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.

INTRODUCTION

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 abun-
dances 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, Xiong 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 2000) or by indirect effects of fire, such as increased light levels or changes in light level experienced by seeds (Roy and Sonie 2000). 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. elliottii...
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), Chapmán’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>
<thead>
<tr>
<th>Measurement</th>
<th>Mean (Standard Error, n)</th>
<th>Pretreatment</th>
<th>Burned Site</th>
<th>t-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Experimental Site</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scrub buckwheat density (ccd²)</td>
<td>0.97 (0.12, 151)</td>
<td>0.51 (0.18, 36)</td>
<td>1.81</td>
<td>0.72</td>
<td></td>
</tr>
<tr>
<td>Rosettes/plant</td>
<td>1.77 (0.07, 158)</td>
<td>2.46 (0.34, 37)</td>
<td>1.98</td>
<td>0.54</td>
<td></td>
</tr>
<tr>
<td>Percent plants flowering</td>
<td>27.9 (3.6, 156)</td>
<td>100.0 (0, 37)</td>
<td>20.2</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td>No. of flowering stems/plant</td>
<td>0.29 (0.04, 158)</td>
<td>2.30 (0.33, 37)</td>
<td>6.07</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>71.3 (1.2, 137)</td>
<td>61.6 (2.2, 29)</td>
<td>2.49</td>
<td>0.016</td>
<td></td>
</tr>
<tr>
<td>Litter cover (%)</td>
<td>75.8 (3.2, 58)</td>
<td>0.00 (0, 29)</td>
<td>23.9</td>
<td>0.000</td>
<td></td>
</tr>
</tbody>
</table>
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 pretreatment, 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.

**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.
tality did not increase with clipping, sug-
resprout and produce inflorescences. Mor­
ire that stimulated scmb buckwheat to
flowering. Volume

Clipping
nutrient addition, consistent with our re-
flowering response was also mediated by
palmettos
ed by fire and top removal but not by
nia)
production.

DISCUSSION

Postfire Resprouting and Flowering of
Scrub Buckwheat

We found that scrub buckwheat plants re-
sprouted and then flowered rapidly after
fire, consistent with prior research (Car-
rington 1999). Clipping of scrub buck-
wheat 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 post-
fire flowering at the burned site. Ash addi-
tion, shrub canopy removal, and litter re-
moval treatments altered microsite condi-
tions 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 micro-
site 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 eto-
nia) that occur in xeric upland habitats in
Florida. Palmetto flowering was stimu-
ed by fire and top removal but not by
nutrient addition, consistent with our re-
sults for scrub buckwheat. For palmettos,
flowering response was also mediated by
light level. In our study of scrub buck-
wheat, shrub removal treatments increased
the openness of the canopy over scrub buckwheat plants but did not stimulate
their flowering.

Clipping of scrub buckwheat plants appar-
ently mimicked the top-killing effect of
fire that stimulated scrub buckwheat to
resprout and produce inflorescences. Mor-
tality did not increase with clipping, sug-
gest that clipping can be used as an
alternative to prescribed burns to generate
reproductive activity in this endemic spe-
cies.

Resprouting immediately after fire may
confer a competitive advantage. Fire cre-
ates a more open tree and shrub canopy,
and resprouting scrub buckwheat individu-
als 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 buck-
wheat seeds are not apparently stored in
soil seed banks (Carrington 1997, Satter-
waite et al. in press), so new seed pro-
duction may be necessary to provide the
opportunity to take advantage of postfire
microsite conditions.

Postfire flowering rates declined in sub-
sequent years in the Loop burned site and
in other ABS sites, and also in sites studied
by Carrington (1999) at ABS and else-
where. However, burned sites may con-
inue to have increased flowering levels for
several years postfire, as compared to un-
burned sites (Carrington 1999).

Seedling Recruitment

Following postfire flowering, seedlings
appeared in the burned site, often near
adults (consistent with results of Carrin-
tong 1999). In the unburned, experimental
site, seedlings were most abundant in the
experimental treatment combinations that
included litter removal. Similar percent-
ages of litter-removal plots (in the experi-
mental 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 pres-
ence of favorable microsites for subse-
quently seedling recruitment. Other compo-
nents 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). There-
fore, without a treatment to increase flow-
ering and seed production (e.g., burning
or clipping), there may be few seeds avail-
able to germinate in microsites with re-
duced litter. Also, litter removal by agents
other than fire may not be a practical man-
agement tool for larger areas.

Most lightning induced wildfires in Flori-
da occur just prior to, and during, the rainy
summer season, when nearly 85% of an-
ual precipitation occurs. Few seedlings
of Florida scrub species are noticeable in
the summer months following fires; in-
stead most species recruit mainly during
the winter months (E. Menges, unpubl.
data). However, scrub buckwheat is an
exception in being able to recruit seed-
lings during the summer (Carrington 1996).
We observed that scrub buckwheat seed-
lings numbered 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 condi-
tions such as the amount of shade, organic
litter, and water, and recruitment decreas-
es with increased litter depths and de-
creased light (Carrington 1996). Litter may
prevent seeds from contacting moist soil
and block sunlight necessary for germina-
tion and photosynthetic activity in emer-
ging seedlings. Litter generally has inhibi-
tory effects on seedling emergence and
recruitment (Xiong and Nilsson 1999).

Life History and Species Management

Scrub buckwheat’s life history is charac-
terized by the ability to resprout repeated-
ly after periodic fire, which is the major
disturbance agent in its two habitats: sand-
hill and Florida scrub. This resprouting is
probably enabled by extensive taproot re-
serves. Furthermore, this species is able to
persist in two communities with different
fire regimes: the frequently burned sand-
hill (fire return interval 1–10 years; Men-
ges 1999) and the less frequently burned
Florida scrub (fire return interval 5–100
years, depending on type of scrub; Men-
ges 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 will be promoted by mechanical methods, their small size (mean = 3.7 mg; Carrington 1996). 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 manage-


