in driving plant community dynamics. Although these shrubs sometimes show slight increase in early postfire years, crown cover of these shrubs rarely exceeds 2 percent. Other plants appear to be little influenced by these shrubs. However, bitterbrush is locally common to abundant on this ecological unit, and at high percent crown cover it appears to have at least moderate capacity to suppress other species.

Graminoids

Average number of graminoid taxa was 12 (table 3). Graminoids with 100 percent site consistency (n = 6) and with quadrat frequency of greater than 33 percent are muttongrass (*Poa fendleriana*), Sandberg bluegrass (*P. secunda*), needle-and-thread grass (*Stipa comata* var. *intermedia*), thickspike wheatgrass (*Elymus lanceolatus*), and squirreltail (*E. elymoides*). Two other grasses had 100 percent site consistency but had less than 33 percent quadrat frequency. These were Junegrass (*Koeleria macrantha*) and Letterman needlegrass (*Stipa lettermanii*). As indicated in table 5, graminoids are most productive when sagebrush canopy cover is less than 10 percent. However, they appear to be able to persist in sufficient abundance and vigor under as high as 30 percent crown cover of sagebrush to be able to rapidly respond to fire that decreases sagebrush cover.

Bluebunch wheatgrass (*Elymus spicatus*) is lacking or of low quadrat frequency at most sites. Grazing does not appear to be the factor in the absence of bluebunch wheatgrass, for it is abundant to dominant on adjacent, warmer ecological units of the south face of the Uinta Mountains with equal grazing history. The one site with over 10 percent quadrat frequency of bluebunch wheatgrass (31-4D) is at the ecotone with the south face of the Uinta Mountains.

Sheep fescue (*Festuca ovina*) had 83 percent site consistency, but average quadrat frequency of this plant was only 11 percent. Low frequency of this plant does not seem to be a function of grazing. More frequent graminoids are used equally or to a greater degree than is sheep fescue on this ecological unit. Also the sheep fescue complex is not found in great abundance in many areas of the Uinta Mountains that have been quite protected from livestock. Inherent factors appear to limit plants of this complex here.

Muttongrass appears to be the graminoid most capable of persisting at moderate to high frequency under high percent canopy cover of sagebrush. The ability of muttongrass to persist under dense canopy of sagebrush on this ecological unit indicates value of this plant as a descriptor of the sagebrush community type or habitat type for the area. Needle-and-thread grass appears to be the graminoid most capable of rapid increase following fire.

Graminoids appear to drive community dynamics in early successional stages. They dominate production in the early years following fire and following herbicide application. However, they appear to be highly compatible with high diversity of forbs in the early years following disturbance.

Forbs

As high as 37 forb taxa have been recorded for a site with sample size of 100 quadrats of 2.7 ft^2. Average number of forb taxa was 31 (table 7). Those with 100 percent site consistency and greater than 33 percent quadrat frequency (table 2) are ballhead sandwort (*Arenaria congesta*), Hooker balsamroot (*Balsamorhiza hookeri*), and hollyleaf clover (*Trifolium gymnocarpon*). Others with 100 percent site consistency but with less than 33 percent quadrat frequency are pussytoes (*Antennaria microphylla*), bluebells (*Mertensia fusiformis*), many-flowered phlox (*Phlox multiflora*), common dandelion, and death camas (*Zigadenus paniculatus*).

Of these forbs ballhead sandwort, hollyleaf clover many-flowered phlox, and hooker balsamroot seem to be of some importance to classification of this ecological unit. By themselves they are not unique to this ecological unit, for they are widely distributed. However, collectively they appear to be quite descriptive of the unit. This ecological unit appears to be the principal habitat for many-flowered phlox in Utah.

Forbs appear to react to community dynamics more than to drive these dynamics. They decrease or increase in reaction to shrub and graminoid changes. Some, including ball head sandwort, dandelion, and pussytoes might be expected to increase with increasing intensity of ungulate grazing.

Fire

References that indicate fire of rather high frequency burned in communities of this ecological unit include Houston (1973) and Winward (1991). Additional evidence of comparatively high fire frequency includes the volatile nature of mountain big sagebrush communities. Based on a large number of prescribed fires and attempted prescribed fires on the Ashley National Forest, basin big sagebrush and mountain big sagebrush communities are among the most easily ignited communities with capability to carry fire under weather conditions that will not support fire in many other plant communities.

The capability of sagebrush/grass communities to carry wildfire was well demonstrated in the Dry Fork Fire of 2000 on the south slope of the Uinta Mountains. In this fire, a sagebrush/grass community of the south face of the Uinta Mountains was the ignition source. From that point the fire was carried onto sagebrush communities of the Bishop Conglomerate Formation. These communities carried the fire into aspen and lodgepole pine communities.

Fire adapted species that occupy plant communities of this ecological unit are additional evidence of high fire frequency. As high as 37 forb taxa, 12 graminoid taxa, and 4 shrub taxa have been found in burned areas at two growing seasons postfire (site 32-78). Plants found in postfire communities are the same ones found prior to burning. Fire alters abundance of various taxa in different ways, but it seems to do little to change the presence of taxa.

Although sagebrush is greatly reduced by fire, it is not uncommon to find seedlings of sagebrush the year after fire. Indeed the dynamics of mountain big sagebrush itself is a strong indication of high adaptability to fire. It is common for mountain big sagebrush to return to 20 percent canopy cover within 15 to 25 years after fire. The recovery interval of sagebrush of 15 to 25 years could, perhaps, be an indicator of the fire return interval common to the history of this ecological unit.

Postfire response of bitterbrush appears to be more varied than for sagebrush. It generally increases after the initial reduction following fire, but recovery is much slower on some sites than on others.

Some other species increase rapidly in the first 1 to 3 years following fire including annuals such as blue-eyed Mary (*Collinsia parviflora*) and ground smoke (*Gayophytum* spp.). Abundance of these appears to be fire-dependant, as these

Table 7—Comparison of features of Wyoming big sagebrush communities (ARTRW) from pediments associated with the Green River and mountain big sagebrush communities (ARTRP) on the Bishop Conglomerate Plateau.

Community feature	ARTRW (n = 9)	ARTRP (n = 6*)
Crown cover of sagebrush (percent)	0–22	0–38
Total number of vascular plant taxa	51	93
Total number of shrub taxa	7	7
Total number of graminoid taxa	13	20
Total number of forb taxa	26	66
Ave. number taxa/site (alpha diversity)	18	47
Ave. number of taxa/quadrat (beta diversity)	2.92	11.35
Ave. number of shrub taxa/site	4	4
Ave. number of graminoid taxa/site	6	12
Ave. number of forb taxa/site	7	31‘
Shrubs with 100 percent consistency	1	3
Shrubs with >49 percent consistency	1	4
Graminoids with 100 percent consistency	1	7
Graminoids with >49 percent consistency	7	12
Forbs with 100 percent site consistency	0	8
Forbs with >49 percent site consistency	4	31
Average ground cover (percent)	58	92

*n = 6 except for crown cover of sagebrush for which n = 42.

species seem to respond from a soil-seedbank of long-lived seeds that are activated by fire. Regardless of the initial response to fire, nearly all species of the ecological unit show adaptability to fire. They increase after fire by soil-seedbanks, by sprouting, or by mobile seeds that are produced elsewhere but are transported to burned areas.

Capabilities and Values

Due to low gradient, the pediment surface, and capacity to produce 90 percent or more ground cover, this ecological unit is resistant to erosion. Roads across the unit are comparatively stable. This ecological unit has supported livestock grazing for about a century with little evidence of accelerated erosion.

Vascular plant diversity and ground cover have been maintained at high levels concurrent with livestock grazing. These features indicate this area has moderate to high capability to support livestock grazing concurrent with maintenance of a number of other values.

McArthur (1984) reported 87 wildlife species for sagebrush communities of the Intermountain Region. While total number of wildlife species can be expected to be less than this on any one ecological unit, high diversity of wildlife species are indicated for this one by the high diversity of plant communities of the unit. It has high capability to produce high value herbaceous forage and browse for wild ungulates.

Bitterbrush is closely hedged across the unit. This indicates high value of this plant for ungulates. However, mountain big sagebrush is lightly, if at all, hedged over much of the area. Hedging of this shrub by ungulates seems to be more prominent toward the lower edges of the unit where it contacts the south face of the Uinta Mountains where wild ungulates spend more time in winter.

This ecological unit has capability to support dense stands of sagebrush of high value for sage grouse nesting. High number of forbs and relative high production of forbs indicate high value brooding habitat for sage grouse. The unit also includes mesic drainages that support graminoid and forb dominated communities of high value for sage grouse brooding. Current numbers of sage grouse are much lower than in past decades. Livestock grazing was equally intense or of greater intensity in past decades than in the past few years. The history of sage grouse populations and the history of livestock grazing indicate factors other than livestock grazing are related to declines in sage grouse populations.

Compared to forested environments, wild ungulates are highly visible in the sagebrush communities of this ecological unit. Wild ungulates are abundantly seen on the unit in spring and mild winters. This indicates high value for recreational wildlife viewing. The high capacity of this unit to support wild ungulates also translates to high value for big game hunting opportunities.

Camping associated with this ecological unit is most common at its margin with the aspen and lodgepole pine ecotone. However, the unit does have low to moderate value for camping.

As discussed above, the ecological unit is highly capable of supporting fire and recovering from fires with frequency of 25 to 40 years.

Comparison of Mountain Big Sagebrush Communities With Wyoming Big Sagebrush Communities

Goodrich and others (1999) reported on Wyoming big sagebrush/grass communities of pediments associated with the Green River in Daggett County, Utah. These communities are at the base of the north flank of the Uinta Mountains where average annual precipitation is about 9 inches and snow depth is commonly less than 1 foot, and continuous snow cover is usually limited to December through February. In that environment crown cover of sagebrush was found from 0 to 22 percent compared to 0 to 38 percent in mountain big sagebrush communities of plateau lands of the Bishop Conglomerate Formation.

Hedging of sagebrush by wild ungulates is heavy in the Wyoming big sagebrush communities associated with pediments of the Green River. Hedging of sagebrush is light to locally moderate in the mountain big sagebrush communities on Bishop Conglomerate. Difference in hedging of sagebrush is likely a function of differences in snow depth and duration. Difference in hedging is also a function of pronghorn antelope (*Antilocarpa americana*). Pronghorn diets can include high percent of sagebrush (Cole 1956; Ngugi and others 1992; Olsen and Hansen 1977). Pronghorn are abundant during parts of the year in some of the Wyoming big sagebrush communities. They are rare to lacking in the mountain big sagebrush communities on Bishop Conglomerate.

While greater hedging of sagebrush by mule deer and pronghorn is a factor in difference of sagebrush crown cover, the primary factor is likely the climate and especially precipitation. Nine inches of annual precipitation of the Wyoming big sagebrush communities does not have the capacity to support as much sagebrush cover as does 12 to 20 inches of the mountain big sagebrush communities. This concept is supported by exclosures in the Wyoming big sagebrush communities that have prevented ungulate access. In these exclosures, sagebrush has not exceeded an average of 22 percent crown cover (Goodrich and others 1999). Other differences between communities of the two sagebrush taxa discussed below are considered to be primarily a function of climate.

Ground cover averaged about 55 to 59 percent in areas protected from livestock or that were grazed at moderate intensity in Wyoming big sagebrush communities compared to 90 percent or more ground cover concurrent with moderate to heavy livestock grazing in mountain big sagebrush communities.

Average number of vascular plant taxa was 19 and 47 for Wyoming big sagebrush and mountain big sagebrush communities respectively. Perhaps the most vivid contrast is seen in the number of forb taxa and production of forbs. Average number of forb taxa was 7 and 31 for Wyoming big sagebrush and mountain big sagebrush communities respectively (see table 7 for these and other comparisons). Production (air dry weight) of forbs in mountain big sagebrush communities of the Bishop Conglomerate Plateau ranged from 25 to 365 lbs/acre depending on the crown cover of sagebrush. Forb production in Wyoming big sagebrush communities of Green River pediments is commonly as low as 3 to 10 lbs/acre.

Another conspicuous difference is the absence of bitterbrush in Wyoming big sagebrush communities and the presence and sometimes abundance of bitterbrush in mountain big sagebrush communities. Plants of *Chrysothamnus viscidiflorus* are present in communities of both sagebrush taxa. However, there is a difference at the level of variety. Sticky rabbitbrush (*Chrysothamnus v.* var. *viscidiflorus*) is specific for Wyoming big sagebrush communities, and yellowbrush is found at high consistency in mountain big sagebrush communities. Also mountain snowberry is consistently found in mountain big sagebrush communities of this ecological unit, but it is lacking in the Wyoming big sagebrush communities along the Green River.

Although needle-and-thread grass was of 100 percent consistency in both Wyoming big sagebrush and mountain big sagebrush communities, the long-awned variety (*Stipa comata* var. *comata*) was found only in Wyoming big sagebrush communities, and the short-awned variety (*S. c.* var. *intermedia*) was found only in mountain big sagebrush communities.

Management Implications

Mountain big sagebrush communities of the Bishop Conglomerate Plateau have diverse capabilities and values. These lands have been managed for multiple uses over the past several decades concurrent with maintaining ground cover and highly diverse plant communities. These uses appear to be compatible with maintaining processes such as fire and successional patterns consistent with the inherent capability of the land. The history of use and response to use indicates these communities have capability to continue to be managed for a number of uses concurrent with maintaining long-term productivity.

Inherent capabilities of mountain big sagebrush/grass communities of Bishop Conglomerate pediments and Wyoming big sagebrush/grass communities of pediments associated with the Green River are vastly different. Values expected of these communities could be outside reality if these differences are not recognized. Expectations for Wyoming big sagebrush communities based on a vision of mountain big sagebrush communities are indicated for disappointment, and they can be expected to lead to expensive failures in terms of habitat improvement projects.

The Wyoming big sagebrush communities have high value as winter range for mule deer and pronghorn and, in places, high value year-long for pronghorn. The mountain big sagebrush communities have high value for mule deer in spring, fall, and mild winters. They have low value for mule deer in normal and heavy winters, and they have low value for pronghorn year-long.

While the Wyoming big sagebrush communities might be of moderate to high value for sage grouse wintering areas, the low capability of these to produce forbs indicates low value for brooding habitat. Number of forbs and production of forbs in the mountain big sagebrush/grass communities of Bishop Conglomerate indicate high value brooding habitat for sage grouse.

Rating systems for condition and trend based on diversity, production, and species composition will not reflect reality unless the inherent differences between communities of these two sagebrush taxa are recognized.

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A Yellowbrush/Grass Community Type From the Uinta Mountains and Utah Plateaus

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Abstract—Ecological inventory and vegetation monitoring in the Uinta Mountains and Utah Plateaus on the Ashley National Forest and Manti-LaSal National Forest of the past several years suggest a community type in which yellowbrush (*Chrysothamnus viscidiflorus* ssp. *lanceolatus*), and slender wheatgrass (*Elymus trachycaulus*) are indicator species. This community type is common at elevations or slope positions where snow depth and duration are sufficient to greatly suppress big sagebrush. Features of this community type are discussed in context of management implications.

Yellowbrush

Yellowbrush (*Chrysothamnus viscidiflorus* spp. *lanceolatus*) is a common plant over much of mid montane Utah. It is known from lower British Columbia east to Montana and south to northern California and Colorado with outlying populations in Arizona and New Mexico (Anderson 1986). By association with some of its generic relatives, yellowbrush has been much maligned. However, yellowbrush has high value for ungulate forage. In late summer, fall, and winter it is highly selected by domestic and wild ungulates. It has been rated with moderate value for watershed protection (USDA Forest Service 1993).

In numerous studies on the Ashley National Forest, it has not displaced other vegetation by forming dense, closed stands as is sometimes the case of other members of the genus. Most often it contributes to species diversity and structural diversity without assuming high dominance that greatly suppresses other plant taxa. In contrast to rubber rabbitbrush (*Chrysothamnus nauseosus*) and big sagebrush (*Artemisia tridentata*), yellowbrush commonly does not overtop associated herbaceous vegetation. It is not uncommon for associated grasses to exceed the height of yellowbrush.

Even at sites where yellowbrush is a dominant with high frequency and high percent crown cover, there is usually a diverse mix of other plant species. Such sites are the focus of this paper.

The common name of yellowbrush is used in this paper to reduce association of this plant with some other members of the genus with less forage value and of more aggressive nature. This common name has a long history. It was used as early as 1937 (USDA Forest Service 1937). Other common names included mountain low rabbitbrush, lanceleaf yellowbrush, lanceleaf rabbitbrush, and Douglas rabbitbrush.

Study Sites

Information for this paper came from seven sites on the Wasatch Plateau, Manti-LaSal National Forest, and from five sites on the Ashley National Forest. Of the Ashley National Forest sites, three were from the western Uinta Mountains, and two were from the West Tavaputs Plateau. Range in elevation of the sites was from 2,743 to 3,048 m (9,000 to 10,000 ft). Average elevation of the sites was 2,936 m (9,633 ft). Study sites included all exposures except northerly. Gradients were mostly from 0 to 15 percent. Study sites from the Manti-LaSal National Forest are identified as RR-102, YB-1, WH-1, TSR-1, WR-1, CB-101, and RR-102N. Those from the Ashley National Forest are identified as 34-2, 34-3, 35-5, 58-1B, and 58-2. Locations for these study sites are documented at the Supervisors Offices of these National Forests at Price, Utah, and Vernal, Utah.

Methods

Data was taken from long-term monitoring sites that are permanently marked and included in study inventories of the Ashley National Forest and Manti-LaSal National Forest. Plots from which information was taken were of various sizes and from various methods of vegetation measurements. These included percent composition based on air-dry weight, rooted nested frequency, and line intercept. Although plot size varied and purpose and design of studies varied, the plot data does provide site consistency and plot frequency. Because various plot sizes and various numbers of plots were used, percent site consistency and percent frequency is used to standardize the information from the data.

Although percent composition by weight might not be statistically friendly, it does provide comparative information. This method of vegetation measurement does provide a comparative measure of the ability of different plant taxa to command the resources of a site. Ability to command resources is perhaps more accurately expressed by relative production than by frequency. Small annuals of high frequency might be much less able to command resources than larger plants of lower frequency. Percent composition by weight (table 1) is one of the parameters used in this paper to define yellowbrush-grass communities.

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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Table 1—Consistency, frequency, and composition by weight of vascular plant taxa in yellowbrush communities

Taxa	Site consistency (%) (n = 12)	Plot freq. % (n = 12)		Composition by weight (%) (n = 11)	
		Range	Average	Range	Average
Yellowbrush	100	13–100	73	12–54	26
Slender wheatgrass	100	20–100	79	7–41	17
Letterman needlegrass	100	30–100	79	2–20	11
Yarrow	92	0–94	49	0–7	3
Peavine	92	0–100	41	0–15	7
Mountain brome	58	0–100	25	0–30	5
Sandberg bluegrass	50	0–100	26	0–37	5
Sedges	58	0–77	22	0–6	3
Everywhere aster	50	0–37	7	0–6	1
Potentilla	50	0–52	19	0–11	2
Dandelion	58	0–100	29	0–4	1
Douglas knotweed	50	0–40	15	0–1	<1
Oniongrass	42	0–80	18	0–3	1
Rockcress	42	0–20	4	0–1	<1
American vetch	42	0–40	12	0–1	<1
Muttongrass	33	1–10	2	0–1	<1
Penstemon	33	0–60	12	0–14	2

Features of Yellowbrush/Slender Wheatgrass Communities

Yellowbrush/slender wheatgrass communities are typically found at higher elevations than mountain big sagebrush communities or on concave leeward slopes where persistent snowbeds suppress sagebrush. They appear to be more common on basic substrates than on acidic or neutral ones. In Utah, they are found in the aspen and spruce-fir belts. They are found in the western Uinta Mountains and on the plateaus that run down through the center of Utah. Ground cover (ground covered by vegetation, litter, and rock greater then 2 cm diameter) varied between 35 and 98 percent with three sites at 35 percent and three sites over 90 percent. Potential for ground cover might be above 90 percent. Sites with lower ground cover values were highly disturbed by northern pocket gophers (*Thomomys talpoides*).

Yellowbrush communities are distinguished by yellowbrush being the dominant shrub and sometimes the only shrub with greater than a trace of crown cover. Line intercept of crown cover of yellowbrush was measured at three of the sites. Crown cover of this shrub ranged from 8 to 37 percent. Graminoid representatives of these communities include slender wheatgrass (*Elymus trachycaulus*), letterman needlegrass (*Stipa lettermanii*), and Hood sedge (*Carex hoodii*). Although mountain brome (*Bromus carinatus*) is occasional to these communities, it is not nearly so common here as in tall forb communities. Forbs common to these communities include peavine (*Lathyrus lanzwertii*), yarrow (*Achillea millefolium*), Rydberg penstemon (*Penstemon rydbergii*) and Watson penstemon (*Penstemon watsonii*).

Although yarrow was found at relatively high site consistency, and high plot frequency, this plant is a generalist of broad ecological amplitude. Its broad amplitude limits the indicator value of this plant for a specific community type. The same might be said of Letterman needlegrass.

Several species had site consistency of 33 percent or greater. However, due to broad amplitude or low plot frequency these plants are not considered reliable or specific indicators of yellowbrush/grass communities. These include Sandberg bluegrass (*Poa secunda*), sedges (*Carex* spp.), everywhere aster (*Aster chilensis*), potentilla (*Potentilla* spp. and mostly *P. gracilis*), dandelion (*Taraxacum officinale*), Douglas knotweed (*Polygonum douglasii),* oniongrass (*Melica bulbosa*), rockcress (*Arabis* spp.), American vetch (*Vicia americana*), muttongrass (*Poa fendleriana*), and penstemon (*Penstemon* spp. and mostly *P. rydbergii* and *P. watsonii*).

Over 70 vascular plant taxa were recorded in plots. The 17 taxa listed in table 1 had site consistency of 33 percent or greater. All other taxa had site consistency less than 33 percent, average plot frequency less than 15 percent, and contributed no more than 1 percent of composition by weight.

The three methods of classifying plants of table 1 all point to the same few taxa as being most reliable as indicators of the community type. These are yellowbrush, slender wheatgrass, Letterman needlegrass, and peavine. The large gap in site consistency from 92 percent to 58 percent between peavine and mountain brome shown in table 1 is likely significant.

These plants have rather broad amplitude. However, the combination of these plants as dominants does seem unique. The name of yellowbrush/slender wheatgrass serves well to identify this community type.

Abundance of slender wheatgrass, mountain brome, peavine, and other plants common to tall forb communities might be considered an indication that yellowbrush/slender wheatgrass communities are degraded tall forb communities. However, the classic indicators of degraded tall forb communities including western cone flower and tar weed were lacking or of comparatively low frequency at these sites. Of the 12 sites, tarweed was found at only one site. Western coneflower (*Rudbeckia occidentalis*) was not recorded in plots at any of the sites. Tall larkspur (*Delphinium occidentale*) was found in low abundance at one site. Additional evidence of two distinct communities includes abrupt boundaries between some tall forb and yellowbrush/slender wheatgrass communities. However, gradual gradients between the two communities can be expected at some locations.

At the warm or low elevation end, yellowbrush communities grade into mountain big sagebrush communities.

Recently burned big sagebrush sites at high elevation can take on the appearance of yellowbrush/slender wheatgrass communities. At one site on the Manti-LaSal National Forest (Baldy Swamp Burn), yellowbrush and Letterman needlegrass were common after burning. However, bluebunch wheatgrass (*Elymus spicatus*) and not slender wheatgrass was the dominant grass.

Topographic position and elevation are also indicators of yellowbrush/slender wheatgrass communities. These communities are most common on leeward slopes and/or at elevations above that commonly occupied by mountain big sagebrush. These communities appear to occupy sites not as productive as tall forb communities and often more exposed to wind. Although they are often on concave slopes, they are more commonly on convex slopes than are tall forb communities.

Resource Values

Although yellowbrush is often held in low esteem as a forage plant by association with other members of the rabbitbrush genus, it is highly selected during parts of the year by mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), cattle (*Bos tarus*), and sheep (*Ovis aries*). Dayton (1931) noted a good representation of this plant by no means necessarily indicates a deteriorating range. He indicated carrying capacity of grass communities was likely increased by presence of this plant.

Stubble height of individual shrubs of yellowbrush monitored over a 10-year period on the face of Mosby Mountain of the Uinta Mountains has been reduced on an average of about 50 percent each winter by elk and deer from an average of 41 cm in the fall to 19 cm in spring (unpublished data on file at the Supervisors Office, Ashley National Forest, Vernal, Utah). Observations on the Ashley National Forest indicate cattle and sheep on the Tavaputs Plateau commonly use the flowers and upper parts of stems in late summer and fall after grasses have cured. These observations are consistent with those recorded by the U.S. Department of Agriculture, Forest Service (1937) that the plant is used by cattle and sheep mostly after the middle of August. The graminoids of yellowbrush/grass communities have moderate to high value for elk and livestock forage. There is often a moderate diversity of forbs associated with these communities. These forbs are of various resource value.

Yellowbrush/grass communities are often within close proximity to aspen and/or coniferous tree cover. Thus, they provide high value elk foraging areas close to hiding cover.

These communities have high potential for uniform dispersion of ground cover, and high percent ground cover. They often have high value for watershed protection. Where pocket gophers have cast up much bare soil, infiltration rates appear to be high and these sites appear to remain highly capable of maintaining watershed values.

Management Implications

Although this is a comparatively minor community type, it is important to recognize this community type and not confuse it as a degraded phase of tall-forb communities. These communities should not be expected to have capabilities of tall forb communities. Although in some cases, yellowbrush/grass communities develop as seral communities in burned mountain big sagebrush sites, there are areas where this community is exclusive of sagebrush sites. To understand capabilities of the land, it is important to recognize yellowbrush community types that have low or no potential to support sagebrush.

Ground cover appears to be highly influenced by pocket gophers. Although ground cover was found at over 90 percent at three sites, it was as low as 35 percent at three sites. Livestock and wild ungulates have used all of the study sites, and ungulate use is a likely factor in reduced ground cover. However, the sites with high percent ground cover have a similar history of grazing to those with low percent ground cover. A conspicuous difference between sites with low percent ground cover and those of high percent ground cover was the abundance of gopher casts. The influence of pocket gophers on ground cover should not be overlooked when making evaluations of ungulate grazing.

Yellowbrush communities are indicated to have high value for watershed stability. This stability has been maintained under light and moderate livestock grazing. These communities are indicated to have moderate to high capability to support livestock and wild ungulates without loss of watershed values under light and moderate grazing intensities.

Yellowbrush is a plant of high resource value especially where associated with high frequency of grasses and forbs. It has been recognized with high capacity to withstand grazing. It is reasonable to expect high abundance, cover, and production of this plant is to some degree a function of livestock grazing at the sites where data was taken for this study. However, this highly competitive plant can be expected at moderate levels in yellowbrush/grass communities not grazed by livestock. Vigor of graminoids at some sites on the Ashley National Forest indicates a history of light to moderate livestock grazing in the past decade or more. Yellowbrush was as abundant here as it was at other sites with a history of higher levels of livestock use.

The studies from which the above information was taken are part of long-term study inventories. The sites can be revisited. Repeat information has already been collected from some of these sites. A clear advantage of this approach is the opportunity to revisit sites in the future to reevaluate management implications. Interpretations or management implications made here are based on data collected to date. Future information might have other implications.

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Rate of Increase of Redberry Juniper (*Juniperus pinchotii*) Canopy Cover in Western Texas: Ecological and Economic Implications

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Abstract—Redberry juniper (*Juniperus pinchotii*) is a major problem on Texas rangelands, yet little is known about the rate it is increasing. This study estimated long-term rates of change of redberry juniper canopy cover on undisturbed sites and adjacent sites that were either chained or grubbed at five locations in western Texas. Juniper cover was estimated from positive transparencies of aerial photographs by the line intercept method using a 10-X monocular lense with a vernier. Juniper cover increased at an average rate of 0.37 percentage unit year^{-1} (range 0.12 to 0.59) on undisturbed sites from the mid 1950s or early 1960s to the late 1990s (34 to 41 years). Following chaining or grubbing treatments during 1970 to 1978, juniper cover increased at an average rate of 1.00 percentage unit year^{-1}, which was significantly faster than the average rate of 0.5 percentage unit year^{-1} on untreated rangeland for the same time interval. Juniper cover returned to pre-treatment levels in an average of 20.6 years (range 11 to 29) following mechanical control. The annual increment in herbaceous production was predicted at –2 to –4 kg ha^{-1} (–1.8 to –3.6 lb acre^{-1}) for sites or periods where juniper cover was increasing at low rates and at –15 to –23 kg ha^{-1} (–13 to –21 lb acre^{-1}) where juniper cover was increasing at high rates. Data from this study suggest that initial or maintenance control practices should be installed before juniper cover exceeds about 12 percent.

Redberry juniper (*Juniperus pinchotii*) infested about 4.7 million ha (12 million acres) of rangeland in Texas in 1982 (Soil Conservation Service 1985), and it is rapidly increasing in abundance and expanding its geographical range (Ansley and others 1995). Only about 34 percent of annual rainfall reaches mineral soil beneath mature redberry junipers because of interception by the tree canopies and litter layers (Thurow and Hester 1997). Mature junipers severely impact the herbaceous vegetation beneath, and on some soils for considerable distances beyond, their canopies (Dye and others 1995), thus, forage production declines as juniper canopy cover increases (Johnson and others 1999; McPherson and Wright 1990). Knowledge on the rate of increase of redberry juniper cover is critical to better understanding its ecology, assessing the economic feasibility of control programs, and scheduling initial and maintenance control practices. The main objective of this study was to determine the rates of increase of redberry juniper cover on undisturbed and mechanically treated rangeland in western Texas. Our hypothesis was that juniper cover increases faster following mechanical control than on undisturbed rangeland. A secondary objective was to apply the knowledge on the rate of juniper cover increase to estimate the temporal effects of redberry juniper cover changes on herbaceous production.

Materials and Methods

Redberry juniper woodlands were studied at five locations across the northern and western Edwards Plateau of Texas (fig.1) along an average annual rainfall gradient from 46 to 62 cm (18.1 to 24.5 inches). Two 16.2-ha (40-acre), juniper-infested sites, one with and one without a history of prior mechanical control that were in close proximity and on the same soil, were selected at each location. Other criteria for site selection were that (1) redberry juniper was the dominant overstory species, (2) there were no other large, evergreen plants that could be mistaken for junipers on aerial photographs taken during winter, (3) maintenance juniper control treatments had not been applied to treated plots subsequent to the initial mechanical control treatments, (4) past management was typical for the region, and (5) topographical or man-made features facilitated precise location of the sites on large-scale aerial photographs.

The soils at all study sites were shallow, with rapid surface runoff, and low to very low water availability. Juniper control treatments included two-way chaining at three sites (1970 in Coke County, 1972 in Irion County, 1978 in Reagan County), one-way chaining in 1971 in Crockett County, and grubbing in 1976 in Nolan County.

Positive transparencies of all available aerial photographs (scale 1 cm = 79 m) (1 inch = 660 ft) of each site were purchased from the USDA Farm Services Agency Aerial Photography Field Office in Salt Lake City, Utah. The earliest photographs were taken in 1955 and the latest in

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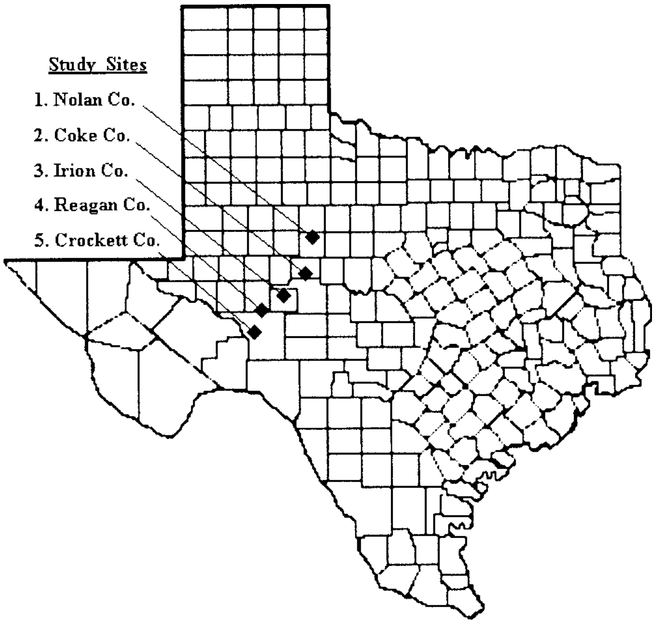

Figure1—Locations of redberry juniper study sites in the Edwards Plateau, Texas.

1997. All photographs were taken in winter and redberry juniper plants or clusters were evident on the photographs as dark or black areas within the grey matrix of dormant grasses and bare ground. A 10-X hand lense with a vernier was used to estimate juniper cover by the line intercept method (Bonham 1989) on each aerial photograph of each study site, while the positive transparency was on a light table. The center one-hundred 0.1-mm (0.0039-inch) increments of the vernier were used for line transects. Forty-five line transects, equivalent to 79 m (259 ft) in length, were sampled on each aerial photograph of each site. The mean canopy cover for each photograph of each site was calculated. Redberry juniper cover on each study plot was estimated in the field by the line intercept method in July 1999 for comparison with estimates from the most recent (1996 or 1997) aerial photographs. Ten 152.4-m (500-ft) line transects were sampled on each 16.2-ha (40-acre) plot. The mean canopy cover was calculated for each plot.

The rate of change of juniper cover (percentage units year^{-1}) for each site was calculated by dividing the percentage point change in cover from photograph A to photograph B by the number of years that had lapsed between the two photographs. Live juniper cover remaining subsequent to chaining or grubbing was assumed to be about 1 percent, based on our observations of commercial chaining and grubbing operations in the region.

Analysis of variance was used to determine if the estimates of juniper cover for each site from the most recent aerial photographs and from field sampling in 1999 were significantly different. Variation among subsamples within each plot (n = 45 for aerial photographs; n = 10 for field sampling) was utilized as the estimate of error. Data on juniper cover from each study site were subjected to analysis of variance to determine if juniper cover changed significantly during the time interval between photographs. Variation among subsamples within treatments was utilized as the estimate of error. Means were separated by LSD at $P \leq 0.05$. Analysis of variance was also used to test for differences in rates of change of redberry juniper canopy cover post treatment on chained or grubbed sites and for this same time interval on untreated plots. Locations (n = 5) were utilized as replications in this analysis.

We used our estimates of the rates of change of juniper cover to estimate juniper cover for each year between the earliest and latest photographs for each undisturbed site. These yearly juniper cover values were then used in the natural log model of the relationship between annual herbage production and redberry juniper cover developed in the Edwards Plateau by Johnson and others (1999) to estimate the decline in total herbaceous production as a function of time. This production function is defined as:

$$Y = e^{7.1626024 - 0.000441X^2}$$

where Y = annual herbage production in kg ha^{-1}, e is a transcendental number 2.718282, X = redberry juniper canopy cover (percent), and $r^2 = 0.9054$.

Results and Discussion

Cover Estimates From Photographs Versus Field Sampling

Estimates of juniper cover from 1996 or 1997 aerial photographs and from field sampling in 1999 were similar for seven of the 10 study sites, but field estimates were significantly ($P \leq 0.05$) lower than those from photographs for three sites (data not shown). Visual estimates of juniper cover on the photographs of these three sites by two observers were in close agreement with the means obtained from the photographs using the 10-X monocular lense method. We concluded that ten 152.4-m (500-ft) line transects were not an adequate sample size for field sampling on these three sites because the juniper was spatially arranged either in patchy or striated patterns. We feel confident that the 10-X monocular lense method provided acceptable estimates of redberry juniper cover on all 10 of our study sites.

Juniper Canopy Cover Changes

Undisturbed Rangeland—Juniper cover decreased or remained relatively static for several years after the mid 1950s on untreated sites where the initial cover was >30 percent (see graphs for Irion and Coke County sites in fig. 2). In contrast, juniper cover steadily increased, usually at increasing rates, on undisturbed rangeland where the initial canopy cover was ≤14 percent (see graphs for Crockett, Nolan, and Reagan County sites in fig. 2). These differences suggest that, following the drought of the 1950s, intraspecific competition may have suppressed juniper growth and seedling recruitment on rangeland with heavy juniper cover, whereas adequate resources were available for juniper growth and seedling recruitment on rangeland with light juniper cover.

The rate of juniper cover increase on undisturbed rangeland escalated over time from the mid 1960s through the late 1990s at most sites (fig. 2). Terminal rates of canopy cover

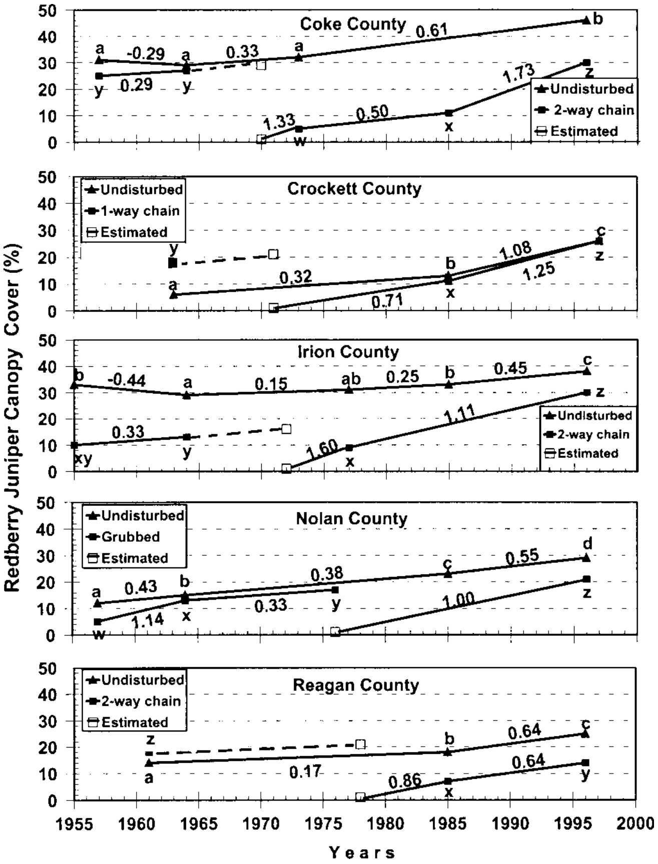

Figure 2—Redberry juniper canopy cover (percent) during 1955 to 1997 on undisturbed rangeland and adjacent sites subjected to chaining or grubbing in Coke, Crockett, Irion, Nolan, and Reagan Counties, Texas, estimated from aerial photographs. Numbers between data points are the rates of canopy cover change (percentage unit year^{-1}). Means within a line accompanied by different lower case letters are significantly different at $P \leq 0.05$.

change on undisturbed rangeland varied from 0.45 percentage unit year^{-1} in Irion County, where cover was approaching 38 percent, to 1.08 percentage unit year^{-1} in Crockett County, where cover was approaching only 26 percent (fig. 2). The Crockett County undisturbed site supported only 11 percent juniper cover in 1985, which was much less than was present on the other undisturbed sites. This suggests that the environment of the Crockett County site during 1985 to 1996 was capable of supporting more juniper cover, whereas juniper populations on the other undisturbed sites were more mature, and perhaps approaching equilibrium with their environments.

The long-term rates of change of juniper cover over 34- to 41-year periods on the five undisturbed sites averaged 0.37 percentage unit year^{-1} (range 0.12 to 0.59). The undisturbed site in Irion County, which supported the greatest initial juniper cover (33 percent) (fig. 2), had the lowest long-term rate of change (0.12 percentage unit year^{-1}). The undisturbed site with the lowest initial juniper cover (6 percent) exhibited the greatest long-term rate of change in juniper cover (0.59 percentage unit year^{-1}) (see Crockett County site in fig. 2). Soulé and Knapp (1999) reported that western juniper (*J. occidentalis* spp. *occidentalis*) cover increased at rates of 0.08 percentage unit year^{-1} on an ungrazed site and at 0.11 to 0.18 percentage unit year^{-1} on grazed sites during 1951 to 1994 in central Oregon where average annual precipitation was 25 cm (9.8 inches). The faster development of redberry juniper woodlands in western Texas may be a function of greater annual rainfall or to inherent differences among these two species in growth rate, seed production, recruitment rates, or the age at which these species reach reproductive maturity.

Mechanically Treated Rangeland—Redberry juniper canopy cover increased at an average rate of 1.00 percentage unit year^{-1} over the 18- to 26-year periods following chaining or grubbing (range 0.72 in Reagan County to 1.21 in Irion County). During this same time interval, the canopy cover of undisturbed juniper increased at 0.50 percentage unit year^{-1}, which was significantly ($P \leq 0.001$) lower than the average rate following mechanical treatments. Short-term rates of cover change (between photographs) subsequent to mechanical treatments ranged from 0.5 to 1.73 percentage unit year^{-1} (fig. 2). Juniper cover increased at similar rates on sites two-way chained, one-way chained, and grubbed.

The more rapid development of juniper cover following mechanical treatments can be attributed to three factors. Redberry juniper seedlings and saplings are often very abundant in the understory of mature junipers in the Edwards Plateau (Dye and others 1995; Ueckert and Whisenant 1982), and these small plants are not effectively controlled by chaining or grubbing. Removal of mature junipers by chaining or grubbing reduces the interference of mature junipers with the growth of these juvenile plants, and they grow very rapidly. On some sites, chaining only removes the aboveground growth of many redberry junipers, and these plants resprout from the basal caudex, then grow very rapidly because of their extensive root system (McPherson and Wright 1989). Also, the soil disturbance and juniper debris created by chaining or grubbing provides seedbeds for juniper seed germination and safe sites for juniper seedling establishment.

Interrelationship of Juniper Cover, Herbage Production, and Time

Linear and polynomial models with r^2 values >0.998 explained the decline in annual herbage production over time in response to increasing redberry juniper cover on our five untreated range sites (fig. 3). Annual herbage production was predicted to decrease at increasing rates over time at the Crockett, Nolan, Reagan, and Irion County study sites, and to decrease at a slightly decreasing rate over time at the Coke County site. The annual increment in herbage production was low (–2 to –4 kg ha^{-1} year^{-1}) (–1.8 to –3.6 lb acre^{-1} year^{-1}) for sites and periods when juniper cover was increasing at low rates (0.15 to 0.32 percentage unit year^{-1}), intermediate (–11 to –14 kg ha^{-1} year^{-1}) (–10 to –12 lb acre^{-1} year^{-1}) when juniper cover was increasing at intermediate rates (0.45 to 0.61 percentage unit year^{-1}), and high (–15 to –23 kg ha^{-1} year^{-1}) (–13 to –21 lb acre^{-1} year^{-1}) when juniper cover was increasing at the highest rate (1.08 percentage unit year^{-1}). The natural log production function predicted

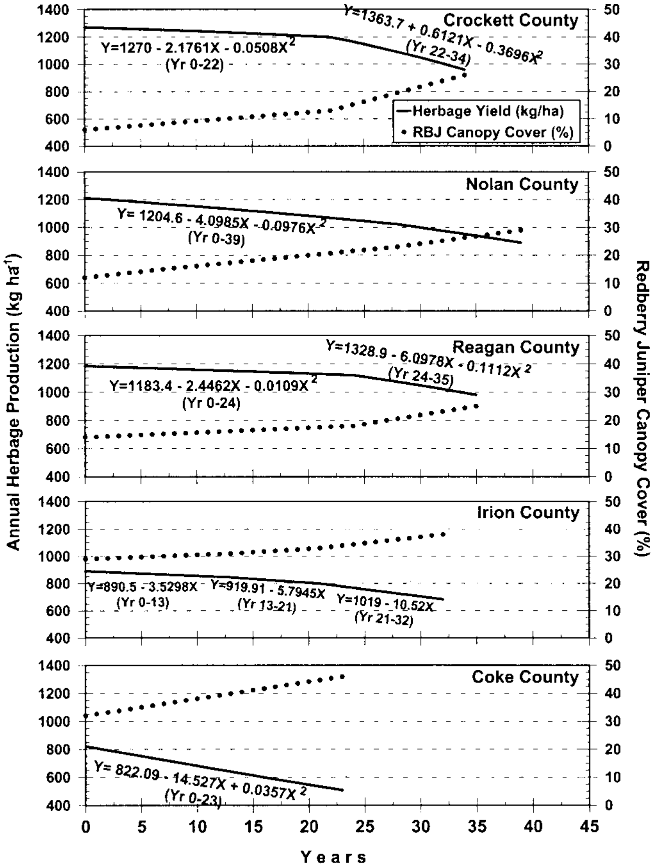

Figure 3—Relationships between annual herbage production (kg ha^{-1}) (Y) and time (years) (X) for undisturbed redberry juniper study sites in Crockett (1963 to 1997), Nolan (1957 to 1996), Reagan (1961 to 1996), Irion (1964 to 1996), and Coke (1973 to 1996) Counties, Texas. The trend lines were developed by integrating our estimates of annual redberry juniper canopy cover (percent) into a natural log model of the relationship between annual herbage production and redberry juniper canopy cover developed in the northern Edwards Plateau, Texas, by Johnson and others (1999). Functional forms were fitted to the trend lines that had r^2 values >0.998. Annual juniper canopy cover (dotted line) is included in each graph for reference only.

that herbage production on our five untreated sites had decreased by an average of 272 kg ha^{-1} (243 lb acre^{-1}) (range 204 to 320 kg ha^{-1}) or 26 percent (range 17 to 38 percent) from the mid 1950s or 1960s to the late 1990s.

Management Implications

The threshold from grasslands, in which graminoid-driven successional processes predominate, to redberry juniper-dominated woodlands is crossed when sufficient numbers of junipers become established and reach reproductive maturity. At this point, juniper-driven successional processes, including (1) a major reduction in diversity, density, basal area, and productivity of the herbaceous undestory, (2) an influx of subsidiary woody and succulent species, (3) further reduction in fire frequency and intensity, and (4) a high incidence and rate of juniper seedling establishment, begin predominating (Dye and others 1995). Data presented in this paper document the rates at which redberry juniper woodlands can develop and recover following chaining or grubbing, and predicted rates at which herbage production concomitantly declines. This study substantiates the conclusion of Dye and others (1995) that conversion of juniper woodlands back to grasslands will not only require initial reclamation treatments, but also sustained use of followup maintenance control practices and proper grazing management. Our data show that annual herbage production on undisturbed rangeland declines slowly as redberry juniper cover initially reaches 12 to 18 percent, rapidly as juniper cover increases from 19 up to 29 percent, and slowly on some sites, but fairly rapidly on other sites, after juniper cover exceeds 29 percent. We suggest that initial or maintenance redberry juniper control practices should be installed before redberry juniper cover exceeds about 12 percent, in other words, before annual herbage production begins declining at peak rates.

Knowledge of the rate woody plant canopy cover changes is essential for determining the economic feasibility of control projects. In a recent study of the economic feasibility of redberry juniper control using two-way chaining as the initial treatment and periodic prescribed burning as maintenance treatments, Johnson and others (1999) utilized empirical linear rates of juniper cover change of 1.6, 2.5, and 5 percentage units year^{-1} across a range of untreated juniper cover of 10 to 30 percent and subsequent to two-way chaining and prescribed burning. Their study showed that net present values of juniper control treatments increased from \$67 to \$130 ha^{-1} (\$27 to \$53 acre^{-1}) and that the optimal burning cycle decreased from 9 to 5 years as the rate of juniper cover change increased from 1.6 to 5 percentage units year^{-1}. The slower rates of juniper canopy cover increase that we report here for untreated and mechanically treated rangeland suggest that the net present value of controlling juniper with chaining and periodic burning would be positive, but substantially less than \$67 ha^{-1} (\$27 acre^{-1}), and that the optimum burning interval would be substantially longer than 9 years. More recently and based on data from our study, SoRelle (2000) used rates of redberry canopy cover increase of 0.12, 0.37, and 1.08 percentage unit year^{-1} for undisturbed stands and rates of 0.5, 1.0, and 1.73 percentage unit year^{-1} subsequent to initial or maintenance control practices in his study of the economic feasibility of redberry juniper control. The net present value to a cattle producer for controlling redberry juniper using two-way chaining as the initial treatment and hexazinone (3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1*H*,3*H*)-dione) individual plant treatments for maintenance control increased from about \$34 to \$56 ha^{-1} (\$14 to \$23 acre^{-1}) as the rate of juniper cover increase without treatment increased from 0.12 to 1.08 percentage unit year^{-1}. The net present value of juniper control decreased from about \$54 to \$25 ha^{-1} (\$22 to \$10 acre^{-1}) when the rate of canopy cover increase following treatment increased from 0.5 to 1.73 percentage unit year^{-1}.

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Ecological Implications of Using Goats for Control of Juniper in Texas

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Abstract—The Edwards Plateau region of central Texas supports a rich diversity of plants and animals. The diversity and abundance of trees and shrubs is especially noteworthy, but two species of juniper (*Juniperus ashei, Juniperus pinchotii*) now dominate much of the landscape. Goats are currently being recommended to control juniper infestations. The concept of using biological methods for the control of nuisance plant species has gained much attention in recent years. Some claim that biological control is more environmentally friendly and cost effective than herbicides or heavy equipment. Because juniper is one of the poorest browse plants in the region, other more desirable shrubs are browsed in preference to juniper. While goats can be managed to cause damage or even death to juniper, this level of browsing is very detrimental to a host of more palatable shrubs and trees. These more palatable species become stunted and unproductive and often die prematurely when subjected to this kind of browsing. Reproduction is impaired and eventually they are lost from the local plant community. These harmful side effects of biological juniper control are not often considered by practitioners. These side effects are easily observed, but have not been scientifically studied nor quantified.

Background and History

The Edwards Plateau region of Texas is a 24 million acre area that lies in the central and southwestern portion of the State. The region is characterized by rolling to steep topography, shallow, rocky, limestone soils, and receives 14 to 32 inches of rainfall on a west to east gradient. The region is biologically very diverse being the transition between forests to the east and deserts to the west and between grasslands to the north and thorn shrublands to the south. There are about 2,500 species of vascular plants native to the region (Hatch and others 1990).

The historic climax plant communities varied greatly, depending on soils, topography, rainfall, and the extent of natural fire. Historic landscapes included mid grass prairies on the flatter divides, oak savannas across the rolling uplands, juniper-oak woodlands in the canyonlands and steep terrain, and riparian forests. Most natural resource professionals agree that periodic and recurring wildfire was responsible for maintaining the open character of the prairie divides and the rolling oak savannas (Smeins 1980). This fact was recognized in the early 1900s (Bray 1904; Foster 1917).

The presence and extent of juniper in pre-settlement times has been hotly debated and argued by ranchers, natural resource managers, ecologists, and environmentalists. Despite the ongoing debate, the historical record is abundant and clear that juniper was common and dominated some sites, and was uncommon or absent on other sites (Curtis 2000; Smeins 1980; Weniger 1984)

The region is almost entirely privately owned ranches and has been grazed by domestic livestock for over 100 years. Various combinations of cattle, sheep, goats, exotic ungulates, and native white-tailed deer are present across the region and are the basis of the ranching and hunting economy.

Because of poor grazing management and the resulting reduction in fires, the vegetation and general appearance of the region has changed dramatically over the past century (Smeins and others 1997). Herbaceous cover has been degraded by heavy and continuous grazing. Tall and mid grasses and desirable forbs have been eliminated or greatly reduced in most pastures. A sparse ground cover of low successional species and excessive bare ground has caused poor infiltration, accelerated runoff, and erosion. The lack of adequate fine fuel has greatly reduced the opportunity for natural or prescribed fire.

Juniper Encroachment

As grasslands were thinned by heavy and continuous grazing, fires were not able to burn with the intensity or at the scale and frequency required to suppress and control increases in woody plants. Several species of woody plants including two species of juniper have taken advantage of this opportunity. Red-berry juniper (*Juniperus pinchotii*) and Ashe juniper (*Juniperus ashei*) have increased in extent in response to the overgrazing and subsequent lack of fire. Rangeland managers often refer to this as an “invasion” as if juniper had some insidious power to overwhelm healthy grasslands. Others consider the increase of juniper merely a natural ecological response to a man-made disturbance.

The spread and increase of juniper into what formerly were grasslands and savannas has caused problems for the rancher. The cover of grass that had already been altered by grazing practices was being weakened further by increases in juniper. The shading of grasses by the juniper canopy, the competition for moisture, and the interception of rainfall all contribute to the progressive loss of grass cover and forage (Thurrow and Carlson 1994; Ueckert 1997). The inability of the rancher to see and manage livestock is also impaired by increases in juniper. Several million acres of once productive grazing land now supports dense canopies of juniper and sparse densities of grass.

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Juniper Control

Since increases in juniper were first observed, ranchers as well as agricultural and conservation agencies have been busy discovering and promoting methods to control juniper (Wolff 1948). Many different methods have been used and millions of dollars spent to kill juniper. Mechanical methods including grubbing, dozing, chaining, and rootplowing with large equipment have been popular (Scifres 1980). Hand cutting of ashe juniper, a nonsprouting species has long been used and is effective. Chemical methods have been tried but with limited and small scale success. The use of prescribed fire is gaining in popularity, yet most landowners are either unwilling or unable to use this method, and less than one-tenth of 1 percent of the acreage in the region is burned each year (Nelle, unpublished data).

Regardless of the method of control or the effectiveness of control, one thing is certain: juniper begins to reappear and increase soon after it has been removed. Many areas within the Edwards Plateau have had all juniper removed several different times in the past 50 years only to see it return to undesirable densities. In the ecological tussle for control of the landscape, juniper is winning and healthy grasslands are loosing.

Goats

Goats have been numerous in the region for over 100 years. The Edwards Plateau has led the country in goat production ever since records have been kept. Goat numbers reached their peak in the mid 1960s with about 4 million head. Since that time, goat numbers have declined (Findley 1990). Goat numbers on individual ranches are commonly as high as one goat per 3 to 5 acres.

Diet and food habit studies have confirmed that goats eat large amounts of browse even when other kinds of forage are available (Bryant and others 1979). The rich diversity and the abundance of desirable woody plants in the Edwards Plateau have provided a natural resource base for a thriving goat industry. When managed on a renewable basis the raising of goats can be very compatible with the sustainability of the browse resource (NRCS 1994)

Are Goats Nature's Herbicide?

Some agricultural professionals have been making the claim in the popular media that goats are "nature's herbicide" and an "environmentally friendly" way to control juniper. The word, "herbicide" literally means "plant killer." It is true that goats or any other kind of livestock can be managed intentionally or unintentionally in a way that causes harm to plants. Grazing or browsing an excessive amount of leaf material will necessarily reduce the photosynthetic ability of a plant to sustain itself. If this excessive level of leaf removal continues, plants will be reduced in vigor and can eventually be killed. When this process is unintentional and unplanned, it is called overgrazing or overbrowsing. When it is planned, it is often called biological control.

There is an important distinction between the normal consumption of juniper by goats and the biological control of juniper. Goats and deer will naturally consume some juniper as a part of their diet, especially in winter when the availability of other green browse is limited. This degree of normal browsing is not heavy enough to exert physiological damage to established plants although some seedling mortality is likely to occur.

Side Effects

When any land management practice is considered, it is wise to evaluate the potential negative side effects prior to full-scale endorsement (Hughs 2000). If a practice successfully meets the intended objective and if associated side effects are minimal or tolerable, the practice might be safely prescribed. If the practice meets its objective, but there are serious unintentional side effects, the practice would at least be considered questionable. The consequences of the side effects would be weighed against the benefits before the practice is recommended. In the case of biological control of juniper with goats, the ecological side effects are substantial.

Juniper is one of the least preferred browse plants of the region. The secondary chemical compounds in the leaves make juniper relatively unpalatable to browsing animals (Launchbaugh and others 1997). This built-in defense mechanism against browsing is one reason why juniper has proliferated in the face of large numbers of browsing goats and deer. Even though juniper is nonpreferred and relatively unpalatable, goats can be managed for an unnaturally high consumption of juniper, even to the point of causing injury and death of juniper.

Goats, like most other herbivores are selective feeders. They will selectively consume the best, most palatable plants in preference to less palatable plants. As the more preferred plants become heavily browsed, goats will move to progressively less and less preferred plants. A host of more palatable woody plants will be very heavily browsed when goats are forced to eat unnaturally high amounts of juniper (table 1). When such heavy use continues over a sustained period, the woody plant diversity of the area suffers loss. Although most ranchers agree that there are many desirable kinds of shrubs and trees, their dislike of a few brush species such as juniper often overshadows their desire to manage the beneficial species.

An experienced observer can easily discern this loss or reduction of desirable woody species across the region. Decades of heavy goat grazing have caused distinct browse lines on preferred and moderately preferred species. All growth within reach of animals is consumed. Shorter plants exhibit severe hedging, a reduction in leaf size, dead twigs and branches, and an overall reduction in vigor. Flowering and seed production is curtailed. Successful reproduction, if it occurs at all, is limited to protected sites where goats and deer cannot browse. This reduction of plant diversity is one of the major side effects of this practice.

Ecological Implications

The reduction of plant diversity is a fairly clear side effect of heavy goat browsing. The long term ecological implications of this loss are less clear but should be considered. There has been little or no research in this area. In the

Table 1—A partial listing of desirable woody plants that are browsed in preference to juniper and that may be lost under heavy browsing.

Common name	Scientific name
Texas kidneywood	*Eysenhardtia texana*
Littleleaf leadtree	*Leucaena retusa*
Texas sophora	*Sophora affinis*
Carolina buckthorn	*Rhamnus caroliniana*
Mountain mahogany	*Cercocarpus montanus*
Texas mulberry	*Morus microphylla*
White honeysuckle	*Lonicera albiflora*
Black cherry	*Prunus serotina*
Hawthorne	*Crataegus crusgallii*
Rusty blackhaw	*Viburnum rufidulum*
Inland ceanothus	*Ceanothus herbacea*
Texas oak	*Quercus texana*
Netleaf hackberry	*Celtis reticulata*
Cedar elm	*Ulmus crassifolia*
American elm	*Ulmus americana*
Black willow	*Salix nigra*
Bumelia	*Bumelia languinosa*
Clematis	*Clematis drummondii*
Roemer acacia	*Acacia roemeriana*
Wild plum	*Prunus angustifolia*
Redbud	*Cercis canadensis*
Grapevine	*Vitis* sp.
Virginia creeper	*Parthenocissus quinquefolia*
Greenbriar	*Smilax bona-nox*
Carolina snailseed	*Cocculus carolinus*
Western soapberry	*Sapindus drummondii*
Elbowbush	*Forestiera pubescens*
Ephedra	*Ephedra antisyphyllitica*
Live oak	*Quercus virginiana*
White shin oak	*Quercus durandii*
Vasey shin oak	*Quercus pungens*
Blackjack oak	*Quercus marylandica*
Skunkbush sumac	*Rhus trilobata*
Evergreen sumac	*Rhus virens*
Littleleaf sumac	*Rhus microphylla*
Flameleaf sumac	*Rhus copallina*
Feather dalea	*Dalea formosa*
Roughleaf dogwood	*Cornus drummondii*
Buttonbush	*Cephalanthus occidentalis*

absence of unbiased scientific studies, general knowledge, common sense, and experience must be used to consider what the implications may be. A reduction in native plant diversity has the probability of impacting native wildlife diversity. Changes in specific cover requirements and the diversity of food items may affect a whole array of bird species. Simplified plant communities are usually less stable and resilient than more diverse communities. Energy and mineral cycling through an ecosystem is impaired when plant diversity suffers. Soil microbes, soil tilth, and soil stability may be affected when plant communities change. Riparian health and stability are most certainly impacted with a loss of key woody species. Consequently, water quality and fish habitat are affected. Indirectly, gradual damage to the natural resource base (soil, water, plants, animals) will lead to insufficient economic returns from ranching and landowners may be forced to subdivide and sell off native ranges for the profits of commercial and residential development.

A Holistic Perspective

Natural resource managers would be wise to take a long term, wide-angle look at land management practices before they are recommended (White 2000). Instead of looking at a single facet of a problem (such as an increase in juniper) and a simple solution, managers need to take a more ecologically holistic view (Nelle 1997). Considering the causes of a problem, distinguishing between symptoms and root causes, and discovering the possible side effects of various treatments are essential elements of wise land management. In the case of juniper and its control with goats, the following considerations are important in gaining a holistic perspective:

1. Juniper–oak woodlands are the native climax vegetation type on certain sites in the region. Juniper control on these sites is ecologically questionable.
2. Juniper has encroached and increased on other sites where it was not a part of the climax vegetation.
3. Under conditions of overgrazing, the increase of juniper is the natural ecological response and provides a degree of protection to the site.
4. Juniper encroachment is due directly to a reduction in fires and indirectly to overgrazing, which prevents the buildup of adequate fine fuel.
5. The increase of juniper to undesirable densities causes significant problems for ranching.
6. The control of juniper where it has encroached should only be considered after a long term commitment has been made to proper grazing management.
7. The periodic use of fire to control small encroaching juniper is strongly encouraged.
8. Goats can be managed to exert some control of juniper, but at the expense of many other desirable woody species.
9. Maintaining the native plant diversity of a site is important to wildlife habitat, soil health, watershed function, ecological stability, and economic viability.

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Habitat Improvement for Wildlife in North-Central Sonora, Mexico

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Abstract—Native vegetation of semiarid grasslands and desert ecosystems that comprise the Arbosufrutescent Desert scrub vegetation in north-central Sonora has been degraded by overgrazing, drought, farming, woodcutting, and a host of other activities over the past century. Several studies were conducted at "Rancho Grande" and at "Rancho El Carrizo," Sonora from 1992 to 1999 to evaluate the effect of several range improvement practices on wildlife habitat. Twenty-five-thousand seedlings of eight native shrubs and trees were transplanted on a site in north-central Sonora. Survival rates among species varied from 55 to 84 percent 1 year after transplanting and from 10 to 41 percent 3 years after planting. Reestablishment of native shrubs represents a promising technique that could restore native woody vegetation on degraded ecosystems that lack diversity. Habitat management by disking and shredding coupled with improvement in grazing management with short-duration grazing, have also resulted in improved native herbaceous conditions on thousands of acres of private ranches. These results are encouraging. The potential impact that re-establishment of native shrubs, control of undesirable brush species, and improvements in grazing management may have on wildlife occupying rangelands in north-central Sonora will be discussed.

Introduction

Extensive areas of desert rangelands that were once productive are now highly infested with less desirable brush species and toxic plants (Vallentine 1971). Overgrazing, droughts, frosts, accidental fires, land clearing for farming and grazing; and the extensive use of wood for fuel, fences, charcoal, and wood carving have caused drastic changes in the vegetation, resulting in low forage productivity, unprotected soils, and a high susceptibility for soil erosion (Scifres 1980; Ibarra and others 1996). Reduction of cattle numbers and good grazing management alone may not be sufficient to restore productivity on these deteriorated rangelands. In most cases range seeding with high quality grasses and shrubs may be the best alternative for restoring productivity (Vallentine 1971; Ibarra and others 1996). Browse species are important because they are a good source of food for humans, livestock, and wildlife; provide shelter, soil protection, and soil stabilization; improve soil fertility; and provide a favorable microhabitat for the establishment of other species (Whisenant and others 1982; Guthery 1986; Ibarra and Martin 1995).

Buffelgrass (*Cenchrus ciliaris* L.) is a warm season bunchgrass widely used in much of Mexico for revegetation following brush removal. Forage production of buffelgrass exceeds that of native grasses and stocking rates are frequently three to ten fold greater than on native rangelands (Martin and others 1995). Brittlebush (*Encelia farinosa* A. Gray) is a deciduous half shrub native to the Sonoran Desert (Benson and Darrow 1981), which infests buffelgrass stands. Densities of this species have almost doubled in 30 years on rangelands near Tucson, Arizona (Shreve and Hinckley 1937), and densities as high as 30,000 plants per hectare have been reported in buffelgrass seeded pastures in Sonora, Mexico (Ibarra and others 1986). High resin and oil contents make brittlebush a plant of low palatability for cattle and wildlife. As the species increase, density, cover, and forage production of buffelgrass declines (Ibarra and others 1996).

Masked bobwhite (*Colinus virginianus ridgwayi*) is an endangered specie restricted to the Buenos Aires National Refuge in Arizona, U.S.A., and to rancho El Carrizo and Rancho Grande in Sonora, Mexico. Densities of masked bobwhite have been drastically declining in the last 20 years, with an actual estimated bird population of close to 3,000 at these three locations. As a result, ranchers and range managers of both countries are applying grazing management and range improvement practices to restore bird population. Additionally, densities of Sonoran mule deer (*Odocoileus hemionus eremicus*) have been drastically declining in some ranches because of severe droughts, deficient range management practices, and poor wildlife management strategies.

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There is a lack of information on the establishment of browse species for cattle and wildlife in the Sonoran Desert. Also, there is not enough information about the effect of vegetation manipulation by mechanical control of unpalatable shrubs and grazing on range productivity and animal responses. A series of range improvement practices were conducted at "Rancho Grande" and "Rancho El Carrizo" from 1992 to 1999 with the following objectives: (1) to evaluate the seeding potential of several browse species by transplanting to restore range productivity, (2) to evaluate the effect of vegetation manipulation by mechanical means to increase forage production for cattle and wildlife, (3) to evaluate the effect of grazing systems on wildlife habitat recovery, and (4) to enhance species diversity and productivity for livestock and wildlife.

Material and Methods

The Rancho Grande site (29° 49' N Lat. and 111° 14' W Long.) is located 90 Km north of Hermosillo, Sonora, Mexico (fig. 1), at an elevation of 700 m on a gently sloping terrain (<5 percent). Mean annual precipitation is 320 mm, 75 percent of which occurs during the summer. Mean annual temperature is 24.5 °C, with a frost-free period of 345 days. Soils are deep sandy loams of granitic origin, with moderate permeability and a pH of 7.0.

The Rancho El Carrizo site (30° 0' N Lat. and 111° 12' W Long.) is located 120 Km north of Hermosillo, Sonora, Mexico (fig. 1), at an elevation of 750 m on a gently sloping terrain (<5 percent). Mean annual precipitation is 330 mm, 75 percent of which occurs during the summer. Mean annual temperature is 24.0 °C, with a frost-free period of 345 days. Soils are deep sandy loams and deep gravelly loams of granitic origin, with moderate permeability and a pH of 7.0.

Figure 1—Location of study sites, Sonora, Mexico.

Transplanting Browse Species

A study site was selected within the Arbosufrutescent Desert shrub vegetation type in the northwestern area of Sonora, Mexico. The site was located at Rancho Grande on a recently planted buffelgrass pasture. Twelve-thousand plants were transplanted in July 1996. Species planted were selected based on previous animal preference trails. Seed used for plant propagation was collected 1 year before at each study site. Plants were grown during 1 full year under nursery conditions before transplanting to achieve a height of 20 to 75 cm. Browse species were distributed randomly and planted every 5 m along contour furrows 40 cm in depth. Furrows were made at 20 to 50 m intervals with a back mounted "v" type plow pulled by a bulldozer.

Species were planted by hand on the bottom of the furrows using shovels. Species planted were: native mesquite [(*Prosopis juliflora*) (Swartz) DC.], chilean mesquite [*Prosopis chilensis* (Molina) Stuntz emend. Burkart], ironwood (*Olneya tesota* A. Gray), blue palo verde (*Cercidium floridum* Bentham), foothill palo verde [*Cercidium microphillum* (Torr.) Rose & Johnston], jojoba [*Simmondsia chinensis* (Link) Schneid], fourwing saltbush [*Atriplex canescens* (Pursh) Nutt.], and zamota (*Coursetia glandulosa* A. Gray). The site was fenced to protect it from cattle grazing. Plant survival (percent) and height (cm) were measured during the peak growing season of 1996 to 1999 by checking 100 previously marked plants by species.

Shredding for Brittlebush Control in Buffelgrass Pastures

This study was conducted at Rancho Grande on three adjoining buffelgrass pastures, 200 hectares each, in poor to regular condition. Pastures were shredded once during 1995, 1996, and 1997. Shredding at a height of 5 cm was conducted in April with a 5 m wide flail shredder powered by a tractor. Initial brittlebush density was 17,570 ± 3,125 plants per hectare, and canopy cover was 46 ± 8.4 percent across pastures. Initial buffelgrass density was 1.3 ± 0.4 plants per hectare, and basal cover was 5.2 ± 0.6 percent across pastures. Vegetational changes were monitored on three 10 x 20 m plots. Total grass and shrub density was estimated on three 10 m^2 permanent quadrats, and cover on three 20 m long transects per plot (Canfield 1941). Total forage production was estimated at the end of the summer growing season in each plot by clipping ten 1 m^2 quadrats per plot. Forage samples were oven dried at 65 °C for 72 hours and results were expressed in dry matter.

Improving Native Rangelands Infested With Brush by Disk Harrowing

Two thousand hectares of rangelands, dominated by the arbosufrutescent brush type, in poor to regular condition and highly infested with catclaw mimosa [*Mimosa laxiflora* (Swarts.) DC.] and creosotebush [*Larrea tridentata* (Moc.&Sesse.) Cov.)], were improved by disk harrowing at rancho "El Carrizo" from 1992 to 1997. Disking at a depth of 20 cm was conducted from March to June by using a disk harrow with 36 disks mounted on the back of a D-4 bulldozer. Mainly catclaw mimosa and creosotebush were selectively controlled by disking, because about 40 percent of the total vegetation cover was composed of these species. Desirable brush and tree species protected during disking were blue palo verde, foot hill palo verde, mesquite, and ironwood. Main grass species present were three awn (*Aristida* spp.), 6 weeks needle grama [*Bouteloua aristidoides* (H.B.K.) Griseb], and rothrock grama (*Bouteloua rothrockii* Vasey). Total dry forage production was low and averaged 350 kg per hectare. Treated areas were protected during a full year from cattle grazing, and they were grazed light to moderate thereafter.

Forage production on disked pastures was estimated at the end of the summer growing season by clipping. Forage production increases by disking were compared with forage production in adjacent untreated pastures. Mortality of catclaw mimosa and creosotebush was estimated by comparing plant densities inside and outside the treated pastures. Masked bobwhite quail densities were estimated by direct observation and by call counts. Quail density increases in disked pastures were compared against bird densities estimated on adjacent untreated pastures. Densities of Sonoran mule deer on treated pastures was estimated by direct animal counting and population changes over time were compared with deer densities on untreated adjacent pastures.

Adopting Grazing Systems for Habitat Improvement

This study was conducted at rancho El Carrizo from 1992 to 1998. The two-thousand hectares of rangelands treated by disk harrowing to improve masked bobwhite quail habitat were subdivided into 12 small pastures. Pasture sizes varied from 140 to 200 hectares. A modified short-duration grazing system (SDG) was implemented in the ranch to control grazing. Stocking rates were set following biologists recommendations to remove no more than 60 percent of the total dry forage production available during the summer growing season of a given year. Grazing periods are set to be 7 days in each pasture during the summer growing season, and 15 days of grazing in each pasture during the rest of the year.

Forage production in the SDG was estimated at the end of the summer growing season by clipping. Forage production and stocking rate increases on the SDG were compared against forage production and stocking rates in adjacent pastures subjected to continuous grazing. Masked bobwhite quail densities were estimated by direct observation and by call counts. Quail density increases in the SDG pastures were compared to bird densities estimated on adjacent untreated pastures. Densities of Sonoran mule deer on pastures subjected to SDG were estimated by direct animal count and population changes over time were compared to deer densities in adjacent pastures subjected to continuous grazing.

Results and Discussion

Transplanting Browse Species

Total precipitation at "Rancho Grande" was 317, 353, 384, and 162.5 mm during 1996, 1997, 1998, and 1999 and was close to the long-term average of (320 mm). In general, growing conditions during all summers were adequate for species survival and growth. Precipitation distribution was adequate during all years, except for the summer of 1996, the year of planting, when more than 60 percent of the total rain occurred during the winter. Because of the dry conditions prevailing during the year of planting, approximately 10 liters of water were added to each plant during the summer of 1996.

Plant survival was different among species after the dry growing season of 1996, and varied from 55 to 84 percent. Between the winter of 1996 and the summer of 1999, 51 to 82 percent of the plants were killed by drought and insects and cattle grazing. Plant survival was different among species by the end of the summer growing seasons of 1997, 1998, and 1999. Species with the greatest survival rate after planting in the four summer growing seasons were native mesquite, chilean mesquite, foothill palo verde, blue palo verde, and ironwood with 41, 35, 33, 30, and 27 percent survival, respectively. Species with the lowest survival were zamota, fourwing saltbush, and jojoba, with 25, 15, and 10 percent survival, respectively.

Plant height was not different among species after the summer of 1996, but it differed in the summer growing seasons of 1997, 1998, and 1999. The height of transplanted species increased from 13 to 138 cm during the four summer growing seasons after planting. Species that achieved the greatest height were chilean mesquite and native mesquite with 138 and 137 cm, respectively. Jojoba had the lowest height with an average of 13 cm, and the height of the remaining species varied from 30 to 68 cm.

High densities of Sonoran mule deer, white tailed deer (*O. virginianus couesi*), javelina (*Tayassu tajacu*), and jackrabbit (*Lepus alleni*) were common at the study site. Low forage availability outside the exclusions during the dry period caused severe wildlife grazing on most planted species. Chilean mesquite (with no thorns), jojoba, and fourwing saltbush were the most preferred species by wildlife. Ten to 25 percent of the fourwing saltbush and jojoba plants were uprooted by wildlife within 3 weeks of planting.

Survival of transplanted shrubby forage species was adequate in the Sonoran Desert when planting was followed by a summer with below average precipitation. Mortality of the browse species was principally due to low moisture availability during the study period, grasshopper consumption, and wildlife grazing. Similar results have been reported with other browse species on rangelands (Whisenant and others 1982; Ueckert and others 1982), although greater plant survival can be expected in years with above average precipitation (Springfield 1970).

Results obtained show that browse consumption by wildlife may be an important factor affecting species survival after transplanting. Similar results had been reported with different browse species (Springfield 1970; Whisenant and others 1982). Watering transplanted species during drought may be risky because plants with green foliage will attract more wildlife. Based on survival and growth characteristics, native mesquite, chilean mesquite, ironwood, blue palo verde, and foothill palo verde appear to have the greatest potential for range seeding in the Sonoran Desert. However, transplanting of these species may be feasible only where a few plants are needed (McMillan 1960). Although there is a high risk of seeding failures on areas with low rainfall, range seeding by transplanting browse species continues to be a future alternative for the restoration of deteriorated Sonoran Desert rangelands.

Good brush and grass cover along with an adequate food source is required to enhance masked bobwhite population recovery (Guthery 1986). Bobwhite habitat conditions are good to excellent on the pasture where browse species were planted. Although the pasture has been protected from cattle grazing during 2 years and has been grazed light to moderate for 2 consecutive years thereafter, no quail has been detected after call counts. Bobwhite possibly already inhabit the area, but it may be too soon to see big changes in bird densities after habitat improvement.

Densities of Sonoran mule deer have certainly increased on brush reseeded pastures. Mule deer numbers have almost doubled since 1996 after planting. Densities of deer were 1.0 per every 25 ± 4.5 hectares inside the shrub-seeded pasture and 1.0 per every 48 ± 5.9 hectares in the neighboring pastures. Browse species planted in this pasture have been found to be an important component of Sonoran mule deer diets (Ibarra and Martin 1995), consequently, this range practice will aid in deer habitat improvement and recovery.

Shredding for Brittlebush Control in Buffelgrass Pastures

Brittlebush was not significantly reduced by shredding and densities declined by 12.2 ± 3.5 percent among pastures. Brush canopy cover was always greater on the control plots as compared to shredded areas during the study period. Brush cover was 8.2 ± 1.9 percent after shredding, and 22.3 ± 3.5 percent in the three growing seasons after treatment application. Buffelgrass density averaged 1.9 ± 0.2 p/m^2 on untreated checks and 3.9 ± 0.3 p/m^2 on shredded areas in the three growing seasons after treatment .

Buffelgrass basal cover was consistently greater during all years on shredded plots. Grass cover averaged 5.2 ± 0.6 percent on untreated control plots and 13.0 ± 1.3 percent on shredded areas in the three growing seasons after shredding. Forage production of buffelgrass was greater on shredded plots during all years as compared to untreated controls. Forage production on shredded pastures varied from 1.9 to 2.7 ton/ha after the first growing season; from 3.5 to 4.1 ton/ha after the second summer growing season, and averaged 4.5 ton/ha after the third growing season. Cumulative forage production after three summer growing seasons on shredded stands was 7.82 ton/ha greater as compared to untreated plots.

Although mortality of brittlebush from shredding was low (8.7 to 15.7 percent) among pastures, top removal temporarily reduced brush canopy cover (Vallentine 1971). Brittlebush cover was reduced by 82 percent after shredding, but the species replaced 48 percent of its original cover three summer growing seasons after shredding. Similar results had been reported with these and other brush species in Mexico and Texas (Wright and Stinson 1970; Ibarra and others 1986). However, the rate of replacement of top growth is variable among species (Reynolds and others 1992), and depends directly on rainfall after shredding (Scifres 1980). Consequently, a faster rate of recovery on brittlebush may be expected when shredding is followed by years of above average precipitation.

In this study, recovery of buffelgrass stands after shredding may be attributed to temporary brush suppression and resulting plant competition reduction (Scifres 1980; Bovey and others 1986). The addition of plant debris to the soil surface after shredding may also protect the soil from erosion, reduce runoff, increase water availability, and add organic matter (Vallentine 1991); afterwards, oxidation of organic matter releases nutrients to the soil for plant use (Kononova 1968). The establishment of new grass seedlings was possibly enhanced by soil disturbance caused by branches, sticks, and shredding blades hitting the soil surface. Results suggest that shredding is an effective range improvement practice to restore productivity in buffelgrass pastures highly infested with brittlebush in the Sonoran Desert.

Although pastures have been rested from grazing during the year of shredding and they have been light to moderately grazed thereafter, it is uncertain if masked bobwhite densities have increased on treated pastures. No birds have been recorded after count calling, despite rancher cowboy reports that they have seen more birds in the area. Hopefully, habitat for quail has improved because brush cover of all other desirable brush and tree species were protected during shredding. Good brush cover is reported to improve habitat for bobwhite quail (Guthery 1986). Densities of mule deer have been consistently greater on shredded pastures as compared to untreated pastures. Deer counting during the fall of three consecutive years show 35 to 57 percent more deer, mainly does, in shredded pastures. The presence of more succulent forage of grasses and shrubs may account for deer population increases after shredding (Scifres 1980). This information suggests that habitat improvement of deteriorated buffelgrass pastures by shredding may play an important role in increasing mule deer populations.

Improving Native Rangelands Infested With Brush by Disk Harrowing

Precipitation at Rancho El Carrizo, Sonora, was close to the long-term average (325 mm) from 1994 to 1999, except for 1998 when only 203 mm of rainfall occurred. Total precipitation at the study site was adequate in quantity and distribution to promote significant vegetational changes after disking. Less than 30 percent of the catclaw mimosa and creosotebush plants were killed by disk harrowing. Plants that survived disking sprouted vigorously from the base and reached original sizes within 3 years of treatment application. Soil disturbance significantly increased density and cover of most grass and forbs species present in the site before disking. Bristlegrass (*Setaria* spp.), buffelgrass, sideoats grama [*Bouteloua curtipendula* (Michx) Torr.], and tanglehead [*Heteropogon contortus* (L.) Beauv.] were species not present on the pasture before disking, but were also substantially increased after soil disturbance. These plants are reported as an important source of feed in masked bobwhite diets (Guthery 1986). Forage production on disked pastures varied from 750 to 1,100 kg per hectare and was two to threefold as compared to untreated pastures.

Sonoran mule deer populations were consistently greater during all years on disking improved pastures. Deer count estimations indicate that deer numbers were 40 to 65 percent greater in improved pastures as compared to adjacent untreated pastures. Greater forage availability and richer species diversity may be attracting more deer to feed inside the improved pastures. Density of mule deer has varied among years from 28 to 33 hectares per deer in disked pastures and from 45 to 51 hectares per deer on untreated adjacent pastures.

Call counts of masked bobwhite quail show that bird densities have at least doubled on disked pastures. Ranchers have reported seeing more birds on the area. Additionally, bobwhites have been recording even in areas where they were not found before. There is no doubt that habitat for masked bobwhite is improved after disking because cover of desirable brush and tree species were protected during treatment. Additionally, disking drastically increased some plants preferred by quail (Guthery 1986). The results of this study show that selective brush control by disking is an important habitat management tool for the recovery of masked bobwhite populations in the Sonoran Desert.

Adopting Grazing Systems for Habitat Improvement

The short-duration grazing system recently adopted in el Carrizo ranch in pastures previously rehabilitated by disking is significantly improving vegetation, cattle performance, and wildlife recovery. Combination of selective brush competition reduction, soil disturbance, forage production increase, and the control of animal grazing have resulted in greater ecological and economical benefits. Actual carrying capacity on treated pastures is at least two to threefold as compared to untreated pastures. Smaller pastures are facilitating the management of animals. The calf crop has been increased from 15 to 20 percent as compared to previous yearly records. Although animal gains are similar in continuous grazing, the number of animals in SDG almost doubled, despite the established forage utilization of 60 percent or less.

Densities of Sonoran mule deer have almost doubled within the SDG. Moderate to light grazing is possibly attracting more deer, as more nutritious feed remains available in the pastures. Masked bobwhite habitat conditions are good to excellent according to wildlife biologists throughout the SDG. Grazing is permitted in the system when cattle can graze forage without damaging masked bobwhite habitat. Controlling grazing intensity should improve herbaceous cover conditions and masked bobwhites will have more chances to colonize new areas within the pasture. Good grazing management is expected to yield improved habitat conditions for quail.

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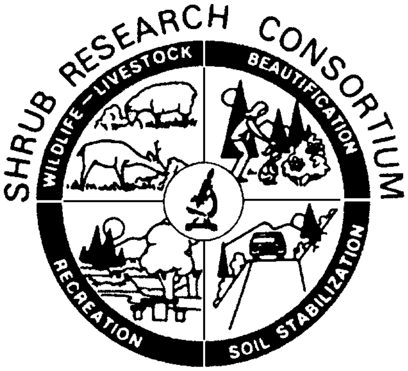
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Field Trip

Colorado Plateau Chenopod Field Trip

Howard C. Stutz

Abstract—The field trip was held on June 14, 2000, in warm, dry weather. It consisted of eleven stops and additional views from the busses. Many saltbush (*Atriplex*) species were observed and their genetical and ecological characteristics described. In addition other chenopod shrubs and annual chenopods were observed and characterized. The field trip is described so that is can be experienced by interested parties on subsequent trips.

Introduction

Much of the Colorado Plateau is occupied by plants in the family Chenopodiaceae. Almost no other kind of plants can tolerate the severe challenge of the salty, alkaline deserts that make up much of the terrain in the Colorado Plateau.

Within the family, the genus *Atriplex* is by far the most common, often occupying vast acreages containing nothing else. Hopefully this tour will serve to introduce a number of Chenopod species and to portray the ongoing evolutionary process that is conspicuous at some of the frontiers.

Stop #1: Carbonville, Carbon County, UT; *Atriplex cuneata* and *A. confertifolia.*

Along the railroad embankment are two of the most common species of *Atriplex* in the Colorado Plateau: *A. cuneata* and *A. confertifolia*.

1. *Atriplex cuneata* ("Castle Valley Clover") is found only in the Colorado Plateau. The common name of this species says a lot about its reputation. Its value as an important forage plant for livestock and other herbivores is derived partly from its high nutritive potential but probably more from its occurrence in landscapes that would be completely empty were it not present.

The distinctive morphological features that distinguish it from other species of *Atriplex* are its low, bushy habit, taproot system, burry fruiting bracts, cuneate leaves and early flowering habit (May). It is mostly dioecious but a few monoecious plants are usually present in most populations. Genetically, it occurs at two chromosome levels: diploids (2n = 18) and tetraploids (2n = 36).

Tetraploid *A. cuneata* is widespread throughout the Colorado Plateau and is morphologically highly variable. Some of the variation may be due to phenotypic plasticity in response to variable environments but most of it appears to be genetic. Some tetraploid forms appear to be direct autoploid derivatives from diploids, others appear to be stabilized segregants from hybrids, and others appear to be products of introgression. Some isolated populations may have acquired their uniqueness from new mutations. There are several distinct forms of diploid *cuneata* throughout the Colorado Plateau. Each is phenotypically distinct and each is restricted to a specific ecological niche.

2. *Atriplex confertifolia* (shadscale) is distinguished from all other saltbushes by its broad obtuse leaves, thorny branches, and two-lipped, unappendaged fruiting bracts. It is widespread throughout Western United States from northern Montana to northern Arizona and New Mexico and from central Colorado to south-central California. On the Colorado Plateau it occurs as diploids (2n = 18), tetraploids (2n = 36), and hexaploids (2n = 54). Elsewhere (Utah, Nevada, Oregon) there are octoploids (2n = 72) and decaploids (2n = 90).

Diploid shadscale, on the Colorado Plateau, is most common in rocky soils, often in association with Utah Juniper. It usually occurs in small, isolated populations in which between-plant variation is conspicuous. In contrast, tetraploid populations are usually much larger and show minimal between-plant variation, suggesting that the tetraploids are autopolyploid derivatives from single or few diploid progenitors.

Interspecific hybrids occur, occasionally, between *Atriplex confertifolia* and *A. canescens*, *A. corrugata*, *A. cuneata,* and *A. garrettii* but no successful product from any of them has yet been found.

The hybrids between *A. cuneata* and *A. confertifolia* as seen here are fairly common where ever these two species meet. Notice that the fruiting bracts of the hybrids have two entire apical lips like those of *A. confertifolia* and numerous basal appendages as in *A. cuneata*. Most hybrid plants are somewhat thorny, like *A. confertifolia*.

Stop #2: Wellington, Carbon County, UT; *Atriplex tridentata, A. utahensis, A. confertifolia, A. cuneata, A. powellii, A. corrugata,* occasional *Atriplex* hybrids, *Sarcobatus vermiculatus, Kochia scoparia,* and *Sueda torreyana*.

About 1 mile south of Wellington, a jumble of ecological sites brings together several species of *Atriplex*. In the wet, alkaline bottoms, there are extensive patches of *A. tridentata*, salt sage. In contrast to all other species of *Atriplex* on the Colorado Plateau, *A. tridentata* shows extensive root-sprouting. Some individual plants may extend, by root sprouts, to several meters. Because it is a dioecious species, the limits of individual plants are usually clearly discernable. Throughout its geographic range it is highly variable, probably because it hybridizes with most of the other *Atriplex* species that it contacts. Hybrids of *A. tridentata* with *A. canescens* are particularly common and, from

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these hybrids, have come several new taxa (*A. nuttallii, A. robusta, A. anomala*).

On the clay slopes above the populations of *A. tridentata* occurs a mixture of chenopods including *A. confertifolia, A. cuneata, A. corrugata, A. utahensis, A. powellii*, *Kochia scoparia, Sueda torreyana,* and *Halogeton glomeratus.*

Atriplex "utahensis" is a distinct perennial diploid species endemic to the Colorado Plateau, mostly in east-central Utah. It is distinguished by its narrow leaves, upright habit, tap-root system, and prominent central beak on the copiously appendaged fruiting bracts.

Atriplex corrugata (mat saltbush) is tetraploid in this area but occurs as a diploid on vast acreages south of here (see Stops 8 and 9). *A. corrugata* occupies some of the most severe habitats found anywhere, often as near monocultures. When populations collapse, as they have been seen to do during severe extended droughts, no species other than *A. corrugata*, come into the vacant sites. Because of its low stature it is of minimal value as a forage plant for livestock but is of high value as a soil stabilizer and habitat for small animals. *A. corrugata* plants are easily distinguished by their small, compact habit, grey color, tiny (3 to 5 mm) linear to oblong leaves, and two-lipped bracts that are burry below.

Stop #3: East side of Wellington; *Sarcobatus vermiculatus.*

Sarcobatus vermiculatus (greasewood) is common in alkaline bottomlands in all of the Western States of North America. Although mostly octoploid (2n = 72) there is considerable between-population variability. Because nursery-grown plants maintain many of their differing, distinguishing features, much of the variation appears to be controlled genetically. Tetraploid populations of *S. vermiculatus* are confined to southern Alberta, southern Saskatchewan, northern Montana, northern California, northwestern Sonora, Mexico, and southern Arizona and may be relic ancestors to the more common, widespread octoploid populations. The genetic variation present among the octoploids may be an indication of polyphyletic origins or/and subsequent introgessive hybridization.

Stop #4: Southeast of Sunnyside, Carbon County, UT; *Atriplex canescens* var. *"cunescens."*

This stop is in a population of *Atriplex canescens* (fourwing saltbush) that appears to be introgressed with genes from *A. cuneata*.

Atriplex canescens (Pursh.) Nutt. is the most widespread species of perennial *Atriplex* in North America, distributed from southern San Luis Potosi, Mexico, to southern Alberta and Saskatchewan, Canada, and from the Pacific Coast of California and Baja California to Texas, Oklahoma, Nebraska, Kansas, and the Dakotas. Throughout its distributional range, *A. canescens* shows considerable between-population variation. Some of this variation may be due to phenotypic plasticity but most of it appears to be genetic. Mutations, polyploidy, introgressive hybridization, and segregation from interspecific hybrids all appear to have contributed to its extensive heritable variation. Polyploidy is unusually common with seven identified chromosome races (2x, 4x, 6x, 8x, 10x, 12x, 20x). *A. canescens* is also the most promiscuous of all species of *Atriplex* and natural hybrids have been found between it and almost all other perennial *Atriplex* species including *A. acanthocarpa, A. confertifolia, A. corrugata, A. cuneata, A. falcata, A. gardneri, A. lentiformis, A. linearis, A. obovata, A. polycarpa,* and *A. tridentata*.

Many of the hybrids show some fertility and some appear to have been the source of new taxa. Seed from this tetraploid population has been valuable in reclamation efforts on BHP mine spoils in New Mexico.

Stop #5: Bottom lands south of the Carbon-Emery County line; *Atriplex tridentata* var. *"minutifolia."*

This extensive population of low-statured, small-leaved, *tridentata*-like plants appear to have been derived from hybrids between *A. tridentata* and *A. corrugata*. As with most other *tridentata* plants, these are hexaploid (2n = 54). The *corrugata* plants here are tetraploid (2n = 36).

As you travel south notice the extensive populations of this still unnamed species on both sides of the road.

Stop #6: Horse Canyon, Emery County, UT; diploid *A. confertifolia* (shadscale) and *Ceratoides lanata* (winterfat).

The *A. confertifolia* plants to the south of the exit road are diploid (2n = 18). The plants to the west are all tetraploid (2n = 36). Throughout the Intermountain West, most populations of *A. confertifolia* are tetraploid. Diploids are routinely on well-drained upland sites. Two hexaploid (2n = 54) populations have been found on the Colorado Plateau, one about 5 miles north of Green River, Utah, and one south of Cortez, Colorado. Both appear to be allopolyploids derived from hybridization between *A. confertifolia* and *A. corrugata*. Elsewhere, some *A. confertifolia* occurs as octoploids (2n = –72) and some as decaploids (2n = 90).

Ceratoides lanata (winterfat) appears to be diploid throughout its wide distribution and shows abundant variation between populations. Some populations consist of plants that are less than 6 inches (15 cm) tall. In other populations the plants grow to more than 1 m.

This species is highly prized for its forage value and in many areas has proven to be valuable in reclamation of disturbed lands.

Stop #7: Approximately 6 miles west of Green River, Emery County, UT.

Just before arriving at highway I-70, turn right (west) on a well-improved road. Continue west for about 1 mile where there is an extensive mixed population of *Atriplex cuneata* and *A. corrugata*. Interspecific hybridization between them appears to be common here and many odd-ball segregants are produced. These species often hybridize in such ecologically "hybrid" habitats and may be responsible for some of the variation seen in both species.

Stop #8: Green River, Carbon County, UT; annual *Atriplex* species: *Atriplex minuticarpa, A powellii,* and *A. rydbergii.*

Most annual species of *Atriplex* have narrowly limited distributions, occupy severely restricted ecological sites and are, within species, morphologically highly uniform. *Atriplex powellii* is the principal exception. It is widely distributed, occupies many different sites, and is morphologically variable, both within and between populations. The reason for this significant difference appears to be due to its sexuality. It is the only native annual *Atriplex*, that is dioecious; all others are monoecious. Because of its dioecy it is obliged to outcross whereas monoecious annuals are perpetually inbred, leading quickly to genetic homozygosity.

A. powellii plants are easily distinguished from those of all other annual *Atriplex* species. In addition to being dioecious, the leaves are prominently three-veined and the fruiting bracts have crown-shaped, two-lipped apices and numerous basal appendages.

Atriplex minuticarpa, a recently, newly described annual species is found only on Tununck shale in eastern Utah. It has previously been confused with *A. powellii* but here, where they grow together, they are clearly distinct. *A. minuticarpa* is monoecious, *A. powellii* is dioecious; leaves of *minuticarpa* are single-veined, those of *powellii* are prominently three-veined, and *A. minuticarpa* is smaller statured with divaricate branching. The severe restriction of *A. minuticarpa* to a single, small, geologic formation suggests an ancient origin.

A. rydbergii is restricted in distribution to eastern Utah, northern New Mexico, and northern Arizona. It usually occurs in small isolated populations but in some places in Industrial Valley and near Bluff, San Juan, County, UT, there are several extensive populations.

Stop #9: 3 miles east of Green River, Grand County, UT; diploid *A. corrugata.*

All of these small plants that cover these hills are diploid (2n = 18) *A. corrugata*. They differ in phenotype from the tetraploids in being smaller and more erect. Following severe drought years it looks like every plant has died. Subsequently nothing comes back into the vacated acreage except more diploid *A. corrugata*. What appears to be an occasional tetraploid *A. corrugata* plant is present in the draws but on the more severe slopes only the diploids survive.

Stop (pause) #10: 10 miles west of Green River on both sides of I-70; more diploid *A. corrugata.*

There is no place to stop here but as we drive along the freeway, observe the vast populations of diploid *A. corrugata* on both sides of the highway. They extend for miles and miles and miles. What a forest this would be if they could grow up to be trees.

Stop #11: Hanksville exit from I-70; *Zuckia arizonica and Atriplex saccaria.*

Turn north on the dirt road for about mile. *Zuckia arizonica* and *Atriplex cuneata* are common here. *Zuckia arizonica* occurs periodically throughout eastern Utah and is very abundant in northern Arizona, particularly in the Painted Desert area south and west of Tuba City, Coconino County. It is a very distinctive species with yellow-green leaves, brittle branches, non-Kranz leaf anatomy, and six-pointed fruiting bracts enclosing a horizontally positioned embryo.

Also, here is a distinctive *Atriplex* annual, *A. saccaria*. Its broad, yellow-green leaves are covered with glistening persistent trichomes that gives the leaf surface a sandpaper appearance. This and *A. asterocarpa* and *A. graciliflora* are the only species with such trichomes. Most of the fruiting bracts are covered with flattened appendages, a few are small, wedge-shaped, without appendages.

As we return to Provo, watch for the vast populations of the chenopod species that you now know. This is truly Chenopod Country! Where there are alkaline, clay slopes devoid of vegetation, “only” chenopods are encroaching at these evolutionary frontiers. If and when new species occupy these empty sites, they will almost certainly be chenopods.

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Contrasts in Utah’s Great Basin and Colorado Plateau Salt-Desert Vegetation

Western Salt Desert (Great Basin)	Eastern Salt Desert (Colorado River Drainage)
1. Many polyploids	Few
2. Few diploids	Many
3. Low predictability of species by ecological site	High
4. Low predictability of ecological site by inhabitant species	High
5. Few well-defined endemics	Many
6. Few families, genera, species	Many
7. Mostly shrubs	Many herbaceous
8. Extensive hybrid swarms	Rare
9. Minimal plant succession	Conspicuous
10. Vast areas of sudden die back	Rare
11. Most species wind pollinated	Many other
12. High within-plant plasticity	Low
13. High within-population diversity	Low
14. Many extensive monocultures	Few
15. Few endemic annuals	Many

Perennial Chenopods in Western North America

Genus	Number of species
Atriplex	30 +
Ceratoides	1
Grayia	1
Kochia	1
Sarcobatus	2
Suaeda	2
Zuckia	2

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