REPRODUCTIVE ECOLOGY OF TWO COASTAL PLAIN LEGUMES: *BAPTISIA ARACHNIFERA* AND *BAPTISIA LANCEOLATA*

by

AMY R. SQUIRE

(Under the Direction of Rebecca R. Sharitz)

ABSTRACT

Several studies were undertaken to assess the reproductive ecology of two southeastern Coastal Plain legumes: *Baptisia arachnifera* and *B. lanceolata*. First, an experimental seed bank study documented *B. lanceolata* seed fate. Forty percent of seeds remained dormant after one year, suggesting that *B. lanceolata* can form a seed bank. Seed banks are thought to buffer the effects of predispersal seed predation on population dynamics of long-lived perennials. A comprehensive suite of reproductive traits was evaluated in a rare-common comparison of the two *Baptisia* species. Most reproductive traits were similar between the rare *B. arachnifera* and its widespread congener *B. lanceolata*. One notable difference was the reduced tolerance for high temperatures in *B. arachnifera*. Finally, reproductive and genetic traits were compared in central (Georgia) and peripheral (South Carolina) populations of *B. lanceolata*. Peripheral populations had decreased cumulative fitness; however, there was no significant difference in genetic variation between regions.

INDEX WORDS: *Baptisia*, Reproductive ecology, Predispersal seed predation, Rare-common comparison, Heat shock, Allozymes

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DEDICATION

To my love, James D. Young
you are my sunshine
and truly a kindred spirit

To my family
for fostering my Mind
even though I solved the Rubik's
cube by cheating

To *Baptisia* and my extended mouse/turtle clan
for reminding me
how to listen to, and love,
those without a voice

And in memory of Leah Deni,
who planted seeds of change
and an infectious love of Life
in many, many souls

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

With 22% of vascular plants deemed worthy of conservation (Falk, 1992), there is a need for more research efforts that could help elucidate the nature of plant rarity. As one might expect, rarity is a complex concept. Rarity is often defined in terms of species abundance or range size (Kunin, 1997; Murray et al., 2002). Geographical distribution, habitat specificity and local population size are three components that have been suggested as a means of partitioning rare species into seven distinct categories (Rabinowitz, 1981). Other researchers stress the merit of synthetic assessments of rarity, which include information on evolutionary history, ecology and population biology (Stebbins, 1980; Fiedler, 1986). Pavlik et al. (1993) depict plant rarity as resulting from the interplay of limiting intrinsic (e.g., inbreeding depression) and extrinsic (e.g., habitat availability) factors. Human activities provide an additional facet to contemporary plant rarity, with an increased number of anthropogenic rarities resulting from the negative consequences of habitat destruction and/or degradation on plant populations (Fiedler and Ahouse, 1992).

An understanding of species biology has been described as "the key to plant preservation" because of its ability to reveal factors that limit long-term persistence (Massey and Whitson, 1980). Nonetheless, insufficient knowledge of species biology is repeatedly cited as a shortcoming of endangered species' recovery plans (Schemske et al., 1994; Tear et al., 1995; Clark et al., 2002). Reproduction and recruitment are considered important biological

components in understanding plant rarity (Kunin and Shmida, 1997; Kaye, 1999; Brown et al., 2003). As such, my Master's research consists of several studies that focus on reproductive ecology as a way to evaluate rarity in two Coastal Plain legumes, *Baptisia arachnifera* and *Baptisia lanceolata*.

Baptisia arachnifera Duncan and *Baptisia lanceolata* (Walt.) Ell. are polycarpic legumes associated with longleaf pine and slash pine forests of the southeastern United States (Larisey, 1940; U. S. Fish and Wildlife Service, 1984). Both species produce terminal racemes of bright yellow flowers and have documented seed predation by Say's weevil (*Apion rostrum*) (U.S. Fish and Wildlife Service, 1984; Faircloth, 1987; Mehlman, 1993; Horn and Hanula, 2004). *Baptisia arachnifera* and *B. lanceolata* both have large rhizomatous rootstocks (Larisey, 1940; Mehlman, 1993; US Fish and Wildlife Service, 1984) and individuals are thought to live at least 15 years. These two species occasionally occur together along roadsides in Wayne Co., Georgia (A. Squire, personal observation).

Baptisia arachnifera is entirely tomentose and possesses simple, cordate leaves, which distinguishes it from other *Baptisia* species (Duncan, 1944; Ceska et al., 1997). It typically flowers in June and July, while pods mature from August through September. A federally listed endangered species, *B. arachnifera* is found only in two southeastern Georgia counties (Wayne and Brantley), with the majority of remaining populations in slash pine plantations (U.S. Fish and Wildlife Service, 1984; Ceska et al., 1997). Within the past twenty years, *B. arachnifera* populations have dramatically declined in size (22-89% fewer individuals) and reverted from primarily mature adults to mostly non-flowering plants (Tassin and McGee, 1999). Since this species was discovered in the 1940s, many botanists have concluded that *B. arachnifera*

population sizes are dwindling despite any reduction in its range (Faircloth, 1987). An assessment of allozyme diversity in ten *B. arachnifera* populations found very low genetic diversity (G_{st} = 0.096) between populations, which is within the range of other endemic species (Ceska et al., 1997).

In contrast, *B. lanceolata* populations are distributed across southern Georgia and extend into Alabama, Florida and South Carolina. *Baptisia lanceolata*, which has the more typical trifoliate leaves, can be found in several habitats, including dry pine woodlands, oak scrub, and sandhills (Larisey, 1940). Flowering commences in early April and pods mature in June and July. Despite having a larger geographical distribution than its endangered congener, *B. lanceolata* is considered potentially threatened in parts of its range. According to the NatureServe ranking system, *B. lanceolata* is considered "apparently secure" overall (G4), with a similar rank in Georgia (S4) and unranked in South Carolina (SNR; NatureServe webpage). However, it is considered a "species of concern" in South Carolina due to its presence in only two counties (Knox and Sharitz, 1990; South Carolina Department of Natural Resources webpage). It is not uncommon for species to be classified as both rare and secure in different parts of their range (e.g., Kartesz, 1981; Edwards and Weakley, 2001). These "apparent rarities" (Rodrigues and Gaston, 2002) often result from geopolitical boundaries coinciding with the periphery of a species' distribution. Thus, species become interpreted as rare when evaluated at a narrower, regional scale (Hunter and Hutchinson, 1994; Lesica and Allendorf, 1995; Bruederle, 1999).

Demographic studies have been identified as a crucial tool for plant conservation efforts (Schemske et al., 1994). Long-lived perennials, such as both *Baptisia* species, present a challenge to these studies because the persistence of older individuals can obscure negative

growth rates that arise from lack of recruitment (Schemske et al., 1994; Kettle et al., 2000). As such, existing populations of long-lived perennials may be more vulnerable than originally perceived (Colling et al., 2002). Oostermeyer et al. (1994) described two opposing types of long-lived perennial populations. Dynamic populations characteristically have high turnover due to steady influx of seedlings whereas static populations consist primarily of older individuals with no successful germination or recruitment. Several rare plant species fit this characterization of static population structure (Mehrhoff, 1989**;** Oostermeyer et al., 1994; Colling et al., 2002). Field germination experiments of long-lived perennials such as *Ipomoea leptophylla* (Keeler, 1991) and *Scorzonera humilis* (Colling et al., 2002) have been completely unsuccessful. In a similar vein, low field recruitment has been noted for *B. arachnifera* and *B. lanceolata*, as well as other *Baptisia* species (Johnson, 1977; Humphrey, 1988; J. Ceska, personal communication; A. Squire, personal observation).

Given this observed lack of *Baptisia* seedlings in natural populations, all of my projects include, to some extent, research on seed dynamics. While *B. arachnifera* and *B. lanceolata* are both capable of vegetative reproduction, seeds remain vital for future colonization events and potentially increasing genetic variation within existing populations.

In Chapter 2, I investigate whether *B. lanceolata* seeds are able to persist up to a year under field conditions. The formation of a persistent soil seed bank has been postulated to potentially buffer the negative effects of predispersal seed predation on the population dynamics of long-lived perennials (Andersen, 1989). By assigning experimental *B. lanceolata* seed banks to one of four microsite treatments, I also test the effect, if any, of canopy openness and litter layer on seed fate.

In Chapter 3, I conduct a rare-common comparison of floral, pod and seed traits in *B. arachnifera* (rare) and *B. lanceolata* (common). This type of contrast could potentially identify reproductive characteristics associated with rarity. In addition, I discuss the results of a heat shock experiment on seeds of both *Baptisia* species, which was performed to determine their range of tolerance to high temperatures. Heat shock can be an effective means of interrupting physical dormancy imposed by an impermeable seed coat (Keeley and Fotheringham, 1998) and, thus, can promote germination in hard-seeded legumes (e.g., Cushwa et al., 1968; Martin et al., 1975, Auld and O'Connell, 1991).

In Chapter 4, I compare a similar suite of reproductive traits (excluding pollen viability and heat shock) in central (Georgia) and peripheral (South Carolina) *B. lanceolata* populations to assess whether there are any significant differences between plants growing in these neighboring states. Allozyme data are also analyzed to test the hypothesis that peripheral populations have reduced genetic variation.

Together, these projects provide a preliminary understanding of the natural history of these two *Baptisia* species, which in turn can be valuable in understanding their status as rare plants. I synthesize and discuss my findings in Chapter 5.

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CHAPTER 2

SOIL SEED BANK DYNAMICS OF A LONG-LIVED PERENNIAL, *BAPTISIA LANCEOLATA*, SUSCEPTIBLE TO PREDISPERSAL SEED PREDATION[1]

[1] Squire, A.R. and R. R. Sharitz. To be submitted to *Journal of the Torrey Botanical Society*.

INTRODUCTION

Persistent soil seed banks are composed of dormant propagules that have the potential to replace existing aboveground vegetation (Baker, 1989). The retention of viable seeds over time influences ecological and evolutionary processes in plant populations. Persistent soil seed banks are presumably made up of seeds produced from multiple generations subjected to varying selection regimes. This genetic memory can influence evolutionary potential by buffering the effects of stochastic events on fitness (Templeton and Levin, 1979) and increasing effective population size (McCue and Holtsford, 1998). Additional benefits of persistent soil seed banks include increased longevity of populations (Kalisz and McPeek, 1992) and source of regeneration in disturbance-prone habitats (Grime, 1989).

Predispersal seed predation by inflorescence-feeding insects is one mechanism that can alter soil seed bank dynamics. Seed loss, delay in seed release, and selective damage to different genotypes are several means by which predispersal seed predation has been shown to influence soil seed banks (Louda, 1989). Within the past thirty years, however, there has been increasing debate about whether such reproductive herbivory truly affects plant population dynamics (e.g., Harper, 1977; Louda, 1982a,b; Andersen, 1989; Louda and Potvin, 1995; Maron and Gardner, 2000). According to Harper (1977), predispersal seed predation should not affect plant density as long as the number of viable seeds remains above a critical threshold for adult recruitment. Recruitment can be limited through inadequate number of viable seeds or lack of microsites suitable for germination and seedling establishment ("safe sites", Harper et al., 1961). For predispersal seed predation to act as a selective force, there must be a direct relationship between seedling recruitment and seed predator damage.

Plant life history can also influence the degree to which predispersal seed predation affects the population dynamics of a species. Predispersal seed predation has been shown to have a negative (Kelly and Dyer, 2002), conditional (Andersen, 1989), or no (Crawley, 1989; Louda and Potvin, 1995) relationship with the population dynamics of long-lived perennials. The ambiguity of the term "long-lived" has been speculated to contribute to this lack of consensus (Kelly and Dyer, 2002). Andersen (1989) argued that seed predation would affect population dynamics of long-lived perennials only if predation interfered with a plant's ability to establish a soil seed bank.

Baptisia lanceolata (Fabaceae) is a long-lived perennial that is found in the southeastern United States from South Carolina to Florida. Several *Baptisia* species, including *B. lanceolata*, have been documented to have high rates of predispersal seed predation by a range of insects, especially weevils and lepidopteran species (Frost, 1945; Evans et al., 1989; Mehlman, 1993; Horn and Hanula, 2004; Schnabel and Sharitz, unpublished data). In this study, we monitored experimental *B. lanceolata* seed banks for one year to determine whether this species was capable of forming a persistent seed bank. Seed banks were assigned to one of four microsite treatments testing the effect, if any, of canopy openness and litter layer on seed fate. Experimental seed bank results were used to evaluate the potential for predispersal seed predation to have long-term population effects on *B. lanceolata*. Predispersal seed predation data from *B. lanceolata* populations in Georgia and South Carolina were included to provide a preliminary assessment of its influence on seed production.

MATERIALS AND METHODS

Species description and study site

Baptisia lanceolata (Walt.) Ell. is a polycarpic, perennial legume that grows in dry pine woodlands, oak scrub, and sandhills along the Coastal Plain of the southeastern United States (Larisey, 1940). Flowers are bright yellow and are either axillary or arranged in terminal racemes of several flowers (Isley, 1990). Flowering commences around late March and early April. Say's weevil (*Apion rostrum*) and an unidentified lepidopteran have been previously reported to feed on the reproductive structures of *B. lanceolata* (Mehlman, 1993; Horn and Hanula, 2004; Schnabel and Sharitz, unpublished data).

This experiment was conducted within an existing *B. lanceolata* population in Barnwell County, South Carolina. *Pinus palustris* and several *Quercus* sp. were the predominant overstory species in this population. The shrub and groundcover layers included *Vitis rotundifolia*, *Vaccinium stamineum*, *Gaylussacia dumosa*, and several grasses.

Experimental seed banks

Seeds were collected throughout July 2003 from three populations in Georgia and South Carolina, including the population where experimental seed banks were eventually placed. Fifteen seeds were placed in 9 cm^2 hard plastic mesh containers ("seed containers") along with a pinch of soil from the surrounding area. There is often heterogeneity in seed color both between and within mature *Baptisia* pods (Mehlman, 1993). To eliminate any potential differences resulting from seed color and/or source, seed containers contained the same composition of seed types. Experimental seed banks were formed by attaching four seed containers to an upright, central piece of PVC using heavy fishing line. At each experimental seed bank, one of three seed containers was randomly collected after one, six or 12 months to assess the temporal change

in seed bank composition. The fourth container housed a Thermochron® iButton temperature data logger, which experienced the same conditions as the seed containers. Hourly soil temperature (°F) readings were recorded for one year (July 2003 – July 2004), with iButton data downloaded approximately every three months; temperature data were later converted into °C. All containers were initially buried in the top centimeter of soil at a distance of one meter from the PVC pipe to exclude any shadow effects.

Sixteen experimental seed banks were assigned to each of the following microsite treatments: closed canopy with litter, closed canopy without litter, open canopy with litter and open canopy without litter. Canopy openness was determined using hemispherical canopy photos taken at 30 m intervals across the entire population and analyzed using Gap Light Analyzer (GLA 2.0; Frazer et al., 2000). Four closed (14-17% canopy openness) and four open (35-39% canopy openness) canopy sites were selected for experimental seed bank placement. Positions were selected within canopy types such that seed banks with litter treatments had similar amounts of litter (1 - 1.5”). All litter was removed within a 1.5 m radius for experimental seed banks without litter treatment.

Upon collection of seed containers, seeds were classified as dormant, germinated, rotten, or unaccounted. Germination estimates were based on the presence of a germinant or an intact empty seed coat. If fewer than 15 seeds could be discerned in a seed container, the difference was considered unaccounted, those that either rotted completely or germinated and subsequently rotted before collection. All dormant seeds were subjected to scarification treatment using fine-grained sandpaper. Seed viability was quantified using the triphenyl tetrazolium chloride (TTC)

test (Grabe, 1970). As a positive control, three replicates of 15 seeds were placed in a drying oven under lethal conditions (140 ºC for eight minutes). Heat control seeds were similarly subjected to the TTC test to determine the efficacy of the tetrazolium stain; none were found to be viable.

Data were analyzed as a three-way factorial analysis of variance (ANOVA)(SAS Institute, 1999). The three factors were time, canopy openness, and litter layer. Response variables were number of dormant seeds (%) and overall seed viability (%). Overall seed viability was calculated for each seed bank as the number of germinants and viable dormant seeds divided by initial number of seeds per seed container. Monthly mean daily and maximum temperatures (° C) were calculated for each microsite treatment.

Predispersal seed predation

In 2004, *B. lanceolata* pods collected from six populations in Georgia and South Carolina were evaluated for predispersal seed predation. Pods attacked by Say's weevil can be identified by small, distinctive exit holes; often the adult weevil can still be found in collected pods. While there is no exterior damage typically associated with lepidopteran-predated pods, these pods are completely filled with silky frass. Only pods with direct evidence of predispersal seed predation (e.g., predator and/or frass present) were classified as such. A frequency distribution of the number of intact seeds/pod was determined for undamaged (N=118), lepidopteran-predated (N=55) and weevil-predated (N=147) *B. lanceolata* pods.

RESULTS

Experimental seed banks

Forty percent of *B. lanceolata* seeds remained dormant in seed banks after one year when all microsite treatments were combined (Fig. 2.1; Table 2.1). At all time intervals, rotten seeds

made up about 30% of each seed bank. There was little direct evidence of germination from the exhumed experimental seed banks. There was a significant loss of dormant seeds between the one and six month sampling periods. Similarly, there was a significant decrease in overall seed viability during the same period, with about 25% of seeds remaining viable after one year (Table 2.1).

Microsite factors had a significant influence on *B. lanceolata* seed fate (Table 2.1). Open canopy seed banks had significantly more dormant and viable seeds than those under closed canopy. The presence of a litter layer had a significant impact only on number of dormant seeds. There were no significant interactions between factors. The four microsite treatments did not have any observable difference in soil temperature when data were analyzed as mean daily temperature (Fig. 2.2a). However, both open canopy treatments tended to have higher maximum daily temperature values than their closed canopy counterparts (Fig. 2.2b).

Predispersal seed predation

All lepidopteran-predated and the majority of weevil-predated pods had no intact seeds remaining (Fig 2.3). In contrast, undamaged pods contained between 0-15 seeds per pod (Fig 2.3).

DISCUSSION

The finding that 40% of *B. lanceolata* seeds persisted after one year in experimental seed banks (Table 2.1) suggests that this species is capable of forming a soil seed bank. Studies of other members of the Fabaceae further support the persistent seed bank hypothesis. Hardseedness, a key characteristic of the Fabaceae (Rolston, 1978), is thought to be largely responsible for legume soil seed bank formation (Degreef et al., 2002). Baskin and Baskin (1998) cite 65 species of legumes capable of producing dormant seeds that remain viable for

extended periods of time. A study of germination trends for 14 herbaceous legumes reported that, on average, 13-92% seeds remained intact after 18 months' burial in experimental seed banks (Van Assche et al., 2003). With respect to other *Baptisia* species, Voß et al. (1994) found that imbibition is not necessarily a precursor to germination for *B. tinctoria* seeds; this may be indicative of some type of dormancy mechanism.

Baptisia lanceolata seed fate was most influenced by time, with the most significant decrease in dormant seeds occurring within the first six months of the experiment (July-January). The steepest increase in unaccounted seeds also occurred during the same period. Unfortunately, the two potential causes of seed loss, germination and senescence, could not be distinguished in the experimental design. While no conclusions can be made about their effect on germination, microsite factors appeared to influence soil seed bank formation. Specifically, open canopy sites had significantly more dormant (57% vs. 44%) and, to a lesser degree, viable (31% vs. 25%) seeds than those positioned under closed canopy. Litter also had a significant effect on seed fate, with an increased number of dormant seeds recovered when litter was initially removed from the surrounding area. One possible explanation is that the higher temperatures recorded at open canopy sites could have reduced soil moisture levels. Similarly, the removal of leaf litter could have also altered the moisture around the seed banks. Drier soil conditions can inhibit fungal growth (Leishman et al., 2000), thus allowing for higher retention of dormant seeds. Fungal pathogens constitute an important, yet often neglected, source of seed mortality (Lonsdale, 1993; Hyatt, 1998; Leishman et al., 2000).

The ability of long lived perennials to maintain a soil seed bank has been postulated to be a factor deciding whether predispersal seed predation has any impact on a species' population dynamics (Andersen, 1989). A recent evaluation of six *B. lanceolata* populations found that

mean pod damage per individual ranged from 18 - 96% (Chapter 4). In the present study, we found that predated pods typically have little to no intact seeds remaining. This substantial reduction in *B. lanceolata* seed production, however, might be buffered over time if seeds from current and previous years remain viable in a soil seed bank.

Our preliminary data suggest that *B. lanceolata* is capable of forming a persistent soil seed bank and, thus, predispersal seed predation may not be detrimental to *B. lanceolata* populations. However, there are several other factors that need to be taken into consideration. First, for some plant species, intensity of predation has been shown to vary between years, especially among individuals within a population (e.g., Ehrlén, 1996). It is feasible that multiple years of high seed predation might severely inhibit the formation of a soil seed bank. As such, a long term study would be necessary to document spatiotemporal trends in predation intensity for *B. lanceolata*. The observed low overall viability of seeds (~ 30%) and their vulnerability to fungal attack suggests that successful recruitment is dependent on the availability of many seeds.

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Table 2.1. The effect of time, canopy type and litter layer on seed fate in experimental *Baptisia lanceolata* seed banks. Values represent mean (SE). Within each factor, values with the same letter are not significantly different at $\alpha = 0.05$ (Tukey's HSD).

Factor	Dormant seeds (%)	Overall viable seeds (%)
Time		
One month	0.66 (0.03)[a] **	0.33 (0.02) [a] *
Six months	0.46 (0.04)[b]	0.24 (0.02) [b]
Twelve months	0.40 (0.03)[b]	0.26 (0.02) [ab]
Canopy type		
Open	0.57 (0.03)[a] **	0.31 (0.02) [a] *
Closed	0.44 (0.04)[b]	0.25 (0.02) [b]
Litter layer		
Absent	0.55 (0.03)[a] *	0.26 (0.02) [a]
Present	0.47 (0.04)[b]	0.30 (0.02) [a]

** $p < 0.001$
* $p = 0.02$

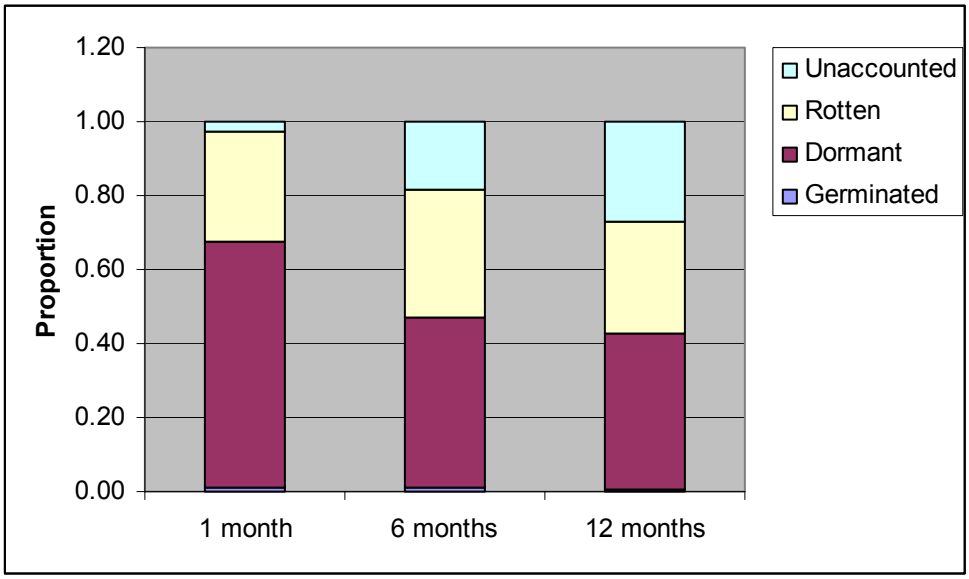
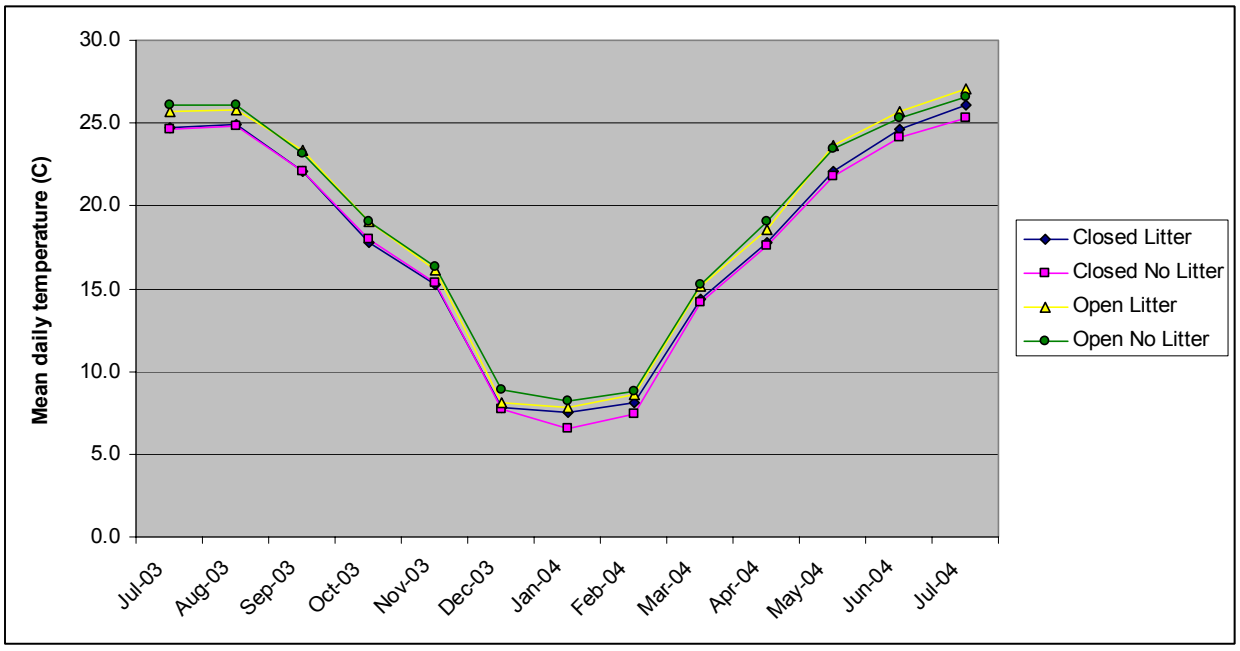


Figure 2.1. Seed fate within *Baptisia lanceolata* experimental seed banks over time. Bars represent proportion of seeds from all 16 seed banks that fall within each seed fate category.

a)



b)

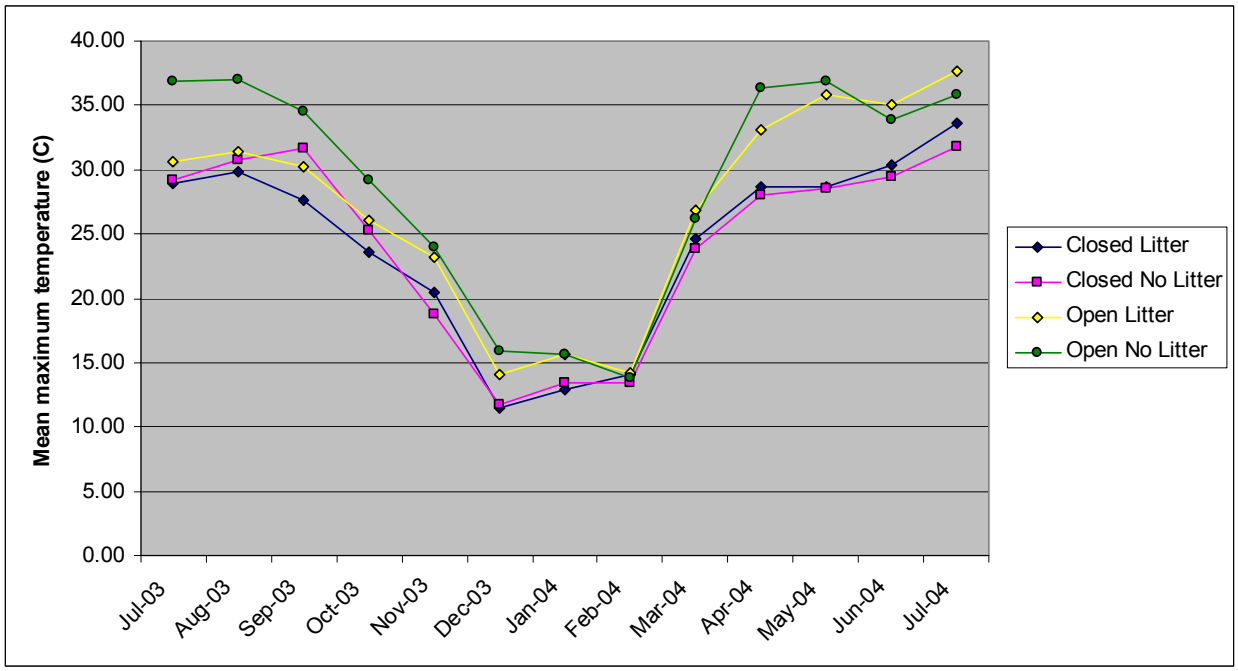


Figure 2.2 (a-b). Mean a) daily and b) maximum soil temperature (°C) recorded at experimental *Baptisia lanceolata* seed banks with four different microsite treatments. All measurements were recorded approximately 1 cm below soil surface.

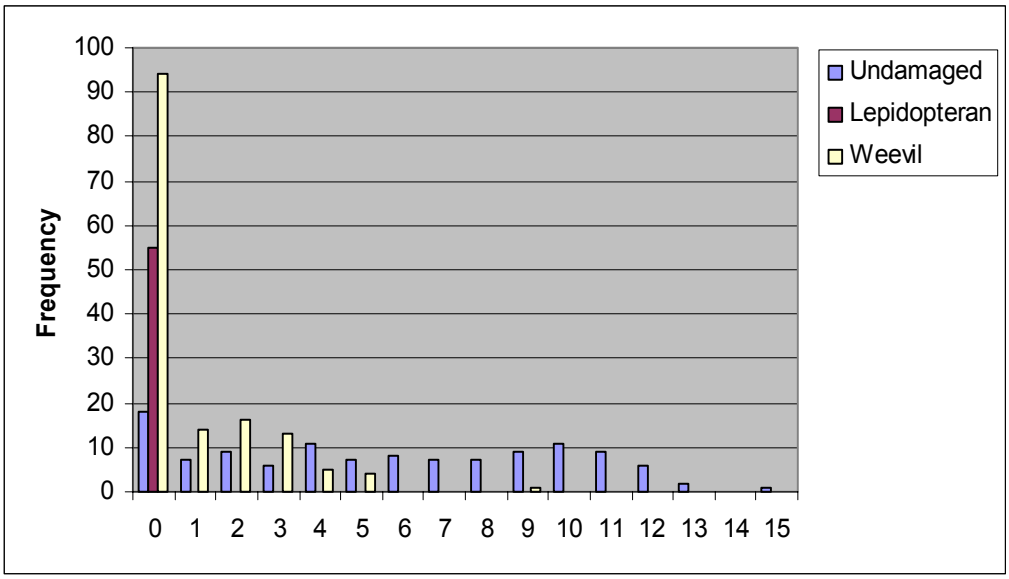


Figure 2.3. Frequency distribution of intact seeds in undamaged (N=118), lepidopteran-predated (N=55), and weevil-predated (N=147) *Baptisia lanceolata* pods.

CHAPTER 3

REPRODUCTIVE ECOLOGY OF A FEDERALLY ENDANGERED LEGUME, *BAPTISIA ARACHNIFERA*, AND ITS MORE WIDESPREAD CONGENER, *BAPTISIA LANCEOLATA*[2]

[2] Squire, A.R., S. M. Chang, and R. R. Sharitz. To be submitted to *Conservation Biology*.

INTRODUCTION

Understanding the natural history of rare plants is crucial to their conservation efforts. Massey and Whitson (1980) identify species biology as "the key to plant preservation" because of its ability to reveal factors that limit long-term persistence. Nonetheless, insufficient knowledge of species biology is repeatedly cited as a shortcoming of endangered species' recovery plans (Schemske et al., 1994; Tear et al., 1995; Clark et al., 2002). By contrasting life history traits of restricted versus more widespread congeneric species, rare-common comparisons can provide essential information for rare plant management (e.g, Kunin and Gaston, 1993; Brown et al., 2003; Burne et al., 2003).

Few rare-common comparisons, however, measure similar sets of traits. For example, Murray et al. (2002) found that 67% (63/94) of traits investigated in rare-common plant comparisons are measured only in one study. Similarly, Bevill and Louda (1999) call for the development of a standardized set of traits to allow for synthesis of general patterns of rarity. Other drawbacks to this comparative method include the tendency of studies to include only one pairwise comparison (Kunin and Gaston, 1993) and the phylogenetic constraints that arise from comparing closely related species (Felsenstein, 1985). In spite of these setbacks, the potential differences in life history traits that arise from rare-common comparisons can still be vital to informing immediate conservation decisions (Kunin and Gaston, 1993).

Baptisia arachnifera Duncan and *Baptisia lanceolata* (Walt.) Ell. are long-lived perennial legumes that occur in the lower Coastal Plain province of the southeastern United States. The federally endangered *B. arachnifera* is restricted to two counties in southeastern Georgia. Within the past twenty years, *B. arachnifera* populations have dramatically declined in size (22-89% fewer individuals) and reverted from primarily mature adults to mostly non-flowering

plants (Tassin and McGee, 1999). In contrast, *B. lanceolata* is considered "apparently secure" in Georgia (NatureServe webpage). Both species have predispersal seed predation by weevils (U.S. Fish and Wildlife Service, 1984; Mehlman, 1993; Horn and Hanula, 2004) and been observed to have low levels of recruitment (U.S. Fish and Wildlife Service, 1984; Humphrey, 1988; A. S., personal observations)

Since many studies emphasize the role of reproduction and recruitment in understanding the life history of rare plants (Gaston and Kunin, 1997; Kaye, 1999; Evans et al., 2003; Brown et al., 2003), we focused on measuring a comprehensive suite of reproductive traits in *B. arachnifera* (rare) and *B. lanceolata* (common). In addition to field measurements on floral, seed pod and seed traits, a heat shock experiment was conducted on seeds of both species to determine their range of tolerance to high temperatures. Seeds were exposed to temperatures comparable to and exceeding those experienced near the soil surface during a prescribed burn. Heat shock can be an effective means of interrupting physical dormancy imposed by an impermeable seed coat prior to germination (Keeley and Fotheringham, 1998). As such, exposure to high temperatures can promote initial water uptake in many hard-seeded legumes (e.g., Cushwa et al., 1968; Martin et al., 1975; Auld and O'Connell, 1991). Since both *Baptisia* species are associated with longleaf pine forests, which are historically fire-dependent, it is feasible that fire might be an important factor for germination and recruitment.

We hypothesized that *B. arachnifera* should have decreased flower, pod, and seed production relative to *B. lanceolata*. Reduced seed production is one of the few generalizations about rare plants substantiated by multiple studies (Murray et al., 2002, see sources cited therein). While measured less frequently, flower (Mehroff, 1983; Fiedler, 1987; Murray and Westoby, 2000; Lavergne, 2004; but see Burne et al., 2003) and fruit (Fiedler, 1987; Young and

Brown, 1998; Brown et al., 2003; Burne et al., 2003; but see Mehroff, 1983) production also tend to be significantly lower in rare plants. Pollen viability, pod initiation, seed weight, seed abortion, and pod volume were also measured. Since these reproductive traits have either not been studied or have no consensus in the rare-common literature, we assumed the null hypothesis that there was no significant difference between *B. arachnifera* and *B. lanceolata*. Based on the one known rare-common comparison of heat shock (Brown et al., 2003), we hypothesized that the rare species (*B. arachnifera*) would tolerate a narrower range of high temperatures than its common congener.

MATERIALS AND METHODS

Study species and experimental design

Baptisia arachnifera Duncan and *B. lanceolata* (Walt.) Ell. are polycarpic legumes typically associated with the longleaf pine and slash pine forests of the lower Coastal Plain (Larisey, 1940; U.S. Fish and Wildlife Service, 1984). Both species produce terminal racemes of bright yellow flowers and have been documented to have seed predation by Say's weevil (*Apion rostrum*; U.S. Fish and Wildlife Service, 1984; Mehlman, 1993; Horn and Hanula, 2004). These *Baptisia* species occasionally occur together along roadsides in Wayne Co., GA (A. Squire, personal observation).

Baptisia arachnifera is entirely tomentose and possesses simple, cordate leaves, which distinguishes it from other Baptisia species (Duncan, 1944; Ceska et al., 1997). It typically flowers in June and July, and fruiting occurs from August through September. A federally listed endangered species, *B. arachnifera* is found only in two southeastern Georgia counties (Wayne and Brantley) with the majority of remaining populations currently occurring in slash pine plantations (U.S. Fish and Wildlife Service, 1984; Ceska et al., 1997). In contrast, *B. lanceolata*

populations are distributed across southern Georgia and extend into Alabama, Florida and South Carolina. *Baptisia lanceolata*, which has the more typical trifoliate leaves of *Baptisia* species, can be found in several habitats including dry longleaf pine woodlands, oak scrub, and sandhills (Larisey, 1940). Flowering commences in early April and pods mature in July and August.

In 2004, three populations of each species were monitored throughout the growing season. All three *B. arachnifera* populations (Powerline, Rayonier, Wire Road) were located in one of the two counties where *B. arachnifera* occurs (Wayne Co.). *Baptisia lanceolata* populations were sampled throughout south Georgia in Wayne (Browntown Road), Coffee (General Coffee State Park), and Appling (Moody Forest) counties. Within each population, a plot between 900 (30 x 30) and 1600 (40 x 40) square meters in size was established in order to obtain 20 focal individuals. To qualify, focal individuals had to be flowering and at least 1 m distant from another conspecific plant since both *Baptisia* species possess rhizomatous rootstocks (Larisey, 1940; U.S. Fish and Wildlife Service, 1984; Mehlman, 1993) and are thought to be clonal to some extent. Although the plot size was selected to capture approximately 20 focal individuals, there were sometimes more than 20 *Baptisia* plants that met these qualifications; emphasis was then placed on randomly selecting acceptable plants across the entire plot. One *B. arachnifera* population (Rayonier) had fewer than 20 individuals that met these criteria and therefore all acceptable individuals were used. During the course of this study, another *B. arachnifera* population (Powerline) was mowed, preventing the collection of mature pod and seed data.

Environmental variables

Canopy openness, soil nutrients and texture were measured to assess potential habitat differences between *B. arachnifera* and *B. lanceolata*. Percent canopy openness was assessed

using 10 hemispherical canopy photographs per population, which were interpreted using Gap Light Analyzer (GLA 2.0; Frazer et al., 2000). A total of fifteen soil samples cores were collected from each population. Five subsamples per population were obtained by pooling five random sets of three cores. Cores were 0.75 inches wide and driven approximately 2 feet into the ground. Soil samples were analyzed by the University of Georgia's Soil, Plant and Water laboratory for soil pH, texture and macro- and micronutrient levels. Efforts were made to distribute sampling locations for both canopy photographs and soil cores across the entire plot.

Reproductive traits

Two floral traits were assessed in *B. arachnifera* and *B. lanceolata* populations: flower production (total # flowers/individual) and pollen viability. To test for pollen viability, an anther was removed from three flowers per focal individual. Pollen grains were dyed with Alexander's stain and evaluated under a compound microscope according to the criteria in Alexander (1980). Three hundred pollen grains per flower were scored using multiple fields per slide. Viability percentage was reported as the average number of viable pollen grains for each individual (3 flowers/individual).

Approximately six weeks after flowering commenced, % pod initiation was determined as the number of developing pods divided by total flower production. Total flower production values were reduced by three to account for flowers destructively sampled for pollen viability. Once pods were mature, several pod and seed traits were measured. Plants were censused for mature pod production (total mature pods/individual), and the presence of weevil exit holes and/or other forms of exterior pod damage also were noted. Pod damage was calculated for each individual plant as the proportion of mature pods with visible pod damage.

Up to five pods were collected from each focal individual for seed and pod measurements. Reproductive failure, however, prevented further analysis of certain plants. Each pod was evaluated for exterior pod damage and the presence of seed predators. Seed production (total # intact seeds/pod), seed abortion (%), seed weight (mg), and pod volume (cm^3) were recorded for each pod and then averaged for each focal individual. Seed abortion measurements included all unfertilized ovules and partially developed seeds; these structures were noticeably smaller than mature seeds. Since *Baptisia* pods are shaped approximately like two adjacent cones, pod volume was calculated as: $2[(1/3\pi)*(W2)*(0.5\ L)]$, where W and L represent pod width and length, respectively. We analyzed data only from undamaged pods in order to exclude the negative effect of pod damage on particular seed measurements. Finally, cumulative fitness (mean # intact seeds/individual) was calculated as: (total # flower/individual) x (# developing pods/ total # flower) x (# undamaged pods/ total mature pods) x (mean # intact seeds/undamaged pod).

Data were analyzed using a nested analysis of variance (ANOVA) (SAS Institute, 1999; PROC GLM) to ascertain species and population effects. Response variables with significant p values were further evaluated using the Tukey-Kramer adjustment for multiple comparisons (SAS Institute, 1999). Several response variables had to be transformed to meet normality assumptions for statistical analyses. Flower production was log-transformed, whereas pod production and cumulative fitness were log x + 1 transformed in order to include individuals with no mature pod production (reproductive failure).

For the heat shock experiment, *B. arachnifera* and *B. lanceolata* seeds collected for the study of reproductive traits were pooled by species. Additional pods from non-focal individuals within the study plots were also collected to increase available seed numbers. Three replicates of

20 seeds per species were subjected to one of six heat treatments in a laboratory drying oven: no heat control, 60 °C, 70°C, 80°C, 90°C and 100°C. All heat treatments lasted for four minutes. The duration of heat exposure and range of temperatures were selected based on previous studies documenting conditions near the soil surface during prescribed burns (Heyward, 1938; Tozer, 1998; Iverson and Hutchinson, 2002; Sullivan et al., 2003).

Following heat treatments, seeds from each replicate were placed in an individual Ziploc bag with a moist paper towel. Since imbibed *Baptisia* seeds were found to be prone to fungal growth, Captan fungicide solution was applied immediately after seeds were subjected to their respective heat treatments; an additional no heat, no fungicide treatment was created to control for the effect of fungicide application. Bags were placed in a greenhouse and randomly repositioned on a weekly basis. Germination under greenhouse conditions was monitored every other day for three weeks. Seeds were classified as germinated, dormant or rotten. After three weeks, seed viability of dormant seeds was quantified using the triphenyl tetrazolium chloride (TTC) test (Grabe, 1970). Overall seed viability (%) was calculated as the number of germinants plus the number of viable seeds from the TTC test divided by the total number of seeds. A one-way ANOVA was used to compare overall seed viability between treatments for each species and significant differences were evaluated using Tukey's Honestly Significant Difference (SAS Institute, 1999).

RESULTS

Environmental variables

Baptisia arachnifera populations occurred under a broader range of % canopy openness (26.0 – 100) than *B. lanceolata* (29.1 - 57.7). However, the maximum % canopy openness value for *B. arachnifera* was reduced to 41.3% when the Powerline population, which had no canopy

due to physical maintenance of utility powerlines, was removed from the dataset. *Baptisia arachnifera* was found on soils with a slightly higher percentage of sand than those of *B. lanceolata* (92% vs. 90%). Overall, both *B. arachnifera* and *B. lanceolata* occurred on acidic soil with low nutrients (Table 3.1). At the species level, soil from *B. arachnifera* populations were more acidic ($p = 0.01$) and had higher levels of carbon ($p < 0.0001$) and phosphorous ($p = 0.02$). *Baptisia lanceolata* populations were typically located on soil with higher potassium ($p < 0.0001$), magnesium ($p < 0.0001$), manganese ($p < 0.0001$) and zinc ($p = 0.002$). Soil nutrient levels were also significantly different at the population level (Table 3.1).

Reproductive traits

While total flower production was similar between species, there were significant differences between populations nested within species (Table 3.2). The Powerline and General Coffee S.P. populations produced significantly more flowers per plant than other populations of *B. arachnifera* and *B. lanceolata*, respectively. Both *Baptisia* species had comparable levels of pollen viability, with mean values ranging from 94.9% (Moody Forest) to 97.6% (Browntown Road; Table 3.2).

Significant differences in pod initiation (%) were apparent only between populations nested within species ($p < 0.0001$) (Table 3.2). In particular, *B. arachnifera* individuals at the Wire Road population were most successful at converting flowers into developing pods. This trend remained consistent over time as the Wire Road population also had significantly higher mature pod production than any other population of either species (Table 3.2). Accompanying this improvement in pod production, however, was a significant increase in pod damage *in B. arachnifera* ($p < 0.001$). Over half (54%) of the pods on *B. arachnifera* individuals had evidence

of pod damage, whereas only 26% of *B. lanceolata* pods were compromised (Table 3.2). There was no significant difference in pod damage between populations nested within species ($p = 0.5$).

Baptisia arachnifera pods were smaller and contained fewer mature seeds than those of *Baptisia lanceolata* (Table 3.3). Both traits were significantly different at the species ($p < 0.0001$) and population nested within species ($p < 0.0001$) levels. *Baptisia arachnifera* seeds were significantly heavier than *B. lanceolata* seeds ($p < 0.002$). While not significant, Wire Road and Moody Forest populations tended to have higher seed abortion (%) than other *B. arachnifera* and *B. lanceolata* populations.

Cumulative fitness was not significantly different between species ($p = 0.18$), however there were distinct patterns among populations nested within species ($p = 0.03$; Figure 3.1). Rayonier, the population with the lowest cumulative fitness, also had the highest percentage of focal plants experiencing reproductive failure, with 6 out of 16 flowering individuals (38%) producing no mature pods. Other populations had either one (Wire Road, Gen Coffee S.P.), two (Moody Forest), or three (Browntown Road) focal individuals completely lacking mature pods.

Finally, our heat shock experiment results showed that seeds from the rare and common *Baptisia* species had markedly different responses to high temperatures (Fig 3.2a-b). *Baptisia arachnifera* seeds tolerated a narrower range of temperatures, with overall seed viability steadily decreasing at temperatures above 60°C. In contrast, approximately 40% of *B. lanceolata* seeds consistently remained viable at all tested temperatures. The number of germinated seeds was also variable between species. A total of 108 *B. arachnifera* seeds germinated in all treatments up to 80°C, of which 40% (43/108) germinated in both controls (i.e., without scarification). Only 5 *B. lanceolata* seeds germinated at 80°C and in the two controls.

DISCUSSION

Environmental variables

Habitat specificity is thought to be an important cause of rarity, especially in endemic species with restricted distributions (Rabinowitz, 1981; Kruckeberg and Rabinowitz, 1985). Nonetheless, only a handful of the numerous rare-common comparisons have quantified differences in environmental variables (Hodgson, 1986; Baskin et al., 1997; Witkowski and Lamont, 1997; Walck et al., 2001; Lavergne et al., 2004). Surprisingly, these comparative studies often found little difference in environmental conditions under which rare vs. common species occur, leading to the speculation that evolutionary and/or historical factors may have a larger bearing on species abundance patterns. In the present study, the environmental conditions under which the species grew also were quite similar. Both species occurred on acidic, sandy soils with variable levels of micronutrients. While most soil nutrients were found to be significantly different at the species level, these results are questionable as they appear to be driven by noticeably elevated levels in one population. Since *B. arachnifera* has historically been found only within a small portion of the lower Coastal Plain, Faircloth (1987) postulated that edaphic factors might be driving this species' endemism. In our study, one notable difference in edaphic conditions between species was that *B. arachnifera* occurs on soil with almost an order of magnitude lower level of manganese than *B. lanceolata*, suggesting that the former has a low tolerance for the micronutrient. Indeed, manganese toxicity tends to be more pronounced on acidic soils in warm climates (Reisenauer, 1988; Smith and Paterson, 1995). Greenhouse experiments and more intensive soil sampling throughout *B. arachnifera*'s distribution, however, would be needed to substantiate this observation.

Reproductive traits

Flower production and pollen viability were comparable in *Baptisia arachnifera* and *B. lanceolata*. This lack of difference in total flower production is contrary to most rare-common comparisons, which characterize rare species as having fewer flowers (Mehroff, 1983; Fiedler, 1987; Murray and Westoby, 2000; Lavergne et al., 2004; but see Burne et al., 2003). Pollen viability was unanimously high in populations of both *Baptisia* species. Mehroff (1983) also found that rare and common orchid species had no significant difference in pollen viability. In contrast, other rare-common comparisons report that rare species often have at least one population with greatly reduced pollen viability (Banks, 1980; Burne et al., 2003). Combined, the floral traits investigated here do not appear to be limiting the reproductive success of *B. arachnifera*. However, other aspects of *Baptisia* life history directly related to floral traits merit future study. Different combinations of breeding systems and growth habit can strongly influence interpretations of the relationship between reproductive biology and rarity (Giblin and Hamilton, 1999). While the breeding systems of *B. arachnifera* and *B. lanceolata* have never been directly quantified, there is some preliminary evidence regarding their nature. Ceska et al. (1997) proposed that *B. arachnifera* populations were predominately outcrossing due to their being in Hardy-Weinberg equilibrium. In contrast, recent allozyme data suggest that *B. lanceolata* populations in Georgia and South Carolina experience moderate levels of selfing (Chapter 4).

Flower abortion, perhaps as a result of pollinator and/or resource limitation, led to substantial reductions in reproduction potential of both *Baptisia* species. On average, only 37% and 28% of flowers on *B. arachnifera* and *B. lanceolata* plants, respectively, initiated pod development. The higher overall level in pod initiation in *B. arachnifera* is due to the high

success of one population (Wire Road), in which over 60% of flowers began developing into pods. All other populations of both species had similar pod initiation (16-36%). The production of surplus flowers is a common phenomenon in plants (e.g., Stephenson, 1981). The ensuing low fruit:flower ratios have been hypothesized to be the result of five non-exclusive mechanisms: pollen limitation, pollinator attraction, bet hedging, selective abortion and increased male fitness via pollen donation (Sutherland, 1987). Additional experiments would be needed to discern which mechanism(s) are most important for our study species. Extremely low pod initiation (9.8%) has been observed in another *Baptisia* species, *B. leucophaea* (Haddock and Chaplin, 1982) as well as several other legume species (< 10%; Stephenson, 1981).

Not unlike the rare-common patterns reported for flower production, mature pod production and pod set are expected to be reduced in rare plants (Fiedler, 1987; Young and Brown, 1998; Brown et al., 2003; Burne et al., 2003; but see Mehroff, 1983). We observed no significant difference in pod production at the species level; however, there were striking differences among populations nested within species. Specifically, the two *B. arachnifera* populations monitored for the full duration of the study possessed both the lowest (Rayonier) and highest (Wire Road) mean pod production values. This disparity in fecundity was also reflected in the finding that reproductive failure was more prominent in Rayonier plants than those in Wire Road (38% vs. 5%).

Evaluation of several seed traits provided the greatest insight into potential differences between *B. arachnifera* and *B. lanceolata*. Pods from the endemic *B. arachnifera* contained significantly fewer mature seeds than those of *B. lanceolata.* The majority of studies compiled in Murray et al. (2002), as well as more recent ones (Mabry, 2004; Lavergne et al., 2004), support the generalization that narrowly-restricted species produce fewer seed than common

species. Reduced seed production in rare species is thought to be a consequence of pollinator limitation, self-incompatibility or inbreeding depression in small populations (Giblin and Hamilton, 1999). In the case of *Baptisia arachnifera*, the relatively low number of intact seeds relative to *B. lanceolata* might also be partially due to the fact that pods are substantially smaller than those of *B. lanceolata*. Unlike seed production, the relationship between seed weight and rarity is inconsistent (Murray et al., 2002). We found, in conjunction with the observed lower seed production, that *B. arachnifera* seeds typically weigh more than *B. lanceolata* seeds. This finding supports the commonly held notion that plants can compensate for low seed production by producing heavier seeds (e.g., Primack, 1987). Such an evolutionary trade-off provides a dispersal advantage to species with high seed production, whereas those that produce heavy seeds have more reserves to help withstand unpredictable hazards (e.g., drought, competition) (Westoby et al., 2002). Finally, there was no significant difference in seed abortion between the rare and common *Baptisia* species. The few rare-common comparisons that have examined seed abortion have also reported mixed results (Murray and Westoby, 2000; Brown et al., 2003; Simon and Hay, 2003).

Our heat shock experiment revealed that *B. arachnifera* and *B. lanceolata* seeds tolerated dissimilar ranges of high temperatures, with the former having a narrower tolerance range. Similarly, previous heat shock experiments have documented species-specific responses in other legumes (Martin et al., 1975; Auld and O'Connell, 1991; Baskin and Baskin, 1998). Brown et al. (2003) propose that rare species possess a narrower regeneration niche (i.e., more specific heat requirements for germination) that, when coupled with intrinsically variable fire conditions, can contribute to species having limited distributions. As a result of habitat fragmentation, many fire-dependent communities, including longleaf pine forests, are maintained by prescribed burns

in lieu of natural fire events (Hiers et al., 2000). Such fire regimes are of utmost concern for the persistence of *B. arachnifera* because this species occurs almost exclusively on land currently managed for pine plantations (U.S. Fish and Wildlife Service, 1984; Ceska et al., 1997). Prescribed burns in longleaf pine forests typically occur between December and April (Hiers et al., 2000). Our data suggest that *B. arachnifera* propagules might not fare well during late spring or summer burns, when elevated ambient temperatures and duration of sunlight might cause soil temperatures to exceed tolerable levels.

One unexpected finding from the heat shock experiment was the high number of *B. arachnifera* seeds that germinated in the unheated control treatments. Legumes often require some mechanism (e.g., scarification, fluctuating temperatures) to break down the hard seed coat prior to germination (Baskin and Baskin, 1989; Degreef et al., 2002, sources cited therein). However, another researcher independently collected mature seeds from *B. arachnifera* populations in 2004 and reported successful germination of seeds that had only been soaked in water overnight (J. Pascarella, personal communication). As such, it is possible that *B. arachnifera* seeds may be capable of germinating in the field prior to the onset of winter conditions. A previous attempt to document *B. arachnifera* field germination monitored populations only in the spring and summer, and reported finding no seedlings (Humphrey, 1988). Given the overall low number of *B. lanceolata* germinants obtained in this study, it is hard to assess whether *B. lanceolata* may also be capable of germinating in the late fall.

Pod damage, which includes the effects of predispersal seed predation, is an extrinsic factor that could limit reproductive success via decreased viable seed production. In recent years, there have been more studies investigating the role of predispersal seed predation in rare plant dynamics (Menges et al., 1986; Hegazy and Eesa, 1991; Bevill et al., 1999; Kaye, 1999;

Vickery, 2002). No trend exists within the rare-common literature as there are reports of rare species experiencing increased (Brown et al., 2003), decreased (Brown et al., 2003; Simon and Hay, 2003) or no difference (Witkowski and Lamont, 1997; Walck et al., 2001) in predispersal seed predation levels relative to common species. Predispersal seed predation is prominent in many *Baptisia* species (Frost, 1945; U.S. Fish and Wildlife Service, 1984; Evans et al., 1989; Haddock and Chaplin, 1982; Horn and Hanula 2004). We found that at the species level *B. arachnifera* individuals had, on average, twice the amount of pod damage as *B. lanceolata* individuals. Our pod damage measurements, however, did not distinguish between damage caused by seed predators (weevils) and other herbivory on reproductive structures. Nonetheless, the amplified pod damage experienced by *B. arachnifera* could still have significant repercussions on reproductive success by providing an additional source of seed loss and increasing exposure of remaining seeds to seed pathogens. *Baptisia arachnifera* seeds have been previously reported to be susceptible to attack from *Fusarium* species (Handaly, 1997). Finally, it is interesting to note that there is experimental evidence that prescribed burns can decrease predispersal seed predation intensity (Mejeur, 1998; Vickery, 2002). For example, Vickery (2002) found that recent (within 12 months) prescribed burns significantly decreased seed predation intensity in populations of a rare grassland perennial, *Liatris scariosa* var. *novae-angliae*. Since prescribed burns are integral to the management of both *Baptisia* species, it would be valuable to determine whether prescribed burns can also alter predispersal seed predation intensity in these species.

Finally, cumulative fitness, which took into account the low pod initiation rate and high extent of pod damage, was used as an overall indicator of reproductive success in *B. arachnifera* and *B. lanceolata*. Counter to generalizations that rare species have reduced fecundity (Fiedler

and Ahouse, 1992; Gaston and Kunin, 1997), our data suggest that there is no significant difference in overall fecundity between *B. arachnifera* and *B. lanceolata*. Cumulative fitness of the Wire Road *B. arachnifera* population was comparable to two *B. lanceolata* populations, with all three populations producing, on average, between 40 – 71 seeds per individual. Individuals in the other *B. arachnifera* population (Rayonier), however, typically produced only 7 seeds per plant. Again, this reinforces other findings that indicate that Rayonier was not a reproductively successful population in 2004.

When evaluated at the species level, very few reproductive traits were found to be significantly different between the rare *B. arachnifera* and its widespread congener*, B. lanceolata*. Additionally, the loss of one *B. arachnifera* population to mowing meant we could monitor only two populations for the full course of the study. These two populations were dramatically different. Wire Road was comparable to *B. lanceolata* in many traits whereas Rayonier had the lowest reproductive potential of all populations. Therefore, more *B. arachnifera* populations need to be studied to determine whether Rayonier or Wire Road is more characteristic of *B. arachnifera* in terms of reproductive traits.

If reproductive traits are not largely responsible for the rarity status of *B. arachnifera*, why then does this species have such a restricted distribution (16 km)? Other studies that comprehensively compared traits of restricted and widespread congeners have speculated that restricted distribution is most likely the result of a relatively recent speciation event, or neo-endemism (Witkowski and Lamont, 1997; Walck et al., 2001). Poor colonization ability, through decreased seed production and different soil seed bank strategies, can also impair a species' ability to expand its range (Walck et al., 2001). Although further studies would clearly be needed to document phylogenetic trends, it is possible that *B. arachnifera* arose from another

simple-leaved *Baptisia*, *B. perfoliata*, which occurs in southern Georgia. Our findings that *B. arachnifera* produced fewer, heavier seeds than *B. lanceolata*, as well as experienced increased pod damage, provide some evidence that reduced colonization ability could additionally be limiting the distribution of *B. arachnifera*. Finally, management practices, such as harvesting and site preparation on pine plantations, are a contemporary factor making *B. arachnifera* populations increasingly vulnerable to extinction.

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Table 3.1. Soil characteristics of *Baptisia arachnifera* (rare) and *Baptisia lanceolata* (common) populations in south Georgia. Values represent mean ± SE. Within columns, values with same superscripts were not significantly different at $\alpha = 0.05$ (Tukey-Kramer adjustment). Traits that were significantly different at the species level ($p < 0.05$) are indicated with an asterisk.

Population	Soil pH	C (%)	N (%)	Ca (g/m^2)	K (g/m^2)	Mg (g/m^2)	P (g/m^2)	Mn (g/m^2)	Zn (g/m^2)
B. arachnifera									
Powerline	4.1 ± 0.0 ^{a}	0.6 ± 0.1 ^{d}	0.02 ± 0.00 ^{a}	4.5 ± 1.2 ^{b}	1.8 ± 0.1 ^{bc}	0.4 ± 0.1 ^{a}	0.6 ± 0.1 ^{b}	0.02 ± 0.01 ^{a}	0.3 ± 0.0 ^{a}
Rayonier	4.1 ± 0.0 ^{a}	0.5 ± 0.1 ^{cd}	0.02 ± 0.00 ^{a}	1.8 ± 0.2 ^{a}	0.9 ± 0.1 ^{ab}	0.4 ± 0.1 ^{a}	0.5 ± 0.0 ^{ab}	0.01 ± 0.00 ^{a}	0.2 ± 0.0 ^{a}
Wire Rd	4.2 ± 0.0 ^{ab}	0.4 ± 0.0 ^{bc}	0.01 ± 0.00 ^{a}	1.8 ± 0.4 ^{a}	0.8 ± 0.1 ^{a}	0.2 ± 0.1 ^{a}	0.4 ± 0.1 ^{a}	0.02 ± 0.01 ^{a}	0.2 ± 0.0 ^{a}
Mean	**4.1 ± 0.0** *	**0.5 ± 0.0** *	**0.02 ± 0.00**	**2.7 ± 0.5**	**1.2 ± 0.1** *	**0.3 ± 0.1** *	**0.5 ± 0.1** *	**0.02 ± 0.00** *	**0.2 ± 0.0** *
B. lanceolata									
Browntown Road	4.2 ± 0.0 ^{ab}	0.2 ± 0.0 ^{ab}	0.01 ± 0.00 ^{a}	1.5 ± 0.3 ^{a}	1.4 ± 0.0 ^{bc}	0.2 ± 0.1 ^{a}	0.5 ± 0.1 ^{ab}	0.1 ± 0.1 ^{a}	0.5 ± 0.1 ^{b}
Gen. Coffee S.P.	4.3 ± 0.0 ^{b}	0.2 ± 0.0 ^{a}	0.01 ± 0.00 ^{a}	1.8 ± 0.3 ^{a}	1.5 ± 0.1 ^{c}	0.5 ± 0.2 ^{a}	0.3 ± 0.0 ^{a}	1.0 ± 0.2 ^{b}	0.2 ± 0.0 ^{a}
Moody Forest	4.1 ± 0.1 ^{a}	0.3 ± 0.0 ^{ac}	0.01 ± 0.00 ^{a}	6.2 ± 0.4 ^{b}	2.3 ± 0.1 ^{d}	6.3 ± 0.9 ^{b}	0.3 ± 0.0 ^{a}	0.4 ± 0.1 ^{a}	0.2 ± 0.0 ^{a}
Mean	**4.2 ± 0.0**	**0.3 ± 0.0**	**0.01 ± 0.00**	**3.2 ± 0.6**	**1.7 ± 0.1**	**2.3 ± 0.8**	**0.4 ± 0.0**	**0.5 ± 0.1**	**0.3 ± 0.0**

Table 3.2. Comparison of *Baptisia arachnifera* (rare) and *Baptisia lanceolata* (common) floral and pod traits. Values represent mean ± SE. Sample size is in parenthesis. Incomplete data are presented for Powerline (*B. arachnifera*) due to mowing of population during the course of study. Within columns, values with same superscripts were not significantly different at $\alpha = 0.05$ (Tukey-Kramer adjustment). Certain data were transformed for ANOVA (see text). Traits that were significantly different at the species level ($p < 0.05$) are indicated with an asterisk.

Population	Flower Production/Plant	% Pollen Viability	% Pod Initiation	Pod Production/Plant	% Pod Damage
B. arachnifera					
Powerline	108.3 ± 16.1 [c] (20)	95.8 ± 0.0 [a] (20)	27.7 ± 0.0 [a] (20)	—	—
Rayonier	41.6 ± 4.8 [ab] (16)	95.6 ± 0.0 [a] (16)	16.0 ± 4.5 [a] (16)	4.4 ± 1.3 [a] (10)	59.8 ± 9.9 [a] (10)
Wire Road	55.2 ± 8.7 [ab] (20)	96.7 ± 0.0 [a] (20)	63.9 ± 4.8 [b] (20)	30.4 ± 7.1 [b] (19)	48.5 ± 6.5 [a] (19)
Mean	**70.3 ± 7.6**	**96.1 ± 0.6**	**37.3 ± 3.7**	**18.8 ± 4.5**	**52.4 ± 5.5** *
B. lanceolata					
Browntown Road	43.2 ± 6.3 [a] (20)	97.6 ± 0.0 [a] (20)	31.3 ± 6.5 [a] (20)	10.6 ± 2.9 [a] (17)	31.9 ± 9.0 [ab] (17)
Gen. Coffee S.P.	95.2 ± 15.0 [bc] (20)	96.9 ± 0.0 [a] (20)	21.2 ± 4.9 [a] (20)	16.8 ± 5.9 [ab] (19)	29.3 ± 8.0 [ab] (19)
Moody Forest	38.2 ± 4.6 [a] (20)	94.9 ± 0.0 [a] (20)	31.9 ± 5.4 [a] (20)	9.3 ± 2.0 [ab] (18)	17.9 ± 6.5 [b] (18)
Mean	**58.8 ± 6.5**	**96.5 ± 0.6**	**28.1 ± 3.3**	**12.2 ± 2.3**	**26.3 ± 4.5**

Table 3.3. Comparison of *Baptisia arachnifera* (rare) and *Baptisia lanceolata* (common) seed traits from undamaged pods. Values represent mean ± SE. Within columns, values with same superscripts were not significantly different at $\alpha = 0.05$ (Tukey-Kramer adjustment). Traits that were significantly different at the species level ($p < 0.05$) are indicated with an asterisk.

Population	N	Seed Production (# seeds/pod)	% Seed Abortion	Seed Weight (mg)	Pod Volume (cm^3)
B. arachnifera					
Rayonier	6	1.0 ± 0.2 [a]	25.8 ± 11.5 [a]	15.2 ± 2.1 [b]	0.6 ± 0.1 [a]
Wire Road	17	2.4 ± 0.3 [a]	46.1 ± 6.8 [a]	10.4 ± 0.5 [ab]	0.7 ± 0.0 [a]
Mean	**23**	**2.0 ± 0.3** [*]	**40.8 ± 6.0**	**11.7 ± 0.8** [*]	**0.7 ± 0.0** [*]
B. lanceolata					
Browntown Road	13	7.2 ± 1.1 [c]	24.1 ± 6.2 [a]	8.7 ± 0.9 [a]	3.5 ± 0.3 [b]
Gen. Coffee S.P.	9	6.3 ± 1.3 [bc]	19.9 ± 8.2 [a]	9.9 ± 1.5 [ab]	3.2 ± 0.3 [b]
Moody Forest	16	3.5 ± 0.8 [ab]	42.3 ± 7.5 [a]	8.6 ± 1.2 [a]	1.9 ± 0.2 [c]
Mean	**38**	**5.4 ± 0.6**	**30.7 ± 4.5**	**9.0 ± 0.7**	**2.8 ± 0.2**

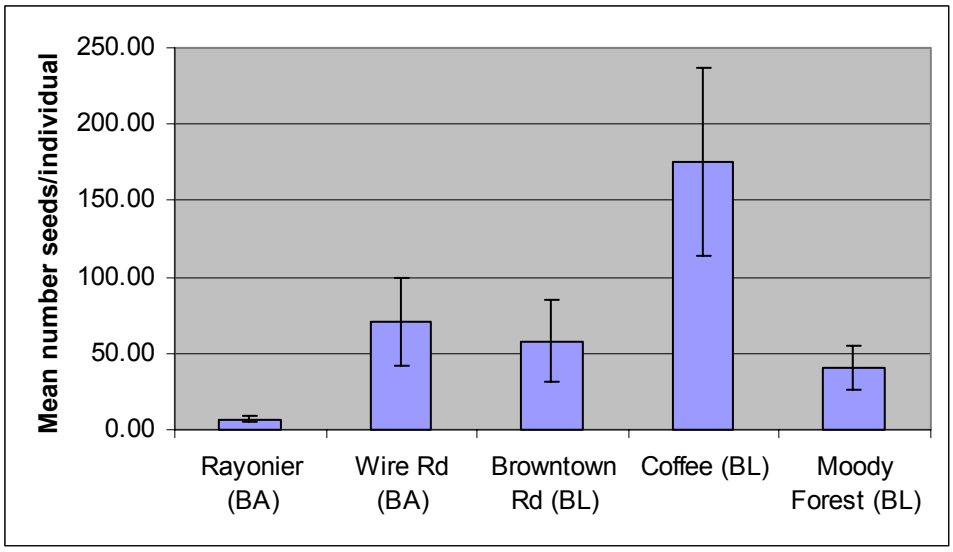
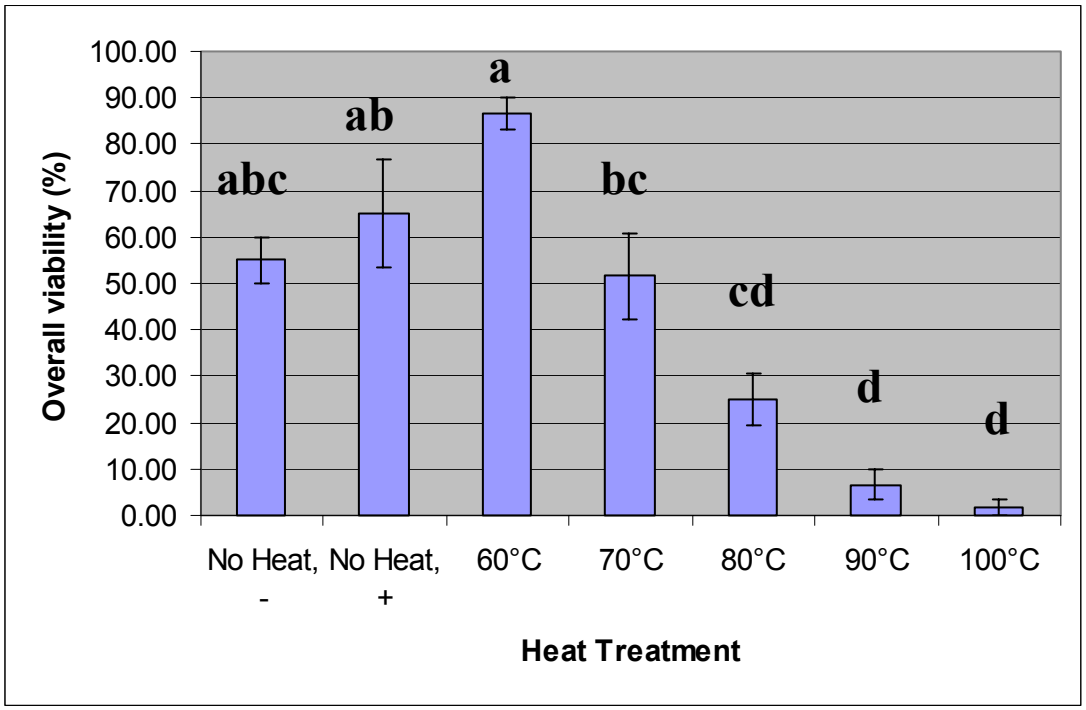


Figure 3.1. Mean cumulative fitness in populations of *Baptisia arachnifera* (rare) and *Baptisia lanceolata* (common). Bars represent mean $\pm$ SE.

a)



b)

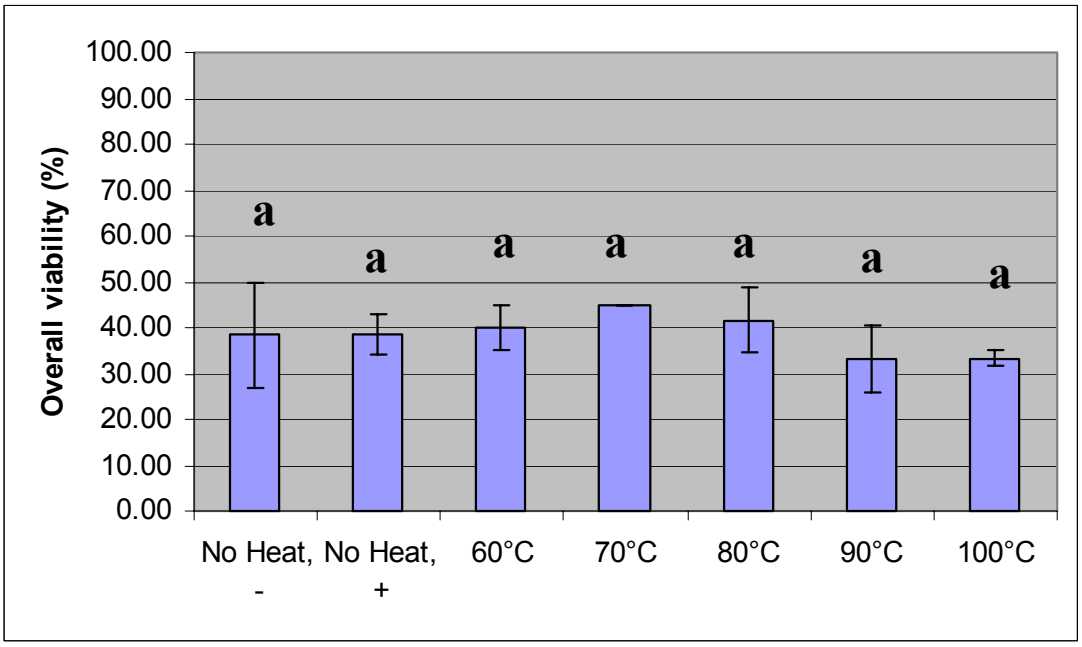


Figure 3.2. Overall seed viability (%) in a) *Baptisia arachnifera* and b) *Baptisia lanceolata* after four minute exposure to heat treatment. Bars represent mean ± SE. Treatments with the same letters were not significantly different at $\alpha = 0.05$ (Tukey's Honestly Significant Difference).

CHAPTER 4

AN EVALUATION OF REPRODUCTIVE AND GENETIC TRAITS IN CENTRAL AND PERIPHERAL POPULATIONS OF *BAPTISIA LANCEOLATA*[3]

[3] Squire, A.R., S. Foré and R. R. Sharitz. To be submitted to *American Journal of Botany*.

INTRODUCTION

Peripheral populations, those that are geographically separated and/or face different environmental conditions from more central populations (Lesica and Allendorf, 1995), remain poorly understood in conservation biology. Species abundance and habitat quality are expected to decrease with increased proximity to the edge of a species' distribution (Lawton, 1993; Mace and Kershaw, 1997; Brown and Lomolino, 1998). Predicted range contractions of endangered species have led to conservation efforts placing increased emphasis on maintaining central (i.e., those more likely to persist) rather than peripheral populations (Wolf et al., 1996). Contrary to this, Channell and Lomolino (2000) reported that 91 endangered species occur only at the edges of their historical distributions, illustrating the need to reassess the role of peripheral population in reserve selection.

Understanding how genetic variation is partitioned is considered an essential component of conservation biology (Godt and Hamrick, 2001) and can influence whether a given population is preserved. It is often assumed that peripheral populations have reduced genetic variation compared to those in the center of a species' range. Mechanisms by which peripheral populations can lose genetic diversity include amplified genetic drift (Nei et al., 1975; Soulé, 1973; Ellstrand and Elam, 1993) and inbreeding (Ellstrand and Elam, 1993; Lienert et al., 2002) in small populations. Empirical studies have found evidence that supports (e.g., Linhart and Premoli, 1994; Bruederle, 1999; Lammi et al., 1999) as well as contradicts (e.g., Schiemann et al., 2000; Faivre and Windus, 2002; Van Rossum et al., 2003) the notion that peripheral populations are genetically depauperate. Similarly, there is no consensus about relative levels of genetic variation in species with restricted (rare) versus widespread (common) distributions (reviewed in Gitzendanner and Soltis, 2000; Cole, 2003). While peripheral populations may be

predisposed to lower amounts of genetic variation, there are also factors that merit their preservation. Peripheral populations have been acknowledged as sources of genetic diversity through the possession of unique alleles (e.g., Hunter and Hutchinson, 1994). Additionally, differential selective forces at the edge of a species' distribution may lead to future speciation events (Lesica and Allendorf, 1995).

The aspect of peripheral populations most in need of reconciliation, however, is their influence on conservation classification systems at the regional level. Formal assessments of threatened species, such as the NatureServe system, are designed to prioritize protection of species based on severity of extinction risk (Master, 1991; Given, 1994). While NatureServe focuses on global rankings of species, individual states also determine their own conservation status by assessing the number of subpopulations and potential threats to a given species within their region (Master, 1991). It is not uncommon for species to be classified as both rare and secure in different parts of their ranges (e.g., Kartesz, 1981; Edwards and Weakley, 2001). These "apparently rare" species (Rodrigues and Gaston, 2002) often result from geopolitical boundaries coinciding with the periphery of a species' distribution. Thus, species become interpreted as rare when evaluated at a narrower, regional scale (Hunter and Hutchinson, 1994; Lesica and Allendorf, 1995; Bruederle, 1999).

Baptisia lanceolata (Walt.) Ell is a long-lived perennial legume found within the Coastal Plain region of the southeastern United States. According to the NatureServe ranking system, *B. lanceolata* is considered "apparently secure" overall (G4), with a similar rank in Georgia (S4) and unranked in South Carolina (SNR; NatureServe webpage). However, it is considered a "species of concern" in South Carolina due to its presence in only two counties (Knox and Sharitz 1990; South Carolina Department of Natural Resources webpage). We compared a suite

of reproductive traits in central (GA) and peripheral (SC) *B. lanceolata* populations to test the null hypothesis that there are no significant differences between plants growing in these neighboring states. In addition, allozyme data were used to analyze genetic diversity and structure at regional (state) and local (population) scales. We hypothesized that peripheral populations would have reduced genetic variation. If there was indeed a reduction in variation between regions, we expected to find high genetic differentiation among populations due to the combined effects of genetic drift, inbreeding and/or founder effects.

MATERIALS AND METHODS

Study species and site description

Baptisia lanceolata (Walt.) Ell. is a polycarpic, perennial legume that grows in sandhills, dry pine woodlands, and along roadsides within the Coastal Plain region of the southeastern United States (Larisey, 1940; Isley, 1990). The center of its distribution occurs in Georgia (Figure 1) with populations extending into South Carolina, Alabama and northern Florida. Individuals have a spherical, shrubby appearance. Flowers are bright yellow and are either axillary or arranged in terminal racemes of several flowers (Isley, 1981). Flowering typically commences in late March and early April, with mature seed pods first present in early summer. Say's weevil (*Apion rostrum*) and an unidentified lepidoteran pest are two insects previously reported to feed on the reproductive structures of *B. lanceolata* (Mehlman, 1993b; Horn and Hanula, 2004; Schnabel and Sharitz, unpublished data).

Three *B. lanceolata* populations each were sampled in Georgia and South Carolina (Table 4.1). Once populations were located, plots between 900 (30 x 30) and 1600 (40 x 40) square meters in size were established in order to obtain 20 focal individuals. To qualify, focal individuals had to be flowering and at least 1 m distant from another *B. lanceolata* plant since *B.*

lanceolata possesses a rhizomatous rootstock (Larisey, 1940; Mehlman, 1993b) and is thought to be clonal to some extent. Although the plot size was selected to capture approximately 20 focal individuals, there were sometimes more than 20 *B. lanceolata* plants that met these qualifications; emphasis was then placed on randomly selecting acceptable plants across the entire plot. Two peripheral populations had fewer than 20 individuals that met these criteria (Table 4.1) and therefore all acceptable plants were used.

Environmental variables

Canopy openness, soil nutrient and texture were measured to determine if there were any distinct habitat differences between central and peripheral populations. Percent canopy openness was assessed using 10 hemispherical canopy photographs per population, which were interpreted using Gap Light Analyzer (GLA v 2.0; Frazer et al., 2000). Five soil samples per population were compiled by randomly pooling together five sets of three soil cores. Cores were 0.75 inches wide and driven approximately 2 feet into the ground. Soil samples were analyzed by the University of Georgia's Soil, Plant and Water laboratory for soil pH, texture, and macro- and micronutrient levels. Efforts were made to distribute sampling locations for both canopy photographs and soil cores across the entire plot.

Reproductive traits

Focal *B. lanceolata* individuals were tracked from April – August 2004. Flower production was the total number of flowers produced/individual. Approximately six weeks after flowering commenced, pod initiation and abortion were assessed. Pod initiation was calculated as the number of pods initiated divided by total flower production. In central populations, total flower production values used to calculate pod initiation were reduced by three in order to account for flowers destructively sampled for pollen viability (see Chapter 3). Pod abortion data

were not included in this analysis as we were unable to differentiate between unpollinated flowers and pods aborted at an early stage. Several months after flowering, individuals were censused for total mature pod production. At this time the presence of weevil exit holes and/or other forms of exterior pod damage was recorded. Pod damage was calculated for each individual as the proportion of mature pods with visible pod damage relative to total pod production.

Up to five pods were collected from as many focal *B. lanceolata* plants as possible; occasional reproductive failure and low fruit set prohibited collection of pods from all focal plants. Each pod was evaluated for damage and/or presence of seed predators. Say's weevil and an unknown lepidopteran species were the only two observed predators. Pods which were attacked by the lepidopteran always had no seeds and were completely filled with silk and frass, whereas pods infested with weevils had at most several intact seeds. To avoid confounding seed measurements with the effect of predation, all damaged pods were removed from the dataset. Seed production (total # intact seeds/pod), seed abortion (%), seed weight (mg), and pod volume (cm^3) were measured from undamaged pods and then averaged for each focal individual. Seed abortion measurements included all unfertilized ovules and partially developed seeds; these structures were noticeably smaller than mature seeds. Since pods were shaped approximately like two adjacent cones, pod volume was calculated as $2[(1/3\pi)*(W^2)*(0.5\ L)]$, where W and L represent pod width and length respectively. Cumulative fitness (mean # intact seeds/individual) was calculated as: (total # flower/individual) x (# developing pods/ total # flower) x (# undamaged pods/ total mature pods) x (mean # intact seeds/undamaged pod). Due to the unequal number of undamaged pods per population, the aforementioned traits were analyzed only at the regional scale (central vs. peripheral).

A nested analysis of variance (ANOVA) was used to analyze the potential effect of regions and populations nested with region for each reproductive trait (SAS Institute, 1999; PROC GLM). Response variables with significant p values were further evaluated using the Tukey-Kramer adjustment for multiple comparisons (SAS Institute, 1999). Two-tailed Student's *t* tests were run for seed traits and pod volume, which could be analyzed only at the regional level due to low sample sizes within populations. Several response variables had to be transformed to meet normality assumptions for statistical analyses. Flower production was log-transformed, whereas pod production and cumulative fitness were $\log x + 1$ transformed in order to include individuals with no mature pod production (reproductive failure).

Genetic analyses

Baptisia lanceolata leaf samples were collected in May 2004 for genetic analyses. The youngest leaf possible was obtained from all 20 focal individuals and up to 10 more plants located within each population. Leaves were individually bagged, labeled and placed on ice. Leaf material was stored at −80°C in the laboratory until shipped on dry ice by overnight express delivery to Truman State University for genetic analysis. Damage in transit caused the subsequent removal of a central population (General Coffee State Park) from the genetics dataset.

Leaf tissue was ground in microbuffer (Werth, 1985) enhanced with 5% PVP-40 and 0.1% 2-mercaptoethanol. Horizontal starch-gel (11% w/v) electrophoresis of allozymes was used to collect genetic data. Preliminary work used all buffers suggested by Ceska et al. (1997) and Clayton and Tretiak buffer (Werth, 1985) to attmpt to resolve the following enzymes: alcohol dehydrogenase, aldolase, aspartate aminotransferase, diaphorase, esterase (colorimetric), glucose-6-phosphate isomerase, isocitrate dehydrogenase, leucine aminopeptidase, malate

dehydrogenase, menadione reductase, phosphoglucomutase, 6-phosphogluconate dehydrogenase, shikimate dehydrogenase, triosephosphate isomerase. Enzymes that were polymorphic and consistently scorable are reported in this study. These enzymes were glucose-6-phosphate isomerase (GPI, E.C. [Enzyme Commission] 5.3.1.9) resolved with buffer 1 (Ceska et al., 1997), aspartate aminotransferase (AAT, E.C. 2.6.1.1) and malate dehydrogenase (ME, E.C. 1.1.1.40) resolved with buffer 2 (Ceska et al., 1997), and malate dehydrogenase (MDH, E.C. 1.1.1.37) and phosphogluconate dehydrogenase (PGDH, E.C.1.1.1.44) resolved with Clayton and Tretiak buffer (Werth, 1985). Stain recipes followed those in Werth (1985).

Genotypes were inferred from stained phenotypes and were scored for each plant. Isozymes and alleles were interpreted based on subunit structure (Kephart, 1990) and scored on the basis of relative mobility (Hickey et al., 1989; Shaklee et al., 1990). An internal standard was included so that relative migration values could be used for initial comparison of alleles from different gel runs. These comparisons were later confirmed by compiling individuals from various runs onto a single gel.

For each population, mean sample size per locus (N), mean number of alleles per locus (A), mean observed heterozygosity (H_o, direct-count estimate), and mean Hardy-Weinberg expected heterozygosity (H_e, unbiased estimate) were computed using BIOSYS-1 (Swofford and Selander, 1981). Significant differences between H_o and H_e within a region, and H_o among all populations, were determined by *t*-tests. Wright's fixation index (*F*) served as another means of assessing whether observed genotypic frequencies met Hardy-Weinberg expectations. A positive *F* value indicates heterozygote deficiency whereas a negative value represents heterozygote excess. Mean F_{IS} was calculated as the inbreeding coefficient for each locus averaged across all populations. Significant differences in fixation for each locus were

determined using the computation, $N(F_{IS})^2$, where N is the total number of individuals in the study, with one degree of freedom in a χ^2 distribution (Baker 1981). To determine fixation at the population level, an additional inbreeding coefficient was calculated for each population [$F^* = (H_e - H_o)/ H_e$] (Wright, 1951).

Chi-square tests were used to determine allozyme frequency differences at both the population and regional level. Bonferroni's procedure was used to adjust for the overall experimental error rate; the overall alpha = 0.05 was divided by the total number of locus comparisons among the regions. The proportion of allozyme variability partitioned among populations (G_{st}) was calculated using GENESTAT (Lewis and Whitkus, 1989). Nei's (1978) unbiased statistic was used to determine genetic identity between regions. Unweighted pair-group method with arithmetic averaging (UPGMA) was used to cluster the populations based on Nei's unbiased genetic identity.

RESULTS

Environmental variables

There were few differences in environmental conditions among the *B. lanceolata* populations, although central populations tended to have more open canopies than their peripheral counterparts (44.1% vs. 38.7% mean canopy openness). Overall, *B. lanceolata* populations in both regions had similar soil characteristics. With the exception of Tennessee Road (peripheral), which was classified as loamy sand, most *B. lanceolata* populations were located on sandy soils. Both central and peripheral *B. lanceolata* populations occurred on highly acidic soils with low carbon and nitrogen levels (Table 4.2). While concentrations of other macro- and micronutrients were largely similar between regions, peripheral populations had significantly higher levels of phosphorous ($p = 0.001$). Magnesium ($p < 0.0001$) and

zinc ($p < 0.001$) were significantly higher in central populations, however, the significance of this finding is likely due to one markedly elevated population (Moody Forest and Browntown Rd, respectively). Soil nutrient levels were also significantly different at the population level (Table 4.2).

Reproductive traits

Flower production was comparable in central and peripheral *B. lanceolata* populations ($p = 0.5$; Table 4.3) when values within a region were combined and regions compared. However, there were significant differences in populations nested within regions (Table 4.3), namely Gen. Coffee S.P. (central) and Road 9 (peripheral) produced more flowers/individual than other populations in the same region. While individuals in central populations had significantly higher pod initiation than those in peripheral populations ($p = 0.01$), the reduction in the latter was primarily due to extremely low pod initiation in Road 9 (Table 4.3). Thus, mature pod production levels were similar between regions ($p = 0.06$; Table 4.3). Reproductive failure, defined as percent flowering individuals with no mature pod production, was higher in peripheral (27%) than central (10%) populations.

There were significant differences in pod damage by insects at both the regional ($p < 0.0001$) and population nested in region ($p = 0.03$) scales (Table 4.3). Overall, individuals in peripheral populations had greater than 2.5 times more pod damage by insects than those in central populations. Although all peripheral populations had high rates of damage, 96% of pods on plants in Road 9 were damaged to some extent (Table 4.3). Additionally, different insects were found to be the primary predator in each region. An evaluation of collected pods with direct evidence of predispersal seed predation (e.g., insect present and/or frass) indicated that

100% of the pods from central populations (N=126) were attacked by weevils. While peripheral populations also had evidence of weevil predation, the majority of damaged pods (55/76) were attacked by an unknown lepidopteran species.

Central *B. lanceolata* populations produced significantly heavier seeds than peripheral populations ($p = 0.03$; Table 4.4). Seed production, seed abortion (%), and volume of undamaged pods were not significantly different between central and peripheral populations (Table 4.4). Comparison of cumulative fitness values indicated that peripheral populations produced, on average, fewer seed/individual than central populations (Table 4.4); however, this difference was not significant ($p = 0.09$).

Genetic analyses

Populations in both regions had similar mean number of alleles per locus (Table 4.5). Browntown Road (central) had significantly reduced observed heterozygosity ($H_{o,}$ direct count) relative to all populations (all values of $t > 2.2$, $df = 10$, $p < 0.01$). Comparisons of H_o and H_e within populations revealed that all populations had significantly lower heterozygosity than Hardy-Weinberg expectations (all values of $t > 3.2$, $df = 10$, $p < 0.01$), with the exception of Kirkland Road (peripheral**).** Nineteen out of 30 fixation indices were positive, suggesting a heterozygotic deficiency in populations (Table 4.6). Analysis of mean F_{IS} values indicated that three loci (AAT, PGDH, ME) had significantly more homozygotes than Hardy-Weinberg expectations in all populations (all values of $\chi^2 > 7.88$, $df = 1$, $p < 0.005$). Similarly, the moderately high F^* values, which ranged from 0.19 – 0.33, suggest an overall excess of homozygotes in *B. lanceolata* populations.

The six putative loci examined were polymorphic in every *B. lanceolata* population (Table 4.7). Of the 16 alleles detected, PGDH-B, MDH2-B, and ME-A were consistently the

most common. While PGDH-C was unique to all peripheral populations, MDH2-C occurred at a low frequency (0.03) in only one central population (Moody Forest). Allele frequency was similar within regions based on valid χ^2 tests (expected values > 1, Lewontin and Felsenstein 1965) obtained for GPI, PGDH, MDH1 and ME. AAT, however, had significantly different frequencies within central populations ($\chi^2 = 16.642$, df = 2, $p < 0.008$). There were no significant differences in allozyme frequencies between regions.

Results suggest that there was little genetic differentiation between all populations (G_{st} = 0.029). Within regions, central populations had slightly more genetic structure between populations (G_{st} =0.06) than did peripheral populations (G_{st} =0.02). It was determined with Nei's (1978) unbiased genetic identity that central populations have higher levels of similarity with peripheral populations than each other (Figure 4.2). One central population (Browntown Road) was identical to two peripheral populations (Tennessee Road, Kirkland Road). Moody Forest was least similar with a genetic identity of 0.955.

DISCUSSION

Baptisia lanceolata was used as a case study to determine whether there was any biological support for state-level conservation classifications, or if some species are considered increasingly at risk as an artifact of the edge of a species' distribution being partitioned by geopolitical borders. Several studies that compared fitness components in central and peripheral populations have reported either a decrease (Grant and Antonovics, 1978; Levin and Clay, 1984) or no difference (Lammi et al., 1999) in reproductive success of individuals in peripheral populations. There is some evidence from the present study that there are significant differences

in reproductive traits between central and peripheral populations of *B. lanceolata*. While populations in both regions were capable of similar levels of flower, pod, and seed production, several factors appear to thwart later stages of reproduction in peripheral populations.

Peripheral populations tended to have lower pod initiation. For example, Road 9, which produced an average of 161 flowers per plant, had only 7.3% of its flowers developing into pods. Haddock and Chaplin (1982) attributed low pod initiation (9.8%) in *Baptisia leucophaea* to lack of pollinator activity. In addition to pollinator limitation, two other non-exclusive mechanisms that can limit pod development are resource conservation and selective fruit abortion. Resource conservation theory postulates that late-blooming flowers are less likely to develop into mature fruit because of competition with already developing fruit for limited maternal resources (Stephenson, 1981). Studies with both cultivated and wild *Phaseolus vulgaris* (Nakamura, 1986) and *Prunus mahaleb* (Guitian, 1994) have documented such trends. Selected pod abortion is predicated on the idea that maternal plants can discriminately abscise less vigorous progeny (Janzen, 1977; Lee, 1988; Marshall and Folsom, 1991). Fruits resulting from self pollination have been shown to be differentially aborted when competing with outcrossed fruit for maternal resources (e.g., Vaughton and Carthew, 1993). Alternatively, obligate fruit abortion may occur regardless of resource levels when recessive lethals are produced in inbreeding plants (Wiens, 1984).

While additional experiments would be needed to ascertain the extent and nature of pod abortion in *B. lanceolata*, our allozyme data provide some preliminary evidence that inbreeding may be important in understanding the reproductive ecology of this species. The finding that observed heterozygosity was consistently lower than expected, as well as the high frequency of positive values for Wright's fixation indices, suggests that these populations are in Hardy-

Weinberg disequilibrium. Additionally, all populations had inbreeding coefficient (F^*) values indicative of moderate levels of selfing. The observed excess of homozygotes might also be attributed to clonality, which can influence reproductive success by increasing the likelihood of geitonogamous pollination, or self pollination from flowers on same genet (e.g., Handel, 1985; Nuortila et al., 2002). Although efforts were made not to sample plants that were part of the same clone (see Materials and Methods), the extent to which *B. lanceolata* vegetatively reproduces remains unknown.

Another striking difference between regions was the significantly increased pod damage by insects in peripheral populations. Peripheral populations are often characterized as occurring in stressful, sub-optimal habitats (Lawton, 1993; Mace and Kershaw, 1997). Louda and Collinge (1992) found evidence that environmental stresses within a population can increase insect herbivory levels via decreased plant resistance. No studies to our knowledge, however, have explicitly looked at the relationship between environmental stress and seed predation in the context of peripheral populations. In general, exposure to different abiotic conditions in these regions can ultimately affect plant-insect interactions (Thompson, 1994**).** For example, Evans et al. (1989) attributed seasonal differences in *Baptisia australis* predation levels to weather fluctuations that can alter seed predator population dynamics as well as disrupt the synchrony between predator emergence and flowering period. There is also some evidence that insect herbivory and predation can vary spatially along environmental gradients (e.g., Louda, 1982; Rand, 2002). Overall, we found that central and peripheral *B. lanceolata* populations did not have any striking differences in canopy openness or soil characteristics. However, it is possible that other abiotic factors (e.g., temperature, precipitation) are influencing the observed differential seed predation to some degree. Finally, peripheral populations experienced a

different type of damage than their central counterparts. The unidentified lepidopteran species was unique to peripheral populations and was found in the majority of predated pods (72%). This unknown pest has the potential to be highly detrimental to germination and seedling establishment in these populations because damaged pods were always devoid of seed (Horn and Hanula, 2004; A. Squire, personal observation).

While differences were not statistically significant, reproductive failure and cumulative fitness values suggest that reproduction is ultimately compromised in peripheral populations of *B. lanceolata*. Plants were more prone to reproductive failure in peripheral populations, with a higher percentage of flowering individuals producing no mature pods. According to cumulative fitness calculations, central populations typically produced almost four times as many seed per individual than their peripheral counterparts. This decline in individual fecundity, coupled with the aforementioned insect damage, could limit seedling recruitment and establishment of new populations at the periphery of *B. lanceolata*'s distribution. Other studies have reported dissimilar demographic trends in central and peripheral populations, with the latter typically having higher demographic turnover (Grant and Antonovics, 1978; Johansson, 1993; Lönn and Prentice, 2002). For instance, Johansson (1993) found that peripheral populations of a clonal aquatic plant had higher vegetative recruitment than central populations.

Bearing in mind the low number of resolvable loci obtained in the present study, peripheral populations of *Baptisia lanceolata* did not exhibit any reduction in genetic variation relative to central populations. While this result contradicts our hypothesis, other comparisons of central and peripheral populations have also found no significant difference in genetic variation (e.g., Schiemann et al., 2000; Faivre and Windus, 2002; Van Rossum et al., 2003). *Baptisia* life history traits and evolutionary history may provide insight into why there were no

observable differences in genetic variation between regions. *Baptisia* species possess large rhizomatous rootstocks (Larisey, 1940; U.S. Fish and Wildlife Service, 1984; Mehlman, 1993b) and individuals are thought to live at least 15 years. Longevity of individuals might obscure potential differences in genetic diversity, as the species investigated in Schiemann et al. (2000) and Van Rossum et al. (2003) were also long-lived herbaceous perennials. High gene flow could account for the similar trends in allele frequencies between regions. *Baptisia lanceolata* pollen has the potential for long distance dispersal as bees are the primary pollinators of *Baptisia* species (Haddock and Chaplin, 1982; Evans et al., 1989). While *B. lanceolata* is capable of tumbleweed seed dispersal (Mehlman, 1993a), it appears that most seed does not travel far from the parent plant (K. Madden, personal communication). Therefore, high gene flow between Georgia and South Carolina populations seems unlikely. An alternative explanation is that *Baptisia* as a genus has low levels of variability due to a historical bottleneck. *Baptisia arachnifera*, the only other *Baptisia* species with published genetic data, has low heterozygosity ($H_e = 0.097$) and percent polymorphic loci (24%) (Ceska et al., 1997). The low genetic variation observed in *B. arachnifera*, however, might be a result of its being endemic to a 16 square kilometer area in southeastern Georgia

The lack of genetic structure between all populations ($G_{st} = 0.029$) provides additional evidence that central and peripheral populations of *B. lanceolata* are more genetically similar than previously anticipated. In fact, measures of genetic similarly revealed that central populations appear to be more comparable to peripheral populations than to each other. For example, Moody Forest had the lowest inbreeding coefficient ($F^* = 0.19$) and highest heterozygosity (0.37) of all populations, whereas the values for Browntown Road were at the other extremes. Since Moody Forest is located in a county with no prior record of *B. lanceolata*

occurrences, it is possible that this population is relatively new and this might partially explain the genetic disparities observed within central populations. Nonetheless, it is apparent that more central populations need to be sampled in the future in order to obtain a better idea of genetic trends of *B. lanceolata* in this part of its distribution.

In summary, our observations of decreased pod initiation, coupled with high rates of insect damage and reproductive failure, suggest that peripheral populations of *B. lanceolata* might indeed be more imperiled than those in the center of its distribution. However, long-term monitoring of reproductive and insect damage trends is necessary as these measurements are expected to vary from year to year. Contrary to our expectations, we found no difference in genetic variation and a lack of genetic structure between central and peripheral populations. The inconsistency within the literature regarding peripheral populations and genetic variation suggests that populations at the edge of a species' distribution may not always fit the genetically depauperate scenario. It would be of interest to identify and comprehensively study the species biology of other "apparently rare" species. Do trends within populations of apparently rare species match those of the more traditionally defined geographically and ecologically marginal populations? How do they compare to central populations? While there is no doubt that peripheral populations merit conservation at the state and local levels (Hunter and Hutchinson, 1994; Lesica and Allendorf, 1994; Abbit et al., 2000), it should also be acknowledged that certain plant species might have an inflated state conservation status due to the influence of geopolitical borders.

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Table 4.1. Summary of sampled *Baptisia lanceolata* populations.

Population	Location	# Focal Individuals	Region
Browntown Road (B)	Wayne Co, GA	20	Central
General Coffee State Park (C)	Coffee Co, GA	20	Central
Moody Forest (M)	Appling Co, GA	20	Central
Kirkland Road (K)	Barnwell Co, SC	15	Peripheral
Road 9 (RD)	Barnwell Co, SC	17	Peripheral
Tennessee Road (TN)	Barnwell Co, SC	20	Peripheral

Table 4.2. Soil characteristics in central (GA) and peripheral (SC) *Baptisia lanceolata* populations. Values represent mean ± SE. Within columns, values with same superscripts were not statistically different at $\alpha = 0.05$ (Tukey-Kramer adjustment). Traits that were significantly different at the species level ($p < 0.05$) are indicated with an asterisk.

Population	Soil pH	C (%)	N (%)	Ca (g/m^2)	K (g/m^2)	Mg (g/m^2)	P (g/m^2)	Mn (g/m^2)	Zn (g/m^2)
Central (GA)									
B	4.2 ± 0.0 ^{ab}	0.2 ± 0.0 ^{ab}	0.01 ± 0.00 ^{a}	1.5 ± 0.3 ^{a}	1.4 ± 0.0 ^{a}	0.2 ± 0.1 ^{a}	0.5 ± 0.1 ^{a}	0.1 ± 0.1 ^{a}	0.5 ± 0.1 ^{b}
C	4.3 ± 0.0 ^{b}	0.2 ± 0.0 ^{a}	0.01 ± 0.00 ^{a}	1.8 ± 0.3 ^{a}	1.5 ± 0.1 ^{a}	0.5 ± 0.2 ^{a}	0.3 ± 0.0 ^{a}	1.0 ± 0.2 ^{b}	0.2 ± 0.0 ^{a}
M	4.1 ± 0.1 ^{a}	0.3 ± 0.0 ^{b}	0.01 ± 0.00 ^{a}	6.2 ± 0.4 ^{b}	2.3 ± 0.1 ^{c}	6.3 ± 0.9 ^{b}	0.3 ± 0.0 ^{a}	0.4 ± 0.1 ^{a}	0.2 ± 0.0 ^{a}
Mean	**4.2 ± 0.0**	**0.3 ± 0.0**	**0.01 ± 0.00**	**3.2 ± 0.6**	**1.7 ± 0.1**	**2.3 ± 0.8** *	**0.4 ± 0.0** *	**0.5 ± 0.1**	**0.3 ± 0.0** *
Peripheral (SC)									
K	4.1 ± 0.0 ^{ab}	0.2 ± 0.0 ^{ab}	0.01 ± 0.00 ^{a}	1.8 ± 0.3 ^{a}	1.3 ± 0.0 ^{a}	0.1 ± 0.0 ^{a}	0.6 ± 0.1 ^{a}	0.2 ± 0.0 ^{a}	0.2 ± 0.0 ^{a}
RD	4.2 ± 0.0 ^{ab}	0.2 ± 0.0 ^{ab}	0.01 ± 0.00 ^{a}	5.2 ± 1.1 ^{b}	1.7 ± 0.1 ^{ab}	0.8 ± 0.2 ^{a}	0.7 ± 0.2 ^{a}	1.0 ± 0.2 ^{b}	0.2 ± 0.0 ^{a}
TN	4.1 ± 0.0 ^{ab}	0.3 ± 0.0 ^{ab}	0.01 ± 0.00 ^{a}	2.6 ± 0.5 ^{a}	2.1 ± 0.2 ^{bc}	0.9 ± 0.3 ^{a}	0.4 ± 0.0 ^{a}	0.3 ± 0.0 ^{a}	0.2 ± 0.0 ^{a}
Mean	**4.2 ± 0.0**	**0.2 ± 0.0**	**0.01 ± 0.00**	**3.2 ± 0.6**	**1.7 ± 0.1**	**0.6 ± 0.1**	**0.6 ± 0.1**	**0.5 ± 0.1**	**0.2 ± 0.0**

Table 4.3. Floral and pod traits in central (GA) and peripheral (SC) *Baptisia lanceolata* populations. Values represent mean ± SE. Pod damage sample sizes are in parentheses. Within columns, values with same superscripts were not statistically different at $\alpha = 0.05$ (Tukey-Kramer adjustment). Certain data were transformed for statistical analyses (see text). Traits that were significantly different at the species level ($p < 0.05$) are indicated with an asterisk.

Population	N	Flower Production/Plant	% Pod Initation	Pod Production/Plant	% Pod Damage
Central (GA)					
B	20	43.2 ± 6.3 [a]	31.3 ± 6.5 [b]	10.6 ± 2.9 [a]	31.9 ± 9.0 [ab] (17)
C	20	95.2 ± 15.0 [ab]	21.2 ± 4.9 [ab]	16.8 ± 5.9 [a]	29.3 ± 8.0 [ab] (19)
M	20	38.2 ± 4.6 [a]	31.8 ± 5.4 [b]	9.3 ± 2.0 [a]	17.9 ± 6.5 [a] (18)
Mean	**60**	**58.8 ± 6.5**	**28.1 ± 3.3** *	**12.2 ± 2.3**	**26.3 ± 4.5** *
Peripheral (SC)					
K	15	27.3 ± 4.0 [a]	22.0 ± 5.4 [ab]	4.6 ± 1.8 [a]	59.2 ± 10.5 [bc] (11)
RD	17	161.3 ± 28.8 [b]	7.3 ± 1.5 [a]	11.4 ± 3.2 [a]	95.7 ± 2.2 [c] (11)
TN	20	66.8 ± 11.5 [a]	22.1 ± 4.7 [ab]	9.9 ± 3.3 [a]	60.9 ± 9.1 [bc] (16)
Mean	**52**	**86.3 ± 12.8**	**17.2 ± 2.6**	**8.8 ± 1.7**	**70.5 ± 5.5**

Table 4.4. Seed and pod characteristics of undamaged pods in central (GA) and peripheral (SC) populations of *Baptisia lanceolata*. Values represent mean ± SE. Cumulative fitness values were log $x + 1$ transformed for statistical analysis. Within columns, values with same superscripts were not statistically different at $\alpha = 0.05$.

Region	**N**	**Seed Production (# seeds/pod)**	**% Seed Abortion**	**Seed Weight (mg)**	**Pod Volume (cm^3)**	**Cumulative fitness (# seed/ind.)**
Central (GA)	38	5.4 ± 0.6^{a}	30.7 ± 4.5^{a}	9.0 ± 0.7^{b}	2.7 ± 0.6^{a}	78.6 ± 17.3^{a}
Peripheral (SC)	14	3.9 ± 1.2^{a}	39.7 ± 10.7^{a}	5.9 ± 1.5^{a}	2.5 ± 2.3^{a}	19.9 ± 29.7^{a}

Table 4.5. Genetic variability at six polymorphic loci in central (B, M) and peripheral (K-TN) *Baptisia lanceolata* populations. Values represent mean ± standard error. Significant differences in observed and expected heterozygosity ($p < 0.01$) are noted with an asterisk. [a]

Population	N	A	H_o	H_e
B	20.3 ± 1.1	2.3 ± 0.2	0.27 ± 0.0 *	0.41 ± 0.1
M	20.0 ± 1.7	2.5 ± 0.2	0.37 ± 0.1 *	0.46 ± 0.1
K	14.7 ± 2.0	2.3 ± 0.2	0.35 ± 0.1	0.43 ± 0.1
RD	17.5 ± 2.2	2.5 ± 0.2	0.31 ± 0.1 *	0.43 ± 0.1
TN	18.7 ± 1.1	2.5 ± 0.2	0.32 ± 0.1 *	0.45 ± 0.1
Central	40.3 ± 2.1	2.5 ± 0.2	0.32 ± 0.1	0.45 ± 0.1
Peripheral	50.8 ± 4.1	2.5 ± 0.2	0.33 ± 0.1	0.44 ± 0.1

[a] N = sample size per locus, A = number of alleles per locus, H_o = observed heterozygosity (direct-count estimate), H_e = Hardy-Weinberg expected heterozygosity (unbiased estimate)

Table 4.6. Inbreeding coefficient (F^*), Wright's fixation index (F), and mean F_{IS} values from central (B, M) and peripheral (K-TN) populations of *Baptisia lanceolata.* Values with an asterisk were significantly different from zero based on χ^2 distribution.

Locus	**B**	**M**	**K**	**RD**	**TN**	**Mean F_{IS}**
F^*	0.33	0.19	0.21	0.28	0.25	
AAT	0.460	0.211	0.564	0.285	0.701	0.442 *
GPI	0.192	- 0.130	- 0.007	0.283	0.377	0.137
PGDH	0.346	0.709	- 0.100	0.451	0.153	0.362 *
MDH-1	0.320	- 0.174	- 0.475	-0.288	- 0.185	- 0.164
MDH-2	- 0.073	0.321	- 0.111	-0.37	- 0.059	0.056
ME	0.389	0.424	0.836	0.626	0.556	0.588 *

Table 4.7. Allele frequency of six polymorphic loci in central (B,M) and peripheral (K-RD) *Baptisia lanceolata* populations.

Locus	Allele	B	M	K	TN	RD	Central	Peripheral
AAT	A	0.18	0.62	0.13	0.21	0.47	0.42	0.27
	B	0.62	0.21	0.63	0.58	0.44	0.40	0.55
	C	0.21	0.17	0.24	0.21	0.09	0.18	0.18
GPI	A	0.62	0.50	0.62	0.54	0.66	0.56	0.61
	B	0.38	0.50	0.38	0.46	0.34	0.44	0.39
PGDH	A	0.24	0.31	0.21		0.21	0.27	0.16
	B	0.77	0.69	0.68	0.91	0.75	0.73	0.76
	C			0.12	0.09	0.04		0.08
MDH-1	A	0.46	0.28	0.32	0.38	0.57	0.39	0.42
	B	0.46	0.47	0.44	0.46	0.40	0.46	0.43
	C	0.09	0.25	0.24	0.17	0.03	0.15	0.15
MDH-2	A	0.07	0.11	0.06	0.10	0.04	0.09	0.06
	B	0.93	0.86	0.94	0.90	0.96	0.90	0.94
	C		0.03				0.01	
ME	A	0.82	0.79	0.75	0.68	0.62	0.80	0.69
	B	0.18	0.21	0.25	0.32	0.38	0.20	0.31

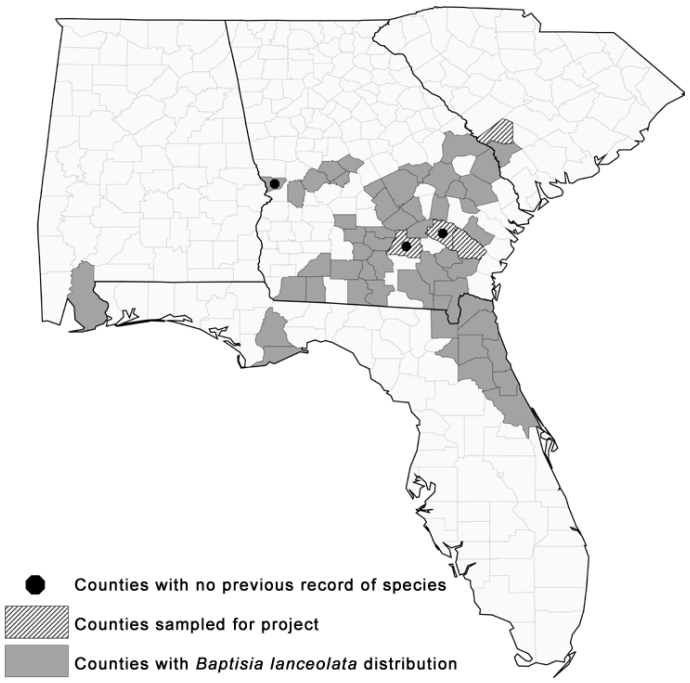

Figure 4.1. Distribution map of *Baptisia lanceolata* based on Larisey (1940), Isley (1981), Jones and Coile (1988), University of Georgia herbarium specimens, and personal observations (A.Squire). Data regarding occurrences of the variety *Baptisia lanceolata var. tomentosa* are not included in this figure.

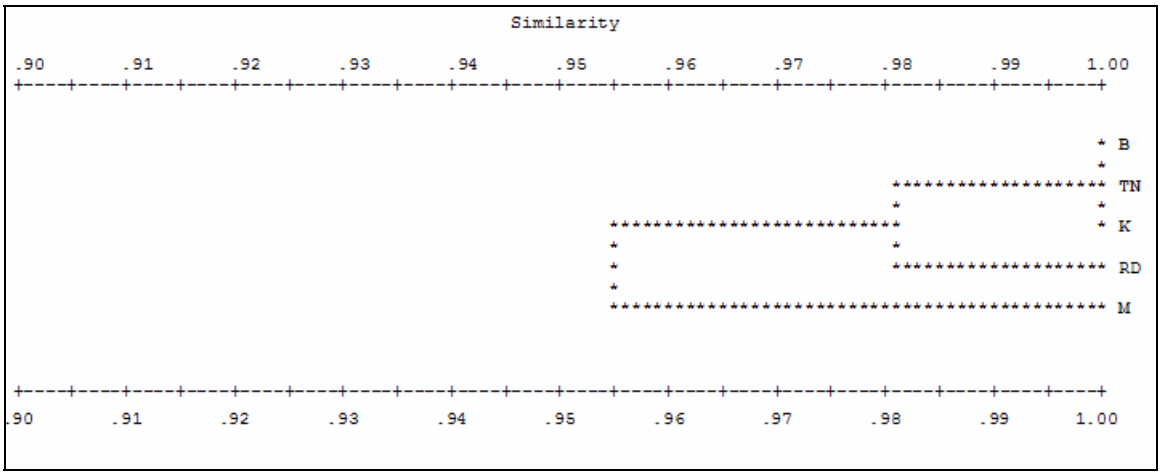

Figure 4.2. Genetic similarity between central (B,M) and peripheral (K, RD, TN) *Baptisia lanceolata* populations. Cluster diagram constructed using Nei's unbiased genetic identity (1978).

CHAPTER 5

CONCLUSION

In the previous chapters, the reproductive ecology of two Coastal Plain legumes, *Baptisia arachnifera* and *Baptisia lanceolata,* was investigated along with information on environmental conditions and genetic characteristics (*B. lanceolata* only). Both species are considered rare to varying extents. *Baptisia arachnifera* is restricted to a 16 km area in southeastern Georgia and is highly vulnerable to management practices on pine plantations. The rarity status of *B. lanceolata*, however, is somewhat ambiguous as it is considered "apparently secure" in Georgia, but is a "species of concern" in neighboring South Carolina. These studies were undertaken to provide a better understanding of *Baptisia*'s species biology, information that is important for assessing rarity.

Predispersal seed predation, which is prevalent in many *Baptisia* species (Frost 1945; Haddock and Chaplin, 1982; U.S. Fish and Wildlife Service, 1984; Evans et al., 1989; Mehlman 1993; Horn and Hanula 2004), varied substantially within each study. Pod damage, which includes the effect of predispersal seed predation, was markedly higher in *Baptisia arachnifera* populations (Chapter 3). Similarly, peripheral *B. lanceolata* populations had elevated pod damage relative to central ones (Chapter 4). Peripheral *B. lanceolata* populations were also the only ones to be attacked by an unknown lepidopteran species that always destroyed all seeds. The resulting decrease in seed production, however, may not necessarily compromise the population dynamics of long-lived perennials, such as *Baptisia*. The experimental seed bank study (Chapter 2) was conducted to assess whether *B. lanceolata* seeds were able to persist up to a year under field conditions. The formation of a persistent soil seed bank has the potential to buffer the negative effects of predispersal seed predation on the population dynamics of long-

lived perennials (Andersen 1989). With 40% of seeds remaining dormant after one year, it is possible that *B. lanceolata* could reduce the impact of predispersal seed predation over time with a persistent seed bank. Since intensity of predispersal seed predation has been shown to vary in space and time (e.g., Ehrlén 1996), long-term monitoring of predispersal seed predation on *B. lanceolata* is necessary to fully evaluate its impact. In the case of *B. arachnifera*, which appears to have compromised seed production (see below), it might be of interest to investigate means of reducing predispersal seed predation levels. Optimal seed production could increase the possibility of sexual recruitment within existing *B. arachnifera* populations or establishment of new populations. Additionally, an experimental seed bank study could be informative for *B. arachnifera* since nothing is known about the fate of its seeds in natural populations.

Few reproductive traits were found to be significantly different between *B. arachnifera* and *B. lanceolata* (Chapter 3), as well as between central and peripheral *B. lanceolata* populations (Chapter 4). Flower, pod and seed production were comparable between central and peripheral *B. lanceolata* populations whereas *B. arachnifera* and *B. lanceolata* were similar only in terms of flower and pod production. Differences at the population level, however, were observed in each comparison. Pollen viability, which was studied only in the rare-common comparison, was unanimously high in populations of both species. Another unexpected similarity came from central and peripheral *B. lanceolata* allozyme data, which revealed that peripheral populations did not have reduced genetic variation relative to central populations. A low G_{st} value (0.029) provided additional evidence that central and peripheral *B. lanceolata* populations are more genetically similar than previously anticipated.

Differences between species (Chapter 3) and plants in different parts of *B. lanceolata*'s distribution (Chapter 4) were most evident in the data collected for pod initiation (%) and several

seed traits. Pod initiation values served as an indicator of how successful plants were at converting flowers into developing fruit. In the rare-common species comparison, both species had similar, moderate levels of pod initiation (38% vs. 27%). In contrast, peripheral *B. lanceolata* populations had significantly reduced pod initiation compared to their central counterparts. At the population level, however, each comparison had one population that was noticeably different from the others. While 60% of flowers initiated pod development at Wire Rd (*B. arachnifera*), Road 9 (*B. lanceolata*, peripheral) had extremely low pod initiation (7.3%). Given this large variation in *Baptisia* pod initiation, future studies should include experiments to assess the mechanisms behind low fruit:flower ratios. For instance, pollinator activity and breeding systems are critical aspects of reproductive ecology that have not been directly studied in *B. arachnifera* and *B. lanceolata.*

Seed weight was another significant factor in both comparisons. *Baptisia arachnifera* produced significantly fewer, yet heavier, seeds than *B. lanceolata*. This finding supports the commonly held notion that plants can compensate for low seed production by producing heavier seeds (e.g., Primack 1987) and could have important implications on future colonization events. Westoby et al. (2002) suggest that species with high seed production experience a dispersal advantage, whereas those with heavier seed have more reserves to help withstand unpredictable hazards. As such, *B. arachnifera* might compensate for its reduced colonization ability by allocating more energy to early seedling development and growth within existing populations. While seed production was comparable in undamaged *B. lanceolata* pods from both regions, central populations produced significantly heavier seeds than peripheral populations. Interestingly, the possession of lighter seeds suggests that plants in peripheral *B. lanceolata*

populations might be capable of dispersing farther than those in more central locations. Perhaps this advantage is unrealized due to habitat limitations not yet identified at the periphery of *B. lanceolata*'s distribution.

Results from the heat shock experiment indicated that *B. arachnifera* and *B. lanceolata* seeds had different tolerances of high temperatures. *Baptisia arachnifera* had a narrower range of tolerance than *B. lanceolata*, which supports the hypothesis of Brown et al. (2003) that rare species have more specific heat requirements for germination than common ones. Specifically, *B. arachnifera* seeds were mostly inviable at temperatures exceeding 80 °C. A good proportion (~40%) of *B. lanceolata* seeds, however, remained viable up to 100 °C. This suggests that *B. arachnifera* propagules might not fare well during late spring or summer burns, when elevated ambient temperatures and duration of sunlight might cause soil temperatures to exceed tolerable levels.

Cumulative fitness, which was calculated using most of the reproductive traits measured, provided a holistic evaluation of fecundity in *B. arachnifera* and *B. lanceolata*. In the rare-common comparison, the most striking difference was not between species but rather amongst *B. arachnifera* populations. One population (Wire Road) produced a mean number of seeds/plant similar to *B. lanceolata* populations, whereas the other (Rayonier) had very low cumulative fitness. In the comparison between central and peripheral *B. lanceolata* populations, peripheral populations had markedly reduced fecundity.

Overall, I would make the following suggestions for agencies (e.g., Department of Natural Resources) in charge of protecting the federally endangered *B. arachnifera*. First, I would recommend continued monitoring of number of individuals and reproductive status within *B. arachnifera* populations, especially since previous reports suggest that populations are

declining. Several experiments could be set up to determine which mechanism(s) are responsible for the highly variable pod initiation in *B. arachnifera* populations. For instance, multiple pollination treatments (self pollen from same individual, self pollen from same genet, outcrossed pollen) would allow researchers to assess the degree of self-compatibility of *B. arachnifera*. In addition, a thorough documentation of pollinator activity could identify whether lack of pollinators is a limiting factor in certain populations of *B. arachnifera*. Finally, I would encourage designing more experiments in conjunction with prescribed burns. A seed addition experiment would allow for a direct measurement of how fire can affect *B. arachnifera* field germination. Monitoring predispersal seed predation levels, as well as pollinator activity, before and after prescribed burns would additionally provide insight into how this common management practice might influence co-occurring insect populations.

To summarize, the soil seed bank experiment (Chapter 2) gave insight into *B. lanceolata* seed fate in natural populations. These findings have potential implications for the impact of predispersal seed predation on long-term plant population dynamics. In the rare-common comparison (Chapter 3), the reproductive traits studied did not provide a clear explanation why *B. arachnifera* has such a limited distribution. The striking difference between the two *B. arachnifera* populations studied, however, suggests that more populations need to be monitored to fully assess the reproductive ecology of this endangered species. Finally, a comparison of reproductive and genetic traits in central and peripheral *B. lanceolata* populations (Chapter 4) revealed that peripheral populations appear to have lower reproductive success than their central counterparts. However, data suggest that there is no significant difference between regions in term of genetic variation and structure.

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