The Ecology and Development of California Oatgrass: the Champagne of Grasses

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California oatgrass (*Danthonia californica*) is a long-lived, cool-season, low- to medium-sized, tufted bunchgrass that grows on sea bluffs, meadows, and valleys from sea level to 7,000 feet in western portions of Canada and the United States. It is found from British Columbia, Alberta, the high plains of Saskatchewan and south into the United States along the coast to California, to the mountain states of the Great Basin and the Rocky Mountains from Montana to Arizona and New Mexico. It is also found in Chile along with other native grasses and flowering plants that have hitched rides north and south along the Pacific flyway. In California, *Danthonia californica* grows along California's north coastal prairie within reach of the summer fog belt, south past the coastal plain near Cambria in San Luis Obispo County, and into the western reaches of Santa Barbara County to Point Conception. Inland, California oatgrass is found in the mid-elevation meadows and forests of the mountains of northern California from the Siskiyou and Warner Mountains, extending south along the north Coast Range and the Sierra Nevada to Tulare County. In Southern Californica, *Danthonia californica* has been found in the higher reaches of the San Bernardino Mountains and the Cuyamaca Mountains of San Diego County (Calflora 2008).

California oatgrass turf-like prairie near San Simeon, California, near the southern extent of its range along the coast. This area was grazed by cattle and African wild game in the 1970s when the photo was taken.

There are two forms of California oatgrass: *Danthonia californica* var. *californica*, which has smooth, often waxy or bluish-whitish (glaucus) leaves, and var. *americana*, which has conspicuously hairy (pilose) blades and sheaths. Both forms are found growing together (sympatric), indicating that the species may be extremely plastic in its response to soil and climatic conditions. Generally, the smooth, glaucus form is found along the north coastal prairie and in moist meadows in the mountains, whereas var. *americana* is found in dryer, thin soil sites in the inland mountains of the north Coast Range and the higher reaches of the Modoc Plateau and the San Bernardino and Peninsular Ranges of southern California. Both varieties of *Danthonia californica* are also adapted to serpentine soils.

Given the significance and distribution of *Danthonia californica*, its use for restoration has been much less than it should be. Its underutilization for restoration can be traced to a poor understanding of the species, whose ecology and physiology are unique compared to most other native perennial bunchgrasses. *Danthonia's* characteristically low initial germination rate as a result of seed dormancy has been the most significant issue. However, today recognition of *Danthonia's* outstanding characteristics, understanding of the intricacies of seed germination, and advances by seed producers are fueling its prominence once again.

The Ecology

California oatgrass is an extremely palatable grass and is relished by all kinds of livestock (Jones 1948). It is one of the few native bunchgrasses that stays green yearlong, and if there is enough soil moisture, the plants shows no obligate dormancy and little seasonal dormancy and maintain a lush green with sufficient soil moisture. California oatgrass attracts grazing by ungulates and has evolved the ability to form low, tight, and almost prostrate bunches with sprawling, flowering culms, which ensures its survival and reproduction under grazing impact. The architecture of the flowering culm is itself unique. It has arching, curved, internodal stems that hold the culm above the ground, stretching close to the ground outward from the plant like a suspended, creeping spider plant. When the culm and seed are mature, the basal joint breaks easily, laying the culm on the ground. Gradually, each culm joint breaks at the nodes, depositing hidden, awnless seeds that are tightly wrapped beneath the leaf sheath above each node. The hidden (cleistogamous) seeds (cleistogenes) are self-fertilized in unopened flowers beneath the sheaths (Dobrenz and Beetle 1966). Grazing animals easily trample and spread these pieces of stems containing the seeds in the immediate vicinity of the mother plant, while the windblown culms also aid in distributing the seed. The straw-colored culms lying on top of the grassland in late summer are a signature of the presence of green California oatgrass bunches blanketing the ground beneath. In the mountains and along the coast, *Danthonia* often flowers during foggy, rainy, and windy conditions. This is not an ideal time for producing viable outcrossing seed. In this case, the cleistogamous seed is a back-up source of fresh seed. The flowering seed produced in the spikelets have awns from the middle of the floret. The awn twists and untwists with changing moisture and dryness, which aids in drilling itself into disturbed soil or catching on the fur of grazing animals. With only three to four spikelets per flowering stem, each flowering culm contains four to eight open-pollinated (chasmogamic) seeds per spikelet, or 21–33 seeds per flowering culm. There are slightly more of the hidden or cleistogamous seeds, which are wrapped in a straight line beneath the leaf sheath above each node or joint (an average of 25–36 seeds per culm), than there are chasmogamic seeds (Dobrenz and Beetle 1966). Both types of seed, the hidden cleistogamic seed and the open-pollinated chasmogamic seed, have similar if not equal germination characteristics (Dobrenz and Beetle 1966, Laude 1949).

Aspect of a *Danthonia californica* grassland with abundant flowering culms arching horizontal on the surface of the vegetation on a remnant East Bay prairie on the bayside U.C. Richmond Field Station, Richmond, CA. Associated plants included coyote thistle (*Erygium arnatum*), patches of mules ears (*Wyethia augustfolia*), buttercups (*Ranunculus californica*), the rare coastal slender wheatgrass (*Elymus subsecundum*), purple needlegrass (*Nassella pulchra*), hayfield tarweed (*Hemizonia conjesta*), sun cups (*Camissonia ovata*), morning glory (*Calystegia occidentalis*) and lady tresses (*Spiranthes* sp.).

The vigor and persistence of *Danthonia* relies on its massive, deep, fibrous root system and its ability to form long-lived buds within and around the root crown where it develops leafy shoots (Jones 1948). Under the natural pressure of elk grazing and intermittent fires, California oatgrass was responsible for building some of the deepest, blackest, and richest soils in California's coastal prairies and mountain meadows. Perhaps in the distant past (over 12,000 BP), during the conclusion of the cooler, moister Pleistocene epoch when mega-herbivores, including mammoth (*Mammuthus columbi*), bison (*Bison antiquus*, *B. latifrons*), camel (*Camelops hesternus*, *Hemiauchenia macrocephala*), elk (*Cervus elaphus*), and horse (*Equus occidentalis*) frequented California, oatgrass was likely much more abundant and widespread, providing a tasty, resilient forage throughout the plains and mountain meadows (Edwards 1992, 1996). The low oatgrass bunches enlarge under moderate grazing pressure. Under heavy persistent grazing, California oatgrass creates a low, tight, turf-like or sod-like cover. In many ways, the mouth structure, size, and diet of cattle is very similar to that of the native elk. Both cattle and elk, along with the majority of grazing mammals (deer, goats, sheep, pronghorn, etc.), lack upper incisors. The tongue and bottom teeth brought against the hardened upper palate cannot get close enough to the oatgrass crown to fatally injure it. Oatgrass thrives under seasonal, intermittent grazing by cattle. The more time allowed for regrowth between grazing events, the larger the oatgrass plants grow. California oatgrass is well adapted to

compaction and disturbance, including cutting and treading by grazing animals. Oatgrass is commonly found populating compacted trail and roadside margins.

A view into the Pleistocene past. Undisturbed Coastal prairie dominated by California oatgrass and tufted hairgrass (*Deschampsia holciformus*) along a coastal bluff south of Fort Bragg, California. The domanant forest trees behind are shore pine (*Pinus contorta* ssp. *bolanderi*), Sitka spruce (*Picea sitkensis*) and grand fir (*Abies grandis*). The pilings in the left center shows an old low bridge alignment of the coast highway of the late 1800's. Associated species includes many of the same species found in the high Sierra: Corn lily (*Veratrum sp.*), Labrador tea (*Ledum glandulosum*), and bearberry (*Arctostaphylos uva-ursi*).

California oatgrass has delayed germination, which is probably related to both embryo and seed coat dormancy (Laude 1949, Darris and Gonzalves 2008). Seed dormancy (both embryo and seed coat dormancy) is a survival strategy that delays seed germination until conditions are favorable for germination and growth. Delayed germination also spreads out germination, increasing the chances of plant establishment, and allows seed to survive for many years in the soil as a seed bank. Most cool-season grasses found in higher elevations with snow and/or freezing temperatures have delayed germination and require cold stratification to germinate. In many ways, the coastal conditions found in central to northern California are similar to montane conditions in the Sierra and southern mountain ranges, where seed deposited in the late summer and fall do not germinate until the following spring, after having been exposed to wet and cold conditions during the winter.

The Soil Seed Bank

Most of California's perennial bunchgrasses do not produce seed that lives longer than a single season and thus do not provide a seed bank for changing conditions (Major and Pyott 1966). California oatgrass is perhaps the only California native grass that forms a readily available seed bank in the soil. Amme (1983) demonstrated this during a field survey at Jug Handle State Reserve (1 mile north of the town of Caspar, south of Fort Bragg) while preparing a restoration plan for controlling gorse (*Ulex europaea*) on the first terrace grassland. To help sample and identify the terrace vegetation in late summer when few plants were flowering, ten 4-inch-square × 4-inch-deep soil plugs were carefully lifted out of the ground with the vegetation intact in a variety of areas to collect from as many different plants and representative sites as possible. The plugs were put into 4-inch-square plastic nursery pots and raised in a greenhouse for identification. The plants from each pot were gradually lifted out, one at a time, and transplanted into smaller 2.25-inch pots to be grown and identified. The soil in the 4-inch pots was kept moist along with the smaller pots during the time they were being transplanted. Over a period of 2 months, small new grass shoots began to germinate and were potted up until no more plants would come up when the experiment was ended. The grasses that germinated during this 2-month period were all *Danthonia californica*. *Danthonia* plants were collected from each of the original ten pots, ranging from two to eight plants in each pot, with an average of four plants per pot. This was seat-of-the-pants science with only ten pots and no replications. But doing the math, this could potentially represent over 300 viable *Danthonia* seeds/plants in a square yard area (81 4-inch pots).

Dremann and Shaw (2002) recounted a similar experience documenting the apparent presence of viable *Danthonia* seed in the soil near Aptos, California. In this instance, Dremann and Shaw worked over a period of 12 years to cut and clear both annual and perennial exotic grasses and weeds from a weedy grassland near the coast, following what could be termed the Bradley methodology of restoration (Fuller and Barbe 1985). What began as a weed-infested grassland with only a few scattered individual California oatgrass plants, gradually evolved into a thick, pure, healthy stand of oatgrass as they improved the conditions for the germination and establishment of seed in the soil seed bank.

Cold stratification, seed scarification, and applications of gibberellic acid, sulfuric acid, and potassium nitrate have been used to break dormancy of seeds of all kinds of plants (Toole 1927, Trumble 1927, USDA 1974, Dobrenz and Beetle 1966). Curiously, planting *Danthonia* seed in moist greenhouse conditions immediately after collection can result in very high germination results (85%) (Amme 1983). This happens with many hard-seeded perennials. With lupines, for example, the soft, tender, pea-like seeds germinate immediately when planted, but once the seeds have shrunk and hardened, they can take much longer to absorb moisture and germinate (USDA 1974). Hot-water treatments have been used to enhance germination of many seeds under the assumption that fire (heat) may be a natural factor that sparks water absorption and germination. Laude (1949) waited 4 months after collecting the seed until fall when moisture conditions would be an ideal time to plant the seed. Laude reported very poor germination with untreated *Danthonia* seed planted in the fall, finding only a slight three-fold rise (0.5 to 3%) in germination up to 16 months after planting under ideal, moist greenhouse conditions. Seeds treated with a 30-minute sulfuric acid bath or with mechanically nicking of the seed coat with a scalpel increased germination up to 30 percent in greenhouse conditions and up to 85 percent raised in Petri dishes with two Humboldt and Mendocino accessions.

The Recent History of the Oatgrass Prairies and Meadows

California oatgrass grasslands and prairies were once much more widespread along the coast and central California's adjacent valleys close to the foggy coast. During the mid 19th century, as the early American settlers moved into the coastal prairies and mountain meadows of California, the oatgrass prairies and meadows were prime sites for livestock grazing and farms. During the Gold Rush era, the rich grasslands were initially grazed by cattle and sheep (Burcham 1957). As the American population increased, most of the rich flatlands and hillsides were converted to cultivation for grain crops, potatoes, vegetables, and fruit trees. Concurrent with this impact was the wholesale seeding and spreading of a variety of competitive European perennial forage grasses along the coastal and mountain regions. These grasses included sweet vernal grass (*Anthoxanthum odoratum*), browntop bentgrass (*Agrostis capillaris*), velvet grass (*Holcus lanatus*), orchard grass (*Dactylis glomerata*), Harding grass (*Phalaris aquatica*), and the annual and perennial ryegrasses (*Lolium multiflorum* and *L. perenne*). During this time, the tall, fast-growing annual Mediterranean grasses with abundant large seeds and seed quantities (Baker 1978), including wild oats (*Avena barbata* and *A. fatua*), ripgut brome (*Bromus diandrus*), soft chess (*B. hordeaceus*) and a "Who's Who" of European thistles and mustards, were competing with the natives for light and soil moisture. The overall effect of these Mediterranean grasses and weeds in temperate and moist conditions was that they overtopped, smothered, and shaded out the native perennial grasses in the spring. They also contribute to the drying out of the soils quickly during the spring growing flush.

The expansion of cattle and sheep ranching in California in the 1880s resulted, in part, from overstocking (or overgrazing) in certain key areas and some of the most severe drought years in California history that occurred in the 1860s, 70s and 80s (Burcham 1957). During these times there were widespread die-offs of livestock throughout the state. As more cattle and sheep were concentrated on the meadows and grasslands they consistently overgrazed the palatable oatgrass, rapidly depleting the good stands, despite its ability to adapt to close cropping (Crampton 1974). This may have contributed more to the reduction of oatgrass cover than any other factor. Hungry, fenced-in cattle are capable of tearing the grasses out by their roots, devouring the flowering culms, leaving little seed to replace the overutilized plants that could recharge the soil seed bank (Jones 1948). As the rich oatgrass prairie soils were mined by excessive grazing, so was the soil washed away and robbed of its moisture by the fast-growing introduced annuals. This began an irreversible spiral of loss—first, the loss of establishing oatgrass seedlings in droughty, eroded soils, then, the gradual exhaustion of the last of the dormant *Danthonia* seeds in the soil seed bank.

One of the earliest and best examples of proper management of California oatgrass with cattle resulted in the marked increase of oatgrass at the expense of annual grasses and the dominant medusahead (*Taeniatherum caput-medusae*). In the early 1950s on a 24,000-acre ranch in northwestern Californica, Lee Rice implemented a yearlong deferred-rotation grazing program on his cattle ranch, based on "the growth requirements of the principal native grass" (Cooper 1960). In an old seeded hay field grazed in this manner, California oatgrass out-performed the previously seeded pasture composed of exotic perennial grasses (orchard grass, Harding grass, tall fescue) and subclover. In 3 years, wild oatgrass, "the champagne grass of these ranges" (Cooper 1960), increased to 80-percent cover, while the seeded mix dropped from 36 to 10 percent cover. In 1960, the ranch produced more pounds of beef with 550 head compared to 1,000 head during the previous years of heavier grazing. The grazing tradition has continued.

Today Lee Rice's son and wife, John and Peggy Rice, continue to increase beef production by harvesting the surplus of the California oatgrass capital (Macon and Reeves 2000).

A thick stand of California oatgrass in a wet meadow in Annadel State Park, on the outskirts of Santa Rosa, California.

Producing Danthonia Seed in the 21st Century

Interest in growing California oatgrass for seed was strong in the mid-1940s, when U.C. Extension researchers Burl Jones and Merton Love identified oatgrass as *the* most outstanding native forage grass in the state (Jones and Love 1945, Jones 1948). The realization of delayed and poor germination in the lab (Laude 1949) and the need to treat or stratify the seed has tended to discourage any try at establishing a research field, and none was established until very recently. As late as 1987, a way was found to clean purple needlegrass (*Nassella pulchra*) seed, but picking the lock of producing native oatgrass seed still defied and frustrated researchers, agronomists, students, and producers.

This has changed. In the late 1990s and early 2000s, producers began to collect and tinker with California oatgrass in Oregon and California. Today there are a handful of sources of *Danthonia californica,* including two Oregon sources: the Eugene BLM variety from the West Eugene Wetlands–Amazon Creek, and the Basket Slough population, recently developed by the Plant Material Center in Corvallis (Darris and Lambert 2001). Craig Edminster of Pacific Northwest Natives near Albany, Oregon, has been working with *Danthonia californica* for almost 10 years (Edminster 2008a). Edminster was instrumental in collecting and producing the Tehama Ranch population from the Cañada de la Segunda Golf Ranch on the Monterey Peninsula near Carmel. In addition to these accessions (collected ecotypes), in the last 6 years, a

California Napa Marsh accession has been collected and produced by Hedgerow Farms in Winters, California (Anderson 2008). Hedgerow Farms has now added native oatgrass plugs and seed to its restoration services. Recently, Triangle Farms, in Silverfalls, Oregon, is growing a local form of native oatgrass collected east of Salem, Oregon, at 1,500-foot elevation (Loe 2008). First-year production is usually around 75 lb/acre, but second and third year production figures are above 200 lb/acre. There are approximately 90,000 to 165,000 seeds per pound of seed (Darris and Lambert 2001). A well-managed native oatgrass field will probably last for decades, forcing out all the weeds. The seed producers are also cutting and combining both the flowering seed and cleistogamous stem seed during the harvesting process (Anderson 2008).

For a seed producer, a clean field seeded in the fall will not germinate or begin to establish until the following spring (~5–6 months) with no stratification. To get this kind of result for planting in a grassland restoration setting, some form of seed treatment is recommended to boost germination of dormant seed. Several types of seed treatment have produced varied results. Simple chilling produced no germination in some tests (Dobrenz and Beetle 1966). Sulfuric acid treatments in a seed germinator produced high germination (up to 85%) in some tests, although field emergence and survival after the same treatments were still quite low at 24 percent or less (Laude 1949). Lab tests with gibberellic acid also yielded relatively high germination of up to 68 percent (Trask 1996).

In a true-to-life nursery test where the resulting seedlings were planted for restoration, *Danthonia* seed was scattered over plug trays and allowed to germinate. Seed aged from 6 to 16 months and treated with gibberellic acid and chilled had the highest (up to 37%) germination. However, multiple seedlings germinated in each cell of the plug trays, resulting in a probable germination rate closer to 85 percent.

Seed soaked in water and stratified in cold storage for up to 3 months reduced seed dormancy and produced a good spring stand that was planted in the previous fall (Edminster 2008b, Darris 2008). Alternatively, seed kept in dry bags in a cool seed barn in northern California showed increased germination and decreased dormancy with little loss of total viability after 2 years of storage. One-year-old seed maintained elevated dormancy (Anderson 2008).

Pure live seed (PLS) rate calculations need to be based on total seed viability and not just percent germination. Given the propensity for highly variable seed dormancy, it is strongly recommended that all seed lots of California oatgrass be given a TZ (tetrazolium chloride) test to determine total viability, along with the requisite germination test (Darris 2008). The TZ test is an accurate method to determine if the dormant seed is alive, filled, and viable. Anderson (2008) tested two seed lots for 3 years comparing germination and dormancy (TZ) of untreated seed. Germination increased and dormancy decreased each year. The total viability of germination and dormancy combined varied from 86% to 92% during this period. This viability range is similar with other growers (Darris 2008, Edminster 2008a, Loe 2008). We conclude that *Danthonia* seed has good viability and generally will make an excellent stand within 2 years. With any pre-treatment or storage method, when planted, the ungerminated seed is not lost but stays viable in the soil seed bank until conditions and disturbance circumstances are right. Seed should be planted in the fall and will generally not begin to germinate until early to late winter from California to Oregon. The cool, wet periods in the fall and early winter provide the conditions that gradually break down its dormancy and delayed germination. This also gives the farmer or restorationist plenty of time to kill or mow weeds before the *Danthonia* begins to germinate.

Sowing, Planting, and Managing *Danthonia*

Sowing, planting, and managing California oatgrass is an enjoyable experience. It stays green with irrigation, is very nutritious for livestock, can become a low sod grass, taking the punishment of a pick-up truck or a practice field for football, or provide a soft pillow for viewing the clouds. Restoring oatgrass grasslands and meadows is definitely the right thing to do. Oatgrass is an important component for restoring the structure and function of coastal and mountain wet meadows. An oatgrass meadow or grassland should be seeded as a pure mix. Unmowed, oatgrass is a sprawling dense bunchgrass 10 to 12 inches in height and 14 to 16 inches across. Mowed or grazed plants can form tight sod-like stands no more than a few inches high. Establishing an oatgrass meadow or grassland requires patience. *Danthonia* establishes slowly but is a persistent grower (Amme 1986). Like the tortoise, it is the first to the finish line. Because of its deep roots, oatgrass does not require frequent irrigation. It thrives in rich, loamy, and clay soils and is well adapted to the home garden setting. It stays green throughout the year if it is cut back and receives a little additional moisture. A good oatgrass "turf" can be established by planting plugs 6 to 8 inches apart (Amme 2003). For establishing a single-species meadow, sow at 3 ounces per 1,000 square feet or about 8 PLS pounds per acre. Darris and Gonzalves (2008) recommend 10–18 PLS pounds per acre. Selective herbicides can help control broadleaf weeds, or mowing at a 3- to 4-inch height two to three times the first year will keep the weeds down and allow the oatgrass to mature and stabilize (Kephart and Amme 1992).

Because of its delayed germination, Edminster (2008b) and Darris and Gonzalves (2008) have recommended nurse crops for establishing an oatgrass meadow or grassland. Edminster has had good success mixing the oatgrass with equal parts of Roemer's fescue (*Festuca roemeri* aka *F. idahoensis roemeri*), which is also the California north coast range form of Idaho fescue. Darris and Gonzalves recommend mixing oatgrass with a species that has similar seed dormancy characteristics, like Lemmon's needlegrass (*Achnatherum lemmonii*) or a less-competitive short-lived grass, which could include slender hairgrass (*Deschampsia elongata*), meadow barley (*Hordeum brachyantherum*), or spikebent (*Agrostis exarata*), or with the long-lived tufted hairgrass (*Deschampsia caespitosa*) in wet or mesic grassland sites. In the latter example, the oatgrass and tufted hairgrass will dominate in their respective preferred sites. A mowing or grazing regimen will gradually select against the "nurse crop" grasses, eventually developing a *Danthonia*-dominated meadow.

Mowing, grazing, and raking are the best tools to manage an oatgrass meadow stand. Close cropping (i.e., mowing or heavy, persistent grazing) will develop a low turf-like or sod-like stand. Higher mowing or occasional light grazing will encourage a less dense stand with much larger plants. Irrigation or existing high soil moisture will maintain a green stand, but if the site dries out during the late spring and summer months the plants are fully capable of becoming dormant, appearing dried out with folded, thin leaves. There is always a hint of green with a closer look. When the moisture returns in the winter, the oatgrass greens up and produces another crop of leaves, stems, and seeds. For the tidy gardener, the sprawling and arching flowering stems hiding the plants can be raked up with a steel rake, revealing a spotless green meadow. Save the stems in a container, crush it up and apply back onto the meadow in the fall. Little seedlings are sure to appear in the open sites the following spring.

California oatgrass has a tough time competing against super-productive exotic perennial bunchgrasses, especially velvet grass (*Holcus lanatus*), tall fescue (*Festuca arundinacea*), and Harding grass (*Phalaris aquatica*). Close mowing will select against the tall fescue and Harding grass, favoring establishment of the oatgrass. However, velvet grass keeps regrowing,

developing a thatch that suppresses the tiny oatgrass seedlings. The introduced creeping turf grasses like colonial bentgrass (*Agrostis capillaris*) and creeping bentgrass (*A. stolonifera*) will also weaken and gradually swamp out a developing native oatgrass stand. The exotic annual grasses are a little easier to control with well-timed mowing or grazing, enabling the oatgrass to gradually increase in cover. The best time for mowing/grazing is just before the exotic perennial or annual grasses can form seed during their peak flowering periods. The cutting also releases more ground moisture for the oatgrass. Always collect and dispose of the cuttings so light can reach the ground. Oatgrass thrives in the sun.

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