SPECIES BIOLOGY AND LIFE HISTORY OF THE FEDERALLY ENDANGERED *SCHWALBEA AMERICANA* L. (SCROPHULARIACEAE)

by

AMY HEATHER NORDEN

(Under the direction of L. Katherine Kirkman)

ABSTRACT

The federally endangered *Schwalbea americana* L. (Scrophulariaceae) is one of nearly 200 rare, fire-dependent plant species associated with the fire-maintained longleaf pine ecosystem of the southeastern Coastal Plain. Development of appropriate management and recovery plans is hindered by the lack of knowledge of the species biology and life history of this extremely rare species. I examined the fire-induced flowering response, herbivory, species longevity and dormancy, and seed germination requirements of *S. americana* in both field & greenhouse conditions.

Flowering in *S. americana* is stimulated by a combination of above-ground stem removal and increased light availability. Individuals are relatively long-lived and exhibit periods of dormancy. Seed germination in the field may be associated with earthworm castings.

INDEX WORDS: *Schwalbea americana*, American chaffseed, Endangered species, Fire-induced flowering, Longleaf pine, Dormancy, Seed germination

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Longleaf pine (*Pinus palustris* Mill.) communities once dominated the southeastern Coastal Plain of the United States. Historically, this fire-maintained ecosystem covered close to 100 million acres, ranging from southern Virginia to eastern Texas (Platt *et al*. 1988, Noss 1989). However, decades of fire suppression, along with conversion of forested land to agricultural use and planted pine plantations, has led to the decline of this biologically rich ecosystem. More than 97% of the original extent of longleaf pine has been destroyed, which classifies it as one of the world's most endangered ecosystems (Means & Grow 1985, Noss 1989).

The plant species richness in this fire-maintained ecosystem rivals that of many tropical rainforests, often up to and exceeding 40 species per square meter (Walker & Peet 1983, Peet & Allard 1993, Drew *et al*. 1998). The ground cover is dominated by grasses, including wiregrass (*Aristida beyrichiana* Trin. & Rupr.), sedges, and many herbaceous species. Nearly 200 of these species are considered rare or endangered (Hardin & White 1989), and approximately 70 of these are endemic to the longleaf pine community (Walker 1993). Fire is crucial in maintaining the open understory and ground cover, and many herbaceous species depend on frequent fires for reproduction, with increased flower and seed production following a burn (Parrott 1967, Platt *et al*. 1988, Brewer & Platt 1994, Outcalt 1994). Knowledge of the species biology and life history of such fire-dependent plants is critical in developing recovery and management plans for rare and endangered species within the longleaf pine community.

One such species is the federally endangered hemiparasite, *Schwalbea americana* (Scrophulariaceae). Primarily a Coastal Plain species, *S. americana* historically ranged from New York to Texas, but it has been reduced to its current range of seven states (AL, FL, GA, LA, NC, NJ, & SC), with remaining populations that are small and fragmented (USFWS 1992, 1995). As a fire-dependent species, it is unknown how long populations of *S. americana* can persist in the absence of fire (Kirkman 1996). It is known that *S. americana* requires fire for successful reproduction (Kirkman *et al*. 1998), but the specific mechanisms involved in this fire-induced flowering response, along with their associated effects on seed production and viability, are unknown. Knowledge of the underlying mechanisms involved in stimulating flowering and seed production is an important factor in establishing and implementing management options to ensure population persistence.

Ecology & Species Biology of *Schwalbea americana*

Schwalbea americana is a relatively long-lived, non-rhizomatous perennial herb (Kirkman *et al*. 1998). Following a fire (regardless of season of burn), *S. americana* produces abundant flowers and seeds that germinate readily in the greenhouse without special treatment. There is no evidence of a persistent seed bank (Kirkman *et al*. 1998), and it is unknown how long seeds remain viable following dispersal or exactly when germination occurs in the field. Seeds stored in refrigeration remain viable for at least eight years (Norden, unpublished data). Despite large numbers of seeds and high germination, it has been reported that seedling establishment and survival are often low (Obee & Cartica 1997), or quite variable from plot to plot in the same population (Kirkman *et al*. 1998). There is no correlation between the density of reproductive individuals the prior year and the number of successful seedlings recruited, and although seedling recruitment is spatially clustered, proximity to reproductive adult is not positively associated (Kirkman *et al*. 1998). Host preference does not seem to be a limiting factor in seedling establishment because this hemiparasite is capable of utilizing numerous species as potential hosts (Helton *et al*. 2000), and the preferred host, *Pityopsis graminifolia*, is an extremely common species in this community. Thus, in addition to habitat loss due to fire suppression or destruction, seedling establishment and survival may be potential bottlenecks for population expansion, even in suitable habitat.

One factor that may increase seedling establishment in the field is availability of microsites (small-scale areas of soil disturbance). Microsite limitation is an important factor for many rare plant populations (Eriksson & Ehrlen 1992, Jordan & Hartman 1995, Hilton & Boyd 1996, Quintana-ascencio & Menges 1996). If microsite availability is found to enhance establishment of *S. americana*, future reintroduction techniques could include small-scale soil disturbances, such as raking, followed by direct seeding.

Hemiparasitic plants

Facultative hemiparasitic plants are those that contain chlorophyll and can complete part or all of their life cycle in the absence of a host (Sahai & Shivanna 1982, Musselmann & Press 1995). As in all parasitic plants, hemiparasites attach to a host by the formation of haustoria. Haustoria contain modified xylem that originates from the roots and serves as a bridge to the host for nutrient (primarily nitrogen and carbon compounds) and hormone uptake (Sahai & Shivanna 1982, Stewart & Press 1990, Musselmann & Press 1995). Haustorial initiation and growth are induced by chemical signals from nearby roots, and it has been proposed that parasitic plants can even utilize allelopathic defense compounds as host recognition cues (Stewart & Press 1990, Riopel & Timko 1995). Facultative hemiparasites can survive without a host; however, if a potential host is available, haustorial attachments are made and growth is enhanced (Heckard 1962, Nwoke & Okonkwo 1974).

Because of their unique life histories, hemiparasites probably exhibit a trade-off between host facilitation and competition for resources. Given that facultative hemiparasites do not require germination cues from the host plant, host facilitation might not be as important during germination (Sahai & Shivanna 1982, Boone *et al* 1995). The trade-off between facilitation and competition during germination and seedling establishment is most apparent in times of drought or high temperature, when neighboring plants help retain soil moisture and decrease temperature by shading (Callaway 1995, Callaway & Walker 1997). In other words, as physical conditions become unfavorable for seedling establishment and growth, the importance of neighboring plants (and thus, future host attachment) increases (Bertness & Callaway 1994, Holmgren *et al*.1997). Conversely, competition becomes more important under favorable conditions. The effects of competition within the host-parasite relationship depend on the availability of resources to both plants and what percentage is lost to the parasite (Graves 1995). In the case of infection with a long-lived perennial hemiparasite, competition for resources is probably not as strong as infection with an annual or biennial because continued survival of the host is necessary to ensure optimal growth of the hemiparasite. Evidence indicates that hemiparasites often rely on their hosts for nutrients and carbohydrates, but the fact that host nutrient deficiency is rare suggests that competition for resources might be weak (Graves 1995).

It is possible that presence of neighboring plants could have a negative effect on the seed-soil contact of *S. americana* because small-scale microsite disturbances may be needed for direct contact with the soil. Microsite disturbances resulting from pocket gopher, small mammal, or insect foraging and burrowing behavior often result in exposed patches of bare, mineral soil (Inouye *et al.* 1997, pers. obs.). These microsites can provide “safe-sites” for seed germination and increase seedling establishment and growth by increasing moisture, light, and nutrient availability (Klinkhamer & de Jong 1988, Martinsen *et al.* 1990, Davis *et al.* 1991).

Flowering Physiology

Many factors, both environmental and internal, stimulate flower induction in angiosperms (Bernier *et al.* 1993, Kinet 1993, Meilan 1997, Hempel *et al.* 2000). Perhaps the most widespread is photoperiodic induction, in which photoreceptors (mainly phytochrome) in the leaves of plants perceive changes in daylength and light availability. The leaves then produce “flowering signals” that are transmitted to apical meristems via the phloem (O’Neill 1992, Bernier *et al.* 1993, Hempel *et al.* 2000). Despite much speculation about the nature of these signals, the exact chemical components remain largely unknown. One hypothesis is that the signals are universal hormones, florigen and antiflorigen, that are responsible for promoting and inhibiting flowering (Lang 1984, Bernier *et al.* 1993). Another hypothesis states that floral induction results from a shift in nutrient allocation within the plant so that the apical meristem receives more nutrients under inductive environmental conditions (Sachs & Hackett 1983, Bernier *et al.* 1993). A third alternative is that a combination of chemicals and hormones (discussed below) act together as the inductive signal (Bernier 1988).

For plants that do not require specific photoperiods to flower (autonomous plants), other external factors involved in floral induction include water and nutrient availability, changes in temperature and light irradiance, herbivory, and defoliation (Bernier et al. 1993, Kinet 1993, Meilan 1997). The phenomenon of fire-induced flowering is also well documented (Old 1969, Myers & Boettcher 1987, Herndon 1988, Brewer & Platt 1994, Johnson *et al* 1994, Outcalt 1994, Kirkman *et al.* 1998), but the specific mechanisms involved are not fully understood. Previous studies examining fire-induced flowering have proposed increased light availability through removal of above-ground understory vegetation and litter as an inductive cue (Haddad & Valio 1993, Abrahamson 1999, Huffman & Werner 2000). Nitrogen and phosphorus pulses in the soil following a fire (Lewis 1974, Christensen 1977, Gholz *et al*. 1985, Seastedt *et al*. 1991, Blair 1997) could also have inductive effects, as nutrient addition has been shown to stimulate flowering in many field and greenhouse experiments (Lockshin & Elfving 1981, Hulbert 1988, Thompson & Clark 1993). Smoke has also been shown to induce flowering in greenhouse experiments (Keeley 1993), and ethylene, a major gaseous component of smoke (Rodriguez 1932, Chanton *et al*. 2000), is a common plant hormone that is known to induce flowering in certain species (Abeles 1973, de Greef *et al*. 1989, Lurssen 1991, Reid & Wu 1991, Meilan 1997). It has been proposed that in the case of partial plant destruction, as in fire, the remaining parts (roots) serve as substitutes in providing nutrients and transporting floral induction signals to the re-sprouting meristem (Bernier *et al*. 1993).

In addition to the environmental factors discussed above, several internal factors are also potentially involved in floral induction. Plant hormones and chemicals including auxin, gibberellin, cytokinin, miscellaneous phytohormones, and ethylene are all potential inductive cues (Bernier *et al*. 1993, Kinet 1993, Blazquez *et al*. 1998).

Additionally, endogenous carbohydrates, proteins, and amino acids have been found to play a role in floral induction (Khurana *et al*. 1988, Bernier *et al*. 1993, Kinet 1993). There has been recent interest in the idea of genetic control of flowering, in which so-called "floral-meristem-identity-genes" or "flowering genes" control daylight or temperature sensitivity within leaves (Bernier *et al*. 1993, Kinet 1993, Mandel & Yanofsky 1995). Mutations in such genes can either enhance or delay flowering time (Bernier *et al*. 1993).

Plant dormancy

Long-lived perennial plant species must employ life history traits to allow persistence through periods of unfavorable environmental conditions (Vaughton & Ramsey 2001, Pnueli *et al*. 2002). One such trait is plant dormancy, which is the temporary absence of above-ground growth of a plant (Lesica & Steele 1994, Anderson *et al*. 2001). Two types of dormancy are ectodormancy (or facultative dormancy), in which dormancy is controlled by environmental factors, and endodormancy (or obligate dormancy), in which dormancy is controlled by physiological factors within the plant (Anderson *et al*. 2001, Vaughton & Ramsey 2001). Ectodormancy is extremely beneficial in areas where environmental conditions are unpredictable and variable from year-to-year, whereas endodormancy can be detrimental to a plant in such areas, particularly if conditions conducive for growth and development are not exploited (Vaughton & Ramsey 2001). Prolonged dormancy is a type of ectodormancy in which a plant can remain dormant through one or more growing seasons (Lesica & Steele 1994). This type of dormancy is often associated with drought (Epling & Lewis 1952, Lesica &

Steele 1994), but the onset and duration of prolonged dormancy may also be affected by the performance of the plant in previous years (Mehrhoff 1989, Lesica & Steele 1994).

Periods of ectodormancy are induced by physiological responses to thresholds of environmental conditions, such as low soil moisture (Vaughton & Ramsey 2001). In response to environmental stress, plants increase internal levels of regulatory compounds and hormones, such as abscisic acid (ABA), which can subsequently affect growth and development by reducing or stopping cell division (Anderson *et al*. 2001). Abscisic acid has been shown both to induce and maintain periods of dormancy (Nooden & Weber 1978, Suttle & Hultstrand 1994, Anderson *et al*. 2001), and it is likely that other hormones, such as cytokinin and auxin, play a role in breaking periods of dormancy following the onset of more favorable environmental conditions (Anderson *et al*. 2001).

Project overview

Knowledge of the species biology and life history of the federally endangered hemiparasite *Schwalbea americana* (American chaffseed), is essential in developing appropriate recovery and management plans. However, studies on the most critical stages of the life history of this species, such as the fire-induced flowering response, seed germination, and seedling establishment, are virtually nonexistent. This thesis examines several aspects of the species biology and life history of *S. americana* through a combination of field and greenhouse studies. Chapter 2 investigates the mechanisms involved in the fire-induced flowering response exhibited by *S. americana*, as well as insect herbivory levels following experimental treatments. Chapter 3 examines the current status of four natural populations of *S. americana* following previous experimental management techniques. Several germination studies are presented in

Chapter 4, and Chapter 5 synthesizes the results of these studies and discusses the implications for recovery and management of this species.

CHAPTER 2

FIRE-INDUCED FLOWERING AND HERBIVORY OF *SCHWALBEA AMERICANA* L. (SCROPHULARIACEAE)[1]

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ABSTRACT

The fire-maintained longleaf pine ecosystem of the southeastern Coastal Plain harbors nearly 200 rare and endangered plant species, many of which depend on frequent fire for persistence. One such fire-dependent species is the federally endangered hemiparasite, *Schwalbea americana* L. (Scrophulariaceae). Regardless of season of burn, fire stimulates flowering and subsequent seed production in this species, but the specific mechanisms involved in this fire-induced flowering response are unknown. The purpose of this study was to determine the mechanism controlling the flowering response to fire. Using experimental treatments in the field and greenhouse, we examined the effect of variables associated with fire on flowering of *S. americana.* Our field treatments included fire, shading immediately following fire, adding phosphorus, stem clipping, excluding competing vegetation, stem clipping plus vegetation exclusion, and mowing plus raking. Greenhouse treatments consisted of ethephon application, smoke incubation, and a gradient of light levels plus stem clipping. Our findings indicate that flowering is stimulated by a combination of clipping and increased light. Flowering was not induced by phosphorus, ethephon, or smoke treatments. An unexpected result of our field study was the occurrence of insect herbivory at one site, with the greatest amount of herbivory in the stem clipping plus competing vegetation exclusion treatment.

Key words: *Schwalbea americana,* American chaffseed, endangered species, fire-induced flowering, prescribed fire, longleaf pine, herbivory

INTRODUCTION

The longleaf pine (*Pinus palustris* Mill.) ecosystem of the southeastern Coastal Plain requires frequent, low-intensity fires to maintain stand structure and diverse ground cover. Consequently, many herbaceous species in these communities have evolved specific life history traits to persist through, and even take advantage of, frequent fire disturbances (Pickett & White 1985, Kirkman *et al*. 1998). One such potential adaptation is the occurrence of a fire-induced flowering response.

There are many plant species associated with fire-maintained communities that depend on fire for reproduction, experiencing increased flower and seed production following a burn (Myers & Boettcher 1987, Herndon 1988, Platt *et al*. 1988, Johnson *et al* 1994, Outcalt 1994). In some species, this fire-induced flowering response is season specific (i.e., flower production is increased after growing season burns) (Parrott 1967, Hartnett 1987, Seamon *et al*. 1989, Brewer & Platt 1994, Van Eerden 1997). In other species, flowering will increase following fire in the dormant season, as well as in the growing season (Kirkman *et al*. 1998, Hiers *et al*. 2000, McConnell & Menges 2002). Many variables associated with fire, which have physical or physiological impacts on vegetation, may stimulate flowering. For example, increased light availability following removal of above-ground vegetation and litter facilitates flowering in some species (Old 1969, Hulbert 1988, Abrahamson 1999, Huffman & Werner 2000). Additionally, phosphorus pulses in the soil following fire and ash deposition have been shown to induce flowering (Lamont & Runciman 1993, Thompson & Clark 1993). Partial plant destruction, or removal of the above-ground stem by clipping, is also a common flowering stimulus (Haddad & Valio 1993, Abrahamson 1999, McConnell & Menges 2002). For other species, incubation in smoke or addition of ethylene, a common plant hormone released from burning biomass, induces flowering (De Greef *et al*. 1989, Reid & Wu 1991, Keeley 1993). Fire-induced flowering responses are quite variable from species to species, however, it is likely that flowering in most fire-dependent species is stimulated by a combination of several factors (Hulbert 1988, Abrahamson 1999, McConnell & Menges 2002). For many species in the southeastern United States, the particular mechanisms that trigger flowering as a result of fire remain unknown. This lack of knowledge becomes especially problematic when dealing with rare or endangered fire-adapted species of the longleaf pine ecosystem. An understanding of how fire elicits the reproductive response of such species is necessary to develop successful recovery plans and to suggest alternative management options to ensure long-term population persistence, particularly during periods when prescribed fire cannot be used.

The federally endangered hemiparasite *Schwalbea americana* is one of these fire-dependent plants. Primarily a southeastern Coastal Plain species, *S. americana* historically ranged from New York to Texas. However, fire suppression and habitat fragmentation have reduced it to a fraction of its original range (USFWS 1992, 1995) (Figure 2.1). Regardless of season of burn, this species produces abundant flowers (and large numbers of viable seeds) following fire (Kirkman 1996, Kirkman *et al*. 1998). Knowledge of the species biology of *S. americana* is still limited, and the specific mechanisms of the fire-induced flowering response have not been studied. The purpose of this study is to examine several variables associated with fire that may be involved in the fire-induced flowering response of *S. americana*. Specifically, we address the following question: Is flowering and subsequent seed production induced by fire as a result of: a) increased light availability due to removal of surrounding vegetation, b) partial plant destruction due to removal of above-ground stems, c) pulses of phosphorus or ethylene released following combustion of vegetation, or d) smoke exposure?

METHODS

This study was conducted on Ichauway, an ecological reserve of the Joseph W. Jones Ecological Research Center located in Baker County, Georgia, and on the Lorraine Erwin tract, a privately owned property in neighboring Mitchell County, Georgia (Figure 2.2). Both of these sites are characterized by fire-maintained longleaf pine savannas, with a diverse, intact native groundcover dominated by grasses and forbs.

We examined the flowering response of *S. americana* to fire, and variables associated with fire, using a combination of field and greenhouse studies. Initial experiments were conducted in 2001 to identify potential factors stimulating flower production, and the experiments were refined in 2002 to further isolate the flowering response. For the field study, seven naturally occurring populations of *S. americana* were used (four on Ichauway and three on the Erwin tract). The four Ichauway populations occur in moist, ecotonal areas between upland longleaf pine savannas and seasonally-inundated depressional wetlands. The transitional soils in these ecotones range from well-drained loamy sands in the uplands (Wagram, Norfolk, and Duplin series) to poorly-drained sandy clay loams in the wetlands (Grady series) (USDA 1986, Goebel *et al.* 1998, Kirkman *et al.* 1998). The three Erwin tract populations occur in upland longleaf pine savannas, with dense wiregrass (*Aristida beyrichiana* Trin. & Rupr.). Soils in this area are sandy loam to sandy clay in texture, and are classified as clayey, kaolinitic, thermic Typic Paleudults (Esto series) (USDA 1986). Past land use at both sites includes frequent (2-3 year) dormant and growing season prescribed burns for bobwhite quail management, selective timber harvest, and limited deer hunting for herd management (Kirkman *et al.* 1998, C. Erwin, pers. comm.).

Field plot layout consisted of a randomized complete block design, with populations as blocks (total of 7 blocks). For the Ichauway study, a subset of previously established, permanent plots (3m x 7m) within each population was used (see Kirkman *et al.* 1998). Additional plots were set up within each population at the Erwin tract in the winter of 2002. Plot corners were marked with rebar and mapped using a Trimble Global Positioning System unit.

Preliminary experiments (2001)

In March 2001, we randomly assigned the following treatments to each of five field treatment plots within each Ichauway population: a) fire, b) fire + shading, c) exclusion of competing vegetation, d) phosphorus addition, and e) stem clipping (total of 5 treatments x 4 blocks = 20 plots). We protected the latter three treatment plots from fire by mowing and burning a band of vegetation around each plot prior to the prescribed burn treatment. For the fire + shading treatment, we suspended a commercial shade cloth (80% shade) over the entire plot using metal support frames the day after the prescribed burn. This level of shading was chosen to simulate the percent of relative light intensity that would penetrate dense groundcover vegetation in an unburned area (approximately 20%) (see Kirkman *et al.* 1998). For the above-ground vegetation exclusion treatment, we used landscape staples to bend and anchor neighboring vegetation away from *S. americana* individuals. Although a completely "shade-free" environment across the entire plot was unattainable, this treatment created a high light environment around the immediate vicinity of individual *S. americana* plants. This treatment was designed to isolate the effect of increased light availability with no loss of above- or below-ground biomass, as competing vegetation remained rooted in the ground. To simulate phosphorus increase through ash deposition following fire (C. Wilson, pers. comm.), we applied a single application of Triple Super Phosphate fertilizer at a rate of 50 g (approximately 10 g phosphorus) per plot. We clipped each *S. americana* stem at the soil surface using scissors to simulate physical removal of the above-gound portion by fire. Plots were monitored bi-weekly for the onset of flowering, censused in May 2001 for percent flowering per plot, and mature seeds were collected and tested for germination in August 2001. To test for germination, we extracted and combined seeds from 1-5 fruits of each flowering individual per plot. We randomly selected 40 seeds from the total number of seeds, placed the seeds on wet filter paper in plastic Petri dishes at room temperature and ambient light conditions, and recorded the number of germinated seeds twice a week for approximately 2 months (until germination ceased). Seeds were removed from the dishes following germination.

To control for possible host species differences and variable environmental conditions encountered in the field, we conducted additional experimental treatments in the Joseph W. Jones Ecological Research Center greenhouse in 2001. In the summer of 2000, we sowed locally-collected *S. americana* seeds into one gallon pots, each containing a mature individual of the preferred host species, *Pityopsis graminifolia* (Michx.) Nutt. (silkgrass) (Helton *et al*. 2000). We used a bark-based soil mix (gravel, pine bark, Osmocote® slow release fertilizer, Micromax®, and Triple Super Phosphate®) in all pots, and plants were hand-watered daily for soil moisture consistency with water filtered by reverse osmosis. In early spring 2001, we removed any weedy species from the pots, and, if necessary, *S. americana* individuals were transplanted to ensure that each pot and host contained at least one S. *americana* individual.

For the initial greenhouse experiments, we used a factorial design to explore the effect of different light levels and stem clipping on flowering. In May 2001, we randomly assigned the following treatments to groups of 52 pots of *S. americana* / *P. graminifolia*: a) low light, b) low light + stem clipping, c) medium light, d) medium light + stem clipping, e) high light, and f) high light + stem clipping. The number of *S. americana* individuals per treatment ranged between 83 and 117. The low light treatments were achieved using commercial shade cloth (63% shade) draped over metal support frames, which provided approximately 8% light (PAR) relative to light conditions outside the greenhouse (no canopy cover). For the medium light treatment, we hung aluminum hoods over groups of pots, which provided approximately 16% of available light. The high light level was ambient greenhouse light, approximately 22% of available light.

Flowering response to smoke incubation was investigated using 59 individuals (51 pots). Pots were placed on the lid of a large (~38 L), inverted plastic container, and a commercial beekeeper's smoker was packed with plant litter (pine needles, silkgrass leaves, and oak leaves). After the biomass was ignited, the smoker was used to fill the plastic container, and plants were kept incubated overnight for 12-15 hours. In order to prevent smoke from escaping, the container was secured to the lid using duct tape. The effect of ethylene exposure was explored by spraying ethephon (Florel®), an ethylene releasing compound, onto the stems and leaves of *S. americana* individuals. One of five concentrations of ethephon (0 ppm, 125 ppm, 250 ppm, 500 ppm, and 1000 ppm) was sprayed onto individuals in five pots (total of 25 pots, between 17 and 45 *S. americana* individuals per concentration of ethephon). Plants in all treatments were monitored weekly throughout the summer for flowering and mature seeds were collected and tested for germination in September 2001 using the method previously described.

Revised experiments (2002)

In 2002, we modified our field treatments to account for the interaction of increased light availability and stem removal through fire, and for increased replication of treatments by adding plots to three populations at the Erwin tract. We randomly assigned each of four plots at each Ichauway population to one of the following treatments: a) fire, b) fire + shade, c) competing vegetation exclusion + stem clipping, and d) mowing + raking. Treatments were identical at the Erwin tract, but due to public access to the area, we omitted the fire + shade treatment to avoid directing attention and possible vandalism to the plots. We used a string-fed weed-eater to mow all vegetation at the soil surface, and then raked the mowed vegetation from the plot. As in 2001, plots were monitored bi-weekly for the onset of flowering and censused in May 2002 for percent flowering per plot. In August 2002, 5-10 mature capsules were collected from each flowering individual per plot. We counted the total number of seeds in each of five randomly selected capsules per plot. Then we randomly selected 100 seeds from the total collection and tested them for germination in the manner described above.

Photosynthetically active radiation (PAR) was measured using a quantum sensor (LI-190SA, Li-Cor, Lincoln, NE) for the competing vegetation exclusion + stem clipping treatment and a line quantum sensor (LI-191SA, Li-Cor, Lincoln, NE) for all other treatments immediately following initial treatment application in March 2002 and again at the time of plot census in May 2002. To quantify relative light penetrating to the ground and available to resprouting *S. americana* individuals, we measured light intensity at ground level (below the ground cover vegetation), with reference measurements taken immediately above ground level, approximately 1 m above the ground cover vegetation.

An unexpected result at the Erwin tract was an extreme degree of herbivory by buckeye butterfly larvae (*Junonia coenia*, Lepidoptera, Nymphalidae), resulting in destruction of flowers and flower buds prior to plot census. Therefore, we compared degrees of herbivory among our treatments at this site, and only data from Ichauway was used to examine the fire-induced flowering response. To quantify the varying degrees of herbivory, we added a control (no treatment) plot at each of the three populations and assigned each plant within all treatment plots to one of the following herbivory classes: 0 = no evidence of herbivory (no damage), 1 = some minor herbivory (holes in leaves or flowers), 2 = partial stem defoliation (some leaves remain but top portion of stem defoliated), 3 = total stem defoliation (no leaves remain on stem, but stem still present), 4 = basal leaves remain (no stem above basal leaves), and 5 = major to complete herbivory (< 1 cm of stem, no leaves remain).

In early spring 2002, we conducted a greenhouse study similar to that of the previous year, but with modifications to the light regime and experimental design. In April 2002, we randomly assigned surviving 1½-year old *S. americana* individuals to the following treatments: a) low light, b) low light + stem clipping, c) medium light, d) medium light + stem clipping, e) high light, and f) high light + stem clipping. These treatments were similar to those in 2001 except that light sources and PAR were altered to apply a wider range of light conditions. The high light treatment was achieved with high pressure sodium, 430-watt grow lights (kept on for 12 hours per day), providing approximately 42% light (PAR) relative to light conditions outside the greenhouse (no canopy cover), and the medium light level was ambient greenhouse light, providing approximately 28% relative light. A split-plot design was used, with greenhouse tables as replicates (5 tables per light treatment, for a total of 15 tables), and 12-14 pots per table (½ clipped, ½ not clipped). To ensure the health of the host plants, we fertilized all individuals in each treatment monthly with a commercial 20-20-20 (NPK) fertilizer (Peter's Professional All Purpose, Scotts-Sierra Horticultural Products) at the rate suggested by the fertilizer manufacturer (~150 mL of fertilizer solution applied per pot). Plants were monitored weekly throughout the summer for flowering, and mature seeds were collected and tested for germination in September 2002 as described above.

Data analyses

We used a General Linear Models Procedure (PROC GLM; SAS Institute Inc. 1989) for a randomized complete block design for all analyses of field-collected data. Because individuals with small leaves do not produce flowers (Kirkman *et al*. 1998), percent flowering was calculated as the number of flowering individuals per large size class individuals (i.e. those with leaves > 1.0 cm long). Due to non-normal data, we used Friedman's distribution-free test for a randomized complete block design to compare mean percent flowering and mean percent seed germination among treatments in 2001 (PROC RANK, PROC GLM; SAS Institute Inc. 1989). Herbivory classes were combined into two classes for analysis (classes 0, 1, and 2 combined = none to minor herbivory, and classes 3, 4, and 5 combined = major to complete herbivory), and a Friedman's distribution-free test for a randomized complete block design was used to analyze differences in proportion of individuals in the major to complete herbivory class due to treatments (PROC RANK, PROC GLM; SAS Institute Inc. 1989). In 2002, percent flowering data were log transformed prior to analysis due to slight skewness of the data. In all analyses, Tukey's multiple comparison test was used to examine differences among treatment means. Due to low total numbers of flowering individuals in both years, statistical analyses were not used for greenhouse flowering data.

RESULTS

Fire-induced flowering response (2001)

Percent flowering was significantly higher in the fire treatment than in the competing vegetation exclusion, phosphorus addition, or stem clipping treatments ($p < 0.05$, $F = 6.89$) (Figure 2.3a). Shading immediately after fire did not reduce the rate of flowering. Mean percent seed germination was higher due to the fire treatment than that of the competing vegetation exclusion treatment ($p < 0.05$, $F = 14.90$) (Figure 2.3b). Seeds produced by the few flowering individuals in the phosphorus addition or clipped stem treatments failed to germinate.

Flowering was not stimulated in the greenhouse as a result of the smoke incubation or ethylene exposure treatments. Of the 12 individuals that flowered in the greenhouse, 7 occurred in the high light plus stem clipping treatment, 4 in the medium light, and only 1 in the medium light plus stem clipping. Percent germination (mean ± SE) was 46% ± 10.7 for seed collected from individuals in the high light plus stem clipping treatment, 9% ± 7.1 for seed collected from individuals in the medium light and 0% for seed collected from individuals in the medium light plus stem clipping treatments.

Fire-induced flowering response & herbivory (2002)

In 2002, there was no difference in percent flowering between the fire, competing vegetation exclusion + stem clipping, and mowing + raking treatments. Flowering in the fire + shading treatment was lower and significant at $a = 0.10$ ($p = 0.08$, $F = 3.80$) (Figure 2.4a). Percent germination was significantly lower in the fire + shading treatment ($p < 0.05$, $F = 22.51$) (Figure 2.4b), and mean number of seeds per capsule was nearly identical for individuals in all treatments ($p > 0.1$, $F = 0.08$) (Figure 2.4c). Immediately following treatment application, mean percent light penetration to the ground was equal across all treatments except the fire + shade treatment ($p < 0.01$, $F = 332.11$) (Figure 2.5a). Two months following treatment application, the light environment in the mowing + raking treatment closely approximated the light environment in the fire treatment, but differed from the other treatments ($p < 0.01$, $F = 33.36$) (Figure 2.5b).

In 2002, flowering in the greenhouse occurred exclusively as a result of the high light + stem clipping treatment. Percent seed germination (mean ± SE) was 35.6% ± 16.4, and number of seeds per capsule for these individuals (mean ± SE) was 218.3 ± 41.8.

Major to complete herbivory (i.e., all leaves gone, stem partially or completely destroyed) was nearly restricted to individuals in the competing vegetation exclusion + stem clipping treatment. Nearly 50% of the individuals in the vegetation exclusion + stem clipping treatment were seriously impacted by herbivory, whereas only 4% of individuals in the mowing + raking treatment experienced major to complete herbivory ($p < 0.01$, $F = 22.00$). None of the individuals responded to partial or complete herbivory by inducing flowering. None of the individuals in either the fire or control treatments experienced major to complete herbivory, and only minor damage was observed in these treatments, mainly as holes in the leaves or flowers.

DISCUSSION

This study indicates that flowering in *S. americana* is strongly stimulated by a combination of above-ground stem removal during fire and increased light availability following fire. Flowering is not induced by these two factors alone, nor by phosphorus addition, smoke incubation, or ethylene exposure. It is possible that stem removal induces a chemical or hormonal signal within the remaining tissue that alters plant growth and development. Ethylene, a common plant hormone known to stimulate flowering in other species, did not stimulate flowering in this study, but there are several other plant hormones, such as auxin or gibberellin, that may be involved (Bernier *et al*. 1993, Kinet 1993, Blazquez *et al*. 1998). It is also possible that, by removing the above-ground portion of the plant, the roots re-allocate nutrients and resources (including floral induction signals) to the re-sprouting meristem (Bernier *et al*. 1993).

Removal of above-ground understory vegetation and litter following partial plant destruction increases light availability and, subsequently, stimulates rapid resprouting and enhances shoot growth (Hulbert 1988). It is likely that increased light can act in combination with stem removal to alter physiological processes and facilitate the expression of floral induction signals or hormones (LeMaitre & Brown 1992, Huffman & Werner 2000). Abrahamson (1999) found that flowering in two palmetto species was greater as a result of increased light following clipping, and McConnell & Menges (2002) reported that shrub canopy removal following clipping enhanced flowering of *Eriogonum longifolium*. Similarly, increased light can also act in combination with nutrient addition to stimulate post-fire flowering (Hulbert 1988), and Brewer & Platt (1994) found that flowering of clipped *Pityopsis graminifolia* individuals was enhanced by nutrient addition. It is possible that flowering in *S. americana* could be stimulated by other combinations of fire effects, such as fertilization + light or fertilization + clipping.

It is unlikely that the flowering response of the host plants, to which *S. americana* individuals were attached, influenced our results, as it is non-host specific and has been shown to parasitize multiple host species (Helton *et al*. 2000). It is likely that the *S. americana* individuals in our field study were attached to several different species, and therefore potentially represent a range of physiological effects that reflect host plant response to our treatments.

Although the initial experimental results suggested that some flowering was stimulated in all of our 2001 field treatments, these results were likely attributable to problems associated with treatment application. For example, the stems of the plants that flowered in the competing vegetation exclusion treatment appeared to have been broken off accidentally at the time of plot census, with flowering occurring after this stem removal. Additionally, the flowering individuals in the clipped stem treatment were located at the edge of the plot, where light availability may have been greater due to the protective band mowed around the plot to exclude fire. Flowering in our fire + shade treatment in 2001 may have been influenced by early problems with the shade cloth. The initial material used as the shade cloth was not durable enough to withstand wind and had to be replaced within the first two weeks following treatment application. Due to tears in the original material, there was a short period immediately following the burn when portions of the plots were not completely shaded and some direct light penetrated to the ground. It is possible that the period immediately following stem removal is when high light exposure is critical in inducing flowering, and thus a brief exposure to light could explain why we did not detect any significant difference in flowering between the fire + shade treatment and the fire treatment in 2001.

The low number of flowering individuals in the greenhouse in 2001 is most likely explained by the light levels of the treatments relative to field conditions. Even with the addition of grow lights in 2002, light levels inside the greenhouse were below that of ambient outside conditions. It is possible that, if we repeated our greenhouse experiment and were able to increase the light availability, we would see a dramatic increase in the number of flowering individuals.

Our 2002 field experiments were designed to quantify the observations of flowering resulting from the combination of broken stems and increased light, and consequently clarified the ambiguous results obtained in 2001. The flowering response from the revised fire + shade treatment indicate that, although reduced, flowering was not completely inhibited by the low light levels of this treatment. These results are consistent with previous reports that occasional flowering of *S. americana* individuals occurs even in the absence of fire (i.e., lower light availability) (Kirkman et al. 1998). The amount of flowering that we observed in our fire treatment was slightly lower than expected (only 35% of individuals flowered, compared to 52% as reported by Kirkman *et al.* 1998), but it is possible that the prolonged drought conditions prior to and during the study period were responsible for increased dormancy, or possibly decreased plant vigor and overall reproductive output of *S. americana* individuals.

Our findings demonstrate that abundant flowering in *S. americana* can be achieved without fire, which is an important issue in determining management options for years in which prescribed fire is not feasible. Kirkman *et al*. (1998) did not find mowing to induce a flowering response similar to that following fire, but the mowed biomass in that study was not completely removed from the plots; therefore, re-sprouting individuals were not exposed to the degree of increased light that was created in our study. We suggest that mowing, followed by complete biomass removal through raking, could be used in place of prescribed fire to stimulate flowering and subsequent seed production, which in turn could potentially enhance future seedling establishment. This approach should only be considered as a temporary means to stimulate flowering, as the long-term effects of mowing + raking on seedlings and seedling establishment is unknown. Additional studies must be conducted to determine the impact of repeated use of alternative management options (such as mowing + raking), on survival and recruitment. It is likely that seedling establishment following flowering is correlated with microsite availability (Kirkman *et al*. 1998, H. Norden, unpublished data), and the relationship between creation and distribution of such microsites and fire is unknown. The effect of repeated use of fire substitutes on competition, as well as any effects on the health or quality of possible host plant species, must also be examined.

We have not previously observed caterpillar herbivory of *S. americana* to the extent that occurred at the Erwin tract in 2002. The absence of herbivory to individuals in the fire treatment may be explained simply by the fact that we burned after the butterflies had oviposited; consequently, eggs may have been destroyed in the fire. Many lepidopteran species (particularly specialists, such as the buckeye butterfly, which concentrates on species in the family Scrophulariaceae) oviposit directly on the desired host plant due to limited mobility of the larvae (Feeney *et al*. 1983). However, host selection does not explain the lack of caterpillar damage in our control plots, which were not burned. Also, because this species of butterfly has a continual life cycle and oviposits throughout the year (J. Neel, pers. comm.), opportunities for ovipositing on resprouting *S. americana* individuals following fire would have occurred.

A more likely explanation for our findings involves the host-search behavior of female butterflies, which use a combination of visual and chemical recognition cues in search of a suitable host plant on which to oviposit (Feeney *et al*. 1983, Rausher 1978, Parmesan *et al*. 1995). A female butterfly must visually locate and physically contact a potential host plant using special chemoreceptors on her forelegs. Therefore, if appropriate host plants are physically and chemically difficult to detect because of dense vegetation, they may not be utilized (Stanton 1982). It is probable that the buckeye butterfly females in our study area were not able to detect *S. americana* individuals in the fire treatment due to thick re-growth of wiregrass and other ground cover species. This host-search behavior also explains the lack of herbivory in our control (unburned) areas, in which wiregrass was extremely dense and *S. americana* plants were often obscured by the ground cover. In the competing vegetation exclusion + stem clipping treatment, re-sprouting *S. americana* individuals were visually exposed and thus were particularly vulnerable to detection by searching butterflies. Stanton (1982) proposed that female butterflies concentrate their egg-laying behavior in patches where host plants are abundant, once located. Such behavior could be considered a type of optimal foraging, in which resources (i.e., host plants) are located in distinct patches (i.e., our treatments), and to exploit these patchy resources, one option is to decrease foraging distance (MacArthur & Pianka 1966, Stanton 1982). This foraging model is consistent with the concentrated herbivory we observed in the treatment where the host plants were extremely obvious.

While individuals in the mowing + raking treatment did not experience severe amounts of herbivory, there were more individuals with damaged flowers in this treatment than in the fire treatment. One implication of severe herbivory is decreased reproductive output, and these results indicate that fire is the best option to stimulate flowering while minimizing severe herbivory.

ACKNOWLEDGMENTS

Funding for this study was provided by the Robert Woodruff Foundation and the Joseph W. Jones Ecological Research Center. We would like to thank Kathy Aleric, Kim Coffey, Dee Davis, Ivy Godbois, Eamonn Leonard, Erin O’Brien, and Slaton Varner for their assistance in field treatment application and data collection. Special thanks to Charles, Bill, and Parrish Erwin for their interest, cooperation, and permission to access their land.

Figure 2.1. Geographical distribution of *Schwalbea americana*. Counties with extant occurrences are indicated in grey.

Figure 2.2. Study site locations in southwestern Georgia.

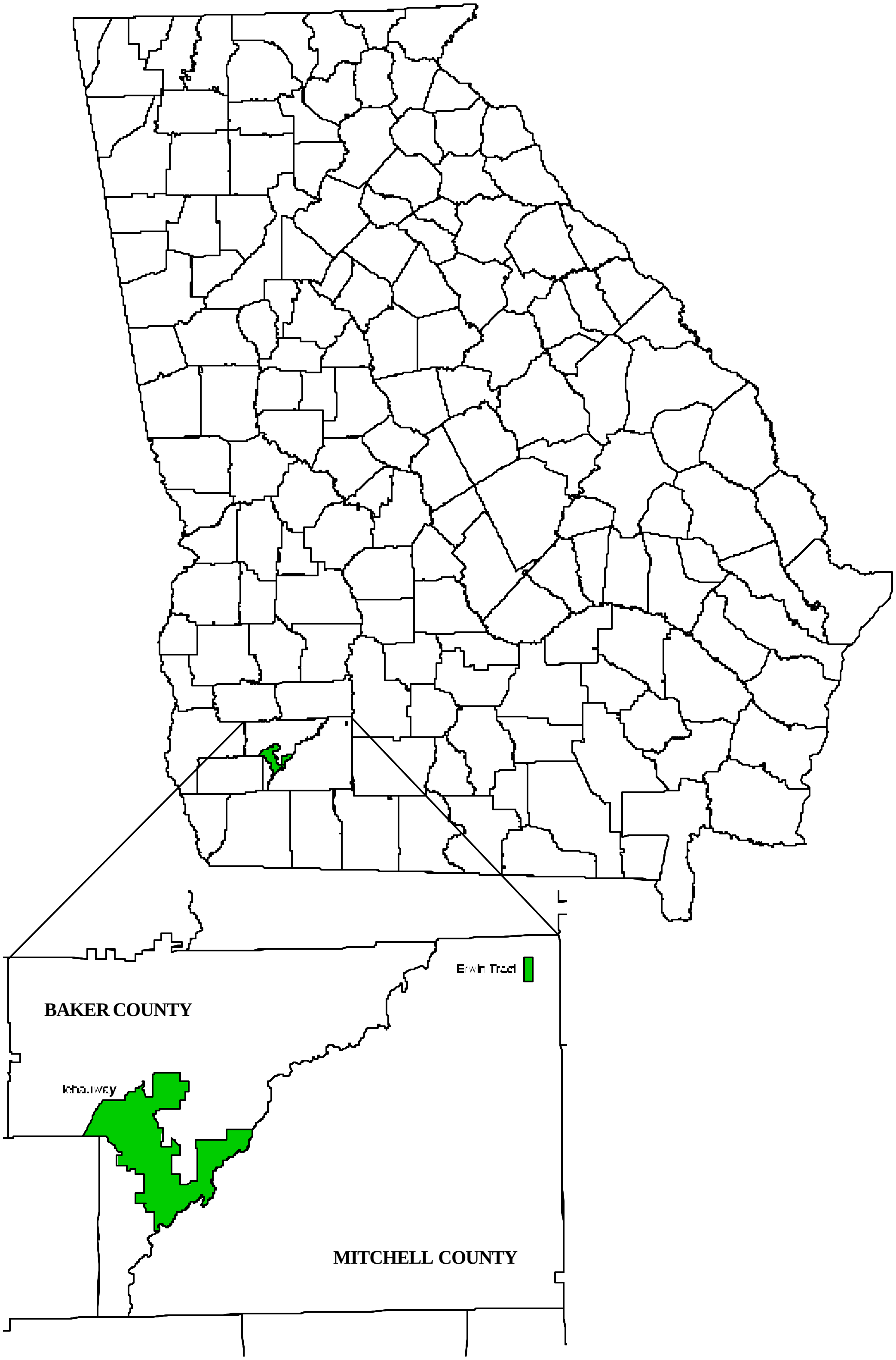

Erwin Tract 🟩
BAKER COUNTY
Ichauway
MITCHELL COUNTY

Figure 2.3. Reproductive response in 2001 (a) % flowering (mean ± SE) (b) % germination (mean ± SE). Treatment means with different letters are significantly different ($p < 0.05$). Competing vegetation exclusion treatment is abbreviated as veg. excl.

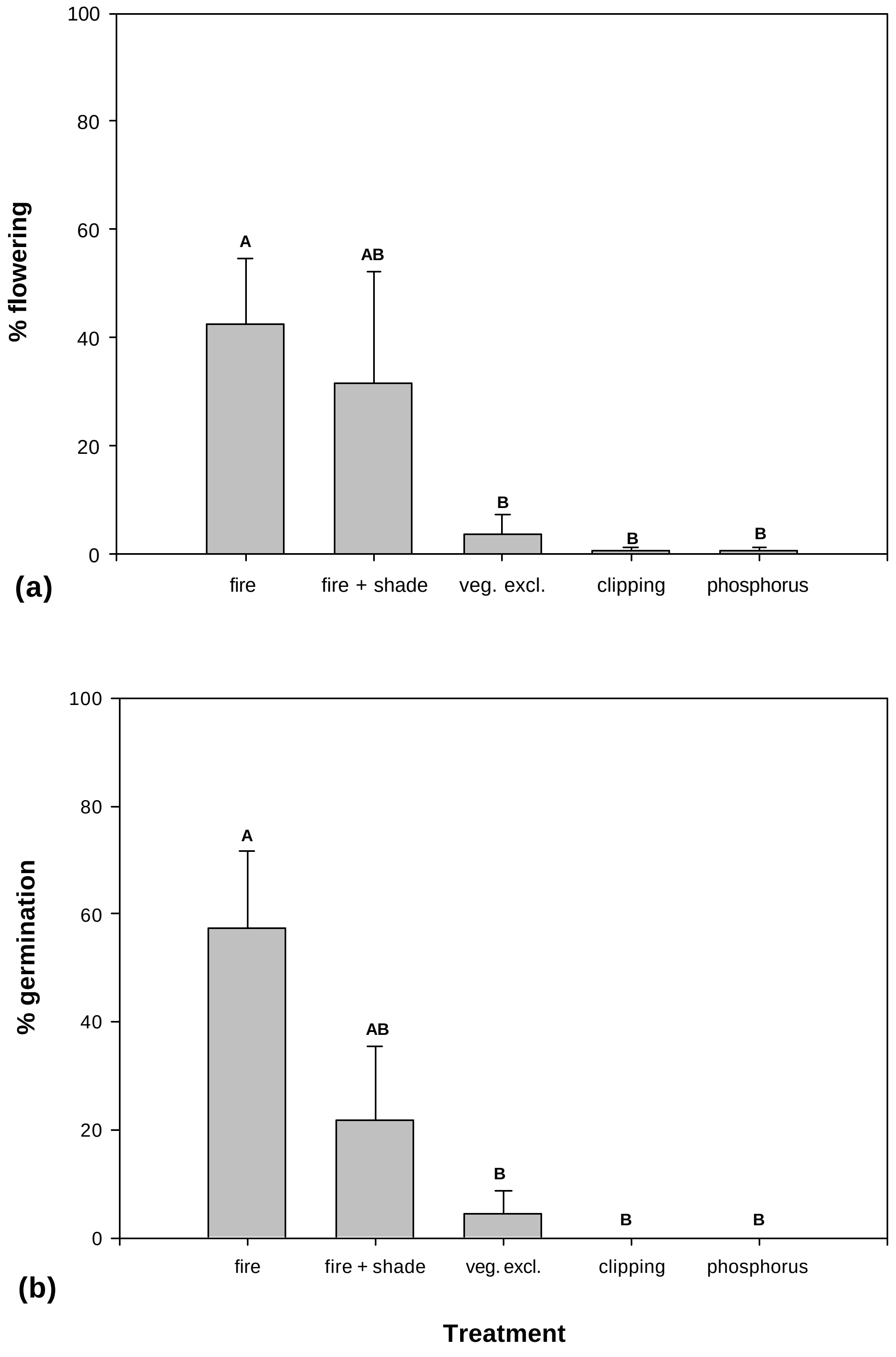

100
80
60
40
20
0
% flowering
A
AB
B
B
B
fire
fire + shade
veg. excl.
clipping
phosphorus
(a)
100
80
60
40
20
0
% germination
A
AB
B
B
B
fire
fire + shade
veg. excl.
clipping
phosphorus
(b)
Treatment

Figure 2.4. Reproductive response in 2002 (a) % flowering (mean ± SE) (b) % germination (mean ± SE) (c) # seeds per capsule (mean ± SE). Treatment means with different letters are significantly different ($p < 0.1$). Competing vegetation exclusion treatment is abbreviated as veg. excl.

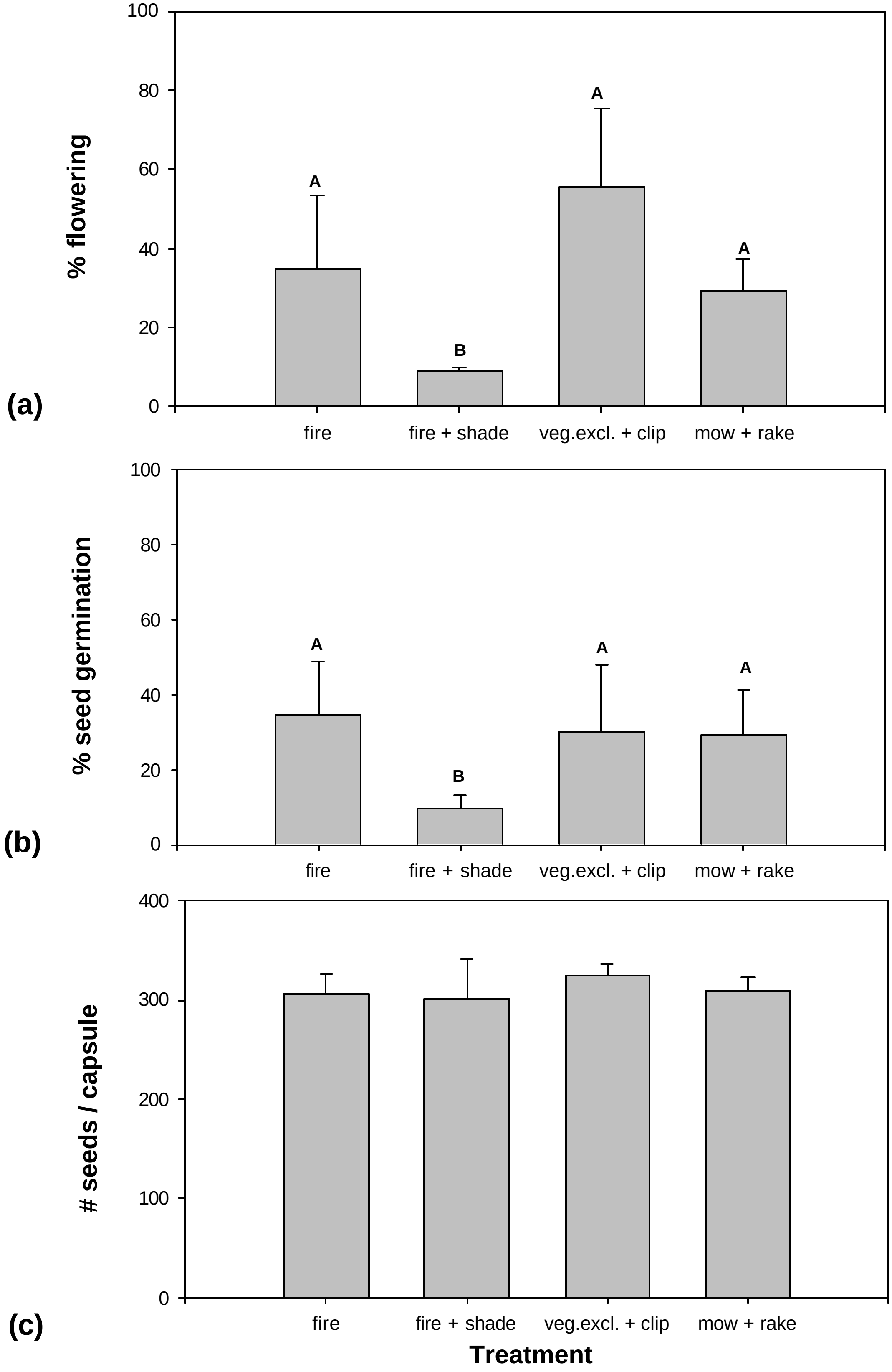
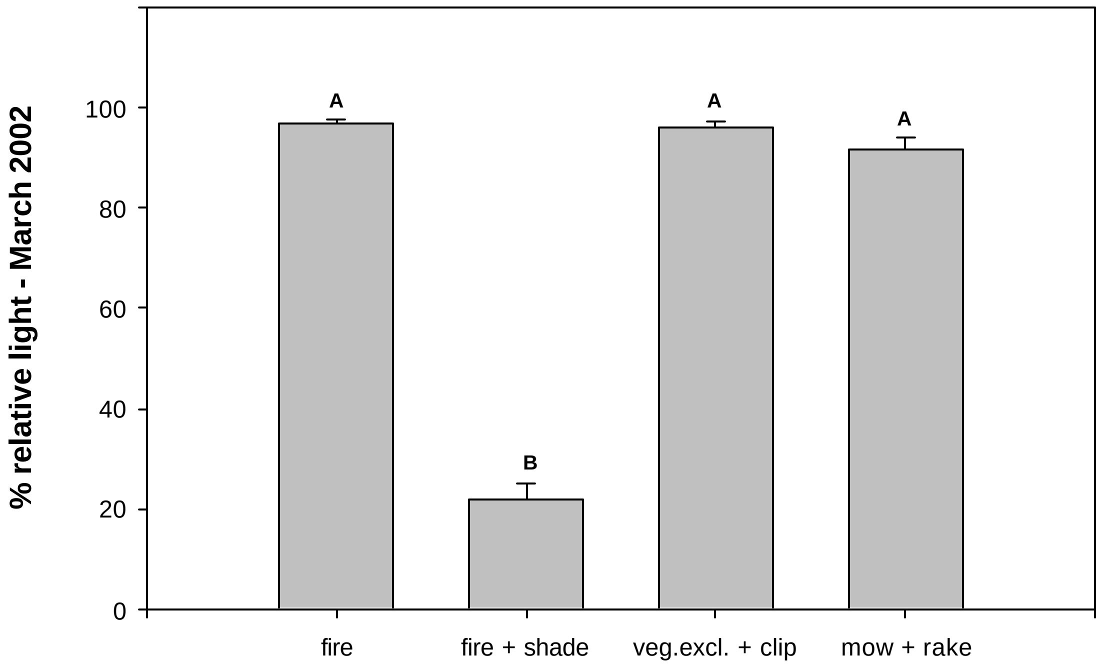
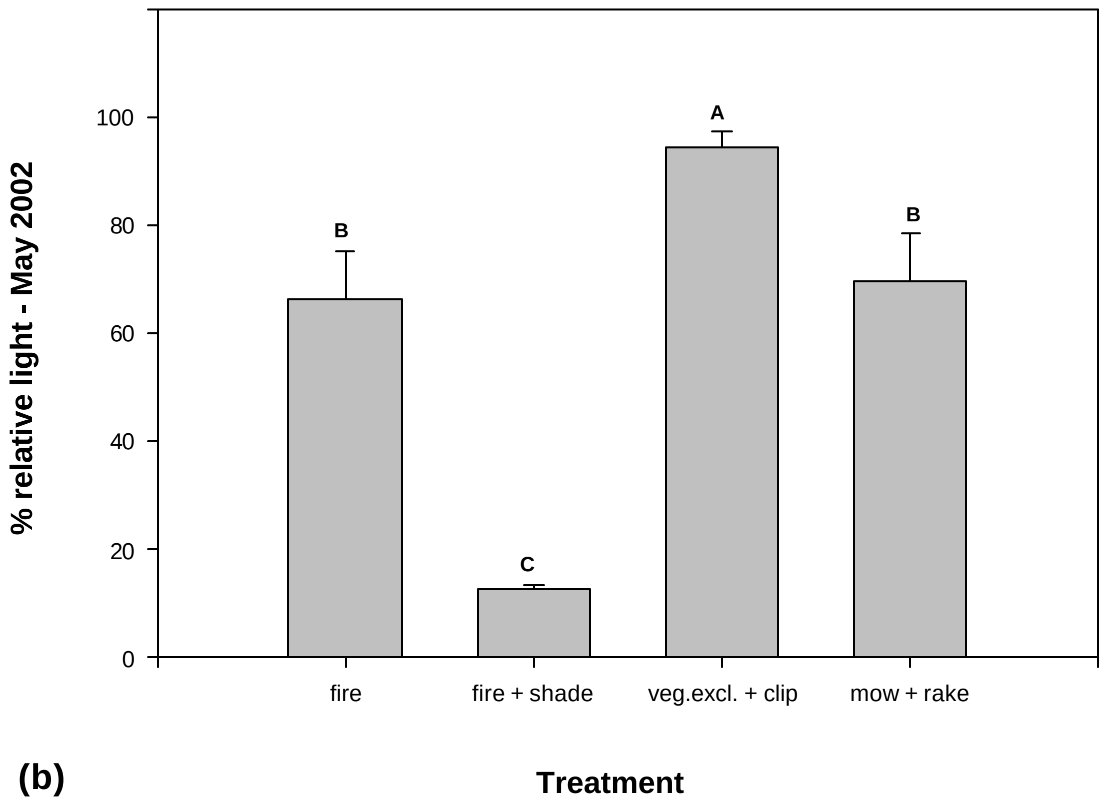

(a)
% flowering
100
80
60
40
20
0
A
B
A
A
fire
fire + shade
veg.excl. + clip
mow + rake
(b)
% seed germination
100
80
60
40
20
0
A
B
A
A
fire
fire + shade
veg.excl. + clip
mow + rake
(c)
seeds / capsule
400
300
200
100
0
fire
fire + shade
veg.excl. + clip
mow + rake
Treatment

Figure 2.5. Percent relative light availability (a) March 2002 (mean ± SE) (b) May 2002 (mean ± SE). Treatment means with different letters are significantly different ($p < 0.01$).


% relative light - March 2002
0
20
40
60
80
100
A
B
A
A
fire
fire + shade
veg.excl. + clip
mow + rake

(a)


% relative light - May 2002
0
20
40
60
80
100
B
C
A
B
fire
fire + shade
veg.excl. + clip
mow + rake
Treatment

(b)

CHAPTER 3

PERSISTENCE AND DORMANCY OF *SCHWALBEA AMERICANA* L. (SCROPHULARIACEAE) FOLLOWING EXPERIMENTAL MANAGEMENT TECHNIQUES [1]

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[1] Norden, A. H. & L. K. Kirkman. To be submitted to *Natural Areas Journal*.

ABSTRACT

The federally endangered hemiparasite, *Schwalbea americana* L. (Scrophulariaceae) is a long-lived perennial herb adapted to fire-maintained ecosystems, such as the longleaf pine-wiregrass community of the southeastern Coastal Plain. *Schwalbea americana* exhibits fire-induced flowering and populations reportedly decline in the absence of fire; however, the long-term population response to alternative management options, along with recovery potential following short-term fire exclusion, is unclear. The purpose of this study was to determine the population status and recovery of *S. americana* following short-term population declines associated with prior experimental management techniques. Specifically, we examined density of individuals and new recruits in 2001, along with 2001 survivorship of individuals present since 1992, in four natural populations that were subjected to experimental management techniques between the years 1992-1996. Previous management techniques included dormant season burn (March), growing season burn (June), growing season mowing (June), and control (no treatment). Our findings indicate that short-term experimental management techniques do not appear to have a detrimental effect on long-term population persistence, and the population fluctuations that we observed may be related more to precipitation patterns than to residual effects of experimental treatments. Additionally, *S. americana* exhibits periods of dormancy that may facilitate long-term population persistence during unfavorable environmental conditions or fire suppression.

Key words: *Schwalbea americana*, American chaffseed, endangered species, dormancy, fire-adapted, longleaf pine

INTRODUCTION

Disturbance-adapted plant species often have evolved specific life history traits to persist through frequent and repeated disturbances (Pickett & White 1985). In fire-dependent ecosystems, such adaptations include rapid post-fire resprouting (Abrahamson 1984), fire-stimulated flowering and seed production (Parrott 1967, Myers & Boettcher 1987, Platt *et al*. 1988), and heat or smoke-stimulated germination (de Lange & Boucher 1990, Brown 1993). In addition to life history traits that allow persistence through frequent fire return intervals, long-lived perennials in fire-adapted ecosystems must also possess traits that allow them to survive unfavorable environmental conditions, such as drought or periods of fire suppression. This is especially important for populations of rare and endangered fire-adapted species, which may be particularly vulnerable to extinction because of low densities of individuals and high degrees of fragmentation (Walker & Peet 1983, Hardin & White 1989). In these species, the ability to survive periods of environmental stress between fire events is crucial in ensuring long-term population persistence.

Schwalbea americana L. (American chaffseed) is a federally endangered hemiparasite in the family Scrophulariaceae. Primarily a coastal plain species, *S. americana* historically ranged from New York to Texas but has been reduced to a fraction of its original range (Figure 3.1), with the majority of remaining populations small and fragmented. Habitat loss and destruction due to fire suppression and agricultural land use are the primary reasons for the decline of this species (USFWS 1992, 1995). This species is closely associated with fire-maintained ecosystems, such as the longleaf pine-wiregrass ecosystem of the southeastern Coastal Plain, and similar to many other fire-adapted species, it has evolved life history traits that facilitate persistence through frequent fire, such as a fire-induced flowering response (Kirkman 1996, Kirkman *et al*. 1998, Norden & Kirkman in review). However, development of appropriate management plans is constrained by the lack of information regarding long-term population persistence and recovery potential of this species, particularly following periods of short-term fire supression.

The purpose of this study was to determine the current population status and stability of four populations of *S. americana* following experimental management techniques imposed from 1992 to 1996 (Kirkman 1996, Kirkman *et al*. 1998). Specifically, we addressed the following questions: 1) Are the population differences observed in 1996 due to treatments still apparent in 2001, following resumption of prescribed fire? 2) What is the percent survivorship of the original 1992 cohort? 3) What are the roles of species longevity, recruitment, and reappearance in long-term population persistence, recovery, or decline?

METHODS

Field methods

The initial study was implemented at Ichauway, a privately owned reserve of the Joseph W. Jones Ecological Research Center in Baker County, Georgia in summer 1992. Each of the four naturally occurring populations of *S. americana* used in this study occur in moist, ecotonal areas between upland longleaf pine savannas and seasonally-inundated, depressional wetlands. Transitional soils in these ecotones range from well-drained loamy sands in the uplands (Wagram, Norfolk, and Duplin series) to poorly-drained sandy clay loams in the wetlands (Grady series) (USDA 1986, Goebel *et al*. 1998, Kirkman *et al*. 1998). All of the populations are characterized by a fire-maintained longleaf pine overstory and a diverse native ground cover dominated by grasses (including wiregrass, *Aristida beyrichiana* Trin. & Rupr.) and forbs. Past land use includes frequent (1-3 year) dormant season prescribed burns for bobwhite quail management and selective timber harvest (Kirkman *et al*. 1998).

Plot layout consisted of a randomized complete block design with populations as blocks and plots as subsamples within each treatment. At three of the four sites, 12 (3 m x 7 m) plots were established. Small population size at the fourth site allowed for only 9 plots to be established. Each block was divided into four experimental sections, and the following treatments were randomly assigned to blocks of three plots each: 1) dormant season burn (March), 2) growing season burn (June), 3) growing season mowing (June), and 4) control (no treatment). At the fourth site with fewer plots, the mowing treatment was omitted. All populations were burned in March 1992, and treatments were imposed in 1993 and applied annually until 1996. However, in 1994 the growing season burn was omitted due to excessive precipitation and regional flooding.

A pre-treatment population census of all plots was made in 1992. Plants were tagged, and number of stems per individual, maximum stem height per individual, leaf size class (small = = 0.5 cm; medium = > 0.5 cm = 1.0 cm; large = > 1.0 cm) and number of flowers and fruits per individual were recorded. All plots were sampled again in 1993. In 1994, 1995, and 1996 a sub-sample of plots (only two of the three plots per treatment) was sampled. Each year, all previously tagged plants were located and re-measured (any plants not located were considered missing), and all new plants were tagged, mapped, and measured.

For a more detailed description of treatment application and sampling procedures, as well as population demographics and spatial patterns following the experimental treatments, see Kirkman (1996) and Kirkman *et al.* (1998). Prescribed fire across all treatment plots was resumed in spring 1998 and 2001, and in summer 2001, the sub-sample of plots was sampled for density of individuals (previously tagged and new recruits) per plot. Here, we present results derived from the 2001 plot census.

Data analysis

We used a General Linear Models Procedure (PROC GLM; SAS Institute Inc. 1989) for a randomized complete block design for all analyses, using plot means (taken over pairs of treatment plots at each site) as the variable of analysis. All data were log transformed prior to anaylsis due to normalize the data.

RESULTS

Mean density of individuals did not differ among treatments in 2001, six years following the last treatment application (F = 1.99, p = 0.19). Although extremely variable, percent change in density of individuals from 1996 to 2001 and from 1992 to 2001 did not differ among treatments (F = 0.93, p = 0.44, and F = 1.07, p = 0.38, respectively). Mean percent survivorship of the original 1992 cohort did not differ among treatments (F = 0.02, p = 0.99), and ranged from 10-17% per treatment. Percent survivorship of 1993 and 1994 recruits showed similar patterns, with survivorship of 1993 recruits ranging from 8-13% per treatment (F = 0.07, p = 0.97) and survivorship of 1994 recruits ranging from 7-11% (F = 1.55, p = 0.28). Of the surviving 1992 cohort, 4–15% per treatment was reported as missing in 1996, and these values were similar across all treatments (F = 0.69, p = 0.60). Mean density of new recruits (new individuals tagged in 2001) was similar across all treatments (F = 2.50, p = 0.13), and ranged from 3-15 individuals per plot per treatment.

Regardless of treatment, all plots have experienced fluctuations in mean densities of individuals since 1992 (Figure 3.2a). Although annual population fluctuations are not available between 1996 and 2001, our census data suggest that the largest total population size coincides with the year of highest rainfall (National Climatic Data Center, NOAA) (Figure 3.2b).

DISCUSSION

Our results do not provide evidence to indicate that any of the experimental management techniques have had any long-term beneficial or detrimental effects on populations of *S. americana*. Within the 9-year study period, the year-to-year fluctuations across all treatment populations suggest a population response to the highly variable environmental conditions experienced regionally since 1992. It is possible that the overall decline in individuals since 1996 is due to extremely variable rainfall patterns, rather than a residual effect of the experimental treatments. The lack of population demographic data between the years of 1996 and 2001 prohibits us from determining a direct correlation between annual fluctuations in population density and precipitation patterns.

The most important findings of this study are the longevity of established *S. americana* individuals and verification that individuals exhibit periods of dormancy. Additional studies exploring potential environmental variables responsible for inducing and breaking plant dormancy are needed to fully understand the relationship between reappearance of individuals and long-term population dynamics. If periods of dormancy in *S. americana* are stimulated by unfavorable conditions, such as drought or periods without fire (as in our control treatment) (Lesica & Steele 1994, Kirkman *et al*. 1998, Lesica 1999), it is likely that dormant individuals could play a major role in population persistence and recovery as conditions become favorable again. The potential for re-emergence, however, emphasizes the possibility of overestimation of annual mortality rates due to year-to-year absence and reappearance of individuals, as noted by Kirkman *et al*. (1998), and the presence of dormant individuals makes it difficult to obtain accurate population sizes and monitor population demographics over time (Lesica & Steele 1994). Longer-term studies (>10 years), with year-to-year demographic data, would reveal important information on how species longevity and dormancy affect population dynamics through prolonged periods of environmental stress, fire suppression, and/or experimental management techniques, such as mowing followed by raking, as suggested by Norden & Kirkman (in review).

It is possible that the relatively low recruitment rates across all treatments between 1996 and 2001 reflect a combination of effects from the experimental treatments and environmental conditions. If individuals in the control treatment persisted in vegetative and dormant states until they were burned in 1998 (Kirkman *et al*. 1998) and then produced flowers and seed following this burn, there could have been an abundance of new recruits in 1998. Despite this, it is likely that any young seedlings would have been vulnerable to the extremely dry conditions in 1999 and 2000 and probably did not reach a reproductive state, resulting in the low number of recruits observed in 2001. Alternatively, if seedlings were able to become established and are currently persisting in a dormant state as a result of the drought, it is possible that an increase in population density and recruitment would occur as soon as environmental conditions become more favorable.

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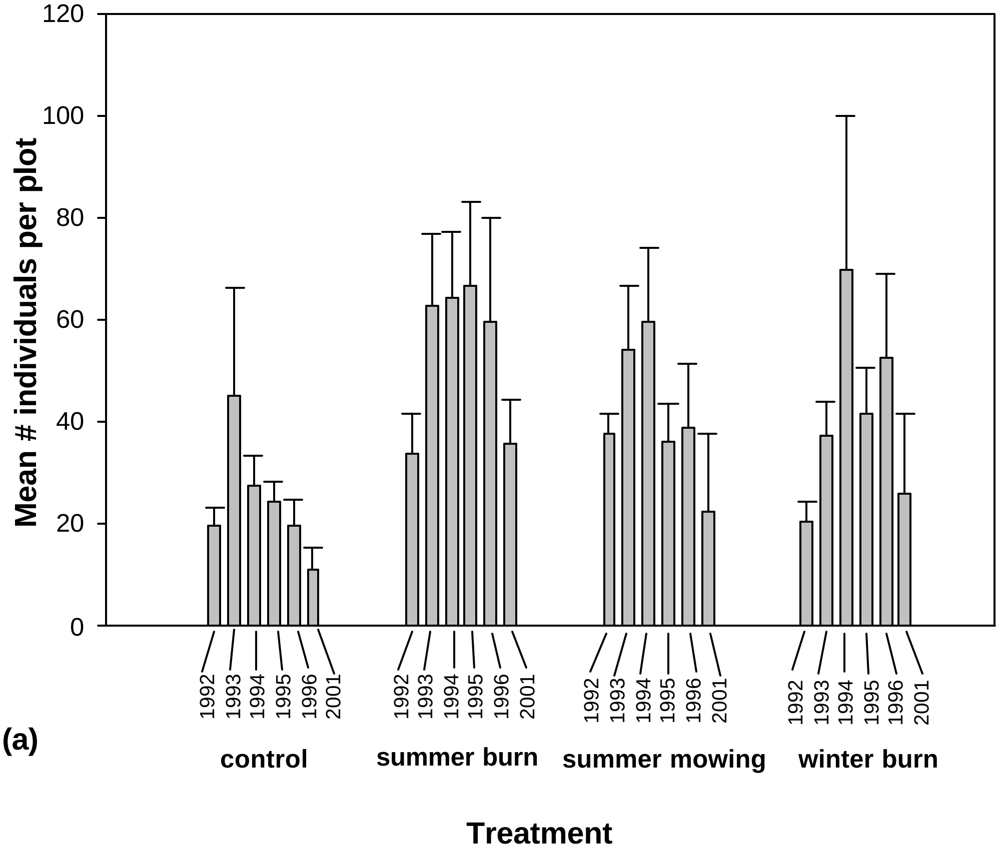
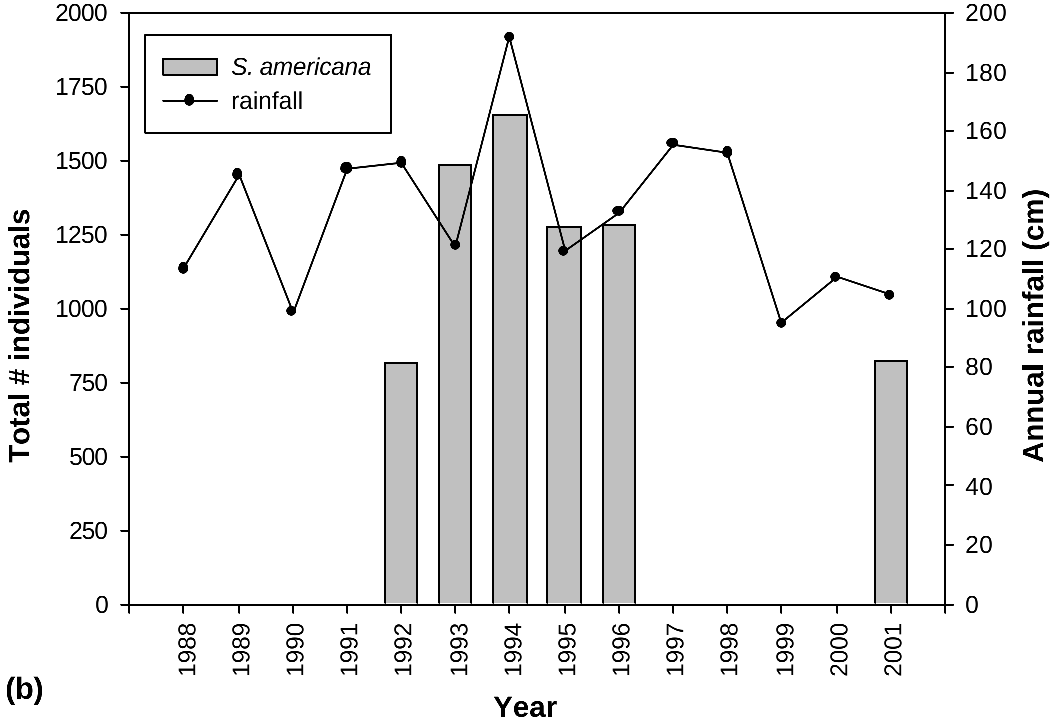
Funding for this study was provided by the U.S. Fish & Wildlife Service, the Joseph W. Jones Ecological Research Center, and the Robert Woodruff Foundation. We thank Kathy Aleric, Kim Coffey, Dee Davis, and Slaton Varner for their assistance in data collection.

Figure 3.1. Geographical distribution of *Schwalbea americana*. Counties with extant occurrences are indicated in grey.

Figure 3.2. (a) Density of individuals in each census year (mean ± SE) (b) total population size in each census year and annual rainfall.


(a)
Mean # individuals per plot
0
20
40
60
80
100
120
1992
1993
1994
1995
1996
2001
control
summer burn
summer mowing
winter burn
Treatment


(b)
S. americana
rainfall
Total # individuals
0
250
500
750
1000
1250
1500
1750
2000
Annual rainfall (cm)
0
20
40
60
80
100
120
140
160
180
200
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
Year

CHAPTER 4

GERMINATION STUDIES

INTRODUCTION

The federally endangered hemiparasite *Schwalbea americana* L. (Scrophulariaceae) is associated with fire-maintained ecosystems, such as the longleaf pine ecosystem of the southeastern Coastal Plain. Following fire, *S. americana* produces numerous flowers and viable seeds that germinate readily in the lab without treatment (Kirkman 1996, Kirkman *et al*. 1998). Despite large numbers of seeds (~ 10,000 per plant) and high germination rates in Petri dishes (up to 98%) (Norden, unpublished data), *S. americana* seedling establishment and survival in the field are reported to be low (Obee & Cartica 1997) and patchy in distribution (Kirkman *et al*. 1998).

Seed germination and seedling establishment in many populations of rare plants are limited by availability of microsite soil disturbances that alter environmental factors (Eriksson & Ehrlen 1992, Menges 1995, Hilton & Boyd 1996). Such factors are potentially involved in regulating seed germination and include light, moisture, temperature, and nutrients (Klinkhamer & De Jong 1988). Information on the germination of *S. americana* seed in the field is limited and largely based on anecdotal observations. Kirkman *et al*. (1998) suggested that patchy distributions of *S. americana* seedlings reflect a relationship between seed germination and small-scale disturbances that expose bare soil, such as pocket gopher activity or earthworm castings. If microsite availability is a limiting factor in seedling establishment, recovery could be facilitated by either amending populations with suitable microsites (Pavlik & Manning 1993) or by adding seeds to existing, unoccupied microsites (Hilton & Boyd 1996).

Successful recovery and reintroduction attempts also depend on the success of greenhouse-grown seedlings in transplant experiments. Successful germination and establishment of large numbers of *S. americana* in the greenhouse often requires multiple attempts, depending on the soil mix (Norden, personal observation), and can waste substantial amounts of viable seeds.

In the following preliminary investigations, our goal was to explore the germination ecology of *S. americana*, including seed reintroduction and germination in association with microsite soil disturbance and earthworm castings, the testing of different soil mixes to enhance seed germination in the greenhouse, and the long-term viability of seeds buried in the soil over time.

METHODS & RESULTS

Seed reintroduction

Seed reintroduction techniques were explored in a restoration site located on Ichauway. This site is an ecotonal area between an open herbaceous wetland and an upland longleaf pine savanna, in the vicinity of a natural population of *S. americana*. In May of 2001, we established a 361-m^2 (19 m x 19 m) garden plot in this site, with 100 1-m^2 sub-plots arranged in the garden plot such that each sub-plot was separated from neighboring sub-plots by 1 m (allowing for paths between sub-plots) (Figure 4.1a).

To each of 50 sub-plots, we randomly assigned one of two treatments: 1) microsite soil disturbance, or 2) no disturbance. For sub-plots without disturbance, we spread 100 seeds as evenly as possible by hand to half of each 1-m^2 sub-plot. For sub-plots with soil disturbance, we created five small bare patches (approximately 5 cm diameter) in half of the sub-plot by removing leaf and pine needle litter and raking the soil with a small comb to expose bare soil (Figure 4.1b). We placed 20 seeds into each small disturbance, for a total of 100 seeds per 0.5 m^2. We sowed seeds into the first half of each sub-plot in mid-June 2001 and to the other half of the sub-plot in early September 2001. In April 2002, we created 90 additional sub-plots between existing sub-plots (45 sub-plots per treatment), and sowed seeds into half of each sub-plot in the same manner described above. We monitored the garden plot weekly for germination following seed addition.

We predicted that by raking the soil and creating available microsites, germination would occur either earlier or exclusively in the disturbances. However, we observed no germination in any of the treatment sub-plots.

Germination on earthworm casts

We explored earthworm castings as possible microsite conditions for enhancing seed germination. We collected fresh earthworm castings from a naturally occurring *S. americana* population, placed four cast piles (approximately 2-3 cm in diameter) in each of 8 flats (filled with Fafard-3b potting mix), and placed 20 *S. americana* seeds on each cast pile. We also placed seeds directly on potting soil adjacent to the earthworm casts, for a total of 160 seeds per flat. We maintained the flats in a timer-regulated misting greenhouse, which misted every 5 minutes for 5 seconds, and we monitored the flats twice a week for approximately 2 months for germination.

We used a Wilcoxon rank-sum nonparametric t-test (PROC NPAR1WAY; SAS Institute Inc. 1989) to contrast percent germination on earthworm casts with germination on bare soil. Mean percent germination per tray differed significantly between earthworm casts and no casts (Figure 4.2a, W = 89.0, p = 0.01).

Germination on soil mixes

To explore potential soil mixes to facilitate optimal germination of *S. americana* for use in future greenhouse projects, we tested seed germination on three different soil mixes. We tested seed germination on Jiffy-7 Peat Pellets® (composed of pure compressed sphagnum peat moss encased in a thin mesh bag), a potting soil mix (1 part Fafard-3b® potting mix, 1 part sterile, washed play sand), and a bark-based, soil-less mix (gravel, pine bark, Osmocote® slow-release fertilizer, Micromax®, and Triple Super Phosphate®). We placed each soil mix into a seedling flat, with 20 seeds in each of 48 cells per flat (total of 960 seeds per soil mix). Seeds were simply placed on top of the soil mix and not covered or pressed into the soil. We misted the seeds daily with water filtered by reverse osmosis, and each flat was covered with a clear, plastic humidity dome to retain moisture. We maintained the flats at room temperature and ambient light conditions, and we recorded germination twice a week from August 2001 to December 2001. Germinated seeds were carefully removed from the soil mix to minimize disturbance to other seeds.

We used a General Linear Models Procedure (PROC GLM; SAS Institute Inc. 1989), with Tukey's multiple comparison test, to examine differences in percent germination among soil mixes. Mean percent germination differed significantly among the three soil mixes (Figure 4.2b, $F = 42.48$, $p < 0.001$), with the highest rate of germination occurring on the peat pellets.

Buried seed bags

To test long-term seed viability, we collected *S. americana* seeds from a naturally occurring, local population in fall 2000 and tested the seed for viability. We then buried

100 seeds in each of 100 small, sand-filled mesh bags (total of 10,000 seeds buried) in March 2001, at a depth of 5 cm, in a 60-year old slash pine plantation. Every year for five years, 20 bags will be extracted and all seeds will be counted and tested for viability by germination tests. We removed the first set of 20 bags in February 2002 and conducted germination tests in March 2002 by placing seeds on wet filter paper in plastic Petri dishes and allowing seeds to germinate at room temperature and ambient light conditions for approximately 2 months.

Following seed collection in 2000, percent germination (mean ± SE) was 55.0 % ± 5.0. In 2002, 97.0 % ± 0.8 of the seeds buried were recovered, and percent germination of these recovered seeds was 44.75% ± 2.62.

DISCUSSION

Our results suggest that germination of *S. americana* in the field may be associated with microsite soil disturbances, specifically earthworm castings. Earthworm castings often contain higher amounts of nutrients, including NH_4, NO_3, and P, relative to parent soil (Ganeshamurthy *et al*. 1998, Parkin & Berry 1994, Rangel *et al*. 1999), and casts may provide nutrient-rich microsites for plant growth and development (Zaller & Arnone 1999). It is also likely that earthworm casts have a higher water-holding capacity than surrounding soil (Edwards & Bohlen 1996, Zaller & Arnone 1999), which may enhance seed germination and seedling establishment.

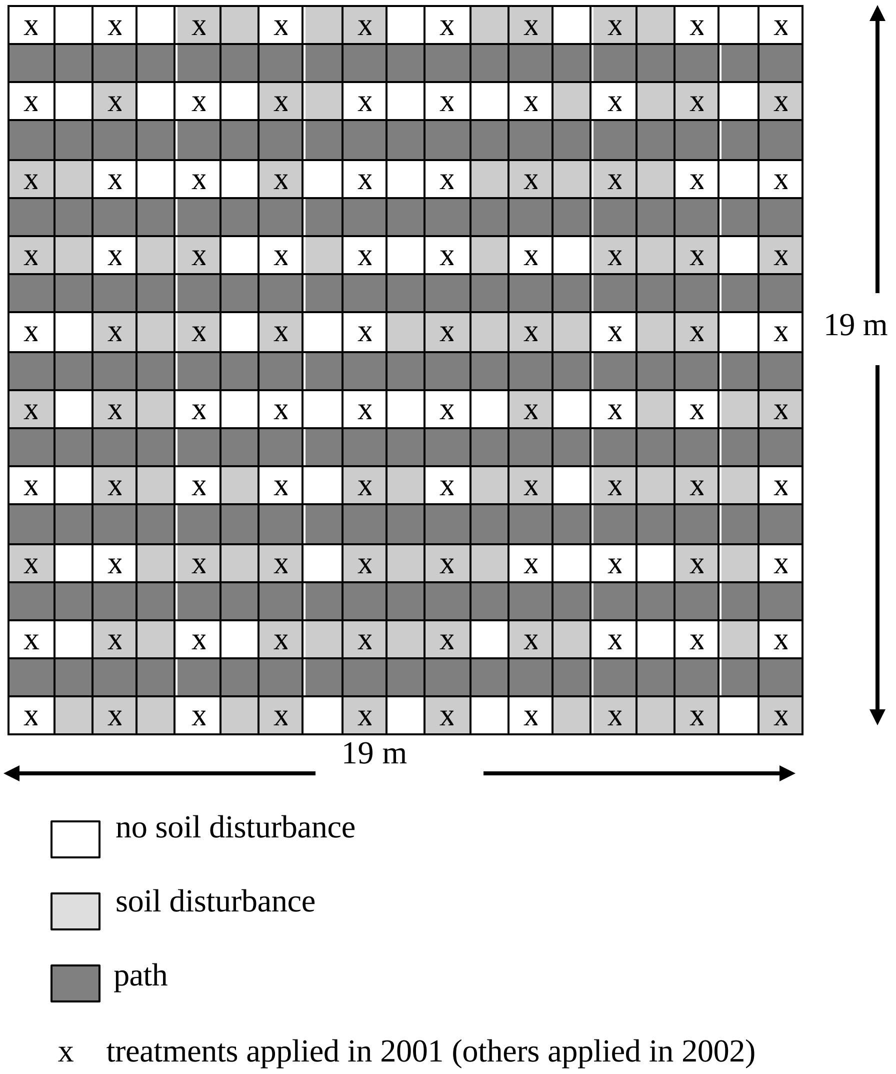
Although we found significantly more germination in association with earthworm casts, germination may have been stopped prematurely by mold growth in several of the flats early in the experiment. Moreover, our earthworm cast experiment was conducted in a controlled greenhouse environment. To determine the impact on population recruitment, the relationship between germination and casts should be investigated under field conditions. In addition, the relationship between cast creation and distribution and fire events, along with the timing of germination events in the field, must be explored to determine possible reintroduction options.

The lack of germination in our garden plot experiment may be due to extremely low precipitation and drought conditions during the study (National Climatic Data Center, NOAA, Asheville, NC). Throughout the study period, the soil in the garden plot was extremely compacted and dry (personal observation), and it is possible that seed germination was inhibited simply by inadequate soil moisture. Therefore, our results might have differed if we had provided supplemental water to the garden plot.

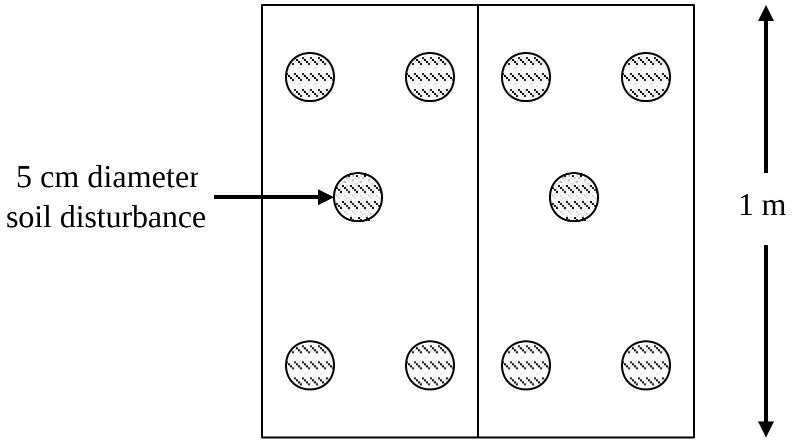
Peat pellets appear to enhance germination of *S. americana* in greenhouse or field conditions. The increased germination is probably due to greater availability of water to the seeds, as peat moss has a higher water-holding capacity than sand or bark mixes (Cornell Cooperative Extension, Cornell University, Ithaca, NY). To minimize root disturbance during transplanting and reintroduction, it is possible that an entire pellet could be planted with or near a host species in either the greenhouse or the field. Because obtaining an accurate count of germinated individuals required removing seedlings from the pellet, we do not know how these pellets might have affected subsequent growth and development. It is also unknown if haustoria of *S. americana* would be able to penetrate the mesh-like bag encasing the peat moss to allow successful host attachment.

Our results demonstrate that *S. americana* seeds buried in soil in field conditions will persist and remain viable for at least one year. The germination rate of seeds not buried was relatively low for this species (55%), but these seeds were not tested until approximately a year after collection, and it is possible that some viability was lost during cold storage. However, the germination rate of the recovered seeds was similar to that of seeds not buried, and even though the buried seeds may have been afforded some protection from deterioration or granivory by mesh bags, these findings support observations of seeds remaining dormant in greenhouse pots for a year before germination (H. Norden, pers. obs). Although not conclusive for naturally dispersed seeds, our results provide evidence that *S. americana* seeds have the potential to exist in a persistent soil seedbank.

Figure 4.1. Seed reintroduction experiment (a) garden plot layout (b) soil disturbance treatment.

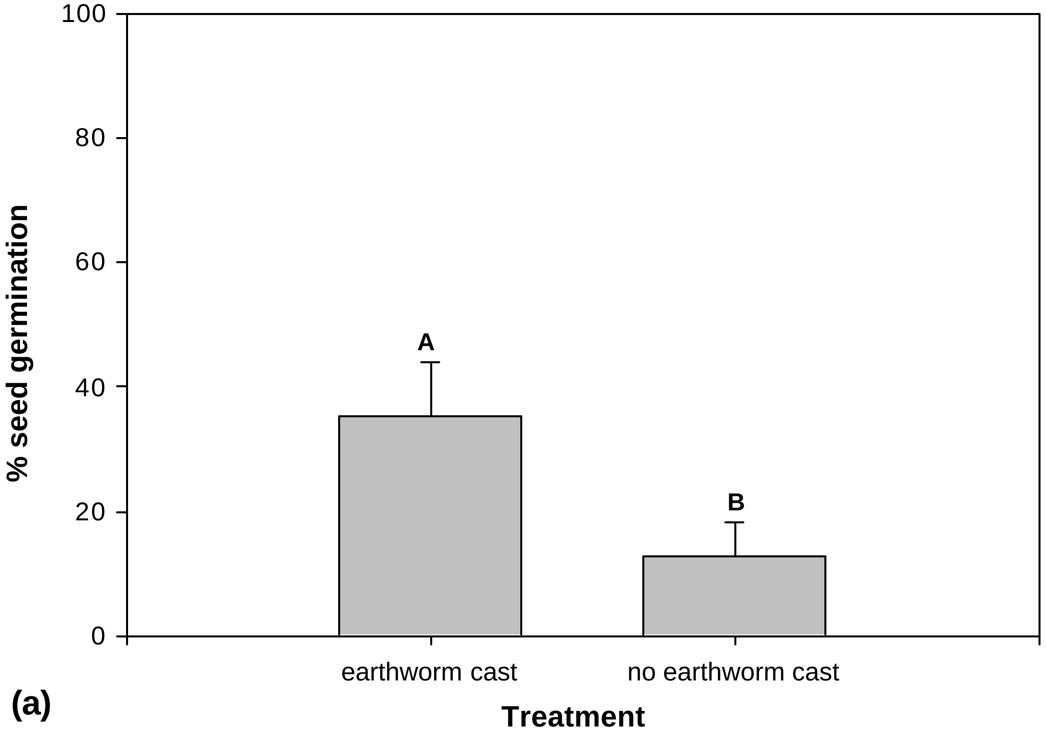

19 m
19 m
no soil disturbance
soil disturbance
path
x treatments applied in 2001 (others applied in 2002)

(a)

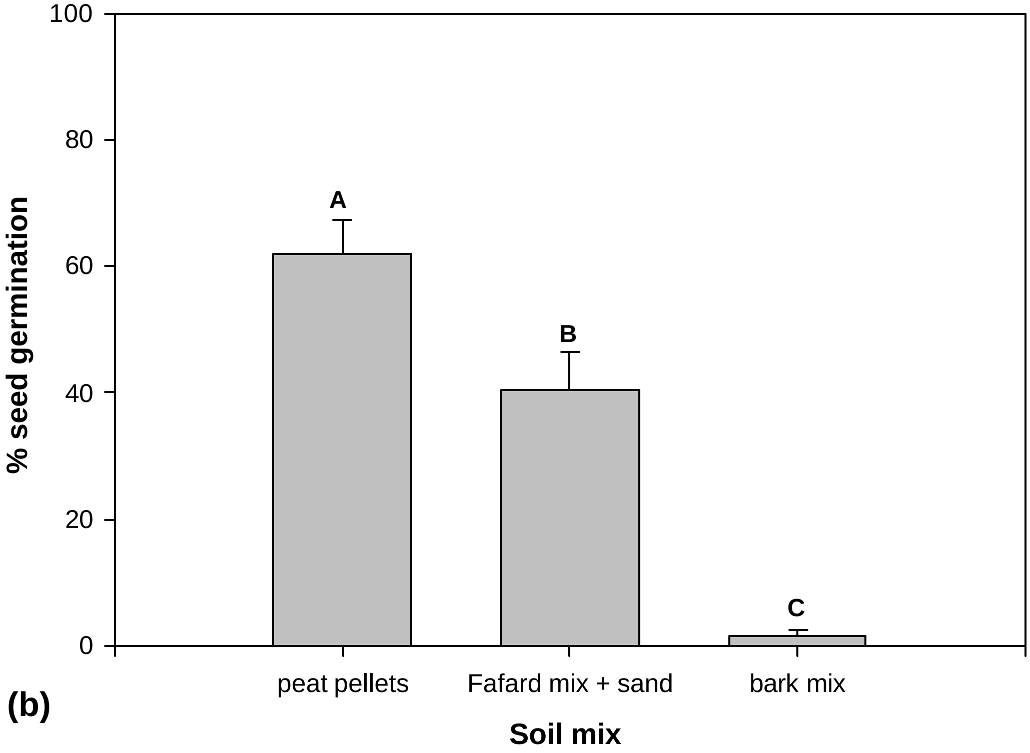

5 cm diameter soil disturbance
1 m
1 m

(b)

Figure 4.2. *Schwalbea americana* germination (mean ± SE) (a) % germination on earthworm casts (b) % germination on soil mixes. Treatment means with different letters are significantly different ($p<0.05$).


100
80
60
40
20
0
% seed germination
A
B
earthworm cast
no earthworm cast
Treatment

(a)


100
80
60
40
20
0
% seed germination
A
B
C
peat pellets
Fafard mix + sand
bark mix
Soil mix

(b)

CHAPTER 5

CONCLUSIONS

The federally endangered hemiparasite, *Schwalbea americana* L. (Scrophulariaceae) is one of nearly 200 rare plant species associated with the fire-maintained longleaf pine ecosystem of the southeastern Coastal Plain. *Schwalbea americana* requires frequent, low-intensity fires for reproduction and population persistence. Because of this, remaining populations of *S. americana* often occur on private land managed with prescribed fire to maintain suitable bobwhite quail habitat, or on military bases, where training activities result in fires. Development of appropriate management and recovery plans for existing *S. americana* populations, along with future reintroduction attempts, is hindered by the lack of knowledge on the species biology and life history of this extremely rare species. In this study, several key components of the species biology of *S. americana* were studied under field and greenhouse conditions, including the fire-induced flowering response, herbivory, species longevity and dormancy, and seed germination requirements. A life cycle of *S. americana* is presented in figure 5.1, and letters (A-D) indicate areas of research focus in this study. Question marks (?) indicate areas where future research is needed.

Overview of results

The fire-induced flowering response exhibited by *S. americana* is stimulated by a combination of above-ground stem removal during fire and increased light availability following fire (Figure 5.1, A). This particular combination of fire effects possibly induces or enhances a hormonal change within the re-sprouting stem to facilitate floral initiation. These findings demonstrate that abundant flowering in *S. americana* can be achieved without fire, but the long-term effects of mowing plus raking on seedlings and seedling establishment are unknown. Additional studies are needed to determine the impact of repeated use of such alternative management options on survival and recruitment. Furthermore, the response of host plant species, as well as competitor species, to alternative management options should be examined to ensure future persistence and health of existing *S. americana* populations.

Results indicate that seeds buried in the soil will persist and remain viable for at least one year and suggest that they may have the potential to exist in a persistent soil seedbank (Figure 5.1, B). Germination of *S. americana* in the field may be associated with earthworm castings. Earthworm castings may enhance seed germination by creating nutrient- or moisture-rich microsites and may play an important role in seedling establishment (Figure 5.1, C). However, the relationship between cast creation and distribution and fire, as well as the timing of germination events, is unknown, and further examination of germination on earthworm casts must be conducted in the field to determine implications for future seed reintroduction attempts.

Individual *S. americana* plants are relatively long-lived, and plant dormancy is common (Figure 5.1, letter D). It is possible that dormancy is stimulated by periods of environmental stress (i.e., drought or fire suppression) and therefore may play a major role in population persistence and recovery. Longer-term studies, relating year-to-year demographic and environmental conditions, are needed to reveal information on how dormancy patterns affect population dynamics over prolonged periods of environmental stress and/or fire suppression.

Implications for management of *Schwalbea americana*

A schematic representation of a management plan for *S. americana* is shown in Figure 5.2. For existing populations, prescribed fire is the best management option to stimulate flowering and maintain appropriate habitat. However, if populations occur in areas where prescribed fire is not feasible (such as roadsides), or if weather or habitat conditions prohibit the use of prescribed fire, then mowing followed by complete biomass removal by raking may be used to stimulate flowering.

Germination and seedling establishment in the field seem to be limiting factors in population recovery and reintroduction. Because each flowering individual is capable of producing up to 10,000 viable seeds, collection of large numbers of seeds is relatively quick and easy, making seed addition the most cost- and time-efficient method for establishing new populations in restored habitats or supplementing existing populations with additional individuals. Furthermore, seed kept in cold storage can remain viable for at least 8 years, allowing large numbers of seeds to be stored for future reintroduction projects. These findings suggest that creation of microsites, particularly amendments of earthworm castings, may facilitate germination and establishment of reintroduced seeds. However, if increased moisture associated with earthworm casts is the mechanism found to enhance field germination, success of seed reintroduction projects may rest on the practicality and feasibility of watering restoration areas. Although more time- and labor-intensive, reintroduction of greenhouse-grown seedlings, or seedling-host units, may prove to be optimal and should also be explored in future studies.

Managing populations of *S. americana* for long-term persistence may be facilitated by the plant’s long-lived nature and ability to persist in a dormant state. Dormancy, which permits plants to persist through unfavorable environmental conditions such as drought and fire suppression, indicates that existing populations are more stable than previously thought, barring any major disturbances that would dramatically alter or disturb the habitat (such as plowing or disking). The results also suggest that this species is resilient to minor changes in management and that annual fluctuations in population sizes are typical, particularly in moist, ecotonal areas where this species has adapted to varying degrees of moisture and patchy fire events. However, the period of persistence of individuals in a dormant state, along with the effects of more severe environmental conditions on population structure, is unknown. Long-term fire suppression would not only cause a sharp decline in recruitment of seedlings, but it would also have a detrimental effect on the habitat, eventually leading to the encroachment of woody species and increased competition for resources.

Due to the longevity and dormancy exhibited by *S. americana* individuals, it is possible that remnant populations occur in areas that have experienced short-term fire suppression, particularly if periods of dormancy are stress-induced. With the reintroduction of frequent prescribed fire for longleaf pine conservation and restoration efforts, formerly dormant populations of *S. americana* may re-emerge. Consequently, recovery efforts should not only focus on reintroduction of this species into suitable, restored habitat, but should also include intensive investigation of areas with a high probability of harboring dormant populations.

Figure 5.1. Life cycle of *Schwalbea americana.* Letters A-D indicate research focus of this study, and question marks (?) indicate areas where future research is needed.

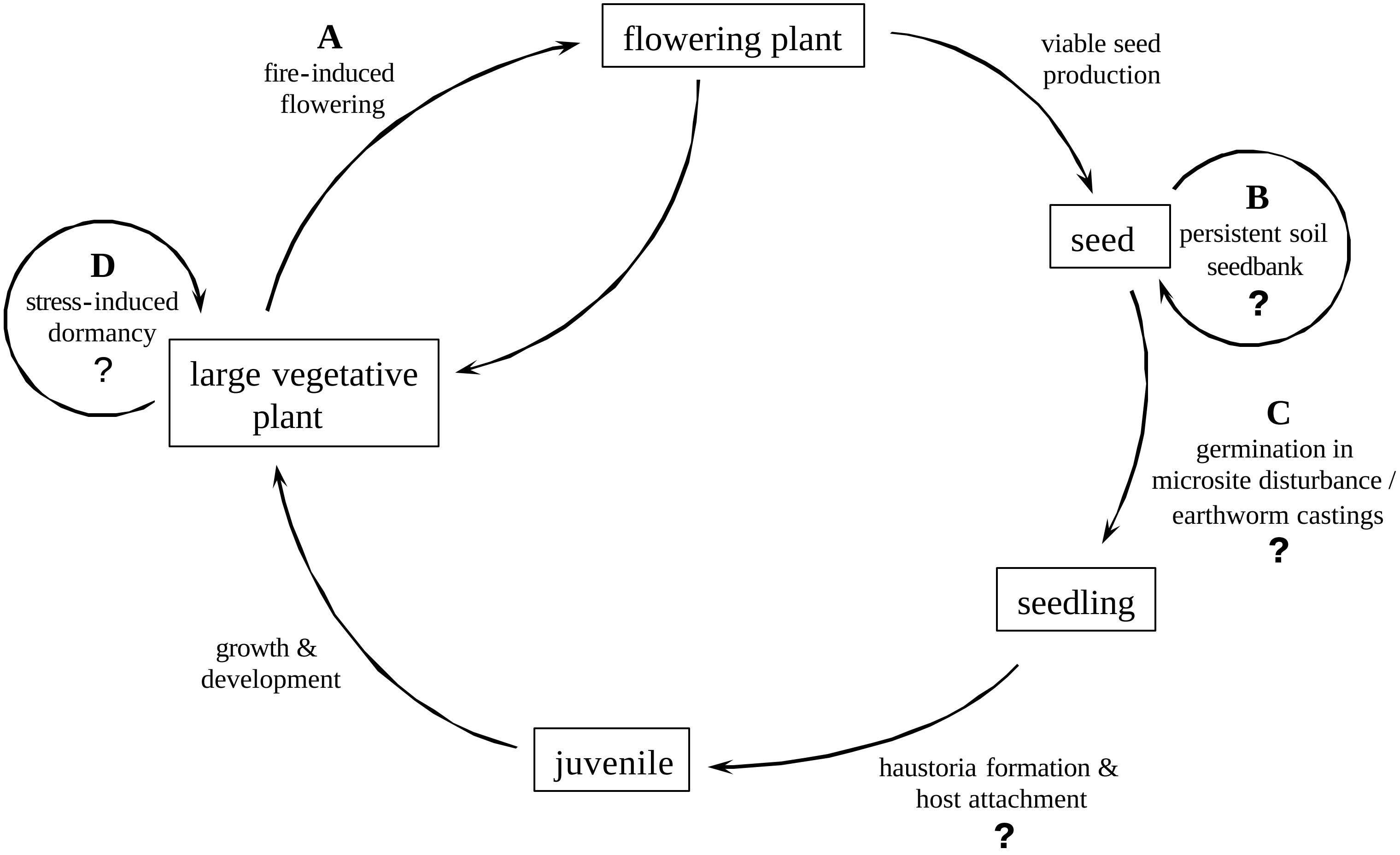
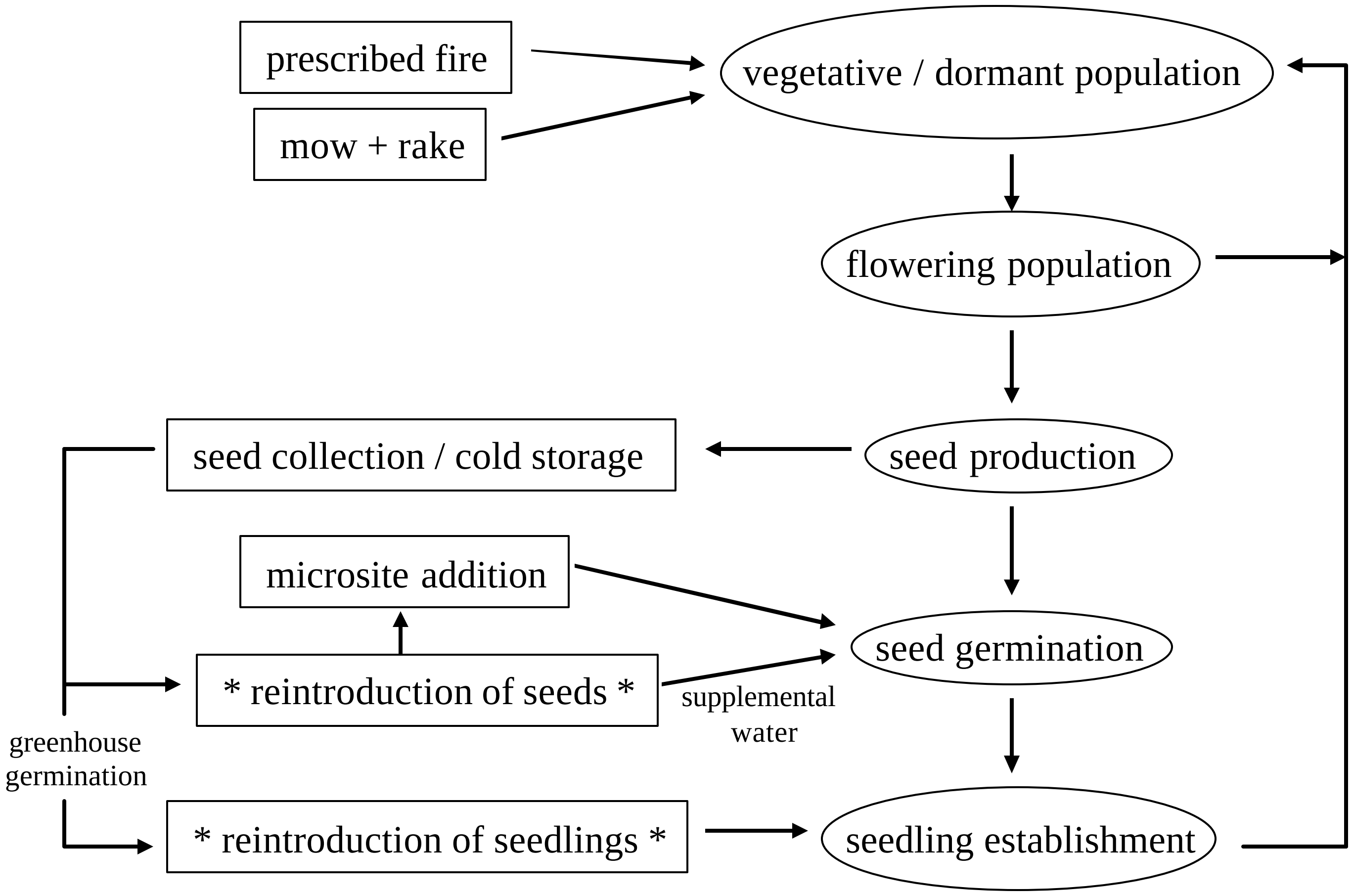

A
fire-induced flowering
flowering plant
viable seed production
seed
B
persistent soil seedbank
?
C
germination in microsite disturbance / earthworm castings
?
seedling
haustoria formation & host attachment
?
juvenile
growth & development
large vegetative plant
D
stress-induced dormancy
?

Figure 5.2. Schematic representation of a management plan for *Schwalbea americana*. Boxes in the left-hand column indicate management options and suggestions, and ovals in the right-hand column indicate life history stages. Asterisks (*) indicate options for establishing new populations of *S. americana*.


prescribed fire
mow + rake
vegetative / dormant population
flowering population
seed production
seed collection / cold storage
microsite addition
* reintroduction of seeds *
supplemental water
seed germination
greenhouse germination
* reintroduction of seedlings *
seedling establishment

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