

RESEARCH ARTICLE

Seed Germination Strategies of Species With Restoration Potential in a Fire-Maintained Pine Savanna

Kim L. Coffey^{1,2}

L. Katherine Kirkman

Joseph W. Jones Ecological Research Center, Ichauway
Route 2 Box 2324
Newton, GA 39870 USA

¹ Corresponding author:
coffekl@co.mecklenburg.nc.us

² Current address:
Mecklenburg County
Division of Natural Resources
9401 Plaza Road Extension
Charlotte, North Carolina 28215 USA

ABSTRACT: Seed germination phenology studies are important tools for determining whether seeds exhibit dormancy and what environmental conditions trigger germination. Within longleaf pine (*Pinus palustris* Miller) ecosystems of the southeastern United States Coastal Plain, little is known about dormancy patterns and germination cues of the suite of native species composing the diverse fire-maintained ground cover vegetation. We used two methods to determine if several dominant or functionally important herbaceous species were capable of forming a persistent soil seed bank, including: (1) a germination phenology study and (2) a buried seed bag study. Results indicate that within species studied from three common families (Asteraceae, 2 species; Fabaceae, 8 species; and Poaceae, 3 species), species within the Fabaceae family seem most capable of forming long-term persistent seed banks. Although most of the Poaceae and Asteraceae species examined exhibited little dormancy in the germination phenology study, evidence from the buried seed bag study indicates that several species may form transient or even short-term persistent seed banks under favorable conditions. The absence of evidence of persistent seed banking potential for several dominant species examined in this study suggests that seed reintroduction will likely be a necessary component in restoration efforts in longleaf pine ecosystems.

Index terms: hard seed coat, restoration, seed bank, seed dormancy, seed germination

INTRODUCTION

An understanding of how environmental cues elicit germination and the role of persistent seed banks is useful in developing species reintroduction strategies in a restoration context. Seeds of most temperate species have some form of primary dormancy and may display annual cycles in germination requirements in response to seasonal changes in temperature and precipitation (Parker et al. 1989, Baskin and Baskin 1998). These responses vary widely among species and are difficult to predict. Information pertaining to the presence of a seed bank, which affects both the potential recovery and rate of recovery of the ground cover following disturbance, can provide insights into the seed pool available for natural recruitment over time (Bakker et al. 1996, Bekker et al. 1998a). Seed banks are particularly important for disturbed sites where the surrounding landscape has been severely altered and no longer serves as a source of propagules for dispersal.

Seed dormancy and germination data are also necessary for developing field establishment and nursery production techniques for native species restoration efforts. Such information is especially relevant to grassland and savanna ecosystem restoration where re-establishment of a diverse perennial ground cover is usually dependent on seed germination rather than outplanting propagated seedling material. For most grassland and savanna ecosys-

tems, it is difficult to obtain propagated native seedlings, and where plant materials are available, the cost is prohibitively high for large-scale restoration (Holliday 2001, Coffey and Kirkman 2004).

Germination phenology studies are an effective tool for understanding conditions required for germination and detecting seed dormancy (Baskin and Baskin 1998). Although numerous studies have addressed dormancy characteristics in perennial herbaceous plants, little is known about specific germination requirements, transient (< 1 year) versus short-term persistent (1–5 year) and long-term persistent (>5 year) seed-banking potential (Bakker et al. 1996, Thompson et al. 1998), and long-term seed viability of species found in the critically endangered fire-dependent longleaf pine (*Pinus palustris* Mill.) savannas of the southeastern United States Coastal Plain (Glitzenstein et al. 2001).

Restoration efforts in longleaf pine ecosystems have focused predominantly on establishment of longleaf pine only, particularly through plantations on old fields (e.g., longleaf pine seedlings planted through the USDA's Conservation Reserve Program, [Holliday 2001]). Although recognition of the functional importance of native ground cover has led to increased interest in herbaceous species reintroductions, commercial sources of seed native to longleaf pine ecosystems are unavailable, and many key questions remain unanswered regarding growth and establishment

of these native species (Pfaff and Gonter 1996, Glitzenstein et al. 2001).

Ground cover vegetation of longleaf pine ecosystems is dominated by perennial and presumably long-lived species (Drew et al. 1998, Mitchell et al. 1999), and no evidence of a strong role of seed banking has been documented for longleaf pine-wiregrass upland vegetation. Cox et al. (2004) have suggested that potential seed banking occurred in longleaf pine sandhills, where species richness increased following ground chopping, presumably due to breaking up soil crust and exposing dormant seeds. Varner et al. (2000) noted the recovery of native herbaceous ground cover species after fire was reintroduced into the Flomaton Natural Area, a longleaf pine site in Alabama, from either long-term survival of individual perennial plants or the presence of a persistent seed bank. Maliakal et al. (2000) found evidence of a soil seed bank in longleaf pine-wiregrass flatwoods in peninsular Florida, but concluded that the seed bank and existing vegetation were dissimilar, suggesting a low potential vegetation recovery from the seed bank. Species recruited in this seedling emergence study were generally "weedy" species or species representing historical ecological conditions (Maliakal et al. 2000). The study was conducted for only four months, and dormant seeds (those that would represent a persistent soil seed bank) would not have been detected; therefore, an assessment of persistent seed bank potential is somewhat inconclusive. Similarly, without differentiation between transient and persistent seed banks, Jenkins (2003) found that species represented in the seed bank of a longleaf pine flatwoods site versus a restoration site in central Florida differed from each other and from the representative vegetation located in the study plot area. In another recent seedling emergence study comparing seed banks of longleaf pine flatwoods to disturbed areas, Cohen et al. (2004) found that species indicative of flatwoods flora germinated from soil cores; however, most germinants were wetland species that have been observed in other seed bank studies (Kirkman and Sharitz 1993, Poiani and Dixon 1995) rather than dominant ground cover species typical to longleaf pine savannas.

Although the technique of charting seedling emergence from soil cores has been widely used to assess seed bank potential (Roberts 1981, Benoit et al. 1989, Leck 1989, Gross 1990), the application of this approach to a spatially diverse vegetation cover, such as the species-rich longleaf pine ecosystem, is probably limited (Roberts 1981, Gross 1990, Cohen et al. 2004). Heterogeneity among soil samples, even when composited over large areas, may suggest that the sampling effort is inadequate to capture seed from numerous species, and potentially those species targeted for restoration. Such studies can verify the seed bank potential of some species, but they do not necessarily address the seed bank potential of specific dominant components of the native ground cover of the longleaf pine ecosystem.

Asteraceae (composites), Poaceae (grasses), and Fabaceae (legumes) families dominate the flora of the longleaf pine ecosystem. They comprise the primary structural and functional components in upland, fire-maintained longleaf pine ecosystems. Native grasses, particularly warm-season C4 species, are dominant ground cover species and are desirable for restoration due to their importance in reintroducing fuel for fire management, although little information is available regarding their dormancy except for weedy or commercially valuable species (Simpson 1990). Legumes are also abundant ground cover species (Martin et al. 1975, Hains et al. 1999), and are believed to contribute nitrogen to an environment where nitrogen is volatilized by frequent fires (Boring et al. 1990, Hendricks and Boring 1999). Additionally, legumes provide important food and cover for wildlife (Hains et al. 1999, Yarrow and Yarrow 1999). Composites represent one of the most abundant and diverse families in longleaf pine ecosystems (Drew et al. 1998), contributing to the exceptionally high species diversity of this ecosystem. In addition, numerous composite species are considered desirable for ground cover restoration because they are aesthetically prominent and important as forage, host, or nectar plants for native birds, butterflies, and insects (Byre 1997, Taron 1997, Yarrow and Yarrow 1999).

In some grasslands (e.g., Konza prairie), dominant grass species rely primarily on vegetative reproduction rather than regeneration through a large and persistent seed bank (Abrams 1988). Grime et al. (1981) found a high percentage of both annual and perennial grasses capable of germinating immediately, also suggesting the lack of a long-term persistent seed bank. In general, grasses contribute less to the seed bank than composites and other forbs (Roberts 1981), and perennial grasses are less likely to be present in the seed bank than annual grasses (Abrams 1988, Rice 1985), as short-lived species commonly have more persistent seeds (Thompson et al. 1998).

Numerous legume species have seeds that exhibit physical dormancy in the form of an impermeable seed coat (Quinlivan 1971; Rolston 1978; Baskin and Baskin 1989, 1998). This dormancy mechanism delays germination from time of seed maturity until environmental conditions become favorable to promote softening of the seed. This hard seed coat may not be present immediately at maturity, as some species will readily germinate prior to being collected and stored (Pfaff and Gonter 1996, Glitzenstein et al. 2001). However, hard-seededness is commonly induced soon after maturity (Pfaff and Gonter 1996) and likely results in moisture reduction within the seed (Quinlivan 1971). Such physically dormant seeds can persist in the seed bank for long periods of time (Hull 1973, Lewis 1973, Roberts and Boddrell 1985) until environmental conditions favor germination.

Several mechanisms may contribute to dormancy break, including daily temperature fluctuations (Rice 1985), relative humidity (Cushwa et al. 1968, Rolston 1978), and high temperatures potentially associated with fire (Cushwa et al. 1968, Martin et al. 1975). McKeon and Mott (1982) found that the highest soil surface temperatures occurred immediately before the rainy season and postulated a mechanism for some species that ensured germination prior to precipitation and favorable growing conditions. Peak germination season is often the same from year to year for a given species (Baskin and Baskin 1998).

This study was designed to test for seed dormancy and seed banking potential of several functionally and compositionally important ground cover species in longleaf pine ecosystems. Specific questions addressed include: (1) Do seeds of common perennial ground cover species exhibit dormancy?, (2) What phenological conditions promote seed germination?, and (3) Which of the selected species have the potential to form persistent soil seed banks?

MATERIALS AND METHODS

Study site

This study was conducted on Ichauway, the privately owned reserve of the Joseph W. Jones Ecological Research Center, in the lower Gulf Coastal Plain of southwestern Georgia. The 11,600 ha property consists of approximately 7000 ha of mature longleaf pine forest, and nearly half of this area has intact native ground cover. Frequent prescribed surface fires have been used to manage the site since the early 1900s. Dominant soils are primarily Ultisols. The region receives approximately 132 cm of rainfall per year, and average daily temperatures are 11 °C in winter and 27 °C in summer.

Experiment 1: germination phenology

Species selected for this study are perennials common to frequently burned, undisturbed longleaf pine savannas and represent three major families with important functional and compositional roles as described earlier. Seed from these species was absent in previous seed bank studies (L.K. Kirkman, unpubl. data), leading us to question the role of seed banking in some common species within longleaf pine ecosystems. While there are hundreds of species to examine, species were selected for this initial study based on seed availability and their propagation potential in native nursery seed production for restoration purposes. Furthermore, our goal was to examine some of the most common species in a few major plant families and to select those representing varied dispersal mechanisms (e.g., wind, gravity, and

animal-transported seeds). Seed from 13 frequently occurring species was hand-collected at maturity on Ichauway during the growing seasons of 2001-2003.

Following collection, all seed was stored inside at room temperature (23 °C, with controlled humidity) until the study was initiated. Species planted included three dominant grasses [*Aristida stricta* Michx., *Sorghastrum secundum* (Elliott) Nash, and *Sporobolus junceus* (P. Beauv.) Kunth], two commonly occurring composites [*Solidago odora* Aiton and *Vernonia angustifolia* Michx.], and eight legumes [*Centrosema virginianum* (L.) Benth., *Desmodium ciliare* (Muhl. ex Willd.) DC., *D. strictum* (Pursh) DC., *Lespedeza angustifolia* (Pursh) Elliott, *L. hirta* (L.) Hornem., *Mimosa quadrivalvis* L., *Orbexilum lupinellus* (Michx.) Isley, and *Tephrosia virginiana* (L.) Pers.]. More legume species were selected for study due to their restoration value for wildlife food and cover. Species nomenclature follows Wunderlin and Hansen (2003).

Standard seedling flats (28 cm x 54 cm x 6 cm) were filled with a mixture of Fafard 3B-mix potting soil and sand (4:1 ratio), and thoroughly watered. Potting soil was used instead of native soil to eliminate the presence of non-target native seeds, and sand was added to aid in drainage. Three replications of 300 seeds per species were placed in flats (one species per flat; three flats per species; N=900 total seeds per species) and randomly arranged on outside benches under greenhouse shade cloth (63% shade). Shade cloth decreased extreme heat conditions and diffused raindrop impact on the soil surface. Seed of the 13 study species was spread over the soil in flats in December 2001. Seed was lightly pressed by hand onto the soil to ensure soil contact without complete burial, mimicking natural seedfall. Flats were watered using untreated well water once weekly for 15 minutes using automatically timed overhead sprinklers, and were exposed to ambient outdoor temperatures and light/dark periods. Germinants were monitored weekly throughout the study, with radicle or coleorhiza protrusion as the germination criterion. Once scored, germinants were removed from the flat to prevent

recounting. Daily weather conditions on-site (Newton, GA) were monitored using information on the Georgia Automated Environmental Monitoring Network (www.griffin.peachnet.edu/bae). Flats remained under shade cloth through April 2004, when the project was terminated.

Low precipitation occurred in spring 2002, and we altered the watering schedule beginning in May to 15 minutes daily to prevent dessication of seeds and new germinants. This cycle coincided with the typical period of afternoon thunderstorms, which would have provided natural moisture, but were absent during drought years. Watering schedule returned to weekly the first week in October 2002. This same watering scheme was applied in 2003.

Upon termination of the project in April 2004, we attempted to recover seed remaining in the flats. We were unable to recover any grass or composite seeds from the soil; however, hard-seeded legume seeds were recovered and tested for germinability. To recover seed, soil was dried in a drying oven at 41 °C for 24 hours, and sieved twice (2 mm followed by 1 mm sieve opening) to isolate seeds. Retrieved legume seeds were counted, scarified using a straight razor to break the hard seed coat (C. Baskin, pers. comm.), and placed on moist filter paper in Petri dishes to test for viability based on germination. Because viable legume seed readily germinates after the seed coat is broken (pers. observation of numerous trials), we used germination rate to indicate viability rather than the more labor-intensive method using a 1% solution of 2,3,5-triphenyl-2H-tetrazolium chloride (Moore 1973) to stain viable seeds. Soft and moldy seed was considered non-viable (Baskin and Baskin 1998, Bekker et al. 1998b). Moldy seed was removed from the dishes as discovered and seed that did not germinate after three weeks was tested for firmness, indicating viability. Firm seeds were retained until germination occurred or were discarded when they became moldy or soft.

Experiment 2: buried seed bags

To determine seed-banking potential, we

initiated a long-term study using buried bags, projected for completion in 2018. This study utilizes data collected during the first three sample periods (2001-2005). Ten thousand seeds (100 bags per species; 100 seeds per bag) of each of 11 of the 13 species in the phenology study described earlier (Table 1) were placed in nylon mesh bags (6.5 cm x 7 cm; mesh size 100 microns). Sand was added to each bag (9.0-9.5 g) to keep seeds from clumping together, and each bag was sewn shut. Bags were strung on 18-gauge galvanized wire, with enough room between bags to avoid overlap in the soil (approximately 10 cm apart). Multiple species were placed on each strand (number of species per strand varied with number of species buried each year) to avoid total loss of a single species in the event of soil disturbance.

Seed bags (N=100 bags per species) were buried within an open, frequently-burned 68-year-old slash pine (*P. elliotii* Englem.) plantation that is, over several decades, being gradually restored to a longleaf pine canopy. Seed of three grass species (*Aristida stricta*, *Sorghastrum secundum*, and *Sporobolus junceus*), six legumes (*Cen-*

trosema virginianum, *Desmodium strictum*, *Lespedeza angustifolia*, *L. hirta*, *Mimosa quadrivalvis*, and *Tephrosia virginiana*), and two composites (*Solidago odora* and *Vernonia angustifolia*) was collected and buried on Ichauway from 2001-2003. An insufficient quantity of *Desmodium ciliare* and *Orbexilum lupinellus* seed (two of the species used in the germination phenology experiment) prevented burial experiments with these two species. Bags were strung onto galvanized wire strands through a small hole punched near the edge of the bag seam and the strands of bags were buried to a depth of 5 cm. Each strand was attached to a tagged metal curly stake above ground. Twenty bags of each species were removed in the winter at one and two years post-burial (N=2000 seeds per species per year). Species buried in 2001 were also tested at four years post-burial. Each curly stake with attached wire strand was lifted with a trowel inserted beneath the wire to loosen bags from soil. All bags were brought into the lab for processing. The remaining bags will be retrieved during the winter at four, eight, and 16 years post-burial.

Aristida stricta and *Sorghastrum secundum* seeds in Petri dishes frequently develop mold that destroys seed prior to germination (pers. observation), so rather than conducting germination tests for these species, they were tested for viability using a 1% solution of 2,3,5-triphenyl-2H-tetrazolium chloride (Moore 1973). Seed from all other species that were not prone to mold attack was placed on moist filter paper in Petri dishes (seed from one bag per dish), maintained in a greenhouse, watered daily, and monitored for germination. Prior to germination tests, seed coats of all legume seeds recovered were scarified using a straight razor to break the impermeable seed coat (C. Baskin, pers. comm.). Composite and grass seed was not treated in any way prior to tetrazolium or germination tests. Germinants were removed and recorded daily until three weeks passed without germination, at which point the trials were concluded. Soft seed was also removed and considered non-viable. All results are based on the total number of seeds that germinated or stained (indicating viable seed) out of the total number of seeds per species buried each year (N=2000 per species per year).

Table 1. Percent seed germination (number of seed germinated or stained with Tetrazolium out of possible 2000 seeds per year). ^a = seed bag burial in 2001; ^b = seed bag burial in 2002; ^c = seed bag burial in 2003; NA = no data available; * = all germination occurred in year one.

Family	Species	% germination from seed bags 1 year after burial	% germination from seed bags 2 years after burial	% germination in flats (mean ± SE) 2 years in flats
Asteraceae	<i>Solidago odora</i> ^b	34	12	66 ± 4.34*
Asteraceae	<i>Vernonia angustifolia</i> ^b	5	<1	15 ± 1.28*
Fabaceae	<i>Centrosema virginianum</i> ^c	14	10	72 ± 0.19
Fabaceae	<i>Desmodium ciliare</i>	NA	NA	93 ± 2.61
Fabaceae	<i>D. strictum</i> ^b	2	0	91 ± 0.89
Fabaceae	<i>Lespedeza angustifolia</i> ^b	82	74	69 ± 2.50
Fabaceae	<i>L. hirta</i> ^b	90	89	83 ± 5.61
Fabaceae	<i>Mimosa quadrivalvis</i> ^c	56	51	31 ± 1.87
Fabaceae	<i>Orbexilum lupinellus</i>	NA	NA	58 ± 4.41
Fabaceae	<i>Tephrosia virginiana</i> ^b	61	50	73 ± 1.09
Poaceae	<i>Aristida stricta</i> ^a	0	0	57 ± 7.12*
Poaceae	<i>Sorghastrum secundum</i> ^a	26	34	17 ± 2.89*
Poaceae	<i>Sporobolus junceus</i> ^b	1	<1	30 ± 0.56*

RESULTS

Germination phenology

Seed from all grass and composite species germinated within the first six months of the study, though germination rates were highly variable among species (Figures 1a and 1b).

Legume germination varied widely among the eight species, but distinct seasonal patterns were identified among groups of species, particularly among congeners. Seed from both *Desmodium ciliare* and *D. strictum* had total germination rates above 90%, the majority of which occurred during the first year (Figure 1c), suggesting that these legume species do not exhibit the strong physical dormancy attributed to an impermeable seed coat found in many legume species. All other legume species

we examined germinated throughout the 28 months of the study. Germination response to changing environmental conditions in February and March can be seen most clearly in two species, *Centrosema virginianum* and *Tephrosia virginiana* (Figure 1d), although *Orbexilum lupinellus* and *Mimosa quadrivalvis* (Figure 1e) exhibit a similar pattern. For *Lespedeza angustifolia* and *L. hirta*, little germination occurred during the first spring (2002) following warming temperatures, but by January of 2003 and again in 2004, germination rates sharply increased following coldest temperatures, with lows averaging near freezing (0 °C) in both years (Figure 1f).

Recovery of seeds in buried seed bags

Seed viability based on buried bag extractions over time varied considerably, even

within families. Among grass species buried in seed bags in 2001 (species with four years of buried bag data available), *Aristida stricta* showed no sign of a soil seed bank while *Sorghastrum secundum* still had 9% seed viability after four years of burial. Only 1% of *Sporobolus junceus* seeds recovered in year one were viable and even fewer following two years of burial (Table 1). In composite species, 12% of *Solidago odora* seed remained viable after two years of burial, whereas <1% of *Vernonia angustifolia* seed remained viable during this period (Table 1).

With the exception of *Desmodium strictum*, seed of legume species remained viable for at least one year after burial (Table 1). Over 70% of both species of *Lespedeza* seed was recovered and germinated following two years of burial. *Tephrosia virginiana* seed had a lower recovery rate, but of those recovered, 50% germinated after

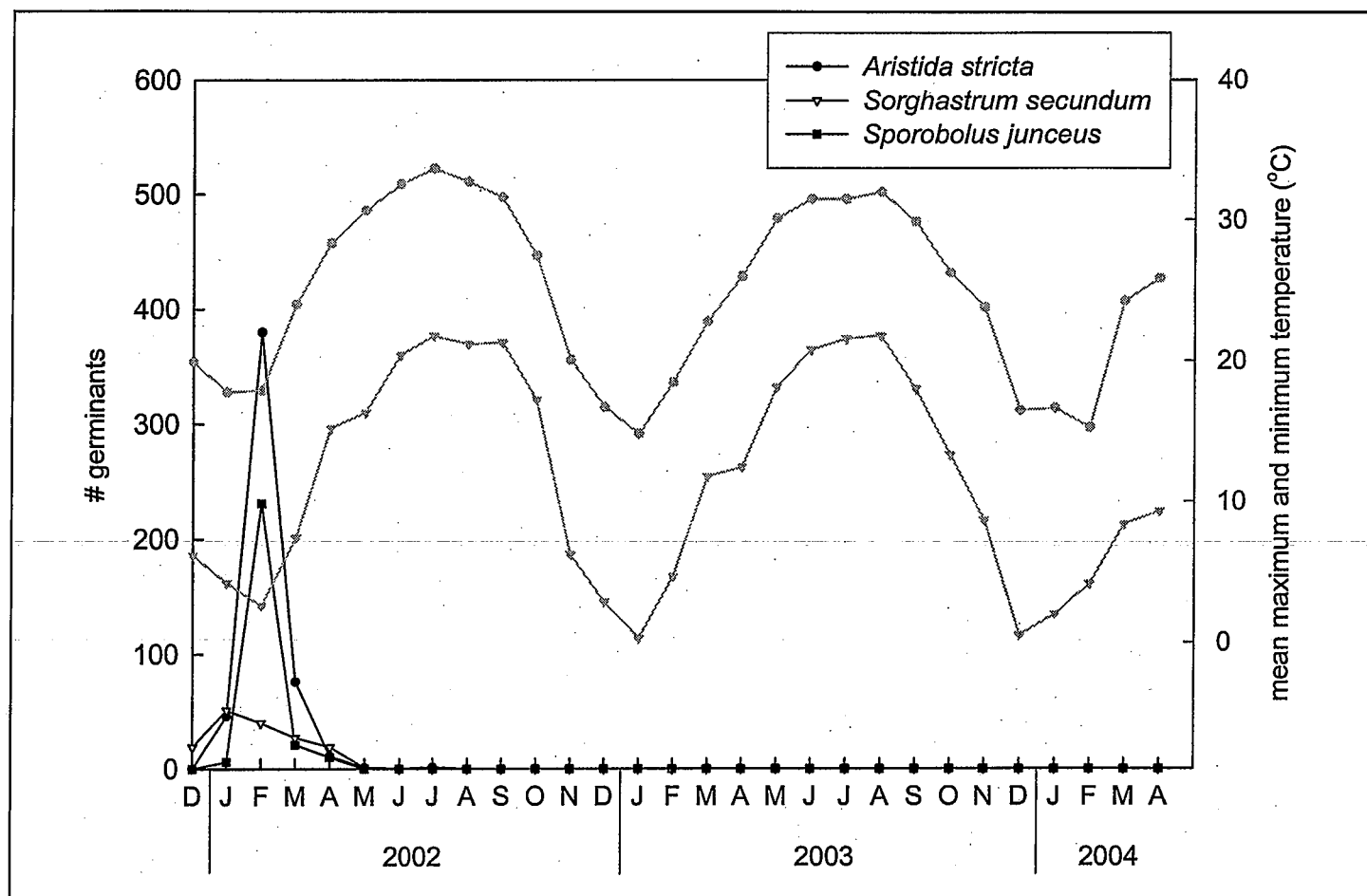


Figure 1a. Monthly germination patterns of grass species in seedling flats – germination only within the first six months of the study. Maximum and minimum mean monthly temperatures are represented by gray background lines.

two years. *Centrosema virginianum* and *Mimosa quadrivalvis* both appear to have hard seed coats with viable seed persisting for at least two years in the seed bank (Table 1).

DISCUSSION

This study indicates that at least a short-term persistent soil seed bank (two years) is present for some species in longleaf pine-wiregrass savannas, whereas, other species have little or no seed dormancy. Although we recognize that our results are limited to only a few of the many ground cover species in this species-rich ecosystem, the germination patterns within the three major plant families studied appear to have similarities to other grassland ecosystems (Grime et al. 1981, Rabinowitz 1981, Freeman 1998, Stöcklin and Fischer 1999). Germination of legume species tested in this study appeared to be triggered by exposure to cold winter temperatures followed by warming trends in the spring

with the largest fluctuation between high and low temperatures (24 °C difference between average high and average low temperatures). Our finding that *Desmodium* species lacked the hard seed coat present in *Lespedeza* and other legume species has also been reported elsewhere (Cushwa et al. 1968, Martin et al. 1975). Species with hard seed coats are likely capable of forming long-term persistent seed banks, and continuation of the buried seed bag portion of this study will yield long-term data on this subject. Greater seed longevity of legumes than of grasses and forbs has also been demonstrated in storage and in buried seed bags (Hull 1973). Admittedly, in our study, fewer species of grasses and forbs were examined than of legumes, limiting broad generalizations across families.

While all germination of grass and composite seed placed on the soil surface in this study occurred within the first year, suggesting non-dormant seed or at most a transient seed bank, contrasting evidence

from buried seed of *Sorghastrum secundum* and *Solidago odora* indicates that these species can persist in the soil for at least two years, and in the case of *Sorghastrum secundum*, a limited number of viable seeds were present (9%) four years post-burial. Although we were unable to directly address the fate of seeds in flats, we offer the following alternative explanations for these differing results. The discrepancy in the data between seedling flats and buried seed bags could indicate that non-dormant seed is inhibited from germinating due to a light requirement unavailable because of depth of seed bag burial (Baskin and Baskin 1989, Qi et al. 1996), yet is still capable of forming a seed bank. If exposure to light is necessary for germination, seed of these species would be considered non-dormant, and germination phenology results and buried seed bag results would then be consistent in terms of dormancy absence. In addition, we also acknowledge that there was a potential loss of seed from the soil surface of the seedling flats during the first

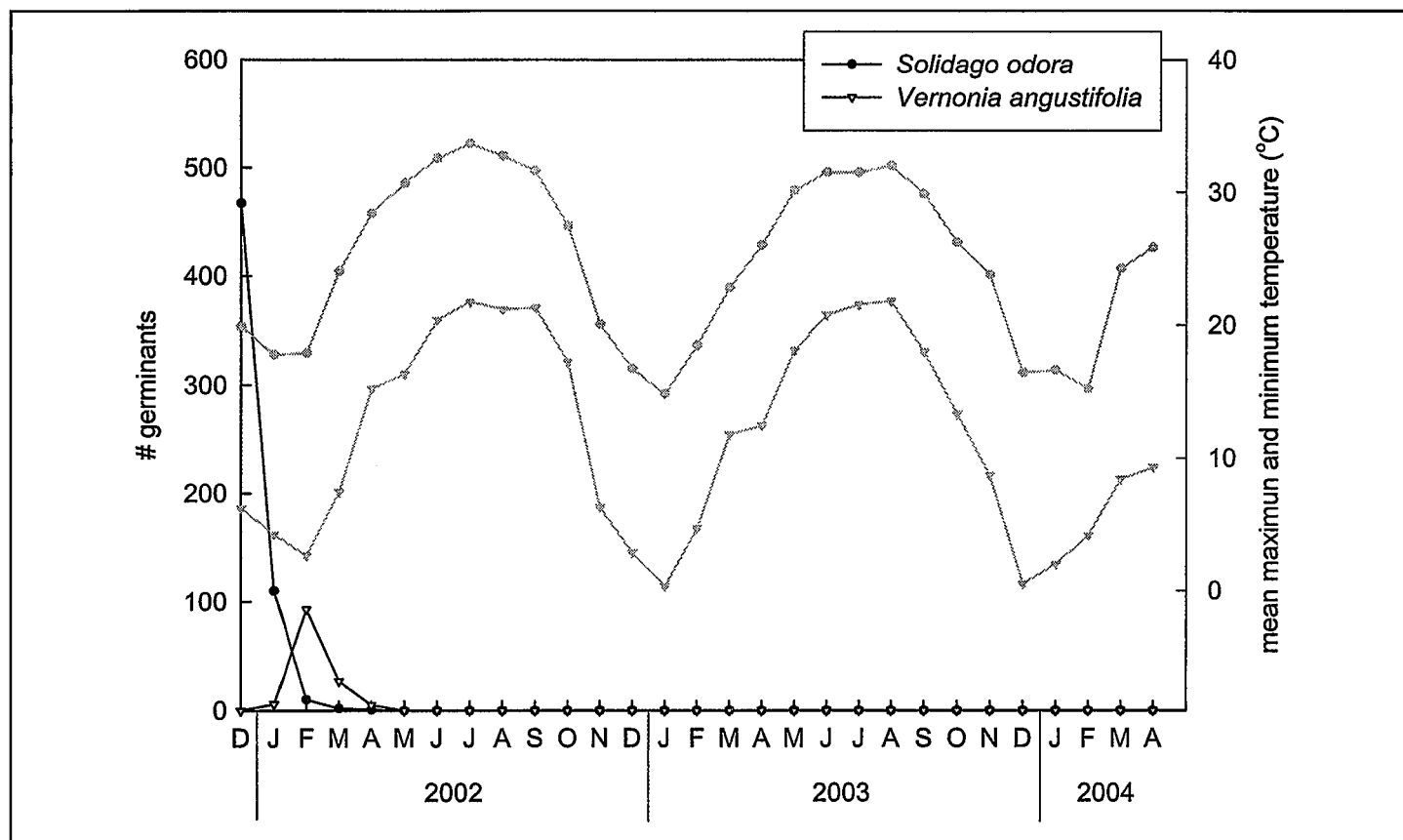


Figure 1.b. Monthly germination patterns of composite species in seedling flats – germination only within the first six months of the study. Maximum and minimum mean monthly temperatures are represented by gray background lines.

year due to either wind or rain displacing small seed, or even predation by animals. This could be of particular importance in the case of *Sorghastrum secundum*, where evidence from buried seed bags contradicts that from the flats and suggests a strong possibility of at least some seed persisting for four years. Future studies should include covering seedling flats with screening material (a method used to prevent rodent seed predation) (Greene and Curtis 1950) to eliminate the possibility of seed loss prior to study conclusion.

Even though data from *Aristida stricta* seed in our studies suggests that this species is unlikely to form a persistent seed bank, other field studies suggest that at least short-term (two year) seed persistence may occur in the soil (Seamon 1998, Mulligan and Kirkman 2002, Cox et al. 2004). Thus, it may not be possible to entirely generalize our experimental conditions to field conditions, perhaps concerning timing of precipitation events or even prolonged drought conditions. Espinar et al. (2005)

found that environmental conditions for the seed bank (represented in our study by buried seed bags) during the “no-growth” season affected the seed response at germination. By retrieving bags in winter every year, we might not be able to fully address seasonal effects on dormancy and germinability.

Different germination patterns were also observed between buried seed bags and seed placed in flats in both *Lespedeza* species. These results could be due to specific light requirements associated with burial (Qi et al. 1996), as discussed earlier. Another possible explanation is that *Lespedeza* seed placed in flats experienced larger daily temperature fluctuations or higher daily temperatures than seed buried in the soil, leading to increased germination of seed closer to the soil surface (Cushwa et al. 1968). Disturbances that decrease canopy vegetation, exposing seeds in the soil to more extreme temperature conditions, trigger seed coat softening and induce germination of hard-seeded species (Rolston

1978, Baskin and Baskin 1989). Although perennial species of longleaf pine ecosystems, such as *Lespedeza*, persist through frequent fire, fire exposes seeds in soil to higher temperatures and higher amplitudes of temperature fluctuation (Grime 1989), leading in some cases to germination.

Long-lived seeds constitute a buffer against risks of local extinction due to stochastic processes (Stöcklin and Fischer 1999). Such buffering capacity suggests that vegetation subjected to frequent disturbance benefits from producing a persistent seed bank (Thompson et al. 1998); however, this adaptive advantage does not necessarily apply to fire-maintained longleaf pine vegetation, where most species are perennials that sprout back from below-ground perennating organs after fire. Once established, individuals of these species presumably persist for many years (Kirkman et al. 2001), and long-lived adult plants are generally unlikely to form a persistent seed bank (Rees 1994). This situation resembles a stable community

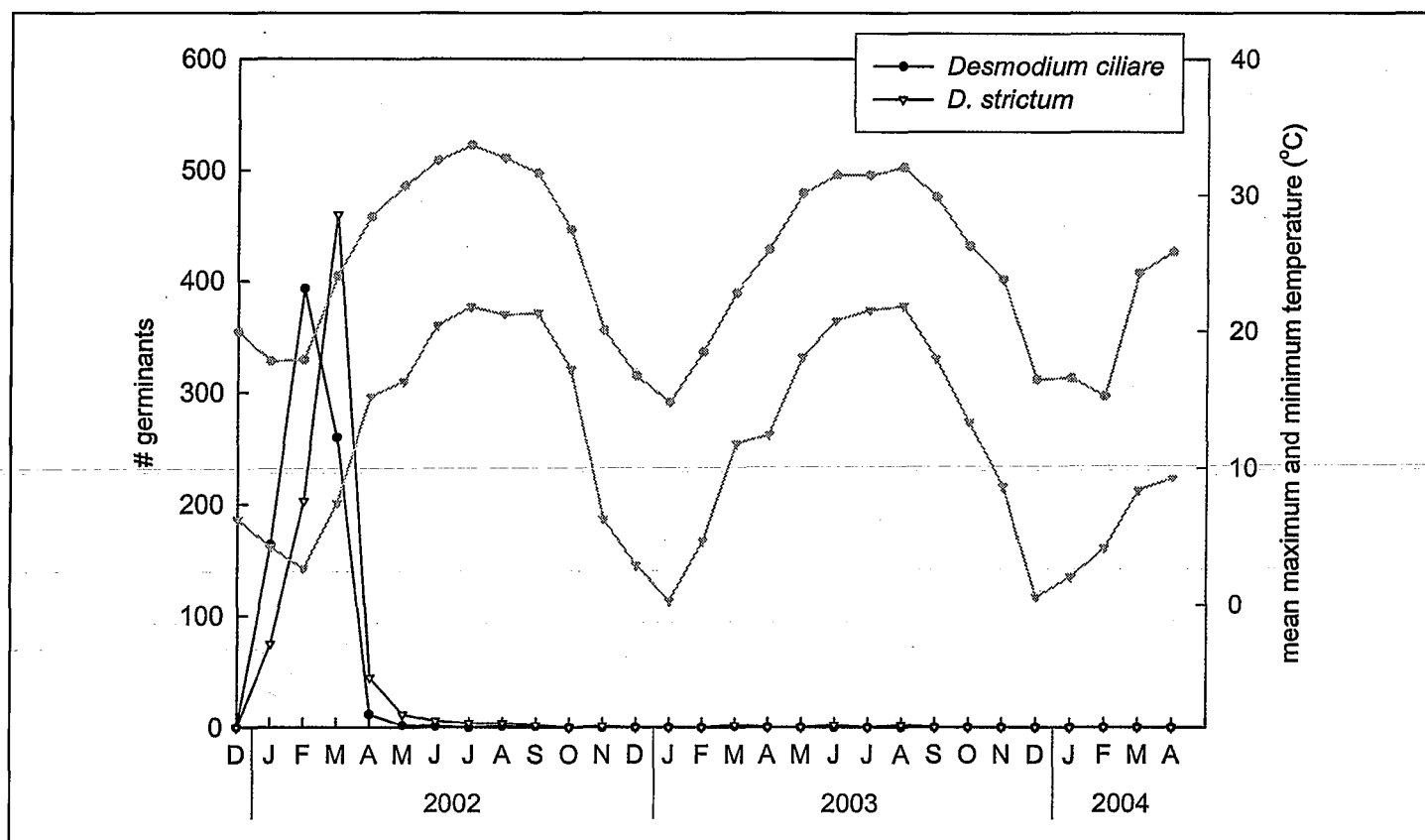


Figure 1.c. Monthly germination patterns of *Desmodium* species in seedling flats – most germination occurred within year one of the study. Maximum and minimum mean monthly temperatures are represented by gray background lines.

that is more likely to favor a transient seed bank (Thompson et al. 1998). In this type of savanna community, variable environmental conditions suitable for seedling establishment are likely associated with precipitation events and microsite variations that provide adequate moisture, as well as with fire that removes aboveground competition for light. The combination of periodic recruitment events and persistent vegetation likely balance the necessity of a persistent seed bank for population survival. Furthermore, regular removal of aboveground biomass with frequent fire in longleaf pine ecosystems does not promote the introduction of weedy annual species (Drew et al. 1998), which do tend to form persistent seed banks (Bekker et al. 1998b). Thus, the degree of seed bank persistence in longleaf pine grassland communities can probably be viewed as intermediate between temperate deciduous forest communities and highly disturbed lands (Bekker et al. 1998b). Validation of this

perspective will require knowledge of seed longevity traits of a greater percentage of the total flora over a long time period.

The presence of persistent seed banks has direct implications for restoration areas by providing propagules of an initial suite of native ground cover species in disturbed areas, particularly in areas where propagule dispersal from neighboring high-quality sites is limited or non-existent. However, the limited amount of viable seed of several dominant species in the seed bank suggests that these species have alternative mechanisms for long-term persistence in agriculturally undisturbed areas, such as re-sprouting or asexual / vegetative reproduction associated with plant longevity (Abrams 1988, Jenkins 2003, Laughlin 2003). Based on results from these studies, it appears unlikely that many of the study species produce seed capable of forming persistent seed banks. This lack of long-term persistent seed banking potential in

some dominant species also confirms that seed reintroduction will likely be necessary for restoration of many dominant grasses and forbs in longleaf pine ecosystems where seed dispersal into the site over time is not an option.

ACKNOWLEDGMENTS

The authors acknowledge the assistance of S. Baumann, K. Bell, J. Biggs, J. Bowen, D. DeBruyne, R. DeMots, E. Leonard, K. Mawhinney, H. Norden, E. O'Brien, K. Schmitt, E. Schuett, and S. Wheeler with seed collection and seed bag processing. R. Mitchell provided helpful comments regarding the manuscript. The Robert W. Woodruff Foundation provided funding for this study to the Joseph W. Jones Ecological Research Center at Ichauway.

Kim Coffey is a Natural Resources Coordinator in Charlotte, N.C. Her interests

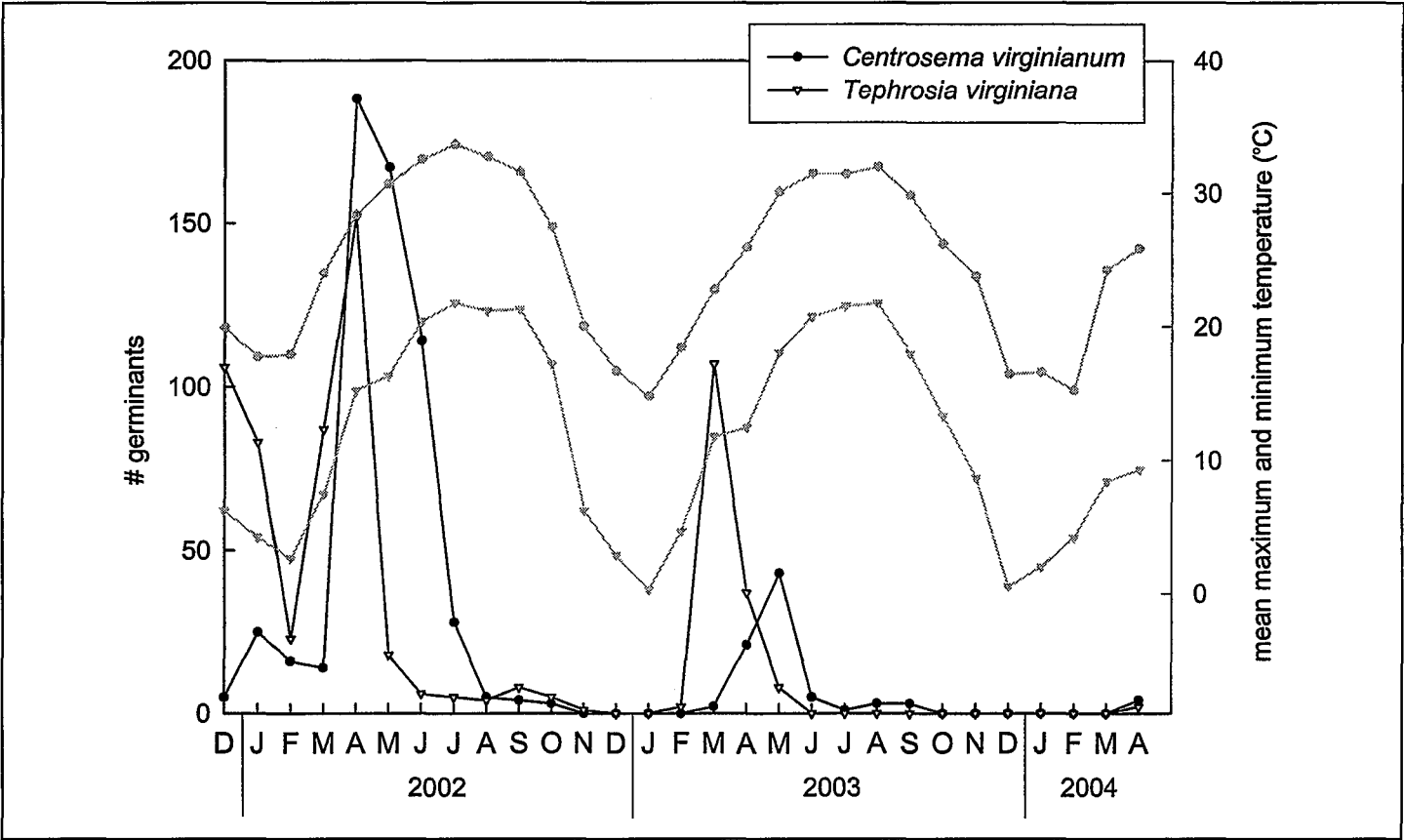


Figure 1.d. Monthly germination patterns of *Centrosema virginianum* and *Tephrosia virginiana* in seedling flats – germination occurred throughout the study period, with pronounced seasonal patterns. Note different scale on y-axis is different from other figures. Maximum and minimum mean monthly temperatures are represented by gray background lines.

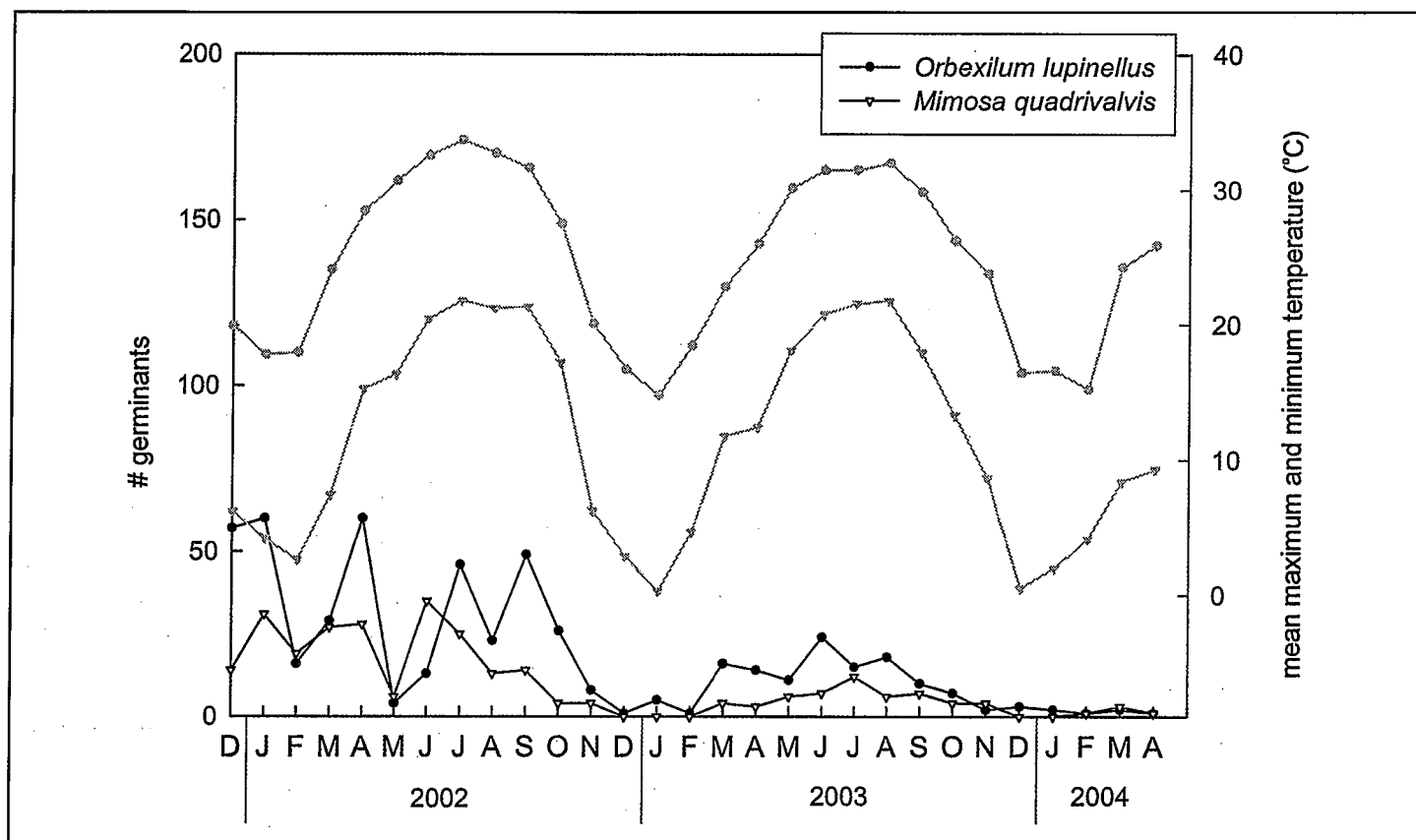


Figure 1.e. Monthly germination patterns of *Mimosa quadrivalvis* and *Orbexilum lupinellus* in seedling flats – germination occurred throughout the study period, with subtle seasonal patterns. Maximum and minimum mean monthly temperatures are represented by gray background lines.

include herbaceous species diversity and restoration and preservation of native ground cover and associated rare plant species. This work was conducted while she was employed as a research technician at the J.W. Jones Ecological Research Center.

Katherine Kirkman is an Associate Scientist with the J.W. Jones Ecological Research Center. Her research interests are in maintenance and restoration of the biodiversity of native ground cover in the longleaf pine ecosystem and associated wetlands.

LITERATURE CITED

- Abrams, M.D. 1988. Effects of burning regime on buried seed banks and canopy coverage in a Kansas tallgrass prairie. *The Southwestern Naturalist* 33:65-70.
- Bakker, J.P., P. Poschlod, R.J. Strykstra, R.M. Bekker, and K. Thompson. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* 45:461-490.
- Baskin, C.C., and J.M. Baskin. 1989. Physiology of dormancy and germination in relation to seed bank ecology. Pp. 53-66 in M.A. Leck, V.T. Parker, and R.L. Simpson, eds., *Ecology of Soil Seed Banks*. Academic Press, San Diego, Calif.
- Baskin, C.C., and J.M. Baskin. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, Calif.
- Bekker, R.M., I.C. Knevel, J.B.R. Tallowin, E.M.L. Troost, and J.P. Bakker. 1998a. Soil nutrient input effects on seed longevity: a burial experiment with fen-meadow species. *Functional Ecology* 12:673-682.
- Bekker, R.M., J.H.J. Schaminee, J.P. Bakker, and K. Thompson. 1998b. Seed bank characteristics of Dutch plant communities. *Acta Botanica Neerlandica* 47:15-26.
- Benoit, D.L., N.C. Kenkel, and P.B. Cavers. 1989. Factors influencing the precision of soil seed bank estimates. *Canadian Journal of Botany* 67:2833-2840.
- Boring, L.R., J.J. Hendricks, and M.B. Edwards. 1990. Loss, retention, and replacement of nitrogen associated with site preparation burning in southern pine-hardwood forests. Pp. 145-153 in S.C. Nodvin and T.A. Waldrop, eds., *Fire and the environment: ecological and cultural perspectives*. Proceedings of an International Symposium, Knoxville, Tenn. General Technical Report SE-69, U.S. Department of the Interior, Park Service, U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, N.C.
- Byre, V.J. 1997. Birds. Pp. 327-337 in S. Packard and C.F. Mutel, eds., *The Tallgrass Restoration Handbook*. Island Press, Washington, D.C.
- Coffey, K.L., and L.K. Kirkman. 2004. Native ground covers partners: re-establishing native ground cover in longleaf pine savannas (Georgia). *Ecological Restoration* 22:288-289.
- Cohen, S., R. Braham, and F. Sanchez. 2004. Seed bank viability in disturbed longleaf pine sites. *Restoration Ecology* 12:503-515.
- Cox, A.C., D.R. Gordon, J.L. Slapcinsky, and G.S. Seamon. 2004. Understory restoration in longleaf pine sandhills. *Natural Areas Journal* 24:4-14.
- Cushwa, C.T., R.E. Martin, and R.L. Miller. 1968. The effects of fire on seed germination.

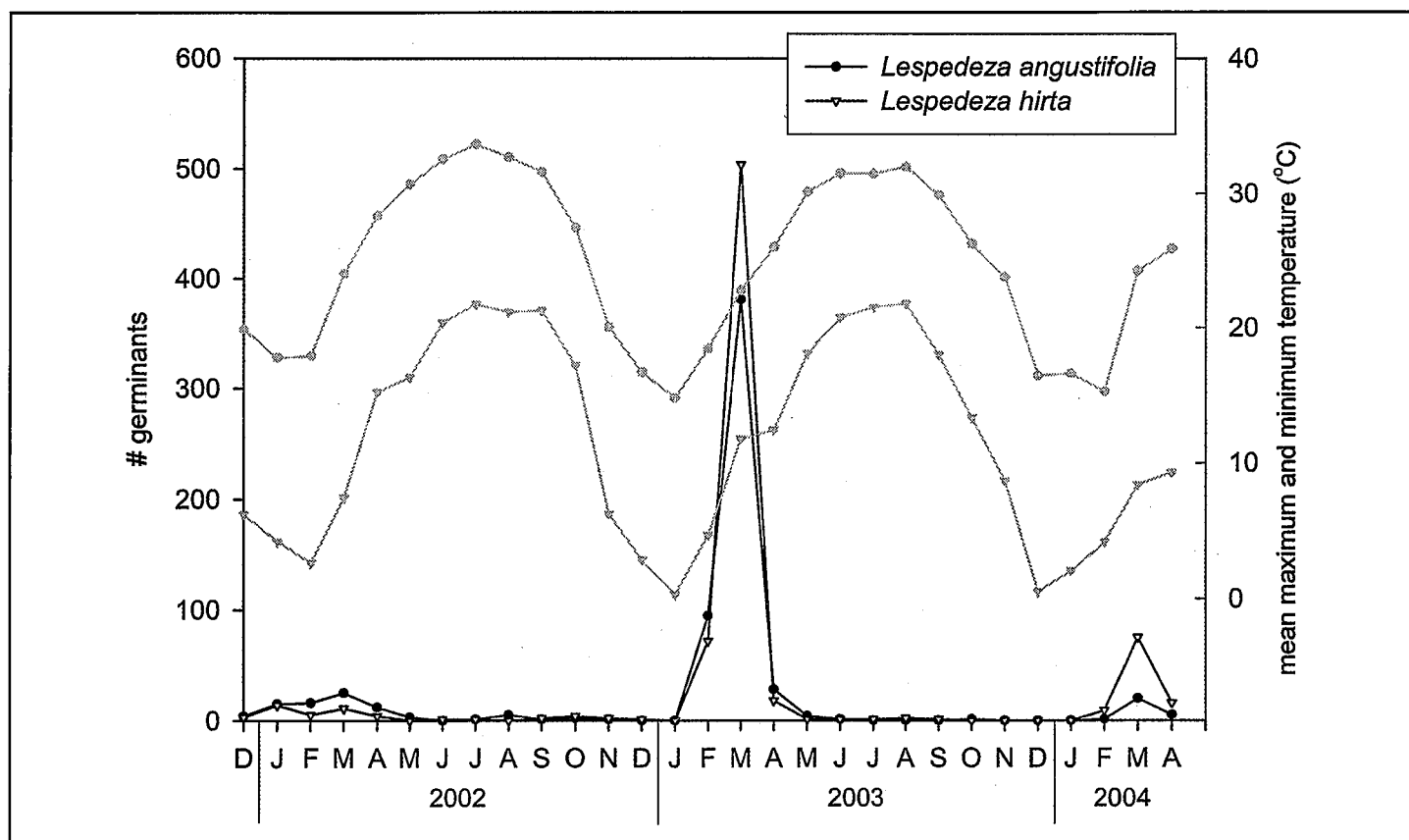


Figure 1.f. Monthly germination patterns of *Lespedeza* species in seedling flats – germination occurred after exposure to warm summer temperatures followed by cold winter temperatures. Maximum and minimum mean monthly temperatures are represented by gray background lines.

- nation. Journal of Range Management 21:250-254.
- Drew, M.B., L.K. Kirkman, and A.K. Gholson, Jr. 1998. The vascular flora of Ichauway, Baker County, Georgia: a remnant longleaf pine/wiregrass ecosystem. *Castanea* 63:1-24.
- Espinar, J.L., L.V. Garcia, and L. Clemente. 2005. Seed storage conditions change the germination pattern of clonal growth plants in Mediterranean salt marshes. *American Journal of Botany* 92:1094-1101.
- Freeman, C.C. 1998. The flora of the Konza Prairie – a historical review and contemporary patterns. Pp. 69-80 in A.K. Knapp, J.M. Briggs, D.C. Hartnett and S.L. Collins, eds., *Grassland Dynamics – Long-term Ecological Research in Tallgrass Prairies*. Oxford University Press, New York.
- Glitzenstein, J.S., D.R. Streng, D.D. Wade, and J. Brubaker. 2001. Starting new populations of longleaf pine ground-layer plants in the outer coastal plain of South Carolina, USA. *Natural Areas Journal* 21:89-110.
- Greene, H.C., and J.T. Curtis. 1950. Germination studies of Wisconsin prairie plants. *American Midland Naturalist* 43:186-194.
- Grime, J.P. 1989. Seed banks in ecological perspective. Pp. xv-xxii in M.A. Leck, V.T. Parker, and R.L. Simpson, eds., *Ecology of Soil Seed Banks*. Academic Press, San Diego, Calif.
- Grime, J.P., G. Mason, A.V. Curtis, J. Rodman, S.R. Band, M.A.G. Mowforth, A.M. Neal, and S. Shaw. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology* 69:1017-1059.
- Gross, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology* 78:1079-1093.
- Hains, M.J., R.J. Mitchell, B.J. Palik, L.R. Boring, and D.H. Gjerstad. 1999. Distribution of native legumes (Leguminosae) in frequently burned longleaf pine (Pinaceae)-wiregrass (Poaceae) ecosystems. *American Journal of Botany* 86:1606-1614.
- Hendricks, J.J., and L.R. Boring. 1999. N₂-fixation by native herbaceous legumes in burned pine ecosystems of the southeastern United States. *Forest Ecology and Management* 113:167-177.
- Holliday, P.P. 2001. Going, going...saving the longleaf pine ecosystem before it's gone. Pp. 55-66 in J.R. Wilson, ed., *The Fire Forest*. Georgia Wildlife Press, Covington.
- Hull, Jr., A.C. 1973. Germination of range plant seeds after long periods of uncontrolled storage. *Journal of Range Management* 26:198-200.
- Jenkins, A.M. 2003. Seed banking and vesicular-arbuscular mycorrhizae in pasture restoration in central Florida. M.S. thesis, University of Florida, Gainesville.
- Kirkman, L.K., R.J. Mitchell, R.C. Helton, and M.B. Drew. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany* 88:2119-2128.
- Kirkman, L.K., and R.R. Sharitz. 1993. Vegetation disturbance and maintenance of diversity on intermittently flooded Carolina bays in South Carolina. *Ecological Applications* 4:177-188.
- Laughlin, D.C. 2003. Lack of native propagules in a Pennsylvania, USA, limestone prairie seed bank: futile hopes for a role in ecological restoration. *Natural Areas Journal* 23:158-164.
- Leck, M.A. 1989. Wetland seed banks. Pp. 283-305 in M.A. Leck, V.T. Parker, and R.L. Simpson, eds., *Ecology of Soil Seed Banks*.

- Academic Press, San Diego, Calif.
- Lewis, J. 1973. Longevity of crop and weed seeds: survival after 20 years in soil. *Weed Research* 13:179-191.
- Maliakal, S.K., E.S. Menges, and J.S. Denslow. 2000. Community composition and regeneration of Lake Wales Ridge wiregrass flatwoods in relation to time-since-fire. *Journal of the Torrey Botanical Society* 127:125-138.
- Martin, R.E., R.L. Miller, and C.T. Cushwa. 1975. Germination response of legume seeds subjected to moist and dry heat. *Ecology* 56:1441-1445.
- McKeon, G.M., and J.J. Mott. 1982. The effect of temperature on the field softening of hard seed of *Stylosanthes humilis* and *S. hamata* in a dry monsoonal climate. *Australian Journal of Agricultural Research* 33:75-85.
- Mitchell, R.J., L.K. Kirkman, S.D. Pecot, C.A. Wilson, B.J. Palik, and L.R. Boring. 1999. Patterns and controls of ecosystem function in longleaf pine – wiregrass savannas. I. Aboveground net primary productivity. *Canadian Journal of Forest Research* 29:743-751.
- Moore, R.P. 1973. Tetrazolium staining for assessing seed quality. Pp. 347-366 in W. Heydecker, ed., *Seed Ecology*. George, Allen, and Unwin, London.
- Mulligan, M.K., and L.K. Kirkman. 2002. Burning influences on wiregrass (*Aristida beyrichiana*) restoration plantings: natural seedling recruitment and survival. *Restoration Ecology* 10:334-339.
- Parker, V.T., R.L. Simpson, and M.A. Leck. 1989. Pattern and process in the dynamics of seed banks. Pp. 367-384 in M.A. Leck, V.T. Parker, and R.L. Simpson, eds., *Ecology of Soil Seed Banks*. Academic Press, San Diego, Calif.
- Pfaff, S., and M.A. Gonter. 1996. Florida native plant collection, production and direct seeding techniques: interim report. U.S. Department of Agriculture, Natural Resources Conservation Service, Plant Materials Center, Brookville, Fla.
- Poiani, K.A., and P.M. Dixon. 1995. Seed banks of Carolina bays: potential contributions from surrounding landscape vegetation. *American Midland Naturalist* 134:140-154.
- Qi, M., M.K. Upadhyaya, and R. Turkington. 1996. Dynamics of seed bank survivorship of meadow salsify (*Tragopogon pratensis*) populations. *Weed Science* 44:100-108.
- Quinlivan, B.J. 1971. Seed coat impermeability in legumes. *The Journal of the Australian Institute of Agricultural Science* 37:283-295.
- Rabinowitz, D. 1981. Buried viable seeds in a North American tall-grass prairie: the resemblance of their abundance and composition to dispersing seeds. *Oikos* 36:191-195.
- Rees, M. 1994. Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *American Naturalist* 144:43-64.
- Rice, K.J. 1985. Responses of *Erodium* to varying microsites: the role of germination cueing. *Ecology* 66:1651-1657.
- Roberts, H.A. 1981. Seed banks in soils. *Advances in Applied Biology* 6:1-55.
- Roberts, H.A., and J.E. Boddrell. 1985. Seed survival and seasonal pattern of seedling emergence in some Leguminosae. *Annals of Applied Biology* 106:125-132.
- Rolston, M.P. 1978. Water impermeable seed dormancy. *The Botanical Review* 44:365-396.
- Seamon, G. 1998. A longleaf pine sandhill restoration in Northwest Florida. *Restoration and Management Notes* 16:46-50.
- Simpson, G.M. 1990. *Seed Dormancy in Grasses*. Cambridge University Press, Cambridge, U.K.
- Stöcklin, J., and M. Fischer. 1999. Plants with longer-lived seeds have lower local extinction rates in grassland remnants 1950-1985. *Oecologia* 120:539-543.
- Taron, D.J. 1997. Insects. Pp. 305-318 in S. Packard and C.F. Mutel, eds., *The Tallgrass Restoration Handbook*. Island Press, Washington, D.C.
- Thompson, K., J.P. Bakker, R.M. Bekker, and J.G. Hodgson. 1998. Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology* 86:163-169.
- Varner, J.M., J.S. Kush, and R.S. Meldahl. 2000. Ecological restoration of an old-growth longleaf pine stand utilizing prescribed fire. Pp. 216-219 in W.K. Moser and C.F. Moser, eds., *Fire and forest ecology: innovative silviculture and vegetation management*, Tall Timbers Fire Ecology Conference Proceedings, No. 21. Tall Timbers Research Station, Tallahassee, Fla.
- Wunderlin, R.P., and B.F. Hansen. 2003. *Guide to the vascular plants of Florida*. University Press of Florida, Gainesville, Fla.
- Yarrow, G.K., and D.T. Yarrow. 1999. *Managing Wildlife*. Sweetwater Press, Birmingham, Ala.