REPRODUCTIVE ECOLOGY OF A FEDERALLY ENDANGERED LEGUME, *BAPTISIA ARACHNIFERA*, AND ITS MORE WIDESPREAD CONGENER, *B. LANCEOLATA* (FABACEAE)[1]

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Comparisons between rare species and their more common congener species can provide valuable information for conservation. Reproductive traits have previously been shown to be critical for reproductive success and persistence of rare species. In this study, we compared floral, seedpod, and seed traits of two *Baptisia* species (one endangered and one common) to assess differences in reproduction between species and among populations. Because heat can trigger germination in hard-seeded legumes, we also exposed *Baptisia* seeds to a range of high temperatures (60–100°C) and determined seed viability. The rare *Baptisia arachnifera* had significantly greater pod damage by insects and produced significantly fewer, yet heavier, seeds than *B. lanceolata*. While *B. arachnifera* seeds were seldom viable at temperatures above 80°C, approximately 40% of *B. lanceolata* seeds maintained viability up to 100°C. Our various seed trait measurements suggest that *B. arachnifera* may be a poorer colonizer than the more widespread *B. lanceolata*. Additionally, *B. arachnifera*'s reduced tolerance for high temperatures may have implications for appropriate fire management regimes for this endangered species.

Key words: *Baptisia*; Fabaceae; heat-stimulated germination; predispersal seed predation; rare–common comparison; reproductive ecology; southeastern USA.

With over 5000 species considered susceptible to extinction within the United States, flowering plants are highly represented in estimates of impending loss of biodiversity (Master et al., 2000). Rarity is often defined in terms of abundance of individuals or range size (Gaston, 1997) and can include species that have limited distribution due to human activities, such as habitat destruction and degradation (Fiedler and Ahouse, 1992). Understanding the natural history of rare plants is crucial to their conservation (Massey and Whitson, 1980). It has long been recognized that basic biological knowledge of a species can help to identify factors that limit long-term persistence. Nonetheless, insufficient understanding 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). Studies that contrast life history traits of restricted vs. more widespread congeneric species address this drawback and can provide essential information for rare plant management (Kunin and Gaston, 1993; Brown et al., 2003; Burne et al., 2003).

Reproduction and recruitment are particularly emphasized in attempts to interpret plant rarity (e.g., Gaston and Kunin, 1997; Kaye, 1999; Brown et al., 2003; Evans et al., 2003). Reproductive traits are tightly correlated with reproductive success and can influence genetic variation in a population (Hamrick et al., 1991; DeMauro, 1993), which is critical in the long-term persistence of a population. Additionally, managers often use fecundity as the primary means to assess rare plant population trends (Giblin and Hamilton, 1999).

Even though many rare–common comparisons include reproductive traits, few generalities can be drawn from these studies because they often measure different sets of traits. For example, Murray et al. (2002) reported that 67% (63/94) of traits investigated in 54 rare–common plant comparisons were measured only in one study, making it difficult to draw general conclusions regarding the differences between rare and common species. Another limitation often associated with this comparative method is the tendency for studies to focus on one pairwise comparison of two closely related species (Kunin and Gaston, 1993). Developing a standardized set of traits for use in rare–common comparisons, however, could potentially address both problems. Studies in which detailed information is gathered on the natural history of a rare plant and a common congener could help inform resource managers in making conservation decisions for the rare species. At the same time, the use of standardized traits would allow studies with only one pairwise comparison to contribute to the overall understanding of rarity via meta-analyses, as proposed by Bevill and Louda (1999).

To approach rare–common comparisons in a more holistic fashion, we measured a comprehensive suite of reproductive traits in *Baptisia arachnifera* Duncan and *B. lanceolata* (Walt.) Ell., two long-lived perennial legumes that grow in the lower Coastal Plain province of the southeastern United States. The federally endangered *B. arachnifera* is restricted to a 260 km² area of southeastern Georgia (GA). Within the past 20 years, *B. arachnifera* populations have dramatically declined in size (22–89% fewer individuals) and have reverted from primarily mature adults to mostly nonflowering plants (K. R. Tassin and A. J. McGee, Georgia Department of Natural Resources, unpublished manuscript). In contrast, *B. lanceolata* is considered "apparently secure" in Georgia (NatureServe, 2005).

Our measurements included flower, pod, and seed production for both *Baptisia* species. 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 (e.g., Mehrhoff, 1983; Fiedler, 1987) and fruit (e.g., Fiedler, 1987; Young and Brown, 1998) production also tend to be significantly lower in rare plants. We also measured pollen viability, pod initiation, seed mass, seed abortion, and pod volume; there is no consensus in the rare–common literature regarding these traits.

Predispersal seed predation, which is prominent in many *Baptisia* species (Frost, 1945; Haddock and Chaplin, 1982; U.S. Fish and Wildlife Service, 1984; Evans et al., 1989; Horn and Hanula, 2004), is an extrinsic factor that could also limit reproductive success via decreased viable seed production. 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 amount of seeds lost to predators relative to common species. We used exterior pod damage by insects as an estimate of predispersal seed predation intensity at the population level.

We also conducted a heat shock experiment on seeds of both *Baptisia* species to assess their range of tolerance to high temperatures. Heat shock can be an effective means of interrupting physical dormancy imposed by an impermeable seed coat before 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). Because *B. arachnifera* and *B. lanceolata* occur in southern pine forests, which are historically fire dependent, fire might be an important factor for germination and recruitment of these leguminous species.

Finally, habitat specificity is thought to influence rarity, especially for endemic species with restricted distributions (Rabinowitz, 1981; Kruckeberg and Rabinowitz, 1985). Nonetheless, only a few 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). To discern potential habitat differences between *B. arachnifera* and *B. lanceolata*, we measured percentage canopy openness, soil texture, and soil nutrients.

For this study, we tested the following hypotheses: (1) The rare *B. arachnifera* has lower flower, pod, and seed production than its common congener, *B. lanceolata*. (2) There is no significant difference between the *Baptisia* species in terms of other reproductive traits (pollen viability, pod initiation, seed weight, seed abortion, pod volume, and reproductive success). (3) Pod damage by insects is not significantly different between the two species. (4) Seeds of the rare *B. arachnifera* will tolerate a narrower range of high temperatures than *B. lanceolata* seeds. (5) There is no significant difference in environmental variables (percentage canopy openness, soil texture, and nutrients) between *B. arachnifera* and *B. lanceolata* habitats.

MATERIALS AND METHODS

Study species and experimental design—*Baptisia arachnifera* and *B. lanceolata* are polycarpic legumes typically associated with the longleaf and slash pine forests of the lower southeastern Coastal Plain (Larisey, 1940; U.S. Fish and Wildlife Service, 1984). Seed predation by Say's weevil (*Apion rostrum*) has been documented in both species (U.S. Fish and Wildlife Service, 1984; Mehlman, 1993; Horn and Hanula, 2004). Seedling recruitment in natural populations has been observed infrequently for *B. arachnifera* (U.S. Fish and Wildlife Service, 1984; L. D. Humphrey, Georgia Department of Natural Resources, unpublished manuscript) and *B. lanceolata* (A. Young, personal observations). These *Baptisia* species occasionally occur together along roadsides in Wayne Co., GA (A. Young, personal observations).

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 fruits from August through September. A federally listed endangered species, *B. arachnifera* is found in only two southeastern GA counties (Wayne and Brantley) with the majority of 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 GA 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, we monitored three populations of each species throughout the growing season. All *B. arachnifera* populations (Powerline, Rayonier, Wire Road) were located in Wayne County, GA. *Baptisia lanceolata* populations were located throughout southern GA in Wayne (Browntown Road), Coffee (General Coffee State Park), and Appling (Moody Forest) counties. Within each population, we established a plot between 900 m² (30 × 30 m) and 1600 m² (40 × 40 m) to obtain 20 focal individuals. To qualify, focal individuals had to be flowering and at least 1 m from another conspecific plant because 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. If there were more than 20 *Baptisia* plants that met these qualifications in a plot, we randomly selected acceptable plants across the entire plot. One *B. arachnifera* population (Rayonier) had fewer than 20 appropriate individuals, and therefore all acceptable plants were used. During the study, another *B. arachnifera* population (Powerline) was mowed, and we could not collect mature pod and seed data.

Reproductive traits—We assessed two floral traits in *B. arachnifera* and *B. lanceolata* populations: flower production (total flowers/plant) and percentage pollen viability. To test pollen viability, we removed one anther from each of three flowers per focal plant, dyed the pollen grains with Alexander's stain (Alexander, 1980), and viewed grains with a compound microscope. Viable grains stained red and nonviable grains stained green. We scored 300 pollen grains per flower within multiple fields per slide. Thus, 900 pollen grains were evaluated per plant to calculate percentage pollen viability.

Approximately 6 wk after flowering commenced, we determined percentage pod initiation (number of developing pods per total flowers produced). We reduced total flower values by three to account for flowers destructively sampled for pollen viability. When pods were mature, we measured several pod and seed traits. We determined mature pod production (total number mature pods per individual) and noted the presence of weevil exit holes and/or other forms of exterior pod damage. We used the proportion of mature pods with visible damage as an estimate of predispersal seed predation intensity.

We collected up to five pods from each focal individual for seed and pod measurements although reproductive failure prevented further analysis of certain plants. We recorded seed production (total number intact seeds per pod), seed abortion (%), seed mass (mg), and pod volume (cm³) for each pod and then averaged these values for each focal individual. Partially developed seeds and any unfertilized ovules were classified as aborted seeds because these structures were noticeably smaller than mature seeds yet could not always be distinguished. Because *Baptisia* pods are shaped approximately like two adjacent cones, we calculated pod volume as: $2[(1/3\pi) \cdot (W^2) \cdot (0.5 L)]$, where *W* and *L* represent pod width and length, respectively. Seed and pod data were analyzed from only the undamaged pods to exclude the negative effect of pod damage on particular seed measurements. However, all *Baptisia* pods with direct evidence of seed predation (e.g., predator and/or frass present) were assessed separately to determine the number of intact seeds remaining. Finally, reproductive success (mean number seeds per plant) was calculated as follows: (total no. flowers/plant) × (no. developing pods/total no. flowers) × (no. undamaged pods/total no. mature pods) × (mean no. intact seeds/undamaged pod).

TABLE 1. Comparison of *Baptisia arachnifera* (rare) and *B. lanceolata* (common) floral and pod traits. Values represent means + SE. Sample size is in parentheses. Incomplete data are presented for Powerline (*B. arachnifera*) because the population was mowed during the study. Within columns, values with same superscripts were not significantly different at α = 0.05 (Tukey–Kramer adjustment). Certain data were transformed for ANOVA (see Methods, Reproductive traits). 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	Damaged pods (%)
B. arachnifera					
Powerline	108.25 ± 16.05[c] (20)	95.79 ± 0.67[a] (20)	27.70 ± 3.26[a] (20)	—	—
Rayonier	41.63 ± 4.78[ab] (16)	95.63 ± 2.04[a] (16)	15.99 ± 4.51[a] (16)	4.38 ± 1.31[a] (16)	59.80 ± 9.89[a] (10)
Wire Road	55.15 ± 8.65[ab] (20)	96.67 ± 0.57[a] (20)	63.88 ± 4.81[b] (20)	30.35 ± 7.12[b] (20)	48.48 ± 6.51[a] (19)
Mean	70.25 ± 7.61	96.08 ± 0.63	37.27 ± 3.65	18.81 ± 4.51	52.38 ± 5.45[*]
B. lanceolata					
Browntown Road	43.15 ± 6.30[a] (20)	97.61 ± 0.37[a] (20)	31.33 ± 6.52[a] (20)	10.55 ± 2.94[a] (20)	31.89 ± 9.04[ab] (17)
General Coffee State Park	95.15 ± 15.03[bc] (20)	96.91 ± 1.08[a] (20)	21.17 ± 4.86[a] (20)	16.80 ± 5.93[ab] (20)	29.25 ± 8.04[ab] (19)
Moody Forest	38.15 ± 4.59[a] (20)	94.92 ± 1.41[a] (20)	31.90 ± 5.40[a] (20)	9.30 ± 2.02[ab] (20)	17.93 ± 6.45[b] (18)
Mean	58.82 ± 6.48	96.48 ± 0.61	28.14 ± 3.26	12.22 ± 2.31	26.31 ± 4.54[*]

We analyzed data from this study using a nested analysis of variance (ANOVA) with species and population nested within species (PROC GLM; SAS Institute, 1999) as the predicting variables. Because both species and population were treated as fixed effects in these analyses, their significance was tested against the Type III mean of squares of the error term for the entire model. We also carried out the Tukey–Kramer adjustment for multiple comparisons when determining pairwise differences between populations (SAS Institute, 1999). Although our variances were found to be homogenous, we transformed several response variables to meet normality assumptions for statistical analyses. Flower production was log-transformed, whereas pod production and reproductive success were log $(x + 1)$ transformed to include individuals with no mature pod production (reproductive failure).

Heat shock experiment—To obtain enough seeds for this experiment, we supplemented the *Baptisia* seeds collected for the reproductive traits study with seeds from nonfocal plants within the study plots. Seeds were then pooled across sites for each species. We subjected three replicates of 20 seeds per species 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 4 min. We based the duration of heat exposure and range of temperatures on previous studies documenting conditions near the soil surface during prescribed burns (Heyward, 1938; Tozer, 1998; Iverson and Hutchinson, 2002; Sullivan et al., 2003).

After heat treatments, we placed seeds from each replicate in a "zipper"-locking bag with a moist paper towel. Because imbibed *Baptisia* seeds are prone to fungal growth, we coated the seeds with a weak solution of Captan fungicide (5% N-trichloromethylthio-4-cyclohexene-1,2-dicarboximide; Drexel Chemical, Memphis, Tennessee, USA) immediately after they were subjected to their respective heat treatments. An additional no-heat/no-fungicide treatment was created to control for the effect of fungicide application. Therefore, 420 seeds (7 heat treatments × 20 seeds × 3 replicates) per species were used.

We monitored germination under greenhouse conditions every other day for 3 wk, classifying seeds as germinated, dormant, or rotten. Bags were randomly repositioned within the greenhouse on a weekly basis. After 3 wk, we used the triphenyl tetrazolium chloride (TTC) test to assess viability of all remaining dormant seeds (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. We used a one-way ANOVA to compare overall seed viability between treatments for each species and evaluated significant differences using Tukey's honestly significant difference (SAS Institute, 1999).

Environmental variables—We measured canopy openness (%), soil nutrients, and texture to assess potential habitat differences between *B. arachnifera* and *B. lanceolata*. We determined canopy openness using 10 hemispherical canopy photographs distributed throughout each population, which we interpreted using the computer program Gap Light Analyzer (GLA 2.0; Frazer et al., 2000). We collected 15 soil cores, each 2 cm in diameter and driven approximately 0.5 m deep, from each population and pooled random sets of three cores to obtain five subsamples per population. Soil samples were analyzed by the University of Georgia's Soil, Plant and Water laboratory for pH, texture and macro- and micronutrients. The environmental variables were analyzed the same way as the reproductive traits. No transformation was necessary for these data.

RESULTS

Reproductive traits—While total flower production was similar between species, there were significant differences between populations nested within species ($F_{4,110} = 7.48$, $P < 0.0001$; Table 1). The Powerline and General Coffee State Park 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 95% (Moody Forest) to 98% (Browntown Road; Table 1).

On average, 37% and 28% of flowers on *B. arachnifera* and *B. lanceolata* plants, respectively, initiated pod development (Table 1). Significant differences in pod initiation were apparent only at the population level ($F_{4,110} = 12.59$, $P < 0.0001$). In particular, *B. arachnifera* plants in the Wire Road population were most successful at pod initiation and also had significantly higher mature pod production than any other population of either species (Table 1).

Pod damage was significantly greater in *B. arachnifera* than *B. lanceolata* ($F_{1,78} = 14.75$, $P < 0.0005$). Over half (52%) of the pods on *B. arachnifera* plants had evidence of damage, whereas only 26% of *B. lanceolata* pods were compromised (Table 1). There was no significant difference in pod damage between populations nested within species ($F_{3,78} = 0.89$, $P = 0.45$). Thirty-nine percent of *B. lanceolata* pods attacked by predators had between 1–9 intact seeds remaining, whereas all *B. arachnifera* pods with evidence of predation were devoid of seed (Fig. 1). In contrast, undamaged pods contained a range of 0–15 (*B. lanceolata*) and 0–6 (*B. arachnifera*) intact seeds.
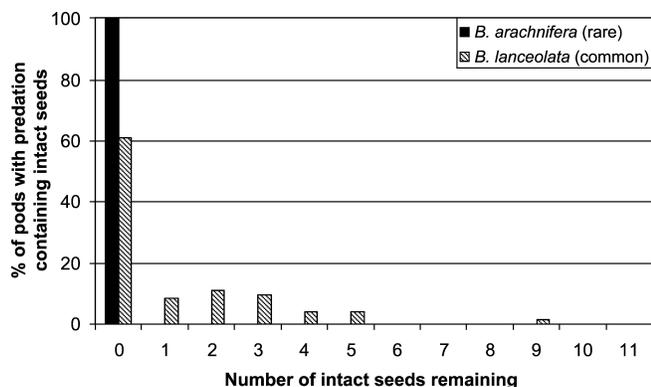
Fig. 1. Distribution of intact seeds remaining in pods of *Baptisia arachnifera* (rare) and *B. lanceolata* (common) with evidence of predispersal seed predation.
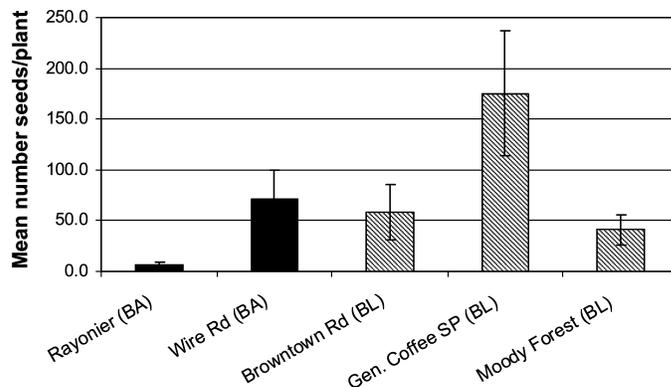

Fig. 2. Mean reproductive success (no. seeds/plant) in populations of *Baptisia arachnifera* (BA; rare) and *B. lanceolata* (BL; common) in southern Georgia. Error bars represent ± SE.

Baptisia arachnifera pods were significantly smaller ($F_{1,56} = 96.81$; $P < 0.0001$) and contained significantly fewer mature seeds than those of *B. lanceolata* ($F_{1,56} = 21.42$, $P < 0.0001$; Table 2). *Baptisia arachnifera* seeds were significantly heavier than *B. lanceolata* seeds ($F_{1,56} = 10.96$, $P = 0.002$). While not significant, Wire Road and Moody Forest populations tended to have higher seed abortion (%) than other *B. arachnifera* and *B. lanceolata* populations (Table 2).

Reproductive success was highly variable but not significantly different between species ($F_{1,56} = 1.87$, $P = 0.18$; Fig. 2); however, there were distinct patterns among populations nested within species ($F_{3,56} = 3.05$, $P = 0.04$). The General Coffee State Park population was the most successful population in our study, producing an average of 175 seeds per *B. lanceolata* plant. The reproductive success of one *B. arachnifera* population (Wire Road) was comparable to that of two *B. lanceolata* populations (Browntown Road, Moody Forest), with all three populations producing, on average, between 40–71 seeds per plant. Individuals in the other *B. arachnifera* population (Rayonier), however, typically produced only seven seeds per plant. Rayonier also had the highest percentage of focal plants with reproductive failure; six of 16 flowering individuals (37.5%) produced no mature pods. Reproductive failure was lower in all other populations: 5% (1/20) for Wire Road and General Coffee State Park, 10% (2/20) for Moody Forest, and 15% (3/20) for Browntown Road.

Heat shock experiment—Seeds from the rare and common *Baptisia* species had markedly different responses to high temperatures (Fig. 3). *Baptisia arachnifera* seeds tolerated a narrower range of temperatures, with overall seed viability decreasing from 87 to 2% between 60°C and 100°C. In contrast, approximately 40% of *B. lanceolata* seeds consistently remained viable at all tested temperatures. The number of germinated seeds also varied between species. Twenty-six percent (108/420) of *B. arachnifera* seeds germinated in all treatments up to 80°C, with the majority in the two controls. Only 1% (5/420) of *B. lanceolata* seeds, however, germinated under greenhouse conditions.

Environmental variables—Canopy openness differed significantly at both the species ($F_{1,54} = 198.99$, $P < 0.0001$) and population ($F_{4,54} = 7779.76$, $P < 0.0001$) levels. In particular, *B. arachnifera* populations were highly variable, with mean canopy openness ranging from 29.4% (Wire Road) to 100% (Powerline; Table 3). There was a weak positive correlation ($r^2 = 0.59$) between percentage canopy openness and flower production for both *Baptisia* species (Fig. 4).

While *B. arachnifera* and *B. lanceolata* populations both occurred on sandy, acidic soils with low nutrients, there were significant differences at the species and population levels (Table 3). The Moody Forest population had the most distinct soil texture, with a significantly lower proportion of sand and, subsequently, higher amounts of silt and clay than other

TABLE 2. Comparison of seed and pod traits in undamaged pods from *Baptisia arachnifera* (rare) and *B. lanceolata* (common). Values represent means ± 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 mass (mg)	Pod volume (cm³)
B. arachnifera					
Rayonier	6	1.01 ± 0.17^a	25.76 ± 11.54^a	15.20 ± 2.12^b	0.55 ± 0.08^a
Wire Road	17	2.35 ± 0.30^a	46.10 ± 6.80^a	10.40 ± 0.46^{ab}	0.68 ± 0.04^a
Mean	23	$2.00 \pm 0.26^*$	40.79 ± 6.03	$11.65 \pm 0.76^*$	$0.65 \pm 0.04^*$
B. lanceolata					
Browntown Road	13	7.15 ± 1.11^c	24.06 ± 6.15^a	8.73 ± 0.87^a	3.53 ± 0.31^b
General Coffee State Park	9	6.26 ± 1.27^{bc}	19.86 ± 8.17^a	9.94 ± 1.51^{ab}	3.18 ± 0.27^b
Moody Forest	16	3.49 ± 0.79^{ab}	42.26 ± 7.50^a	8.60 ± 1.22^a	1.87 ± 0.24^c
Mean	38	$5.40 \pm 0.63^*$	30.73 ± 4.46	$8.96 \pm 0.68^*$	$2.75 \pm 0.20^*$
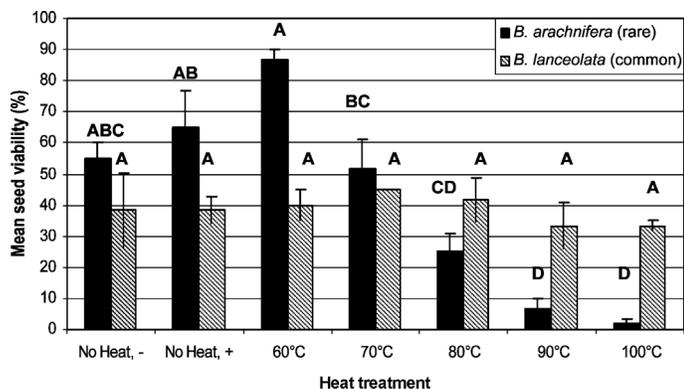
Fig. 3. Mean seed viability in *Baptisia arachnifera* and *B. lanceolata* after a 4-min heat treatment. No heat = control without fungicide, No heat, += control with fungicide. Error bars represent ± SE. Treatments with the same letters were not significantly different at $\alpha = 0.05$ (Tukey's honestly significant difference).
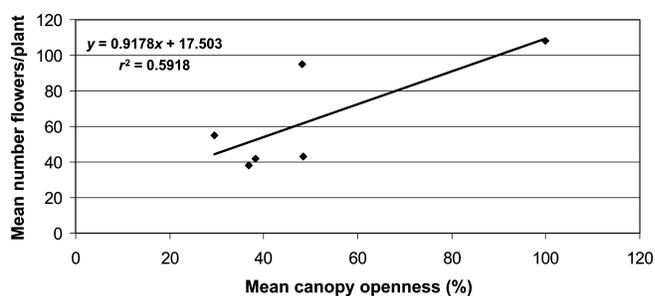

Fig. 4. Correlation between mean canopy openness and flower production in populations of *Baptisia arachnifera* (rare) and *B. lanceolata* (common) in southern Georgia.

Baptisia populations. Soils from *B. arachnifera* populations were slightly more acidic ($F_{1,24} = 6.96$, $P = 0.01$) and had higher levels of carbon ($F_{1,24} = 34.51$; $P < 0.0001$) and phosphorous ($F_{1,24} = 6.75$, $P = 0.02$). *Baptisia lanceolata* populations were typically located on soil with higher potassium ($F_{1,24} = 42.28$, $P < 0.0001$), magnesium ($F_{1,24} = 41.29$, $P < 0.0001$), manganese ($F_{1,24} = 39.77$, $P < 0.0001$), and zinc ($F_{1,24} = 12.24$, $P = 0.002$). The Powerline population tended to have higher levels of soil nutrients than other *B. arachnifera* populations. Magnesium and manganese levels were an order of magnitude higher in two *B. lanceolata* populations (Moody Forest and General Coffee State Park, respectively) relative to all *Baptisia* populations.

DISCUSSION

Rare–common comparisons can be a powerful conservation tool, providing specific biological information often lacking in recovery plans for endangered species and insight into causes of rarity. We addressed a criticism of rare–common comparisons—that they often lack standardized traits (Bevill and Louda, 1999; Murray et al., 2002)—by evaluating multiple reproductive traits and extrinsic factors that could be

contributing to the rarity of a federally endangered legume, *Baptisia arachnifera*.

Floral traits did not differ significantly between the two *Baptisia* species, counter to our expectations. The lack of difference in total flower production is also 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 some populations with greatly reduced pollen viability (Banks, 1980; Burne et al., 2003).

Although flower production and pollen viability do not appear to be limiting the reproductive success of *B. arachnifera*, other reproductive traits merit further study. The breeding system can influence interpretations of the relationship between reproductive output and rarity. For instance, reduced seed production in rare species can be a consequence of self-incompatibility, inbreeding depression, or pollinator limitation (Giblin and Hamilton, 1999). While the breeding systems of *B. arachnifera* and *B. lanceolata* have never been directly examined, there is some preliminary evidence regarding their nature. Ceska et al. (1997) proposed, based on the observation of Hardy–Weinberg equilibria, that *B. arachnifera* populations were predominantly outcrossing. In contrast, recent genetic data suggest that *B. lanceolata* populations in Georgia and South Carolina experience moderate levels of selfing (Squire, 2005).

TABLE 3. Environmental variables sampled within *Baptisia arachnifera* (rare) and *B. lanceolata* (common) populations in southern Georgia, USA. Values represent means ± SE. Within columns, values with same superscripts were not significantly different at $\alpha = 0.05$ (Tukey–Kramer adjustment). Variables that differed significantly at the species level ($P < 0.05$) are indicated with an asterisk.

Population	Canopy openness (%)	Soil texture (% sand)	Soil texture (% silt)	Soil texture (% clay)	Soil pH	C (%)
B. arachnifera						
Powerline	100.00 ± 0.00[d]	93.20 ± 0.49[b]	4.00 ± 0.63[a]	2.80 ± 0.49[a]	4.08 ± 0.04[a]	0.61 ± 0.08[d]
Rayonier	38.25 ± 0.74[b]	92.67 ± 0.40[b]	3.67 ± 0.63[a]	3.67 ± 0.75[a]	4.08 ± 0.04[a]	0.46 ± 0.05[cd]
Wire Road	29.42 ± 0.50[a]	91.20 ± 0.49[b]	4.00 ± 0.63[a]	4.86 ± 0.49[b]	4.18 ± 0.04[ab]	0.40 ± 0.03[bc]
Mean	55.89 ± 5.84*	92.27 ± 0.33*	4.00 ± 0.34*	3.73 ± 0.38	4.11 ± 0.02*	0.49 ± 0.04*
B. lanceolata						
Browntown Road	48.42 ± 0.69[c]	92.40 ± 0.75[b]	4.00 ± 0.63[a]	3.60 ± 0.40[a]	4.20 ± 0.00[ab]	0.24 ± 0.02[ab]
General Coffee State Park	48.18 ± 2.43[c]	90.80 ± 1.02[b]	6.40 ± 0.98[b]	2.80 ± 0.49[a]	4.26 ± 0.02[b]	0.18 ± 0.03[a]
Moody Forest	36.94 ± 1.16[b]	85.60 ± 1.60[a]	7.60 ± 0.75[b]	6.80 ± 1.02[b]	4.10 ± 0.05[a]	0.34 ± 0.03[ac]
Mean	44.10 ± 1.32*	89.60 ± 1.00*	6.00 ± 0.59*	4.40 ± 0.59	4.19 ± 0.03*	0.26 ± 0.02*

We observed that flower abortion substantially reduced the reproductive potential of both *Baptisia* species; less than 40% of flowers initiated pod development. The production of surplus flowers (i.e., those that do not produce mature fruit) is a common phenomenon in plants (Stephenson, 1981) and can serve to increase total plant fitness by attracting pollinators, allowing for selective abortion of inferior progeny and/or improving male fitness via increased pollen donation (Sutherland, 1987). Flower abortion might also be indicative of pollen or resource limitation.

While mature pod production is 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 between species. There were striking differences, however, among populations nested within species. Plants in the two *B. arachnifera* populations monitored for the full duration of the study had both the lowest (Rayonier) and highest (Wire Road) pod production of either species.

Evaluation of seed traits provided the greatest insight into potential differences between the rare and common species. *Baptisia arachnifera* pods contained significantly fewer mature seeds than those of *B. lanceolata*, as we hypothesized. The majority of studies compiled in Murray et al. (2002), as well as more recent ones (Lavergne et al., 2004; Mabry, 2004), uphold the generalization that narrowly restricted species produce fewer seed than common species. The relatively low number of *B. arachnifera* seeds might be partially due to the fact that its pods are substantially smaller. Unlike seed production, the relationship between seed mass and rarity is inconsistent (Murray et al., 2002). We found that *B. arachnifera* seeds typically weigh more than *B. lanceolata* seeds, which supports the commonly held notion that plants can compensate for low seed production by producing heavier seeds (e.g., Primack, 1987). Finally, there was no significant difference in seed abortion between the rare and common *Baptisia* species; however, our inclusion of unfertilized ovules in our seed abortion measurements might have obscured potential differences for this trait. 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).

Researchers in the past several decades have pointed out the potential importance of predispersal seed predation in rare plant dynamics (Menges et al., 1986; Hegazy and Eesa, 1991; Bevill et al., 1999; Kaye, 1999; Vickery, 2002). Most recently, Münzbergová (2005) documented that the population growth rates of a rare and common *Cirsium* species differed significantly only when seed predation data were taken into account. We found that *B. arachnifera* plants had, on average, twice the amount of pod damage as *B. lanceolata* plants; however, our pod damage measurements did not distinguish between damage caused by seed predators (weevils) and other herbivory on reproductive structures. Nonetheless, the higher pod damage for *B. arachnifera* could still have significant repercussions on reproductive success by causing additional seed loss and increasing exposure of remaining seeds to pathogens. *Baptisia arachnifera* seeds have been reported to be susceptible to attack from *Fusarium* species (Handaly, 1997).

Our analysis of a subset of *Baptisia* pods with direct evidence of weevil damage provides preliminary data that predispersal seed predation is in fact more intense in *B. arachnifera*. *Baptisia arachnifera* had no intact seeds in pods lost to seed predators, whereas more than a third of *B. lanceolata* pods that had been attacked by weevils still contained viable seed. It is also interesting to note that there is experimental evidence that prescribed burns can decrease the intensity of predispersal seed predation (Mejeur, 1998; Vickery, 2002). For example, Vickery (2002) found that recent (within 12 months) burns significantly reduced seed predation intensity in populations of a rare grassland perennial, *Liatris scariosa* var. *novae-angliae* Lunell. More studies are needed to evaluate the impact of prescribed burns on seed predators and their plant hosts. Other investigations have focused primarily on the effect of fire on populations of granivores (Zimmer and Parmenter, 1998) and foliar herbivores (e.g., Bock and Bock, 1991; Knight and Holt, 2005). Because prescribed burns are integral to the habitat management of both *Baptisia* species, it would be valuable to determine whether prescribed burns can also alter the intensity of predispersal seed predation in these species.

Counter to generalizations that rare species have reduced fecundity (Fiedler and Ahouse, 1992; Gaston and Kunin, 1997), our reproductive success data suggest that there is no significant difference in overall fecundity between *B. arachnifera* and *B. lanceolata*. One *B. arachnifera* population (Wire Road) produced a similar number of seeds per plant as two *B. lanceolata* populations (Browntown Road, Moody Forest). In contrast, the other *B. arachnifera* population (Rayonier) had the overall lowest reproductive success. The high variability in

TABLE 3. Extended.

N (%)	Ca (g/m²)	K (g/m²)	Mg (g/m²)	P (g/m²)	Mn (g/m²)	Zn (g/m²)
0.02 ± 0.00[a]	4.52 ± 1.15[b]	1.79 ± 0.12[bc]	0.42 ± 0.12[a]	0.64 ± 0.09[b]	0.02 ± 0.01[a]	0.25 ± 0.01[a]
0.02 ± 0.00[a]	1.75 ± 0.19[a]	0.94 ± 0.11[ab]	0.39 ± 0.06[a]	0.45 ± 0.04[ab]	0.01 ± 0.00[a]	0.24 ± 0.02[a]
0.01 ± 0.00[a]	1.76 ± 0.35[a]	0.80 ± 0.10[a]	0.18 ± 0.07[a]	0.38 ± 0.05[a]	0.02 ± 0.01[a]	0.23 ± 0.01[a]
0.02 ± 0.00	2.68 ± 0.51	1.18 ± 0.13*	0.33 ± 0.05*	0.49 ± 0.05*	0.02 ± 0.00*	0.24 ± 0.01*
0.01 ± 0.00[a]	1.54 ± 0.25[a]	1.37 ± 0.03[bc]	0.15 ± 0.05[a]	0.45 ± 0.07[ab]	0.11 ± 0.05[a]	0.47 ± 0.05[b]
0.01 ± 0.00[a]	1.77 ± 0.31[a]	1.51 ± 0.14[c]	0.49 ± 0.15[a]	0.33 ± 0.02[a]	0.99 ± 0.21[b]	0.22 ± 0.01[a]
0.01 ± 0.00[a]	6.16 ± 0.40[b]	2.32 ± 0.10[d]	6.33 ± 0.90[b]	0.32 ± 0.03[a]	0.39 ± 0.07[a]	0.23 ± 0.02[a]
0.01 ± 0.00	3.16 ± 0.59	1.73 ± 0.12*	2.32 ± 0.81*	0.37 ± 0.03*	0.50 ± 0.12*	0.31 ± 0.04*

B. arachnifera reproductive success appears to be related to pod development. While plants in both *B. arachnifera* populations had similar levels of flower production, the Rayonier population had substantially reduced pod initiation relative to Wire Road, which translated into decreased mature pod and seed production for the former. The Rayonier population also experienced notably higher reproductive failure, a measurement of the percentage of plants that produced no mature pods, than all other populations of both species. Finally, the high seed production per plant in General Coffee State Park might be attributed to high flower production coupled with reduced pod damage relative to other sampled *Baptisia* populations.

The narrower heat tolerance range of *B. arachnifera* seeds is consistent with species-specific heat responses in seeds of other legumes (Martin et al., 1975; Auld and O'Connell, 1991; Baskin and Baskin, 1998). Brown et al. (2003) proposed 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. Many fire-dependent communities, including longleaf pine forests, are maintained by prescribed burns in lieu of natural fire events (Hiers et al., 2000); these burns typically occur between February and late April. 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 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 before germination (Baskin and Baskin, 1989; Degreef et al., 2002, sources cited therein). However, another researcher (J. Pascarella, Valdosta State University, personal communication) independently collected mature seeds from *B. arachnifera* populations in 2004 and reported successful germination of seeds that had only been soaked in water overnight. Thus, it is possible that *B. arachnifera* seeds may be capable of germinating in the field before the onset of winter conditions. In a previous attempt to document field germination of *B. arachnifera*, populations were monitored only in the spring and summer and no seedlings were reported (L. D. Humphrey, Georgia Department of Natural Resources, unpublished manuscript). The low number of *B. lanceolata* germinants that we obtained in this study made it hard to assess whether *B. lanceolata* might have similar germination patterns.

Very few reproductive traits were found to be significantly different between the rare and common *Baptisia* species, counter to our expectations. If reproductive traits are not largely responsible for the rarity of *B. arachnifera*, why then does this species have such a restricted distribution (260 km²)? Because *B. arachnifera* historically has been found only within a small portion of the lower Coastal Plain, Faircloth (1987) postulated that edaphic or other environmental factors might be driving this species' endemism.

We found that both *B. arachnifera* and *B. lanceolata* occurred under a relatively open forest canopy on acidic, sandy soils with variable levels of micronutrients. The high variability in canopy openness among *B. arachnifera* populations is largely due to differences in current land management, which includes pine plantations (canopy 29% and 38% open) and a utility right-of-way (canopy 100% open). The significantly higher flower production in the Powerline population led us to investigate the correlation between canopy openness and flower production in both *Baptisia* species. While we observed a weak positive correlation between these two variables, data from an earlier study of eight *B. arachnifera* populations (K. R. Tassin and A. J. McGee, Georgia Department of Natural Resources, unpublished manuscript) provide further evidence that flower production is indeed positively related to the percentage canopy openness ($r^2 = 0.89$) for this endangered plant.

We also found that certain *Baptisia* populations had noticeably elevated levels of soil micronutrients. For example, Moody Forest had magnesium levels that were an order of magnitude higher than all other *Baptisia* populations, while manganese levels were especially high at General Coffee State Park. Overall, *B. lanceolata* occurred on soil with significantly higher levels of manganese than *B. arachnifera*, suggesting that *B. arachnifera* has a low tolerance for the micronutrient. Because the sites of the studied *Baptisia* populations are currently managed for different objectives, it is likely that they also have divergent land use histories, including fire regimens. Land use legacies have been identified as an important component of conservation efforts (Foster et al., 2003) and might help explain some of the differences in environmental variables that we observed.

Another possible explanation for the limited distribution of *B. arachnifera* is that it is the result of a relatively recent speciation event, or neo-endemism (Witkowski and Lamont, 1997; Walck et al., 2001). *Baptisia arachnifera* is one of three *Baptisia* species that have simple leaves (Isley, 1981). Although additional studies are needed to analyze phylogenetic relationships, it is possible that *B. arachnifera* arose from *B. perfoliata*, another simple-leaved *Baptisia* that occurs in the same region of southeastern Georgia. Finally, a species' inability to expand its range might also be due to poor colonization via decreased seed production and/or lack of a persistent soil seed bank (Walck et al., 2001).

Overall, we found that *B. arachnifera* might be most vulnerable during later stages of reproduction. Because it produced significantly fewer, heavier seeds than *B. lanceolata*, as well as had more damaged pods, it is possible that reduced colonization ability is limiting the distribution of *B. arachnifera*. It might be further restricted by its decreased overall seed viability when exposed to temperatures exceeding 60°C, such as occurs during prescribed burns. Thus, seed addition experiments and long-term monitoring of populations would contribute to a better understanding of the seed dynamics of *B. arachnifera* under field conditions. Finally, fostering communication with pine plantation managers is important for the conservation of *B. arachnifera* because the majority of remaining populations exist on lands managed for silviculture.

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