RESEARCH ARTICLE

Effects of Fire and Treatments that Mimic Fire on the Florida Endemic Scrub Buckwheat (*Eriogonum longifolium* Nutt. var. *gnaphalifolium* Gand.)

Kelly McConnell[1]
Graduate Program in Sustainable Development and Conservation Biology
University of Maryland
College Park, MD 20742 USA

Eric S. Menges[2]
Archbold Biological Station
P.O. Box 2057
Lake Placid, FL 33862 USA

[1] Current address: NatureServe, 1101 Wilson Blvd., Arlington, VA 22209 USA.
[2] Corresponding author e-mail: emenges@archbold-station.org

Natural Areas Journal 22:194–201

ABSTRACT: We investigated the responses of scrub buckwheat (*Eriogonum longifolium* Nutt. var. *gnaphalifolium* Gand.), a perennial herbaceous plant endemic to sandhill and Florida scrub in central Florida, USA, to prescribed fire and four treatments mimicking different aspects of fire. Top-clipping of scrub buckwheat individuals, litter removal, shrub canopy removal, and ash addition were imposed in a replicated, factorial study around focal plants. We studied subsequent flowering and seedling recruitment in experimental and burned plants. Fire stimulated flowering, but only top removal produced similarly high flowering levels. Seedling recruitment followed postburn flowering, but, outside of the burn, only litter removal stimulated seedling recruitment. The rapid response of scrub buckwheat to fire allows it to persist under frequent burning typical of sandhill vegetation, while its long life span and plant dormancy allow persistence under the less frequent fire regimes characteristic of Florida scrub. However, no single substitute for prescribed burning is likely to produce the dramatic postburn flowering and seedling responses seen in burned scrub buckwheat populations.

Efectos del fuego y de tratamientos que lo simulan sobre *Eriogonum longifolium* Nutt. var *gnaphalifolium* Gandog, una planta endémica de Florida

RESUMEN: Nosotros investigamos la respuesta del "scrub buckwheat" *Eriogonum longifolium* Nutt. var *gnaphalifolium* Gandog, una planta perenne endémica del "sandhill" y "Florida scrub" en el centro de Florida, USA, a quemas prescritas y cuatro tratamientos que simulan diferentes efectos del fuego. La eliminación de la parte aérea de la planta, la remoción de la hojarasca, la remoción del follaje de los arbustos y la adición de cenizas se impusieron en un diseòo factorial repetido alrededor de las plantas focales. Estudiamos la floración y el reclutamiento de plántulas posteriores a la aplicación del fuego o de los tratamientos. El fuego estimuló la floración, pero, entre los tratamientos experimentales, solo la eliminación de la parte aérea de la planta produjo niveles semejantes de floración. Se observó reclutamiento de plántulas asociado al florecimiento en los sitios quemados. Entre los tratamientos, solo la remoción de hojarasca estimuló el reclutamiento de plántulas. La rápida respuesta del "scrub buckwheat" al fuego le permite persistir bajo regímenes con quemas frecuentes típicas del "sandhill", mientras su largo ciclo de vida y la latencia de la planta le permiten persistir bajo regímens con fuegos menos frecuentes característicos del "Florida scrub." No obstante, ningún sustituto individual del fuego parece producir el dramático florecimiento posterior a la quema y las respuestas de reclutamiento de plántulas observadas en las poblaciones quemadas de *Eriogonum longifolium* var *gnaphalifolium.*

Index terms: fire management, Florida scrub, postfire flowering, sandhill vegetation, seedling recruitment

INTRODUCTION

Fire is a selective agent in many plant communities including Mediterranean and Australian shrublands (Bowen and Pate 1993), California chaparral (Tyler 1995), tallgrass prairie (Hartnett 1991, Vinton and Hartnett 1992), and Florida scrub and sandhill (Abrahamson et al. 1984, Myers 1985, Menges and Hawkes 1998, Menges 1999). Postfire recovery strategies include resprouters that persist through fire by generating successive shoots from belowground reserves (Menges and Kohfeldt 1995, Vila and Terradas 1995). Fire stimulated resprouting is often coupled with immediate and prolific flowering (Abrahamson 1984, Grigore and Tramer 1996, Carrington 1999) and subsequent seedling recruitment (Romme et al. 1997, Carrington 1999).

Florida scrub and sandhill are distinctive and biologically significant plant communities; within North America they support a notable concentration of endemic species (Christman and Judd 1990). In Florida scrub, plant species display characteristic postfire responses, including postfire resprouting, flowering, and seedling recruitment (Menges and Kohfeldt 1995, Hawkes and Menges 1996). Postfire recovery mechanisms may contribute to the abundance and persistence of rare scrub species. In Florida rosemary scrub, many endemic plants are obligate seeders with persistent seed banks (Menges and Kohfeldt 1995, Menges 1999). Their abundances are likely to be affected not only by habitat loss and fragmentation, but also by alterations in fire regime (Menges 1999). In Florida sandhill, most species respond to fire by resprouting and flowering (Olson and Platt 1995, Platt et al. 1988), and the soil seed bank differs markedly from the aboveground vegetation (N. Lang and E. Menges, unpubl. data). Fire in sandhill vegetation prevents shrubs and trees growth from altering habitat structure, although there may be complex effects of fire season and fire intensity on the vegetation (Myers 1985, Platt et al. 1988, Platt 1999).

Although fire management is essential for the maintenance of both Florida scrub and sandhill, it may often be difficult to accomplish fires that are intense enough to allow recovery of fire-adapted species (e.g., Abrahamson and Abrahamson 1996). Using mechanical disturbances to create postfire environmental conditions that may stimulate resprouting and flowering responses in some fire-maintained species has been proposed as a possible management alternative to fire when prescribed burns are impractical (Schmalzer and Hinkle 1992, Greenberg et al. 1995). However, one of the most complete studies of mechanical disturbance on Florida scrub (Greenberg et al. 1995) could not completely separate the effects of clearcutting from those of wildfire without salvage logging. Before mechanical alternatives to fire are used on a large scale, studies of comparative effects on target and nontarget populations, communities, and ecosystems are needed.

The mechanisms by which plants respond to fire are many and varied. Resprouting and flowering cues resulting from fire may include top removal, increased light, increased nutrients, and decreased litter cover. Resprouting and flowering in response to mechanical top removal often are similar to that which occur in response to fire (Matlack et al. 1993, Abrahamson 1999 but see Kirkman et al. 1998). Resprouting may be a general post-disturbance recovery strategy allowing persistence at a site (Bellingham and Sparrow 2000, Bond and Midgley 2001). Increased light occurs in gaps in Florida scrub. Gaps are associated with increased herb density, flowering, and seedling recruitment, survival, and growth (Hawkes and Menges 1996, Lambert and Menges 1996, Quintana-Ascencio and Morales-Hernandez 1997, Abrahamson 1999, Carrington and Keeley 1999, Menges et al. 1999). Such gaps may be expanded or created by fire (Menges and Hawkes 1998). Nutrient additions can sometimes stimulate flowering in a manner similar to fire (Lamont and Runciman 1993, Brewer 1995, but see Abrahamson 1999 for lack of a nutrient effect). Postfire nutrient pulses in Florida scrub and sandhill are transient and therefore difficult to detect (Anderson and Menges 1997, Carrington and Keeley 1999). Litter removal is generally associated with increased seed germination and seedling establishment (Fowler 1988, Xoing and Nilsson 1999).

Many species recruit preferentially in recently burned areas (e.g., Hartnett and Richardson 1989, Tyler 1995, Menges and Gordon 1996). Seed germination and recruitment may be triggered by fire-specific cues such as heat shock, smoke, ash, charred wood, or fire-created chemicals (Enright et al. 1997, Keeley and Fotheringham 1998, Preston and Baldwin 1999) or by indirect effects of fire, such as increased light levels or changes in light level experienced by seeds (Roy and Sonie 1992) or removal of germination-inhibiting litter. Organic litter has been shown to affect seed germination of Florida scrub endemics (Lambert and Menges 1996, Carrington 1996). The presence of ash may potentially affect light reflectivity, soil texture, and temperature with respect to microsite and seed safe sites. Seeds may germinate directly from a persistent buried seed bank, or seeds produced after a fire may germinate in a short time. It is practical to try to determine what mechanisms produce a postfire response if mechanical disturbances are intended to mimic or augment the effects of fire (Greenburg et al. 1995, Schmalzer and Boyle 1998).

This study attempted to isolate the mechanisms of disturbance that cause postfire resprouting, flowering, and seedling recruitment in the perennial herb, scrub buckwheat (*Eriogonum longifolium* Nutt. var. *gnaphalifolium* Gand. [= *E. floridanum* Small.]). Scrub buckwheat is endemic to Florida scrub and sandhill vegetation in central Florida, growing on xeric, yellow sands (Christman and Judd 1990, Coile 2000). Microsites supporting scrub buckwheat individuals have shallower litter than random points, both before and after fire, and have lower canopy cover in unburned areas (Carrington 1999). Nevertheless, scrub buckwheat populations persist in a range of postfire sites (E. Menges, unpubl. data). Individuals produce flowering stalks mainly during the summer flowering season, but can flower at various times of year following burns. Individuals are tap-rooted and nonclonal. This species is known to resprout and flower prolifically after fire (Carrington 1999), irrespective of the season in which fire occurs. Subsequently, strong postfire seedling establishment often occurs, especially within short distances of resprouting adults (Carrington 1999). Scrub buckwheat does not produce a seed bank even in sites with abundant plants (Carrington 1997; Satterthwaite et al., in press). It is currently listed as endangered in Florida and as threatened by the U.S. Fish and Wildlife Service (Coile 2000).

Using scrub buckwheat as a subject, we tested the hypothesis that modifying microsite conditions with experimental treatments that mimic components of fire will elicit resprouting, flowering, and seedling recruitment patterns similar to those observed following fire. Our aim was to understand the mechanisms by which fire causes dramatic responses in plants such as scrub buckwheat, and to evaluate management options for scrub and sandhill plant species that produce characteristic postfire resprouting responses.

METHODS

Study Site

This study was conducted at the Archbold Biological Station (ABS) in Highlands County, south-central Florida USA, located at the southern end of the Lake Wales Ridge. The two sites included in this study were characterized as southern ridge sandhill (Abrahamson et al. 1984, Menges 1999). Sandhill communities at ABS comprise three strata: the tree layer is dominated by pines (*Pinus clausa* and *P. elliotii* var. *densa* Little and Dorman), turkey oak (*Quercus laevis*), and scrub hickory (*Carya floridana*); the shrub layer includes myrtle oak (*Quercus myrtifolia*), sand live oak (*Q. geminata*), Chapman's oak (*Q. chapmanii*), and rusty lyonia (*Lyonia ferruginea*); and the herbaceous layer is dominated by wire grass (*Aristida beyrichiana*), scrub palmetto (*Sabal etonia*), saw palmetto (*Serenoa repens*), and several annual and perennial forbs. (Nomenclature follows Wunderlin 1998 except where noted.)

Experimental Design

We evaluated scrub buckwheat reproductive status, seedling recruitment, and leaf morphology in response to fire (at a burned site) and mechanical disturbances that mimicked fire (at an experimental site). Both sites were long unburned (since 1927) until prescribed fires were conducted in the 1990s. The burned site ("Loop") was burned during prescribed fires in May 1992 and May 1996 and was used to describe the impact of the 1996 fire. The experimental site ("Fire Tower"), adjacent to the burned site, was also burned in May 1992. However, no natural or mechanical disturbances occurred in the experimental site between May 1992 and the start of this experiment in May 1996. These two southern ridge sandhill sites were selected for this study because of similar fire histories, elevations, and locations.

We included 40 and 160 scrub buckwheat individuals in the burned and experimental sites, respectively. All plants were growing at least 1 m from conspecifics. Each plant was characterized on the basis of number of basal rosettes, total number of leaves, total number of flowering stalks, and the area and diameter of basal rosettes. We counted the number of adult and seedling scrub buckwheat plants growing in a 1-m-diameter circular neighborhood around each focal plant so that subsequent seedling recruitment could be noted. Reproductive status and seedling recruitment were monitored beginning shortly after the treatments (May 1996), six times in 1996, three times in 1997, and in June of 1998. We obtained additional data on flowering from four other ABS scrub buckwheat populations studied from 1990 to 2001 (Satterthwaite et al., in press) and subjected to various burn histories.

Experimental Treatments

We imposed four treatments on plants at the experimental site in June 1996. Each treatment had two levels: clipping (focal scrub buckwheat individuals clipped at ground level or not clipped), shrub canopy removal (removed by clipping at ground level or not removed), litter removal (removed or not removed), and ash addition (added or not added). The four-way, two-level factorial design of this experiment generated 16 treatment combinations, with 10 replicate target plants in each. (A few plants were later dropped from the experiment due to herbivory and other unforeseen events.) We assigned experimental plants to size classes based on initial basal rosette measurements and reproductive status. Treatments were then randomly selected within size-stratified classes to minimize any confounding effects of initial size.

Each of the experimental treatments was intended to isolate one of the effects of fire. The clipping treatment, intended to mimic the loss of shoot tissue in fires, consisted of removal of all aboveground biomass of scrub buckwheat focal plants at the soil surface. Shrub canopy removal, intended to simulate postfire reductions in canopy cover (Carrington 1999), was accomplished by removing all foliage within a vertical cylinder whose base was a 1-m-diameter circular plot centered on a focal plant. We recorded the percent canopy, from four ground-level spherical densiometer readings per replicate, before and after canopy removal in the experimental site and after fire in the burned site.

As a result of the 1996 prescribed burn in the burned site adjacent to the experimental site, 100% of the organic litter was consumed in 0.5-m-diameter circular plots centered on focal plants. To imitate fire's effect in removing litter, we removed all organic litter from replicate 0.5-m-diameter circular plots at the experimental site. We generated ash by burning clipped vegetation from five clipped plots. A thin layer of ash (a few millimeters deep) was evenly distributed across the soil surface of replicate 0.5-m-diameter circular plots. The ash was generated by burning sandhill vegetation in a trash can, with the area of clipped vegetation equal to the area of ash addition, to mimic the quality and quantity of ash produced by a complete fire.

Analytical Methods

We used *t*-tests to contrast conditions at the burned site with those at the experimental site before treatments. Categorical reproductive status (flowering vs. not flowering) and presence of seedlings in the experimental site were analyzed using the General Loglinear Model (Fienberg 1985). All proportional spherical densiometer and

Table 1. Differences between the pretreatment experimental site (Fire Tower) and the postburn burned site (Loop) in scrub buckwheat population structure, canopy cover, and litter cover.

Measurement	Mean (Standard Error, n) Pretreatment Experimental Site	Mean (Standard Error, n) Burned Site	*t*-value	*P*
Scrub buckwheat density (/m²)	0.97 (0.12, 151)	0.51 (0.18, 36)	1.81	0.72
Rosettes/plant	1.77 (0.07, 158)	2.46 (0.34, 37)	1.98	0.54
Percent plants flowering	27.9 (3.6, 156)	100.0 (0, 37)	20.2	0.000
No. of flowering stems/plant	0.29(0.04, 158)	2.30 (0.33, 37)	6.07	0.000
Canopy cover (%)	71.3 (1.2, 137)	61.6 (2.2, 29)	2.49	0.016
Litter cover (%)	75.8 (3.2, 58)	0.00 (0, 29)	23.9	0.000

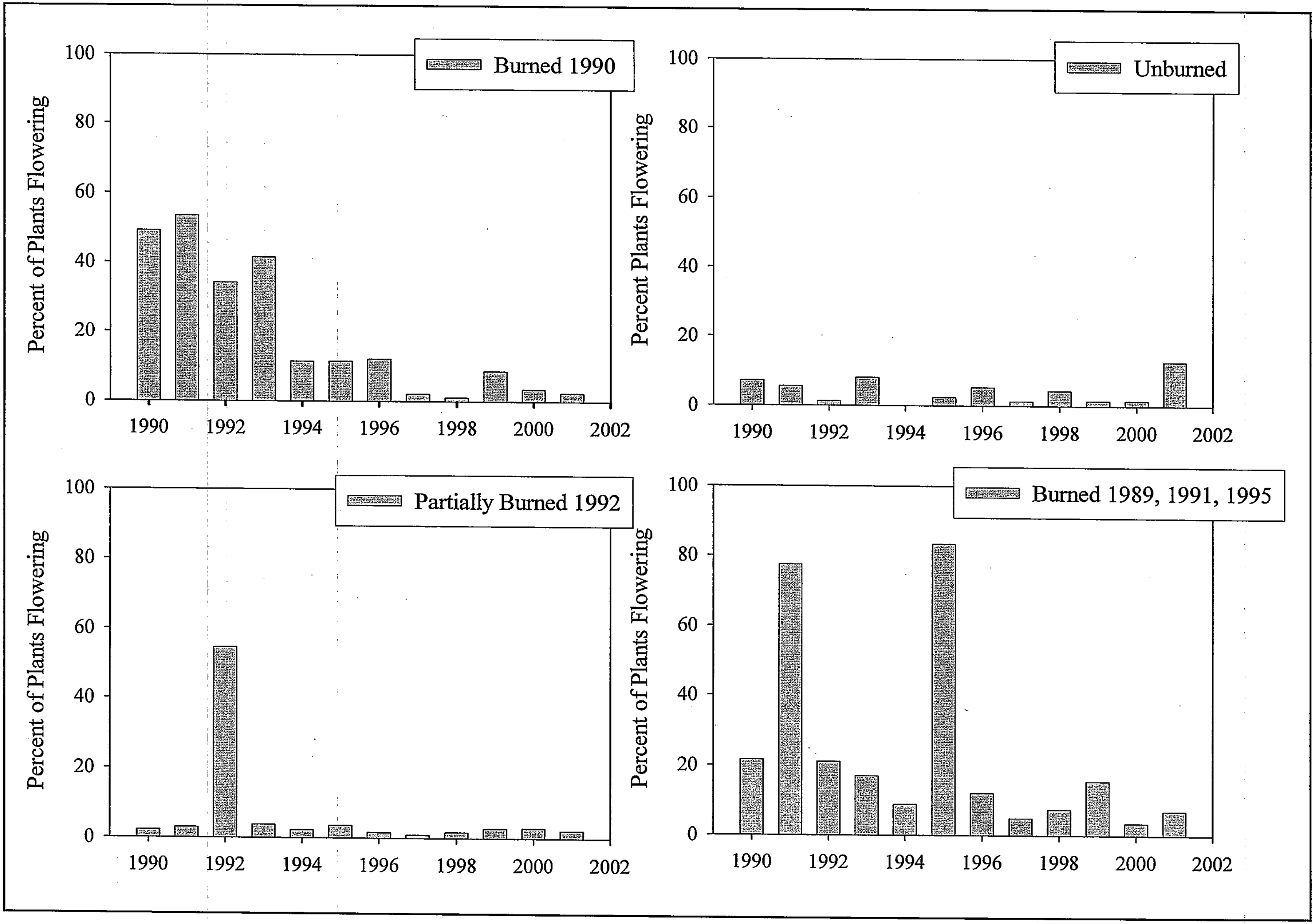

Figure 1. Percent of scrub buckwheat (*Eriogonum longifolium* var. *gnaphalifolium*) plants flowering each summer, 1990–2001, in populations with various burn histories at Archbold Biological Station, Florida.

litter cover measurements were angular (arcsin square root) transformed for analyses. We use $P < 0.05$ to ascribe significance and $P < 0.1$ to ascribe marginal significance.

RESULTS

Effects of Fire at Burned Sites

All scrub buckwheat plants in the burned site (Loop) resprouted, flowered, and produced a large number of flowering stalks immediately following the May 1996 burn. Percent flowering and numbers of flowering stalks per plant were significantly greater in the burned than the pretreatment experimental site (Fire Tower) (Table 1). However, plant density and number of rosettes per plant did not differ between sites.

Postburn canopy cover was lower in the burned site (61.6%) than in the pre-treatment, unburned site (71.3%; t = 2.49, df=164, P = 0.016). Canopy cover in the experimental site declined from 71.3% to 42.8% after the shrub canopy removal treatment. All litter was removed by fire at the burned site, whereas the experimental site was about three-fourths covered by litter before treatments (Table 1).

At three other ABS sites, fires during the 1990s induced scrub buckwheat to resprout, produce inflorescences, and flower at high levels (Figure 1). At two sites, the flowering response occurred primarily in the year of the burn, but high flowering rates (> 30%) continued for four years after a 1990 burn. In the absence of fire, fewer than 20% of plants flowered during the 11 years of observations (Figure 1). In the Loop population, burned in 1996, flowering percentages were 100% in 1996, then 97.3%, 74.5%, 13.1%, 2.1%, and 8.1% in subsequent years through 2001.

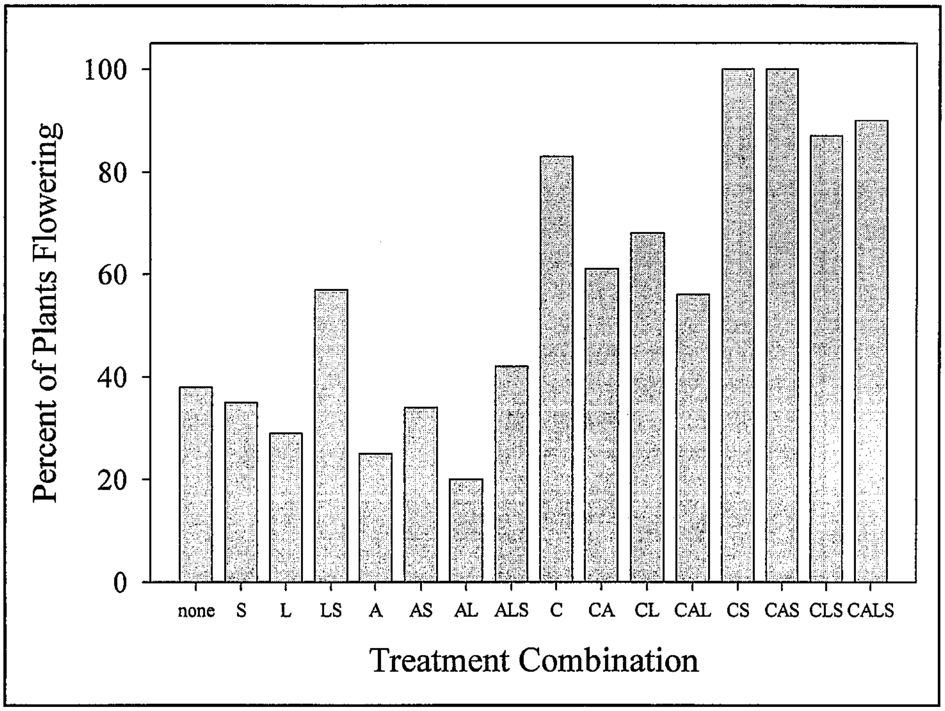

Figure 2. Percent of scrub buckwheat plants flowering, by treatment combination, 6 August 1996, five weeks after treatments were installed. Treatment codes and combinations of treatments are indicated under each bar: S=shrub canopy removal; L=litter removal; A=ash addition; C=clipped scrub buckwheat. Total sample size was 160.

Table 2. General loglinear model indicating the effects of treatments (C=clipping tops of scrub buckwheat individuals; S=shrub canopy removal; A=ash addition; L=litter removal) on categorical flowering response (F) in scrub buckwheat. Based on data collected through 5 December 1996.

Main Effects	df	X	ΔX	df
C, S, A, L, F	26	26.67		
+ C, F	25	17.30	9.36[a]	1
+ S, F	25	26.58	0.09	1
+ A, F	25	25.02	1.65	1
+ L, F	25	26.49	0.18	1

[a] $P < 0.05$.

Effects of Experimental Treatments on Scrub Buckwheat Flowering Response

Clipping of focal plants was the only manipulative treatment that had a significant effect on inflorescence production in the Fire Tower experimental site (Table 2). No significant higher order interactions between the main effects were identified. Flowering in a December 1996 sample did not deviate from results observed in August 1996, five weeks after manipulations were installed. Flowering was highest (>90%) for clipped plants with shrub canopy removal (C and S, Figure 2), was intermediate (60%–80%) for clipped plants with no shrub removal (C without S, Figure 2), and was lower than 60% for all unclipped scrub buckwheat individuals (no C, Figure 2). Mortality through December 1996 was significantly lower in clipped plants (8.5%) than in unclipped plants (28.2%, G = 9.647, df = 1, P = 0.002). Mortality was similar across other treatment combinations on this date, and similar across all treatment combinations by October 1997.

Effects of Experimental Treatments on Scrub Buckwheat Seedling Recruitment

Seedling emergence of scrub buckwheat in both the experimental and burned sites occurred in about 20% to 25% of plots. In the Fire Tower experimental site, seedling numbers peaked in July 1997, when 33 of 161 plots (22.1%) had seedlings, and in October 1997, when 36 of 154 plots (23.4%) had seedlings. Marginally more plots had seedlings when litter was removed (26.0%) than when litter remained

(13.9%, G = 3.39, df = 1, P=0.066). For contrasts of shrub canopy removal, clipping, and ash addition, similar proportions of plots had seedlings (17%–22%) and the overall loglinear analysis (considering all treatments) was not significant (X= 13.5, df=1, P=0.26). In the Loop burned site, seedling numbers also peaked in July 1997, when 21.6% of plots had seedlings.

DISCUSSION

Postfire Resprouting and Flowering of Scrub Buckwheat

We found that scrub buckwheat plants resprouted and then flowered rapidly after fire, consistent with prior research (Carrington 1999). Clipping of scrub buckwheat plants was the only experimental treatment that induced resprouting and high levels of inflorescence production. The proportion of clipped plants that flowered was similar to the high incidence of postfire flowering at the burned site. Ash addition, shrub canopy removal, and litter removal treatments altered microsite conditions in ways that mimicked fires (decreasing shrub canopies, decreasing litter, adding ash), but had no significant effect on scrub buckwheat inflorescence production. Postfire flowering would seem to be cued merely by top removal in scrub buckwheat, and be independent of microsite characteristics such as shrub cover, litter cover, and ash depths. These results are mainly consistent with Abrahamson's (1999) experiments with two species of palmettos (*Serenoa repens* and *Sabal etonia*) that occur in xeric upland habitats in Florida. Palmetto flowering was stimulated by fire and top removal but not by nutrient addition, consistent with our results for scrub buckwheat. For palmettos, flowering response was also mediated by light level. In our study of scrub buckwheat, shrub removal treatments increased the openness of the canopy over scrub buckwheat plants but did not stimulate their flowering.

Clipping of scrub buckwheat plants apparently mimicked the top-killing effect of fire that stimulated scrub buckwheat to resprout and produce inflorescences. Mortality did not increase with clipping, suggesting that clipping can be used as an alternative to prescribed burns to generate reproductive activity in this endemic species.

Resprouting immediately after fire may confer a competitive advantage. Fire creates a more open tree and shrub canopy, and resprouting scrub buckwheat individuals may be able to capitalize on abundant postfire resources. Yet, resprouting also depletes stored reserves (Bowen and Pate 1993). Coupled with immediate flowering, this recovery strategy could result in considerable energy costs to the plant. However, postfire microsite conditions, especially low litter and high light, may be favorable for seedling recruitment in scrub buckwheat (Carrington 1996). Scrub buckwheat seeds are not apparently stored in soil seed banks (Carrington 1997, Satterthwaite et al. in press), so new seed production may be necessary to provide the opportunity to take advantage of postfire microsite conditions.

Postfire flowering rates declined in subsequent years in the Loop burned site and in other ABS sites, and also in sites studied by Carrington (1999) at ABS and elsewhere. However, burned sites may continue to have increased flowering levels for several years postfire, as compared to unburned sites (Carrington 1999).

Seedling Recruitment

Following postfire flowering, seedlings appeared in the burned site, often near adults (consistent with results of Carrington 1999). In the unburned, experimental site, seedlings were most abundant in the experimental treatment combinations that included litter removal. Similar percentages of litter-removal plots (in the experimental site) recruited seedlings as did burned plots (in the site burned in 1996). Fire removes most litter, serving to couple the postfire flowering response with presence of favorable microsites for subsequent seedling recruitment. Other components of fire (shrub canopy removal, ash addition, top removal of scrub buckwheat) did not produce any increases in seedling recruitment relative to the control. Litter removal could be used as a management treatment to increase seedling recruitment in this species. However, scrub buckwheat lacks a seed bank (Carrington 1997). Therefore, without a treatment to increase flowering and seed production (e.g., burning or clipping), there may be few seeds available to germinate in microsites with reduced litter. Also, litter removal by agents other than fire may not be a practical management tool for larger areas.

Most lightning induced wildfires in Florida occur just prior to, and during, the rainy summer season, when nearly 85% of annual precipitation occurs. Few seedlings of Florida scrub species are noticeable in the summer months following fires; instead most species recruit mainly during the winter months (E. Menges, unpubl. data). However, scrub buckwheat is an exception in being able to recruit seedlings during the summer (Carrington 1996). We observed that scrub buckwheat seedling numbers peaked during July 1996, only two months after the fire and a month following the litter removal treatment. During extreme summer temperatures, the threat of seedling desiccation is high. Scrub buckwheat is sensitive to microsite conditions such as the amount of shade, organic litter, and water, and recruitment decreases with increased litter depths and decreased light (Carrington 1996). Litter may prevent seeds from contacting moist soil and block sunlight necessary for germination and photosynthetic activity in emerging seedlings. Litter generally has inhibitory effects on seedling emergence and recruitment (Xiong and Nilsson 1999).

Life History and Species Management

Scrub buckwheat's life history is characterized by the ability to resprout repeatedly after periodic fire, which is the major disturbance agent in its two habitats: sandhill and Florida scrub. This resprouting is probably enabled by extensive taproot reserves. Furthermore, this species is able to persist in two communities with different fire regimes: the frequently burned sandhill (fire return interval 1–10 years; Menges 1999) and the less frequently burned Florida scrub (fire return interval 5–100 years, depending on type of scrub; Menges 1999). Rapid flowering and seedling recruitment following fires provides new genetic individuals, and can also be viewed as a bet-hedging strategy under variable fire regimes (Ostertag and Menges 1994).

While scrub buckwheat is well adapted to fires, it can persist in areas that remain unburned for long periods of time. Its long life span and high survival rates, along with plant dormancy and persistence as small vegetative plants (Satterthwaite et al., in press), allow persistence during decades-long intervals between fires. Modeling of scrub buckwheat population dynamics and extinction risks based on 10 years of demographic data suggests that populations are relatively stable in unburned habitat (finite rates of increase ranging from 0.97 to 1.007) but increase after fires. Unburned populations are predicted to slowly decline without risk of extinction for several decades. In the long run, however, fires are required every 5–20 years to ensure viable populations (Satterthwaite et al., in press).

Postfire seedling recruitment appears to result mostly from the quick and heavy flowering and seed production of scrub buckwheat. Seeds present in the litter and surface soil during fires often suffer mortality (cf. Cheplick and Quinn 1987, Legg et al. 1992). Surface temperatures in Florida scrub fires exceeded 100° C and were lethal to scrub buckwheat seeds (Carrington 1996). Seeds buried deeply enough to survive heating (e.g., 2 cm) are unlikely to germinate and reach the surface due to their small size (mean = 3.7 mg; Carrington 1996). When fresh seeds are placed at the soil surface, germination rates are high (Satterthwaite et al., in press).

Although top removal and litter removal each promote a demographic response in scrub buckwheat, neither is completely sufficient to mimic the effects of fire on this species. Resprouting and flowering will be promoted by mechanical methods, such as mowing, that remove the tops of scrub buckwheat plants. However, the thatch left from mowing is likely to inhibit seedling recruitment during the first summer. Seedling recruitment could be enhanced by treatments that remove litter, although such litter removal treatments other than fire may be impractical for large areas.

Prescribed burning still offers the most appropriate treatment for enhancing both seed production and seedling recruitment, and linking the two in time. Fire may be the most efficient way of managing sandhill vegetation in Florida (Provencher et al. 2001). Scrub buckwheat's response to fire and its other demographic characteristics allow it to exist under a fairly broad range of fire frequencies and fire heterogeneities (Satterthwaite et al., in press), so that typical prescribed fire regimes for both sandhill and Florida scrub do not have to be altered to manage for this species.

ACKNOWLEDGMENTS

We appreciate the field assistance of Carl Weekley, Abby McCarthy, and Holly Lovett and helpful comments on the manuscript by Charles Williams and an anonymous reviewer. Michael Kelrick contributed in many ways to this research, in particular assisting with statistical analyses. Pedro Quintana-Ascencio, Carl Weekley, and Will Satterthwaite provided helpful discussions. Kevin Main provided important information on the prescribed fires at our sites. Our studies of scrub buckwheat have been generously supported by Archbold Biological Station, the Florida Division of Forestry, the Florida Division of Plant Industry, the U.S. Fish and Wildlife Service, and the National Science Foundation (DEB98-15370).

Kelly McConnell works with NatureServe, part of the Natural Heritage Network, where she is researching potential impacts of harvesting on native populations of medicinal plants and designing criteria to assess invasiveness of alien plants in wildlands and natural areas.

Eric Menges has conducted research on the demography of rare plants and fire ecology for several decades, most recently in Florida scrub as a Senior Research Biologist at Archbold Biological Station. He has published over 60 articles on his research. Eric is particularly interested in exploring how variation in fire management techniques affect plant responses.

LITERATURE CITED

Abrahamson, W.G. 1984. Species responses to fire on the Lake Wales Ridge. American Journal of Botany 71:35-43.

Abrahamson, W.G. 1999. Episodic reproduction in two fire-prone palms, *Serenoa repens* and *Sabal etonia* (Palmae). Ecology 80:100-115.

Abrahamson, W.G., and J.R. Abrahamson. 1996. Effects of a low-intensity winter fire on long-unburned Florida sand pine scrub. Natural Areas Journal 16:171-183.

Abrahamson, W.G., A.F. Johnson, J.N. Layne, and P.A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the Southern Lake Wales Ridge. Florida Scientist 47:210-250.

Anderson, R.C., and E.S. Menges. 1997. Effects of fire on sandhill herbs: nutrients, mycorrhizae, and biomass allocation. American Journal of Botany 84:938-948.

Bellingham, P.J., and A.D. Sparrow. 2000. Resprouting as a life history strategy in woody communities. Oikos 89:409-416.

Bond, W.J., and J.J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution 16:45-51.

Bowen, B.J., and J.S. Pate. 1993. The significance of root starch in post-fire shoot recovery of the resprouter *Stirlingia latifolia*. Annals of Botany 72:7-16.

Brewer, J.S. 1995. The relationship between soil fertility and fire-stimulated floral induction in two populations of grass-leaved golden aster *Pityopsis graminifolia*. Oikos 74:45-54.

Carrington, M.E. 1996. Post-fire recruitment in Florida sand pine scrub in comparison with California chaparral. Ph.D. diss., University of Florida, Gainesville. 201 pp.

Carrington, M.E. 1997. Soil seed bank structure and composition in Florida sand pine scrub. American Midland Naturalist 137:39-47.

Carrington, M.E. 1999. Post-fire seedling establishment in Florida sand pine scrub. Journal of Vegetation Science 10:403-412.

Carrington, M.E., and J.E. Keeley. 1999. Comparison of post-fire seedling establishment between scrub communities in Mediterranean and non-mediterranean climate ecosystems. Journal of Ecology 87:1025-1036.

Cheplick, G.P., and J.A. Quinn. 1987. The role of seed depth, litter, and fire in the seedling establishment of amphicarpic peanutgrass

(*Amphicarphum purshii*). Oecologia 73:459-464.

Christman, S.P., and W.S. Judd. 1990. Notes on plants endemic to Florida Scrub. Florida Scientist 53:52-73.

Coile, N.C. 2000. Notes on Florida's endangered and threatened plants. Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville. 122 p.

Enright, N.J., D. Goldblum, P. Ata, and D.H. Ashton. 1997. The independent effects of heat, smoke, and ash on emergence of seedlings from the soil seed bank of a heathy Eucalyptus woodland in Grampians (Gariwerd) National Park, western Victoria. Australian Journal of Ecology 22:81-88.

Fienberg, S.E. 1985. The Analysis of Cross-Categorical Data. 2nd ed. MIT Press, Cambridge, Mass. 191 pp.

Fowler, N.L. 1988. What is a safe site?: neighbor, litter, germination date, and patch effects. Ecology 69:947-961.

Greenberg, C.H., D.G. Neary, L.D. Harris, and S.P. Linda. 1995. Vegetation recovery following high-intensity wildfire and silvicultural treatments in sand pine scrub. American Midland Naturalist 133:149-163.

Grigore, M.T. and E.J. Tramer. 1996. The short-term effect of fire on *Lupinus perennis* (L.). Natural Areas Journal 16:41-48.

Hartnett, D.C. 1991. Effects of fire in tallgrass prairie on growth and reproduction of prairie coneflower (*Ratibida columnifera*: Asteraceae). American Journal of Botany 78:429-435.

Hartnett, D.C., and D.R. Richardson. 1989. Population biology of *Bonamia grandiflora* (Convolvulaceae): effects of fire on plant and seed bank dynamics. American Journal of Botany 76:361-369.

Hawkes C.V., and E.S. Menges. 1996. The relationship between open space and fire for species in a xeric Florida shrubland. Bulletin of the Torrey Botanical Club 123:81-92.

Keeley, J.E., and C.J. Fotheringham. 1998. Smoke-induced seed germination in California chaparral. Ecology 79:2320-2336.

Kirkman, L.K., M.B. Drew, and D. Edwards. 1998. Effects of experimental fire regimes on the population dynamics of *Schwalbea americana* L. Plant Ecology 137:115-137.

Lambert, B.B., and E.S. Menges. 1996. The effects of light, soil disturbance, and presence of organic litter on the field germination and survival of the Florida goldenaster. Florida Scientist 59:121-137.

Lamont, B.B., and H.V. Runciman. 1993. Fire may stimulate flowering, branching, seed production, and seedling establishment in two kangeroo paws (Haemodoraceae). Journal of Applied Ecology 30:256-264.

Legg, C.J., E. Maltby, and M.C.F. Proctor. 1992. The ecology of severe moorland fires on the North York Moors: seed distribution and seedling establishment of *Calluna vulgaris*. Journal of Ecology 80:737-752.

Matlack, G.R., D.J. Gibson, and R.E. Good. 1993. Regeneration of the shrub *Gaylussacia baccata* and associated species after low-intensity fire in an Atlantic coastal plain forest. American Journal of Botany 80:119-126.

Menges, E.S. 1999. Ecology and conservation of Florida scrub. Pp. 7-21 *in* R.C. Anderson, J.S. Fralish, and J.M Baskin, eds., Savannas, Barrens, and Rock Outcrop Plant Communities of North America. Cambridge University Press, New York.

Menges, E.S., and D.R. Gordon. 1996. Three levels of monitoring intensity for rare plant species. Natural Areas Journal 16:227-237.

Menges, E.S., and C.V. Hawkes. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. Ecological Applications 8:935-946.

Menges, E.S., and N. Kohfeldt. 1995. Life history strategies of Florida scrub plants in relation to fire. Bulletin of the Torrey Botanical Club 122:282-297.

Menges, E.S., P.J. McIntyre, M.S. Finer, E. Goss, and R. Yahr. 1999. Microhabitat of the narrow Florida scrub endemic *Dicerandra christmanii*, with comparisons to its congener *D. frutescens*. Journal of the Torrey Botanical Society 126:24-31.

Myers, R.L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. Bulletin of the Torrey Botanical Club 112:241-252.

Olson, M.S., and W.J. Platt. 1995. Effects of habitat and growing season fires on resprouting of shrubs in longleaf pine savannas. Vegetatio 119:101-118.

Ostertag, R., and E.S. Menges. 1994. Patterns of reproductive effort with time since last fire in Florida scrub plants. Journal of Vegetation Science 5:303-310.

Platt, W.J. 1999. Southeastern pine savannas. Pp. 23-51 *in* R.C. Anderson, J.S. Fralish, and J.M Baskin, eds., Savannas, Barrens, and Rock Outcrop Plant Communities of North America. Cambridge University Press, New York.

Platt, W.J., G.W. Evans, and M.M. Davis. 1988. Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia 76:353-363.

Preston, C.A., and I.T. Baldwin. 1999. Positive and negative signals regulate germination in the post-fire annual, *Nicotiana attenuata*. Ecology 80: 481-494.

Provencher, L., B.J. Herring, D.R. Gordon, H.L. Rodgers, K.E.M. Galley, G.W. Tanner, J.L. Hardesty, and L.A. Brennan. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. Restoration Ecology 9:13-27.

Quintana-Ascencio, P.F., and M. Morales-Hernandez. 1997. Fire-mediated effects of shrubs, lichens, and herbs on the demography of *Hypericum cumulicola* in patchy Florida scrub. Oecologia 112:263-271.

Romme, W.H., M.G. Turner, R.H. Gardner, W.W. Hargrove, G.A. Tuskan, D.G. Despain, and R.A. Renkin. 1997. A rare episode of sexual reproduction in aspen (*Populus tremuloides* Michx.) following the 1988 Yellowstone fires. Natural Areas Journal 17:17-25.

Roy, J., and L. Sonie. 1992. Germination and population dynamics of *Cistus* species in relation to fire. Journal of Applied Ecology 29:647-655.

Satterthwaite, W., E.S. Menges, and P.F. Quintana-Ascencio. 2002. Assessing population viability of *Eriogonum longifolium* var. *gnaphalifolium* in relation to fire using multiple matrix modeling techniques. Ecological Applications: in press.

Schmalzer, P.A., and S. R. Boyle. 1998. Restoring long-unburned oak-saw palmetto scrub requires mechanical cutting and prescribed burning (Florida). Restoration and Management Notes 16:96-97.

Schmalzer, P.A., and C.R. Hinkle. 1992. Recovery of oak-saw palmetto scrub after fire. Castanea 57:158-173.

Tyler, C.M. 1995. Factors contributing to post-fire seedling establishment in chaparral: direct and indirect effects of fire. Journal of Ecology 83:1009-1020.

Vila, M., and J. Terradas. 1995. Effects of competition and disturbance on the resprouting performance of the Mediterranean shrub *Erica multiflora* L. (Ericaceae). American Journal of Botany 82:1241-1248.

Vinton, J.M., and D.C. Hartnett. 1992. Effects of bison grazing on *Andropogon gerardii* and *Panicum vigatum* in burned and unburned tallgrass prairie. Oecologia 90:374-382.

Wunderlin, R.P. 1998. Guide to the Vascular Plants of Florida. University Press of Florida, Gainesville. 806 pp.

Xiong, S., and C. Nilsson. 1999. The effects of plant liter on vegetation: a meta-analysis. Journal of Ecology 87:984-994.