RESEARCH NOTE

Persistence and Prolonged Winter Dormancy of the Federally Endangered *Schwalbea americana* L. (Scrophulariaceae) Following Experimental Management Techniques

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ABSTRACT: The federally endangered hemiparasite, *Schwalbea americana* L., American chaffseed (Scrophulariaceae), is a long-lived perennial herb adapted to fire-maintained ecosystems, such as *Pinus palustris* Mill. – *Aristida* spp. (longleaf pine-wiregrass) communities of the southeastern Coastal Plain. *Schwalbea americana* exhibits fire-induced flowering, and populations reportedly decline in the absence of fire; however, 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, and survivorship of individuals between 1992-2001, in four natural populations that were subjected to experimental management techniques between the years 1992-1996. Treatments included dormant season burn (March), growing season burn (June), growing season mowing (June), and control (no treatment). Our findings indicate that none of the short-term experimental management techniques have a detrimental effect on population persistence (five years post-treatment), 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 prolonged winter dormancy that may facilitate long-term population persistence during unfavorable environmental conditions or fire suppression.

Index terms: Schwalbea americana, American chaffseed, endangered species, dormancy, fire-adapted species

INTRODUCTION

Disturbance-adapted plant species have often evolved specific life history traits to persist through frequent and repeated disturbances (Pickett and White 1985). In fire-dependent ecosystems, such adaptations include rapid post-fire resprouting (Abrahamson 1999), fire-stimulated flowering and seed production (Parrott 1967, Myers and Boettcher 1987, Platt et al. 1988, Brewer and Platt 1994), and heat or smoke-stimulated germination (DeLange and 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 and Peet 1983, Hardin and 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 1), with the majority of remaining populations small and fragmented. Habitat loss as a result of fire suppression and habitat destruction due to agricultural land use are the primary reasons for its decline (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 2002). However, development of appropriate management plans is constrained by a lack of information regarding long-term population persistence and post-disturbance recovery of this species, particularly following periods of short-term fire suppression.

The purpose of this study was to determine the current population status and stability of four populations of *S. americana* five years following the termination of experimental management techniques that were imposed from 1992 to 1996 (Kirkman 1996, Kirkman et al. 1998). Specifically, we addressed the following questions: 1)

Figure 1. Geographic distribution of *Schwalbea americana*, with study site location in southwestern Georgia. Counties with extant occurrences are indicated in grey.

Are the population differences due to treatments observed in 1996 still apparent in 2001, following resumption of prescribed fire?; 2) What is the percent survivorship of the original 1992 cohort?; and 3) What are the roles of species longevity, recruitment, and reappearance in population persistence, recovery, or decline over the nine year study period?

METHODS

Study site

The initial study was implemented at Ichauway, a privately owned reserve of the Joseph W. Jones Ecological Research Center in Baker County, Georgia (Figure 1) in summer 1992. Each of the four naturally occurring populations of *S. americana* used in this study occurs 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. 1997, 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. and Rupr., *A. stricta* Michaux.) and forbs. Past land use includes frequent (1-3 y) dormant season prescribed burns for bobwhite quail (*Colinus virginianus*) management and selective timber harvest (Kirkman et al. 1998).

Experimental design & treatments

Plot layout consisted of a randomized complete block design with populations as blocks and plots as sub-samples within each treatment. At 3 of the 4 sites, 12 plots (3 m x 7 m) were established. Small population size at the fourth site allowed for only nine 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 (fire exclusion, no mowing 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 per treatment group was sampled. Two randomly selected plots of each group of three plots per treatment in each block (site) were selected in 1994 and this same sub-sample was re-sampled in each census thereafter. Each year, all previously tagged plants were located and re-measured (any plants not located were considered missing for that year), and all new plants were tagged, mapped, and measured. Due to the relatively wide spacing of individuals, we assumed that individuals located within 1 cm of an aluminum tag were previously tagged.

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). By the end of the former study (1996), population densities of the prescribed burn treatments were greater than the fire exclusion treatment (dormant season fire highly significant, growing season fire marginally significant); however, the mowing treatment did not differ from the fire exclusion treatment. Based on depletion curves, the half life of the initial 1992 cohort was reached in 1996, regardless of treatment. Through the period of this initial study, approximately 30% of the population in the mowing treatment was missing one or more years and then reappeared. Prescribed fire across all treatment plots was resumed in spring 1998 and 2001; and in summer 2001, the same 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, and the term "treatments" refers to the experimental treatments applied between 1992 and 1996.

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 analyses to normalize the data. A depletion curve of the 1992 cohort based on the 1992-1996 annual census data was extended using the 2001 census data. Plants that were located within 1 cm of tags, but had been missing in the 1996 census, were considered to have reappeared.

RESULTS

Mean density of individuals did not differ among treatments in 2001, six years following the last treatment application ($F = 1.99$, $p = 0.19$, $df = 3$), in contrast to the pattern observed at the end of the initial study. Similarly, relative change in density of individuals from 1996 to 2001 and from 1992 to 2001 did not differ among treatments ($F = 0.93$, $p = 0.44$, $df = 3$ and $F = 1.07$, $p = 0.38$, $df = 3$, respectively). Thus, even though overall population densities declined between 1996-2001, values were similar to those initially found in 1992 (Figure 2a). Within the nine-year study period, year-to-year fluctuations occurred across all treatment populations (Figure 2b).

From the 2001 census, the depletion curve of the 1992 cohort was extended from that developed annually between 1992-1996, and ranged from 10-17% per treatment (Figure 3). As documented in 1996, mean percent survivorship of the original 1992 cohort did not differ among treatments in 2001 ($F = 0.02$, $p = 0.99$, $df = 3$). Percent survivorship of 1993 and 1994 recruits showed similar patterns, with survivorship of 1993 recruits ranging from 8-13% per treatment ($F = 0.07$, $p = 0.97$, $df = 3$) and survivorship of 1994 recruits ranging from

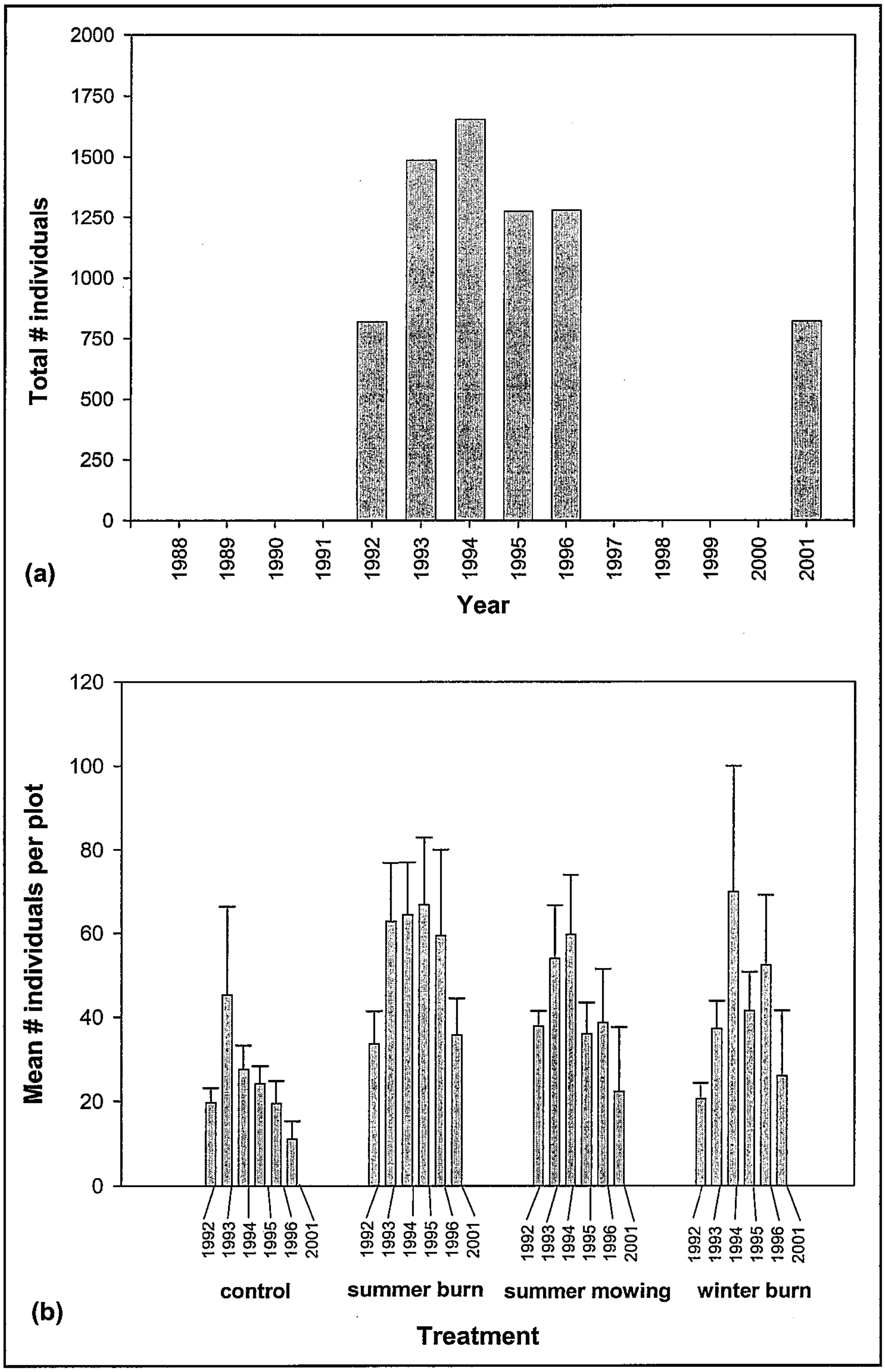

Figure 2. (a) Total density of individuals of all populations (1992-1996, 2001) (b) Density of individuals by treatment in each census year (mean ± SE).

7-11% (F = 1.55, p = 0.28, df = 3). Of the 1992 cohort surviving in 2001, 4-15% per treatment had been reported missing in 1996, and mean proportional values of reappearing individuals were similar across all treatments (F = 0.69, p = 0.603, df = 3). Mean density of new recruits (new individuals tagged in 2001) was similar across all treatments (F = 2.50, p = 0.13, df = 3), and ranged from 3-15 individuals per plot per treatment.

DISCUSSION

Our results do not provide evidence that any of the experimental management techniques have had long-term beneficial or detrimental effects on populations of *S. americana*. Within the nine-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. In particular, we should note that below average precipitation conditions occurred for three years prior to our census. Our data suggest that the largest total population size coincides with the year of highest rainfall (NCDC, 1999). However, 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 apparent longevity (at least nine years) of some established *S. americana* individuals and verification that individuals are absent above-ground some years and then reappear in one or more subsequent growing seasons. Although we cannot be positive that individuals within 1 cm of a tag are the same individuals from year to year, the low recruitment rates and spatial distribution of obvious new individuals suggest that our assumption is reasonable. Additional studies exploring potential environmental variables responsible for inducing and breaking this "prolonged winter dormancy" are needed to fully understand the relationship between reappearance of individuals and long-term population dynamics. Unfavorable growing conditions, such as drought, have been suggested as possible controls of prolonged dormancy for several other species (Epling and Lewis 1952, Thomas et al. 1981, Lesica and Steele 1994). Additional evidence suggests an interacting effect of environmental cues and the condition of an individual, such as performance or size in previous years, may stimulate prolonged dormancy (Hutchings 1987, Mehrhoff 1989, Lesica and Steele

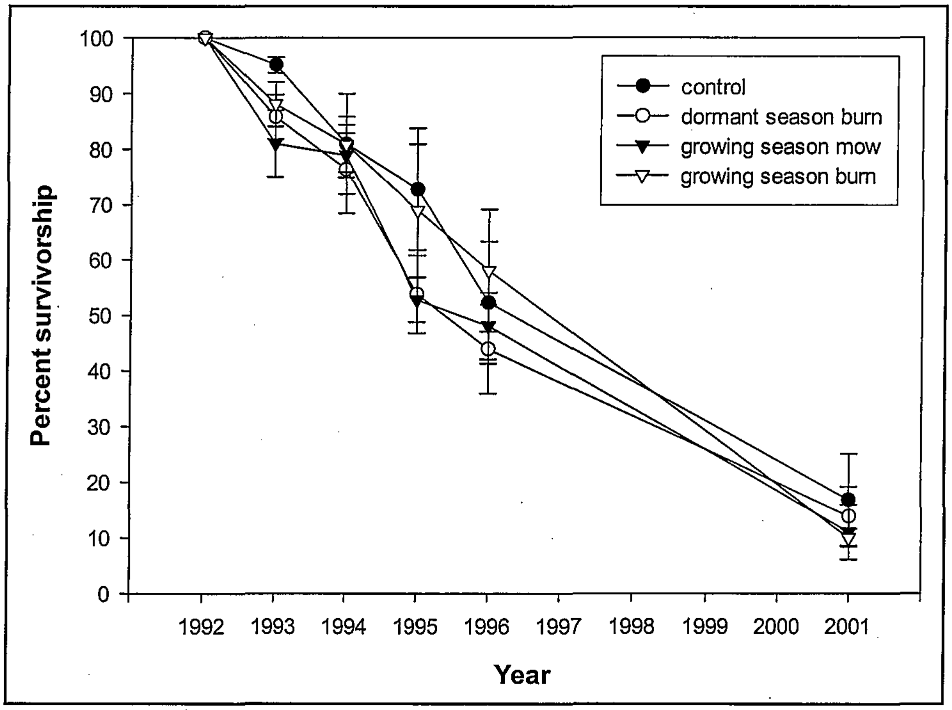

Figure 3. Cohort depletion curve of uneven-age census group in 1992.

1994). It is also possible that the ability of a *S. americana* individual to remain dormant for prolonged periods is linked to its host-parasite relationship, similar to that suggested for mycorrhizal associations with orchids (Montgomery 1990, Lesica and Steele 1994).

The potential for re-emergence 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 and Steele 1994). If periods of prolonged dormancy in *S. americana* are stimulated by unfavorable conditions, such as drought or periods without fire (as in our control treatment) (Kirkman et al. 1998), it is likely that dormant individuals could play a major role in population persistence and recovery as conditions become favorable again (Lesica and Steele 1994, Lesica 1999). Longer term studies (> 10 y), 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 and 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, provided that the use of prescribed fire was maintained for habitat management.

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