

Fellingas a Pre-Treatment for Prescribed Fire Promotes Restoration of Fire-Suppressed Florida Sandhill

Authors: Rickey, Marcia A., Weekley, Carl W., and Menges, Eric S.

Source: Natural Areas Journal, 33(2): 199-213

Published By: Natural Areas Association

URL: https://doi.org/10.3375/043.033.0210

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

RESEARCH ARTICLE

Felling as a
Pre-treatment
for Prescribed
Fire Promotes
Restoration of Firesuppressed Florida
Sandhill

Marcia A. Rickey¹

¹EMPSi Environmental Management and Planning Solutions, Inc. 3775 Iris Avenue, Suite 1A Boulder, CO 80301

> Carl W. Weekley^{2,3} Eric S. Menges²

²Archbold Biological Station 123 Main Drive Venus, FL, USA 33960

•

³ Corresponding author: cweekley@archbold-station.org

Natural Areas Journal 33:199-213

ABSTRACT: Fire suppression in sandhill ecosystems leads to biotic impoverishment and reduces fine fuels needed for frequent fires. We investigated the restoration dynamics of a long-unburned endemic-rich sandhill on Florida's Lake Wales Ridge using prescribed fire with and without prior chainsaw felling of the hardwood subcanopy. Our goals were to promote survival of longleaf pines (Pinus palustris), decrease subcanopy and shrub densities and lichen cover, and increase cover of graminoids and rare forbs. Treatments were applied in 2001 and responses monitored annually through 2005. Prior felling of the subcanopy increased fire temperatures, residence times, and coverage compared to the burn-only treatment. The saw and burn treatment was effective in removing the subcanopy, but caused an undesirable increase in longleaf pine mortality. Pine mortality decreased with distance from saw and burn plots. Post-treatment shrub densities initially decreased, then increased in both treatments relative to controls. Forb densities and graminoid cover increased in both treatments and controls; increases were greater with burn treatments. Both treatments, especially saw and burn, caused compositional shifts relative to the control. Subcanopy felling as a pre-treatment for burning was effective in beginning restoration. We recommend additional fires and protection of longleaf pines to continue restoration progress. Saw and burn treatments can accelerate restoration and are a good first step toward re-establishing a frequent low-intensity fire regime.

Index terms: disturbance ecology, endemic species, pyrometers, sandhill restoration, vegetation sampling

Nomenclature: Wunderlin and Hansen (2003) unless otherwise indicated

INTRODUCTION

Fire is a major ecological disturbance worldwide, shaping evolutionary trajectories, molding biome distributions, and consuming dominant vegetation (Bond and Keeley 2005). However, restoration of fire-suppressed ecosystems may pose significant challenges for conservationists. For example, ecological restoration of southwestern U.S. ponderosa pine (Pinus ponderosa Dougl. Ex Laws.) ecosystems (Moore et al. 1999; Allen et al. 2002) and upland ecosystems in Florida (Menges and Gordon 2010) have included combinations of fire and structural manipulations. The use of fire surrogates and pre-treatments has been controversial because of unintended negative effects (e.g., invasive plants, soil compaction). However, most authorities agree that non-fire steps should be part on an overall goal of restoring the natural range of variability in the fire regime and creating resilient ecosystems (Allen et al. 2002; Noss et al. 2006).

Longleaf pine (*Pinus palustris*) ecosystems, ranging from hydric flatwoods to xeric uplands, were once widespread throughout the southeastern coastal plain (Peet 2006), supporting hundreds of rare and endemic plant species (Hardin and White 1989; Sorrie and Weakley 2006). However, over 95% of longleaf pine ecosystems have been lost to development, with most remaining sites degraded by

fire suppression (Platt 1999; Van Lear et al. 2005). Today, longleaf pine ecosystems are considered among the most endangered ecosystems in the United States (Noss et al. 1995).

Historically, longleaf pine sandhills were characterized by an open canopy of longleaf pine, a sparse shrub layer of oaks (*Quercus* spp.) and other hardwoods, and a ground cover with high herbaceous diversity, including wiregrass (*Aristida stricta*), other graminoids, and forbs (Myers 1990; Platt 1999). Longleaf pine/wiregrass sandhills on the 186-km long Lake Wales Ridge of south-central peninsular Florida have lower herbaceous diversity, more shrubs, and greater endemism than sandhills elsewhere on the southeastern coastal plain (Abrahamson et al. 1984; USFWS 1999).

Longleaf pine sandhills were historically maintained by frequent low-intensity fire, with lightening ignited fires occurring at 2 – 5 year intervals (Myers 1990; Platt 1999). In addition, pre-Columbian indigenous peoples burned sandhills and other pyrogenic ecosystems (Pyne 1982). Restoration of longleaf pine sandhills degraded by logging, habitat fragmentation, and decades of fire suppression is a major conservation goal (Outcalt et al. 1999; Kirkman and Mitchell 2006; Walker and Silletti 2006). Fire suppression on remnant sandhills has resulted in habitat degradation and a loss

of biodiversity (Gilliam and Platt 2006) and has transformed many sandhills into closed canopy hardwood forests (Myers and White 1987). Fire suppression degrades sandhill habitat by reducing longleaf pine recruitment (Peroni and Abrahamson 1986; Hartnett and Krofta 1989), increasing sand pine (Pinus clausa) invasion (Mc-Cay 2001), promoting development of a hardwood subcanopy (Menges et al. 1993), and shading out graminoids and forbs (Walker and Stilleti 2006). As understory cover decreases and oak cover increases, the fine fuels needed to effectively carry frequent fire disappear (Kirkman and Mitchell 2006).

In restoring degraded sandhills, conservation managers seek to promote the survival and recruitment of longleaf pines, decrease hardwood subcanopy and shrub cover, increase the diversity and abundance of herbaceous plants, especially fire-carrying graminoids such as wiregrass, and reduce accumulated woody fuels (USFWS 1999; Reinhart and Menges 2004; Kirkman and Mitchell 2006). Although fire is the preferred tool for sandhill restoration (Rebertus et al. 1989; Menges et al. 1993; Provencher et al. 2001a; Brockway et al. 2009; Outcalt and Brockway 2010), a single fire may be inadequate to achieve these objectives (Glitzenstein et al. 1995; Olson and Platt 1995; Drewa et al. 2002). Multiple fires may be required to increase graminoid and forb cover, reduce litter and lichens, and decrease the cover of woody plants (Drewa et al. 2006). However, hardwood cover may be particularly difficult to reduce with fire alone (Olson and Platt 1995; Provencher et al. 2001a; Reinhart and Menges 2004).

The re-introduction of fire following decades of fire suppression poses several challenges (Provencher et al. 2001a, b). Re-introduced fire may result in patchy burns due to depauperate fine-fuel cover and "hot spots" in areas with dense woody debris or pine needles. In particular, duff accumulation around the base of longleaf pines often results in pine mortality (Glitzenstein et al. 1995; Varner et al. 2009). Similarly, in long-unburned southern ridge sandhills (Abrahamson et al. 1984), south

Florida slash pines (*Pinus elliotti* var. *densa* Little and K.W. Dorman) suffer higher mortality in fire-suppressed than in periodically burned areas (Menges and Deyrup 2001).

Given these difficulties, land managers have resorted to a variety of techniques to facilitate the re-introduction of fire and to accelerate sandhill restoration. These techniques include the use of mechanical and chemical treatments to reduce hardwood cover or alter vegetation structure (Brockway and Outcalt 2000; Provencher et al. 2001a, b; Haywood 2009). Several studies have shown that fire, applied either alone or in combination with herbicides or mechanical treatments, was more effective than any treatment that did not include fire in accomplishing management goals, including shifting degraded longleaf pine sandhills toward reference conditions (Provencher et al. 2001 a, b; Menges and Gordon 2010; Outcalt and Brockway 2010). The use of mechanical and chemical methods as a pre-treatment for prescribed fire may alter fuel loads and increase fire intensity, resulting in undesirable impacts such as longleaf pine mortality. However, most sandhill restoration studies have focused on the response of vegetation to the treatments employed (e.g., Brockway and Outcalt 2000; Provencher et al. 2001a, b; Reinhart and Menges 2004; Haywood 2009), and previous studies have not measured such fire metrics as intensity, residence time, coverage or severity (see Keeley 2009 for usage of these terms), or compared fire metrics among treatments.

Despite extensive work elsewhere on the U.S. southeastern coastal plain, only one previous study has reported on sandhill restoration on the endemic-rich Lake Wales Ridge (Reinhart and Menges 2004). Nevertheless, Lake Wales Ridge land managers have begun to explore various mechanical methods as alternatives or pre-treatments for prescribed fire. In particular, land managers have used chainsaw felling of the hardwood subcanopy as a pre-treatment for prescribed fire, with the objective of promoting fire coverage and encouraging the spread of wiregrass and other fine fuels.

To investigate the efficacy of subcanopy felling as a technique to facilitate and enhance the re-introduction of fire to a long-unburned sandhill and to accelerate its restoration, we compared the effects of prescribed fire, with and without prior chainsaw felling of the hardwood subcanopy (referred to as saw and burn and burnonly, respectively), in a five-year study. We tested the hypothesis that chainsaw felling of the subcanopy, as a pre-treatment to prescribed fire, was more effective than burning alone in advancing our sandhill restoration objectives. Our restoration objectives were to promote survival of longleaf pines, decrease subcanopy and shrub hardwood densities, and increase the abundance of forbs and graminoids. To evaluate the comparative efficacy of the burn-only and saw and burn treatments, our research objectives were to: (1) assess the relationship between fire metrics (temperatures, residence times, severity) and vegetation structure; (2) quantify survival of longleaf pines in the two treatments; (3) measure the impact of the two treatments on the subcanopy, shrub, forb, graminoid and ground cover layers; (4) track the effect of treatments on overall species composition; and (5) analyze post-treatment shifts in plot occupancy for key sandhill species.

METHODS

Study Area

We conducted this study on the Carter Creek tract of the Lake Wales Ridge National Wildlife Refuge near Sebring, Florida, USA (27° 29' N, 81° 26' W). The climate in south-central Florida is characterized by warm wet summers and cool dry winters (Chen and Gerber 1990). Approximately 60% of annual rainfall occurs between May and September, but El Niño events result in higher than normal winter rainfall. At the nearby Archbold Biological Station, mean annual rainfall is 1336 mm (range 694-1949 mm). Mean annual temperature at Archbold is 22.3 °C. January is the coldest month of the year with a mean minimum of 8.6 °C. August is the hottest month with a mean maximum of 34.6 °C (http://www.archbold-station. org/station/html/ datapub/data/data.html).

Carter Creek (Figure 1) comprises 254 ha of xeric uplands and other habitats; about one-third of the site is long-unburned longleaf pine/wiregrass sandhill. The Carter Creek sandhill is characterized by an open canopy of widely-spaced longleaf pines, a discontinuous subcanopy of oaks (Quercus geminata, Q. laevis) and scrub hickory (Carya floridana), a shrub layer of oaks (Q. geminata, Q. chapmanii, Q. myrtifolia, and Q. laevis), and palmettos (Sabal etonia, Serenoa repens), and an herb layer with wiregrass, other graminoids, and forbs. Ground cover includes terrestrial lichens in the genus Cladonia, litter, and patches of bare sand. Eight of the 21 federally listed plants known from the Lake Wales Ridge (USFWS 1999) occur within the Carter Creek sandhill. No non-native plants are known to occur within the study area, although the exotic grass *Rhynchelytrum repens* occurs along some sand roads. The management history of the site before public acquisition in 1999 is largely unknown, but most of the sandhill where this study was carried out had not burned for at least 20 years.

Experimental Design

In spring 2001, we established 12 contiguous experimental units within a 36.5-ha area in the Carter Creek sandhill (Figure 1), utilizing existing roads and firebreaks

where possible. Experimental units averaged 3.0 ha in size (range: 2.1–4.7 ha). We used ArcView 3.2 to generate six random points within each experimental unit. Each point became the center of a 5-m radius circular vegetation plot, 72 plots in all. The center of each plot was located and mapped using a Trimble Global Positioning System (GPS) with sub-meter accuracy. Plots were separated by > 10 m and were > 5 m from roads or firelanes. We conducted pre-treatment sampling of the 72 vegetation plots in March – April 2001.

Each of the three treatments (control, burn-only, and saw and burn) was applied to four experimental units. Assignment of

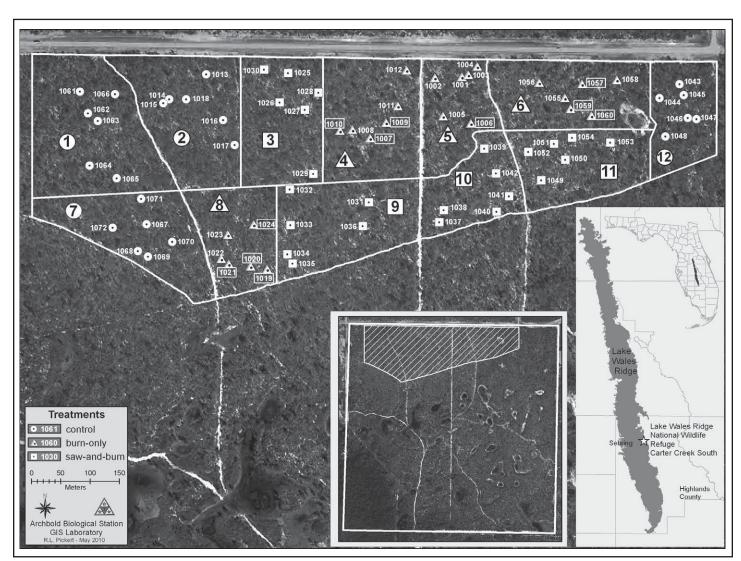


Figure 1. Location of experimental units and vegetation plots at the Lake Wales Ridge National Wildlife Refuge (Carter Creek) near Sebring, Florida. Plot numbers inside boxes indicate vegetation plots that failed to burn and were excluded from analysis. Inset on far right shows the location of the Lake Wales Ridge in central Florida and the location of the Carter Creek tract on the Ridge. Inset near the middle shows the boundaries of the 254-ha Carter Creek tract; hatched area at north end of the tract indicates the 36.5-ha study area.

the control treatment was constrained by the logistical requirements of the burning treatments such that the four control units were at either end of the study site (Figure 1). The burn-only and saw and burn treatments were assigned randomly within the remaining eight units. Pre-treatment data did not show systematic differences in vegetation structure among plots in the three treatments. In addition, control plots did not change markedly in vegetation structure over time. Because a single fire was applied to our study area, we restrict interpretation of our results to our study site and rely on similar studies in other sites to find common patterns.

Felling occurred within 15-m radius "enhanced fuel zones" centered on each of the 24 vegetation plots within the four saw and burn experimental units. Before the burn, we used chainsaws to fell all oaks and other subcanopy trees (except for longleaf pines) within this zone, leaving the felled trees on the ground. Subcanopy felling was carried out during June – July 2001, and a single, landscape-level prescribed burn was conducted on 16 August 2001. The time period between felling and burning allows downed fuels to cure but avoids decomposition of fuels that would occur with longer intervals.

On the day of the burn, the maximum temperature recorded was 35.6 °C and the minimum relative humidity was 39%. Winds were out of the southwest at 5 kph. The Keech-Byram Drought Index was 132, indicating moderate conditions for the fire (for additional burn information, see Wally et al. 2006). The burn included all eight experimental units assigned to the burn-only and saw and burn treatments. Because we wanted the burn to mimic the normal approach of land managers, we did not insist that individual plots be ignited. Consequently, the burn was patchy and did not affect 11 burn-only vegetation plots; these plots were dropped from post-treatment sampling. We sampled the remaining 61 vegetation plots annually in March or April (a time of active plant growth) from 2002 - 2005.

We used pyrometers constructed from copper-tags and temperature-sensitive paints

(Wally et al. 2006) to estimate maximum fire temperatures in the burn-only and saw and burn treatments. To estimate fire residence times, defined as the number of minutes the fire temperature was > 150 °C (Wally et al. 2006), we used CR10X dataloggers (Campbell Scientific Instruments, Logan, UT). Within each of the two burn treatments, two of the 24 vegetation plots received a data-logger with five Type-K thermocouples (n = 20 thermocouples), each thermocouple surrounded by three pyrometers (n = 60). In each of the other 22 vegetation plots in each treatment, we placed two pyrometers (n = 88). CR10X data-loggers also provide other metrics of fire intensity, including instantaneous and mean fire temperatures (Wally et al. 2006). To estimate fire severity, we used the residual twig diameter method described in Menges and Deyrup (2001). More intensely burned locations have smaller twigs completely consumed and thus have larger minimum twig diameters (Moreno and Oechel 1989).

We sampled longleaf pines across the entire 36.5-ha study area 9 and 33 months post-treatment. The location of each pine was mapped with a Trimble GPS. Approximately one-third of the 228 pines censused occurred within each of the three treatments (control = 69, burn-only = 74, saw and burn = 85). We classified pines into four size classes (grass stage [pre-bolting juveniles; n = 2, excluded from analysis], sapling < 3 m tall, small adult 3 - 8 m tall, and large adult > 8 m tall). We assessed the burn status of the pines (burned or unburned) after the burn using consumption or scorching of needles on smaller pines and trunk scorching on larger pines.

To assess changes in community composition and structure due to treatments, we sampled annually from five strata: canopy, subcanopy, shrub layer, herb layer, and ground cover (lichens, litter, and bare sand). Within each 5-m radius vegetation plot (Figure 2), we compiled a list of all vascular plants and ground lichens and counted stems of all canopy (> 8 m tall) and subcanopy (3 – 8 m tall) trees. We recorded the number of shrub stems (woody stems and palmettos 0.5 – 3 m tall) by species

along four 1-m x 4-m belt transects running in cardinal directions from the plot center. We counted forb stems by species within eight 0.25-m radius circular quadrats located at 2 and 4 m from the plot center in the northeast, southeast, southwest, and northwest quadrants. Within these eight quadrats we also made ocular estimates of percent cover by species (to the nearest 10% [e.g., 5-15% cover was coded as 10%] or trace [<5%, coded as 1%]) of graminoids, terrestrial lichens, litter, and bare sand.

We summarized abundance data at the vegetation plot level for canopy, subcanopy, shrub, and forb species based on stem counts (converted to densities). Abundances of graminoids, lichens, litter, and bare sand were based on mean percent cover. For species difficult to distinguish based on vegetative characters, we created species groups for the following genera: Andropogon (A. floridana, A. glomeratus), Asclepias (A. curtissii, A.tomentosa), Cyperus (C. croceus, C. retrorsus), Dichanthelium (D. aciculare, D. portoricense), and Liatris (L. tenuifolia, L. chapmanii). We assessed the impact of treatments on characteristic sandhill species by comparing post-treatment changes in plot occupancy.

Statistical Analyses

Unless otherwise stated, we used SPSS Vers. 11.5 (2002) for all statistical tests. Because fire data (fire temperatures, residence times, and twig diameters) were not normally distributed and were resistant to transformation, we used the nonparametric Mann-Whitney test to test for differences between the burn-only and saw and burn treatments. We used the nonparametric Spearman rank correlation to examine the relationship between fire temperatures estimated by pyrometers and CR10X dataloggers and to assess relationships between pyrometer temperature and stem densities (subcanopy, shrubs, and forbs) or percent cover (graminoids and lichens). Since five tests were run for each vegetation layer, we used the sequential Bonferroni procedure to correct for multiple tests (Holm 1979).

To assess treatment effects on longleaf pine survival, we used a 2 x 2 chi-square con-

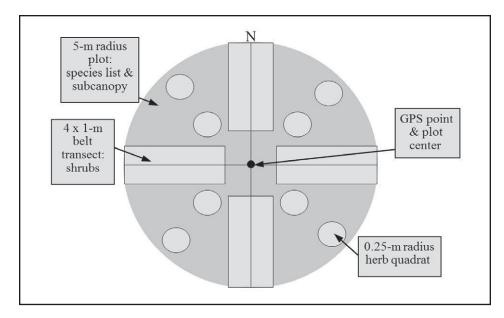


Figure 2. Schematic representation of sandhill vegetation sampling plot. The diagram shows a 5-m radius circle where species list and subcanopy stem densities by species were recorded. Within the plot, we counted shrub stem densities by species in four belt transects. We used eight 0.25-m radius circular quadrats to quantify the herb layer and estimate ground cover.

tingency table to compare survival within and beyond the 15-m radius enhanced fuel zone, and a 3 x 2 chi-square contingency table to test survival differences among the three size classes of pines. We used linear regression to assess pine survival as a function of distance from the center of each vegetation plot in the saw and burn treatment.

Following the approach of von Ende (1993), we used both univariate and multivariate repeated measures ANOVAs (Potvin et al. 1990) to test for differences in vegetation structure resulting from the contrasting treatments (Appendix). For these analyses, we used data scaled up to the 5-m radius vegetation plots (the experimental unit for analyses). We used a number of approaches to accomplish and interpret these repeated measures ANOVAS (Appendix). In addition to the omnibus repeated measures ANOVA, we performed a profile analysis (von Ende 1993) on each component of vegetation structure by conducting within- and between-subject contrasts (SPSS 2002).

To track changes in species composition in response to treatments, we ran Multiple Response Permutation Procedures (MRPP; PC-ORD Vers. 6 [McCune and Mefford 2011]), a nonparametric test for comparing differences among groups (McCune and Grace 2002). MRPP provides A and T statistics and the associated p-values for the global test among three or more groups and for posthoc pairwise comparisons between groups. The A statistic describes within-group homogeneity; A = 1 when all species within groups are identical. The T statistic describes the separation among groups; the lower the T value, the greater the separation. In our analysis, the three groups are the two burning treatments and the control. For the pairwise comparisons, we used a Bonferroni-corrected alpha of 0.017.

We tested for effects of treatment, year, and a treatment * year interaction on the presence/absence of individual species within the 61 vegetation plots using logistic regression. To reduce the number of tests, we selected the six most dominant shrubs, the five most dominant grasses, and five species that are particularly characteristic of sandhill (species selection was made before analyses were conducted). We corrected for multiple tests using the sequential Bonferroni procedure (Holm 1979). We also report the percentage of plots containing each of these 16 species.

RESUITS

Fire Metrics

Fires were more intense in the saw and burn treatment than in the burn-only treatment. Median maximum temperatures recorded by the copper-tag pyrometers were significantly higher (Mann-Whitney U = 944.5, p < 0.001) in the saw and burn (649 °C, range 177 - 704 °C, n = 69) than in the burn-only treatment (413 °C, range 66 – 704 °C, n = 50). There was a strong and significant positive correlation between maximum mean temperatures recorded by the CR10X data-loggers and the associated pyrometers (Spearman's rho = 0.754, p = 0.001, n = 16). Median residence times were also significantly longer (Mann-Whitney U = 10.5, p = 0.021, n = 16) in the saw and burn (3.0 minutes) than in the burn-only treatment (0.5 minutes). Median residual twig diameter (cm) was larger in the saw and burn treatment than in the burn-only treatment (Mann-Whitney U = 309.5, p < 0.001, n = 71). Finally, the saw and burn treatment also had more complete burn coverage; all plots burned in the saw and burn treatment, whereas 11 of 24 plots in the burn-only treatment did not burn even though the larger experimental units were ignited.

Fire temperatures were not significantly related to pre-fire vegetation structure in either the burn-only or the saw and burn treatment, but were strongly associated with post-fire vegetation. Pre-treatment abundance values for the six vegetation components measured did not affect subsequent fire temperatures (Spearman rank correlations, Table 1). However, four of the six post-fire vegetation layers were significantly correlated with fire temperatures. Subcanopy stem densities were negatively correlated with fire temperature in all post-fire years. In contrast, vigorous resprouting by shrubs in areas with higher fire temperatures resulted in an increase in shrub stem density and significant positive correlations between shrub density and fire temperatures in the second through the fourth post-fire surveys. Both graminoid cover and lichen cover were negatively correlated with fire temperature in one or more post-fire surveys. Neither forb density

Table 1. Spearman rank correlations of pyrometer temperature by vegetation layer for pre-fire (2001) and 1- through 4-year post-fire surveys (2002-2005) in burn-only and saw & burn treatments. For each year, the correlation statistic r is given, followed by the p-values. Since five tests were run for each vegetation layer, we adjusted p-values using the sequential Bonferroni procedure (Holm 1979). Significant correlations are in bold font.

| Vegetation measure | 2001 | 2002 | 2003 | 2004 | 2005 |
|--------------------|---------------|----------------|---------------|---------------|---------------------|
| Subcanopy density* | -0.426, 0.146 | -0.828, <0.001 | -0.778, 0.002 | -0.807, 0.001 | -0.678, 0.011 |
| Shrub density | -0.144, 0.396 | -0.070, 0.680 | 0.429, 0.008 | 0.447, 0.006 | 0.403, 0.013 |
| Forb density | 0.088, 0.605 | -0.161, 0.341 | -0.33, 0.845 | -0.163, 0.335 | -0.073, 0.668 |
| Graminoid cover | -0.071, 0.667 | -0.468, 0.003 | -0.156, 0.355 | -0.330, 0.046 | -0.430, 0.008 |
| Lichen cover | -0.157, 0.352 | -0.332, 0.045 | -0.551, 0.001 | -0.492, 0.002 | -0.386, 0.018 |
| Bare sand cover | -0.164, 0.331 | 0.288, 0.084 | 0.202, 0.230 | 0.195, 0.249 | 0.204, 0.225 |

^{*} Includes only subcanopy stem densities from the burn-only treatment because stems in the saw & burn treatment were removed by chainsaw felling.

nor percent bare sand was correlated with fire temperatures.

Longleaf Pine Survival

Longleaf pine survival varied by fire treatment; it was highest for unburned pines (95.7%), lowest for the saw and burn treatment (54.2%), and intermediate in the burn-only treatment (76.1%); survival of burned pines was significantly higher in the burn-only than in the saw and burn treatment ($\chi^2 = 7.950$, df = 1, p = 0.007). In addition, for each size class, survival of burned pines was higher in the burn-only treatment than in the saw and burn treatment (Figure 3), but the difference was significant only for pines > 8 m tall (for saplings: $\chi^2 = 0.676$, df = 1, p = 0.411; for small adults: $\chi^2 = 3.237$, df = 1, p = 0.072; and for large adults: $\chi^2 = 4.629$, df = 1, p = 0.031). Regardless of treatment, larger pines were less likely to die ($\chi^2 = 33.944$, df = 2, p < 0.001).

Longleaf pines (all size classes) within the 15-m enhanced fuel zone of the saw and burn treatment had significantly lower survival than pines in burned areas beyond this zone (25.0% vs. 64.6%; χ^2 = 11.133, df = 2, p = 0.004). In addition, postburn pine survival increased significantly with distance from the center of the saw and burn plots (Wald statistic = 9.726, df = 1, p = 0.002, 67.5% classification success). Within the saw and burn enhanced fuel zones, survival was 43% for saplings, 33% for small pines, and 50% for large pines.

Vegetation Structure

Subcanopy Stem Density

Chainsaw felling eliminated the subcanopy in the saw and burn treatment. The burn-only treatment reduced subcanopy stem density relative to the control (F = 12.801, df = 1, 35, p = 0.001), and the reduction persisted through the fourth post-treatment survey (Figure 4A). Densities differed among treatments between pre- and post-treatment years (Appendix).

Shrub Stem Density

The two burn treatments initially had the lowest post-treatment shrub stem densities, but by the second year post-treatment, shrub stem densities had regained or surpassed pre-treatment levels (Figure 4B). Treatments had significant effects on pre- vs. post-treatment densities and on densities through time; the saw and burn treatment had the largest effect increasing shrub stem densities over time (Appendix).

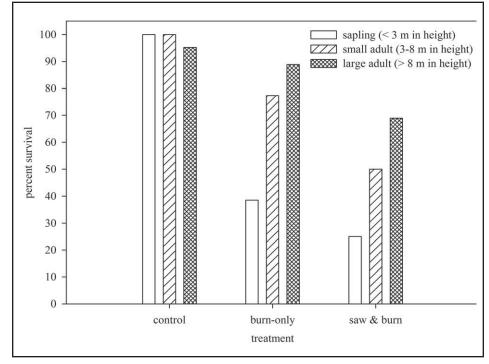


Figure 3. Survival of burned longleaf pines in burn-only and saw & burn treatments by height class, compared to unburned pines in control treatment.

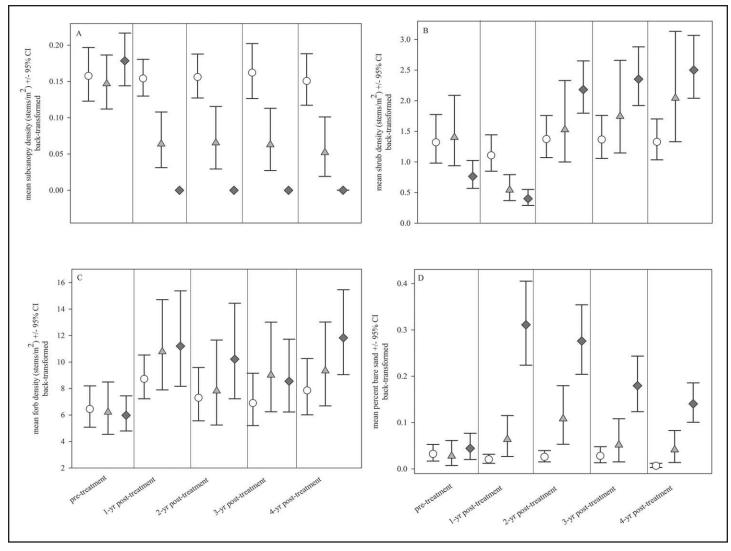


Figure 4. Mean densities of subcanopy stems (A), shrub stems (B), and forb (C) stems, and mean percent cover of bare sand (D) by treatment from pretreatment through fourth year post-treatment. Open circles represent the control, solid triangles represent the burn-only treatment, and solid diamonds represent the saw & burn treatment. Back-transformed means and 95% confidence intervals (Sokal and Rohlfe 1995) are shown, but the analyses were conducted on transformed data.

Forb Stem Density

Post-treatment forb density increased in both burn treatments and in the control (Figure 4C). However, only the final post-treatment year had statistically different treatment effects on forb densities than pre-treatment (Appendix).

Graminoid Cover

Graminoid cover was highly variable for all treatments and for all survey years (Table 2), with a slight increase in graminoid cover in the two burn treatments in the fourth post-treatment year compared to the pre-treatment survey. Treatment effects on

graminoid cover were not consistent among years (Appendix).

Ground Cover

The two burn treatments increased percent bare sand by reducing lichen and litter cover (Figure 4D). Post-treatment bare sand varied significantly from pretreatment levels and the treatments were significant for each year. The saw and burn treatment had greater effects than the burn-only treatment in increasing bare sand (Appendix). Litter and lichen cover were both reduced by burning (Table 2). Although litter cover was dramatically reduced by the saw and burn treatment, it

remained > 60% irrespective of treatment (Table 2). Lichen cover remained a little above 1% for the control, while dramatically decreasing in both burn treatments, particularly the saw and burn treatment (Table 2). Both variables were correlated with percent bare sand (Appendix).

Compositional Responses

Based on the Multi-Response Permutation Procedures (MRPP), we found strong differences in species composition due to management treatments. Overall differences were greater post-treatment (T < -17, A > 0.9, p < 0.001) than pre-treatment (T = -2.9, A = 0.015, p = 0.005). After correcting

Table 2. Mean percent cover ± standard deviation for graminoid, lichen, litter, and bare sand cover in three sandhill restoration treatments at Carter Creek for pre-treatment and four post-treatment surveys. Values shown are based on plot means.

| Survey year | Treatment | Graminoid cover | Lichen cover | Litter cover | Bare sand cover |
|-------------------------------------|------------|-----------------|-----------------|-------------------|-------------------|
| Pre-treatment | Control | 2.40 ± 3.28 | 1.46 ± 2.07 | 95.21 ± 5.17 | 4.51 ± 4.47 |
| | Burn-only | 1.05 ± 1.10 | 2.02 ± 3.89 | 94.59 ± 6.19 | 4.37 ± 5.10 |
| | Saw & burn | 1.61 ± 1.54 | 0.97 ± 1.45 | 92.93 ± 7.91 | 6.70 ± 7.28 |
| 1 st year post-treatment | Control | 1.98 ± 2.62 | 1.42 ± 1.88 | 96.93 ± 3.46 | 2.66 ± 2.45 |
| | Burn-only | 0.81 ± 0.46 | 0.85 ± 2.58 | 91.45 ± 9.23 | 8.12 ± 8.31 |
| | Saw & burn | 0.85 ± 0.92 | 0.03 ± 0.06 | 63.58 ±19.95 | 33.36 ± 18.85 |
| 2 nd year post- | Control | 2.47 ± 4.22 | 1.10 ± 1.78 | 95.57 ± 4.63 | 3.33 ± 3.27 |
| treatment | Burn-only | 1.83 ± 1.62 | 0.34 ± 0.72 | 84.34 ± 11.97 | 12.89 ± 9.94 |
| | Saw & burn | 2.55 ± 3.58 | 0.03 ± 0.08 | 64.23 ± 16.64 | 29.56 ± 15.79 |
| 3 rd year post-treatment | Control | 2.12 ± 3.84 | 1.08 ± 1.98 | 95.73 ± 4.63 | 4.16 ± 5.00 |
| | Burn-only | 1.82 ± 1.52 | 0.28 ± 0.55 | 89.62 ± 10.61 | 7.62 ± 8.60 |
| | Saw & burn | 2.15 ± 2.21 | 0.03 ± 0.07 | 70.08 ± 15.22 | 20.03 ± 13.47 |
| 4 th year post-treatment | Control | 2.44 ± 3.71 | 1.20 ± 1.54 | 96.61 ± 4.24 | 1.09 ± 1.40 |
| | Burn-only | 2.76 ± 2.67 | 0.29 ± 0.56 | 90.48 ± 7.40 | 5.87 ± 6.06 |
| | Saw & burn | 2.77 ± 2.70 | 0.04 ± 0.07 | 71.47 ± 12.99 | 15.40 ± 10.51 |

for multiple tests, the treatment differences pre-treatment were not significant (p > 0.05), but treatment differences were highly significant for all post-treatment years. Differences were greatest when comparing the saw and burn to the control and least when comparing the saw and burn with the burn-only treatment (Figure 5).

Species' Responses

Few of the 104 taxa showed strong responses to treatments. Most dramatically, fire sensitive epiphytic bromeliads (Tillandsia spp.) and ground lichens (Cladonia spp.) were nearly eliminated in the two burn treatments, and the impact was greatest in the saw and burn treatment. In contrast, resprouting shrub dominants (Quercus spp., Serenoa repens, and Sabal etonia) were found in nearly every vegetation plot and were little affected by treatments (Appendix Table A2). Forbs characteristic of sandhills, individual graminoid species, and federally listed endemic species sometimes increased with fire treatments (Appendix Table A2), although sample sizes did not allow statistical testing.

Treatments had inconsistent effects on

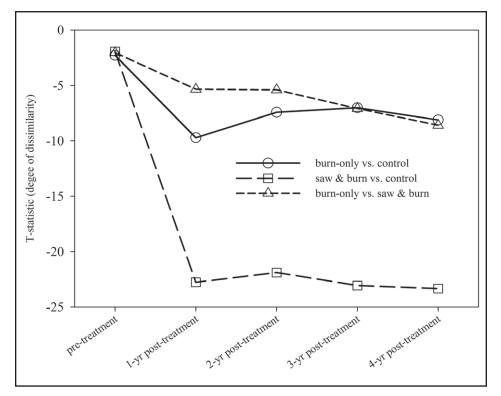


Figure 5. Pairwise comparisons of changes in species composition for two treatments and control. Degree of dissimilarity between treatments increases with decrease in value of T statistic. For all post-treatment years, p < 0.001 for all pairwise comparisons. These differences were not significant for the pre-treatment year after correction for multiple tests.

federally-listed endemic plants. Although we recorded six of the eight federally listed plant species known from the site within our vegetation monitoring plots, only three species were sufficiently abundant to permit statistical analysis. As measured by frequency of occurrence in the vegetation plots over the five years of the study, the long-lived *Eriogonum longifolium* var. gnaphalifolium increased by 16% in the control and by 35% in the burn-only treatment, while decreasing by 21% in the saw and burn treatment (Appendix Table A2). Percent plot occupancy of the short-lived Polygala lewtonii peaked for all treatments in the second or third post-treatment year and then declined (Appendix Table A2); post-treatment increases were most persistent in the saw and burn treatment. The long-lived shrub Prunus geniculata showed little change in the control, increased by 17% in the burn-only plots, and decreased by 14% in the saw and burn plots (Appendix Table A2).

DISCUSSION

Mechanical treatments such as tree thinning, roller-chopping, and mowing are increasingly being used as management tools in ecosystem restoration (e.g., Stephens and Moghaddas 2005; Reinhardt et al. 2008). However, these treatments, especially if

used without a subsequent fire treatment, may be ineffective in achieving management objectives and may also risk adverse effects (Lippincott 2000; Menges and Gordon 2010). In fire-suppressed longleaf pine sandhills of the U.S. southeastern coastal plain, conservationists have used a variety of mechanical and chemical techniques, with and without subsequent burning (e.g., Brockway and Outcalt 2000; Provencher et al. 2001a, b; Haywood 2009), to reduce hardwood cover, increase graminoid cover, and promote forb diversity and abundance. In this study, we explored the use of chainsaw felling of the hardwood subcanopy as a pre-treatment to fire in restoration of a long-unburned longleaf pine/wiregrass sandhill ecosystem.

We found that the saw and burn treatment had higher fire temperatures, longer residence times, and greater fire coverage than the burn-only treatment. However, in other Florida sites, higher fire intensities do not always occur in mechanically treated areas vs. burn-only treatments (Wally et al. 2006). This may be due to differences in the interval between mechanical treatments and fire. Longer intervals result in decomposition of fuels and resulting patchy fires (Weekley et al. 2011).

In our study, felling had both advantages

and disadvantages in comparison to burning alone in achieving the core goals of sandhill restoration: promotion of longleaf pines, bare sand, graminoids, and forbs, and reduction of hardwoods, ground lichens, and litter (Table 3). The saw and burn treatment was more effective than the burn-only treatment in increasing bare sand and reducing the hardwood subcanopy, but resulted in greater longleaf pine mortality. Neither treatment was effective in permanently reducing shrub density or in substantially increasing forb or graminoid abundance relative to controls. Our results are consistent with similar sandhill restoration studies suggesting that multiple fires will be necessary to re-establish the vegetation structure and composition historically maintained by frequent low-intensity fire (e.g., Provencher et al. 2001a; Glitzenstein et al. 2003; Reinhart and Menges 2004).

The biggest disadvantage of the saw and burn treatment was the higher rate of longleaf pine mortality compared to the burn-only treatment. However, pines in the burn-only treatment were also killed by fire, indicating that even relatively low-intensity burns can be a threat to longleaf pines in long-unburned stands. A likely cause of pine mortality was duff buildup and overheating of this layer during the burn (Outcalt 2006; Varner et al. 2009). In our

Table 3. Summary of the effects of two management treatments (in comparison to control) on key components of sandhill restoration.

| Restoration Component Tested | Burn-only | Saw & Burn | Comments |
|------------------------------|-----------|------------|-----------------------------------|
| Survival of longleaf pines | - | | Undesirable effect |
| Reduction of subcanopy | + | ++ | Persistent for 4 years |
| Reduction of shrub density | 0 | 0 | Decrease, then increase |
| Increase in forb density | 0 | + | Increase relative to pre-burn |
| Increase in graminoid cover | + | + | Decrease, then increase |
| Reduction in lichen cover | + | + | Persistent for 4 years |
| Reduction in litter cover | 0 | + | Decrease, then increase |
| Increase in bare sand | + | ++ | Increase, then decrease |
| Shift in species composition | + | ++ | Main shift in first year postburn |
| Key species responses | 0 | 0 | Variable among species |

- + Positive effect; ++ Additional positive effect compared to other treatment
- Negative effect; -- Additional negative effect compared to other treatment
- 0 No significant effects or conflicting effects

study, we observed prolonged smoldering of duff in some areas. Reducing the duff layer by raking is a technique that could be used to decrease longleaf pine mortality in subsequent fires (Outcalt 2006), although this method might be prohibitively laborintensive for large areas.

Chainsaw felling of subcanopy hardwoods within the enhanced fuel zones of the saw and burn treatment eliminated this stratum. Although some of the largest downed stems did not burn completely, moderate-sized felled woody debris was consumed and contributed to the higher fire intensity, longer residence times, and greater fire severity in the saw and burn treatment. However, whether felled by chainsaws or top-killed by fire, resprouting subcanopy hardwoods contributed to increases in shrub density in the three years following the first post-treatment survey. Although few resprouting hardwoods had advanced to subcanopy height by the four-year post-treatment survey, they have done so in recent years. In the absence of frequent fire, the subcanopy will inevitably be reestablished in areas where it was reduced or even (temporarily) eliminated.

Both the burn-only and the saw and burn treatment had only temporary effects in reducing shrub stem densities. Shrub densities steadily increased after the first year post-treatment as a result of clonal growth and resprouting by subcanopy hardwoods top-killed by the treatments. Shrub density increases were most pronounced in the saw and burn treatment, suggesting that greater fire coverage and higher fire temperatures promoted more aggressive resprouting. This result is consistent with previous studies showing that stem cutting may promote aggressive resprouting (e.g., Canadell and Lopez-Soria 1998). However, studies in Florida scrub, a co-occurring xeric ecosystem in which the shrub layer is dominated by the same species of clonal oaks (e.g., Q. geminata, Q. myrtifolia, Q. chapmanii), have shown that the combination of mechanical treatment and fire do not necessarily result in greater post-treatment increases in shrub cover than either mechanical treatment or fire alone (Weekley et al. 2011). Other studies have found that frequent fires can be effective in reducing hardwoods even without prior mechanical treatments (Harrington 2006).

In contrast to our results, sandhill restoration treatments using the herbicide hexazinone (alone or in combination with other treatments) have recorded greater long-term effectiveness in reducing hardwoods (Provencher 2001a, b; Outcalt and Brockway 2010). However, the reduction in hardwoods in these studies did not always result in increases in graminoid or forb abundance (Provencher 2001a). The reason for the lack of a ground layer response in many studies may be that litter accumulation is the primary factor explaining the loss of herb biodiversity and that restoration of the forest floor (Hiers et al. 2007) will promote herb biodiversity and abundance.

In our study, although the saw and burn treatment did not increase forb and graminoid abundances relative to the control, it did reduce litter and lichens more than the burn-only treatment. The saw and burn combination may accelerate restoration progress by providing microhabitat for graminoids needed to carry frequent low-intensity fire. The saw and burn treatment also caused greater compositional shifts (relative to the control) than the burn-only treatment.

Effects of fire regimes on herbaceous plants in sandhill ecosystems outside peninsular Florida have received considerable study (Walker and Silletti 2006). Fire frequency is probably the most important factor influencing the herb layer, with frequent fires promoting the dominance of fire-carrying grasses and increased diversity within the herb layer (Glitzenstein et al. 2003). In contrast, fire suppression can cause marked shifts from more open to closed canopy conditions (Glitzenstein et al. 2003). Shifts in vegetation structure affect subsequent fire. Where grasses have increased, areas are more likely to carry frequent fire. When shrubs and trees have invaded and suppressed graminoids, subsequent fire coverage and frequency will be lower and restoration will be more difficult.

In addition to maintaining longleaf pines and reducing hardwoods, increasing forb diversity is a frequent objective in sandhill restoration (Walker and Silletti 2006). Although several subshrubs and forbs, including some ruderals (e.g., Ambrosia artemisifolia), recruited into the vegetation plots in the post-treatment years, these were all species recorded elsewhere on the site. Thus, the shifts in species composition (especially the divergence of the saw and burn treatment from the control) mainly reflect changes in plot occupancy rather than recruitment of new species to the study site.

Our results, based on a single fire, are consistent with the findings of Reinhart and Menges (2004), the only other published investigation of sandhill restoration on the Lake Wales Ridge. These authors found that even after three prescribed fires within a six-year period, there were only minimal changes in species composition, although several forbs increased in abundance. In contrast, sandhill restoration studies elsewhere in the southeast have reported increases in herb species richness (e.g., Lewis and Harsgbarger 1976; Provencher et al. 2001a). The difference may be due to the reduced species pool for sandhill sites on the southern end of the Lake Wales Ridge (Abrahamson et al. 1984), near the southern range limit for sandhill vegetation, relative to high forb diversity in most longleaf pine/wiregrass ecosystems (Hardin and White 1989; Peet 2006).

Rather than increasing forb diversity, our restoration goal was to increase the abundance of forb species, particularly rare endemics and federally-listed species already present, by creating more open microhabitats for their recruitment. For the federally listed Polygala lewtonii, an obligate reseeding herb (Weekley and Menges 2012), the saw and burn treatment resulted in greater increases than the burn-only treatment, but this pattern was not repeated for the other two federally listed species that occurred with sufficient frequency for analysis. A more detailed analysis of the postburn demography of P. lewtonii has demonstrated that fire promotes seedling recruitment and longevity, greater short-term growth, and earlier flowering (Weekley and Menges 2012). For Erigononum longifolium var. gnaphalifolium, a post-fire resprouter (McConnell and Menges 2002), analysis of treatment effects is complicated by belowground dormancy in this long-lived herb (Satterthwaite et al. 2002). Thus, the apparent decline of E. longifolium in the last three post-treatment years in the saw and burn plots may not signal a negative effect of the saw and burn treatment. More detailed data from annual demographic monitoring of E. longifolium at Carter Creek show short-term increases in growth, flowering, and seedling recruitment in both burn treatments, but especially in the saw and burn treatment (E.S. Menges and C.W. Weekley, unpubl. data). For the long-lived shrub Prunus geniculata, a strong postburn resprouter (Weekley and Menges 2003), the decline in plot occupancy in the saw and burn treatment suggests that it may be vulnerable to hotter fires; this vulnerability may be concentrated in smaller plants (E.S. Menges and C.W. Weekley, unpubl. data).

The results documented in our study of one endemic-rich Lake Wales Ridge sandhill support the consensus among sandhill restorationists that decades of fire suppression will not be reversed by one or a few burns (Provencher et al. 2001b; Reinhart and Menges 2004; Walker and Silletti 2006). The potential adverse effects of the re-introduction of fire can be mitigated in several ways. For example, to lessen the threat of longleaf pine mortality, the duff layer can be gradually reduced by manipulating season and timing of prescribed burns and choosing fire weather and ignition techniques designed to move fire quickly through long-unburned stands (Outcalt 2006). Although mechanical means may contribute to the re-introduction of fire and expedite sandhill restoration, these methods must be employed carefully, with close monitoring of the results (Menges and Gordon 2010).

Similarly, restoration of structure and function in other fire-suppressed ecosystems will generally require a cautious approach with careful monitoring of the effects of different management treatments (Provencher at al. 2001b; Menges and Gordon 2010; Outcalt and Brockway 2010). Efforts to restore typical structure must be coordinated with other objectives, including the protec-

tion of rare or declining species (Noss et al. 2006). While restoration of reference disturbance regimes and conditions is usually the ultimate goal, applications of restoration treatments toward this goal are likely to vary with the ecological history and setting (Moore et al. 1999).

ACKNOWLEDGMENTS

We thank Fred Adrian and Dorn Whitmore of the U.S. Fish and Wildlife Service, Adam Peterson and Steve Morrison from The Nature Conservancy, and their respective staffs for the management treatments that made our research possible. For field data collection, we thank Kim Adams, Mandy Brothers, Laura Calabrese, Gretel Clarke, Martha Ellis, Orou Gaoue, April Hansgate, Betsey Boughton, Becky Hewitt, Sarah Hicks, Tracy Hmielowski, Molly Mathias, David Matlaga, Courtney McCusker, Darien McElwain, Jennifer Navarra, Stephanie Neimeister, Martina Petru, Ian Pfingstein, Beth Stephens, Sonali Saha, Jenny Schafer, Theresa Strazisar, Katie Stuble, Matt Trager, Alaa Wally, Dee White, David Zaya, and Robin Zinthefer. We thank Sarah Haller for statistical advice. Funding was provided by the Florida Fish and Wildlife Conservation Commission (NG02-002), the National Science Foundation (DEB98-15370, DEB-0233899, DEB0812717), and Archbold Biological Station. Finally, we thank editors Ron Hiebert and Jesse Burton for their trenchant and helpful reviews of the manuscript.

Marcia Rickey (M.S. Illinois State University) is an environmental planner and GIS analysis at EMPSi in Boulder, Colorado.

Carl Weekley (M.S., Florida International University) is a Research Assistant in the Plant Ecology Program at Archbold Biological Station. Carl studies the ecology of Lake Wales Ridge endemic plants and the xeric upland ecosystems that support them.

Dr. Eric Menges (PhD., University of Wisconsin) is a Senior Research Biologist in the Plant Ecology Program at Archbold Biological Station. Eric's research focuses on plant population biology, population vi-

ability analyses, fire ecology, conservation ecology, and restoration ecology. He has been working in Florida scrub for 24 years and has authored or co-authored over 125 peer reviewed papers and supervised over 80 students and research interns.

LITERATURE CITED

- Abrahamson, W.G., A.F. Johnson, J.N. Lane, and P.A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. Florida Scientist 47:209-250.
- Allen, C.D., M. Savage, D.A. Falk, K.F. Suckling, T.W. Swetnam, T. Schulke, P.B. Stacey, P. Morgan, M. Hoffman, and J.T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications 12:1418-1433.
- Bond, W.J., and J.E. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in Ecology and Evolution 20:387-394.
- Brockway, D.G., and K.W. Outcalt. 2000. Restoring longleaf pine wiregrass ecosystems: hexazinone application enhances the effects of prescribed fire. Forest Ecology and Management 137:121-138.
- Brockway, D.G., K.W. Outcalt, B.L. Estes, and R.B. Rummer. 2009. Vegetation response to midstorey mulching and prescribed burning for wildfire hazard reduction and longleaf pine (*Pinus palustris* Mill.) ecosystem restoration. Forestry 82:299-314.
- Canadell, J., and L. Lopez-Soria. 1998. Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. Functional Ecology 12:31-38.
- Chen, E., and J.F. Gerber. 1990. Climate. Pp.11-34 *in* R.L. Myers and J.J. Ewel, eds., Ecosystems of Florida. University of Central Florida Press, Orlando.
- Drewa, P., W.J.Platt, and E.B.Moser. 2002. Fire effects on resprouting of shrubs in headwaters of southeastern pine savannas. Ecology 83:755-767.
- Drewa, P.B., J.M. Thaxton, and W.J. Platt. 2006. Responses of root-crown bearing shrubs to differences in fire regimes in *Pinus palustris* (longleaf pine) savannas: exploring oldgrowth questions in second growth systems. Applied Vegetation Science 9:27-36.
- Gilliam, F.S., and W.J. Platt. 2006. Conservation and restoration of the *Pinus palustis* ecosystems. Applied Vegetation Science 9:7-10.
- Glitzenstein, J.S., W.J. Platt, and D.R.Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf

- pine savannas. Ecological Monographs 65:441-476.
- Glitzenstein, J.S., D.R. Streng, and D.D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) in South Carolina and Northeast Florida, USA. Natural Areas Journal 23:22-37.
- Hardin, E.D., and D.L. White. 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in Southeastern United States. Natural Areas Journal 9:234-245.
- Harrington, T.B. 2006. Plant competition, facilitation, and other overstory-understory interactions in longleaf pine ecosystems. Pp. 135-156 in S. Jose, E. J. Jokela, and D.L. Miller, eds., Longleaf Pine Ecosystems: Ecology, Management, and Restoration. Springer, New York.
- Hartnett, D.C., and D.M. Krofta. 1989. Fifty-five years of post-fire succession in a southern mixed hardwood forest. Bulletin of the Torrey Botanical Club 116:107-113.
- Haywood, J.D. 2009. Eight years of seasonal burning and herbicidal brush control influence sapling longleaf pine growth, understory vegetation, and the outcome of an ensuring wildfire. Forest Ecology and Management 258:295-305.
- Hiers, F.K., J.J. O'Brien, R.W. Will, and R.J. Mitchell. 2007. Forest floor depth mediates understory vigor in xeric *Pinus palus-tris* ecosystems. Ecological Applications 17:806-814.
- Holm, S. 1979. A simple sequential rejective multiple test procedure. Scandinavian Journal of Statistics 6:65-70.
- Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18:116-126.
- Kirkman, K.L., and R.J. Mitchell, 2006. Conservation management of Pinus palustris ecosystems from a landscape perspective. Applied Vegetation Science 9:67-74.
- Lewis, C.E., and T.J. Harshbarger. 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina Coastal Plain. Journal of Range Management 29:13-18.
- Lippincott, C.L. 2000. Effects of Imperata cylindrica (L.) Beauv. (Cogongrass) invasion on fire regime in Florida sandhill (USA). Natural Areas Journal 20:140-149.
- McCay, D.H. 2001. Spatial patterns of sand pine invasion into longleaf pine forests in the Florida panhandle. Landscape Ecology 16:89-98.
- McConnell, K., and E.S. Menges. 2002. The effects of fire and treatments that mimic fire on the Florida endemic scrub buckwheat (Eriogonum longifolium Nutt. var.

- gnaphalifolium Gand.). Natural Areas Journal 22:194-201.
- McCune, B., and J.B Grace. 2002. Analysis of ecological communities. MjM Software Design. Gleneden Beach, Ore.
- McCune, B., and M.J. Mefford. 2011. PC-ORD. Multivariate analysis of ecological data, Vers. 6. MjM Software Design, Gleneden Beach, Ore.
- Menges, E.S., W.G. Abrahamson, K.T. Givens, N.P. Gallo, and J.N. Layne. 1993. Twenty years of vegetation change in five unburned Florida plant communities. Journal of Vegetation Science 4:375-386.
- Menges, E.S., and M.A. Deyrup. 2001. Postfire mortality in south Florida slash pine: interacting effects of vegetation, season, burn size, fire intensity, and bark beetles. International Journal of Wildland Fire 10:53-63.
- Menges, E.S., and D.R. Gordon. 2010. Should mechanical treatments and herbicides be used as fire surrogates to manage Florida's uplands: a review. Florida Scientist 73:145-172.
- Moore, M.M., W.W. Covington, and P.Z. Fule. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. Ecological Applications 9:1266-1277.
- Moreno, J.M., and W.C. Oechel. 1989. A simple method for estimating fire intensity after a burn in California chaparral. Acta Oecologica Plantarum 10:57-68.
- Myers, R.L. 1990. Scrub and high pine. Pp. 150-194 *in* R.L. Myers and J.J. Ewel, eds., Ecosystems of Florida. University of Central Florida Press, Orlando.
- Myers, R.L., and D.L. White. 1987. Landscape history and changes in sandhill vegetation in North-Central and South-Central Florida. Bulletin of the Torrey Botanical Society 114:21-32.
- Noss, R.F., P. Beier, D.B. Lindenmayer, J.W. Prather, F. Schmiegelow, T.D. Sisk, and D.J. Vosick. 2006. Recommendations for integrating restoration ecology and conservation biology in ponderosa pine forests of the southwestern United States. Restoration Ecology 14:4-10.
- Noss, R.F., E.T. LaRoe, and J.M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28, U.S. Department of the Interior, National Biological Service, Washington, D.C.
- 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.

- Outcalt, K. 2006. Prescribed burning for understory restoration. Pp. 326-329 in S. Jose, E.J. Jokela, and D.L.Miller, eds., Longleaf Pine Ecosystems: Ecology, Management, and Restoration. Springer, New York.
- Outcalt, K.W., and D.G. Brockway. 2010. Structure and composition changes following restoration treatments of longleaf pine forests on the Gulf Coastal Plain of Alabama. Forest Ecology and Management 259:1615-1623.
- Outcalt, K.W., M.E. Williams, and O. Onokpise. 1999. Restoring *Aristida stricta* to *Pinus palustris* ecosystems on the Atlantic coastal plain, U.S.A. Restoration Ecology 7:262-270.
- Peet, R.K. 2006. Ecological classification of longleaf pine woodlands. Pp. 51-93 in S. Jose, E.J. Jokela, and D.L.Miller, eds., Longleaf Pine Ecosystems: Ecology, Management, and Restoration. Springer, New York.
- Peroni, P.A., and W.G. Abrahamson. 1986. Succession in Florida sandridge vegetation: a retrospective study. Florida Scientist 49:176-191.
- 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, Cambridge, U.K.
- Potvin, C., M.J. Lechowicz, and S. Tardif. 1990. The statistical analyses of ecophysiological response curves obtained from experiments involving repeated measures. Ecology 71:1389-1400.
- 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. 2001a. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in Northwest Florida. Restoration Ecology 9:13-27.
- Provencher, L., B.J. Herring, D.R. Gordon, H.L.
 Rodgers, G.W. Tanner, J.L. Hardesty, L.A.
 Brennan, and A.R. Lit. 2001b. Longleaf pine and oak responses to hardwood reduction techniques in fire-suppressed sandhills in northwest Florida. Forest Ecology and Management 148:63-77.
- Pyne, S.J. 1982. Fire in America: a Cultural History of Wildland and Rural Fire. University of Washington Press. Seattle and London.
- Rebertus, A.J., G.B. Williamson, and E.B. Moser. 1989. Longleaf pine pyrogenicity and turkey oak mortality in Florida xeric sandhills. Ecology 70:60-70.
- Reinhardt, E.D., R.E. Keane, D.E. Calkin, and J.D. Cohen. 2008. Objectives and considerations for wildland fuel treatment in forested ecosystems of the interior western United

- States. Forest Ecology and Management 256:1997-2006.
- Reinhart, K.O., and E.S. Menges. 2004. Effects of re-introducing fire to a central Florida sandhill community. Applied Vegetation Science 7:141-150.
- Satterthwaite, W.S., P.F. Quintana-Ascencio, and E.S. Menges. 2002. Assessing scrub buckwheat population viability in relation to fire using multiple modeling techniques. Ecological Applications 12:1672-1687.
- Sokal, R.R., and F.J. Rohlf. 1995. Biometry, 3rd ed. W.H. Freeman, New York.
- Sorrie, B.A., and A.S. Weakley. 2006. Conservation of the endangered *Pinus palustris* ecosystem based on Coastal Plain centers of plant endemism. Applied Vegetation Science 9:59-66.
- SPSS Version 11.5. 2002. SPSS, Inc., Chicago.
- Stephens, S.L., and J. J. Moghaddas. 2005. Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. Forest Ecology and Management 215:21-36.
- [USFWS] U.S. Fish and Wildlife Service. 1999. South Florida multi-species recovery plan. U.S. Fish and Wildlife Service, Atlanta, Ga.
- Van Lear, D.H., W.D. Carroll, P.R. Kapelcluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. Forest Ecology and Management 211:150-165.
- Varner, J.M., F.E. Putz, J.J. O'Brien, J.K. Hiers, R.J. Mitchell, and D.R. Gordon. 2009. Post-fire tree stress and growth following smoldering duff fires. Forest Ecology and Management 28:2467-2474.
- von Ende, C.N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pp. 113-137 in S.M. Scheiner and J. Gurevitch, eds., Design and Analysis of Ecological Experiments. Chapman and Hall, New York.
- Walker, J.L., and A.M. Silletti. 2006. Restoring the ground layer of longleaf pine ecosystems. Pp. 297-325 *in* S. Jose, E. J. Jokela, and D.L. Miller, eds., Longleaf Pine Ecosystems: Ecology, Management, and Restoration. Springer, New York.
- Wally, A.L., E.S. Menges, and C.W. Weekley. 2006. Comparison of three devices for estimating fire temperature in ecological studies. Journal of Vegetation Science 9:91-102.
- Weekley, C.W., and E.S. Menges. 2003. Species and vegetation responses to prescribed fire in a long-unburned, endemic-rich Lake Wales Ridge scrub. Journal of the Torrey Botanical Society 130:265-282.

- Weekley, C.W., and E.S. Menges. 2012. Burning creates contrasting demographic patterns in an endangered perennial herb: a cradle-to-grave analysis of multiple cohorts. Australian Journal of Botany. 60:347-357. Available online http://dx.doi.org/10.1071/BT11271.
- Weekley, C.W., E.S. Menges, D. Berry-Greenlee, M.A. Rickey, G.L. Clarke, and S.A. Smith. 2011. Effects of mowing and burning on Florida scrub vegetation at two sites on the Lake Wales Ridge. Ecological Restoration 29:357-373. Available online <doi:10.3368/er.29.4.357>.
- Wunderlin, R.P., and B.F. Hansen. 2003. Guide to the Vascular Plants of Florida. 2nd ed. University Press of Florida, Gainesville.

APPENDIX. REPEATED MEASURES ANOVA METHODS AND RESULTS

METHODS

Statistical analysis

To ensure that the data met the ANOVA assumptions of normality and homogeneity of variances, we used frequency histograms, plots of the residuals vs. predicted values, the Shapiro-Wilk test for normality, and the Levene test for homogeneity of variances (SPSS 2002). Data that did not meet the assumption of normality were transformed where possible (Sokal and Rohlf 1995; Table A1). The univariate procedure is more powerful than the multivariate procedure, but has more restrictive assumptions (von Ende 1993; Potvin et al. 1990). For univariate repeated measures ANOVA, we used Mauchly's W test for sphericity. If the assumption of sphericity was not met, degrees of freedom were adjusted using the Greenhouse-Geisser estimated epsilon values (Potvin et al. 1990). For analyses with epsilon values < 0.7, we used the multivariate procedure.

RESULTS

Vegetation structure

Subcanopy stem density

In the omnibus repeated measures ANOVA, subcanopy density differed significantly

over time (F = 5.523, df = 4, 32, p = 0.002), and there was also a significant year * treatment interaction (F = 3.26, df = 4, 32, p = 0.024), indicating that densities differed among treatments over the survey period. In the within-subjects contrasts, each post-treatment year differed significantly from the pre-treatment year (F \geq 10.6, df = 1, 35, p \leq 0.002). The year * treatment interaction also differed from the pre-treatment in each post-treatment year (F \geq 9.6, df = 1, 35, p \leq 0.004).

Shrub stem density

In the omnibus test, shrub density differed significantly among years (F = 45.009, df = 4, 55, p < 0.001), and there was also a significant year * treatment interaction (F = 11.363, df = 8, 112, p < 0.001), indicating that treatments had a significant impact on densities over time. In the within-subjects contrasts, each post-treatment year differed significantly from the pre-treatment year (F \geq 29.1, df = 1, 58, p < 0.001). The year * treatment interaction differed in each post-treatment year compared to the pre-treatment (F \geq 5.4, df = 1, 58, p < 0.001). After the first post-treatment year, both burn treatments increased shrub stem densities relative to the control; this effect was most pronounced for the saw & burn treatment and in the 2-4-year post-treatment surveys (Figure 4B). Averaged over all years, there was no significant difference in shrub density among treatments (F = 0.01, df = 2, 58, p = 0.990).

Forb stem density

In the omnibus test, forb density differed significantly among years (F = 19.801, df = 2.960, 171.7, p < 0.001), and there was a significant year * treatment interaction (F = 2.328, df = 5.921, 171.7, p < 0.035). In the within-subjects contrasts, each post-treatment year differed significantly from the pre-treatment (F \geq 23.5, df = 1, 58, p < 0.001). However, the year * treatment interaction was not significant for the first three post-treatment years (F \leq 2.5, df = 1, 58, p \geq 0.060), while it was significant in the final post-treatment year (F = 4.4, df = 1, 58, p = 0.017). Averaged over all years, forb density did not differ signifi-

cantly among treatments (F = 0.426, df = 2, 58, p = 0.655).

Graminoid cover

In the omnibus test, graminoid cover differed significantly among years, (F = 11.418, df = 2.905, 168.473, p < 0.001) and there was a significant year * treatment interaction (F = 3.084, df = 5.089, 168.473, p = 0.007). In the within-subjects contrasts, the first two and the fourth post-treatment years differed significantly from the pre-treatment (F \geq 4.8, df = 1, 58, p \leq 0.032), but the third year did not (F = 2.9, df = 1, 58, p = 0.094). The year * treatment interaction was not significant in the first two post-treatment years (F \leq

2.4, df = 1, 58, $p \ge 0.097$). Averaged over all years, graminoid cover did not differ significantly among treatments (Figure 8; F = 0.173, df = 2, 58, p = 0.842).

Ground cover

In the omnibus test, bare sand cover differed significantly among years (Figure 4D; F = 38.080, df = 3.397, 197.011, p < 0.001), and there was a significant year * treatment interaction (F = 22.973. df = 6.793, 197.011, p < 0.001). In the within-subjects contrast, all post-treatment years differed significantly from the pre-treatment ($F \ge 4.4$, df = 1, 58, p ≤ 0.041). The year * treatment interaction was also significant in each post-treatment year ($F \ge 19.8$, df = 1, 58, p < 0.001). Averaged over all years,

percent bare sand differed significantly among treatments (F = 29.645, df = 2, 58, p < 0.001). In the between-subjects contrasts, percent bare sand was significantly higher in the saw & burn treatment than in the burn-only treatment (p < 0.001), while the burn-only treatment differed less strongly from the control (p = 0.049). Litter cover was strongly and significantly negatively correlated with percent bare sand (Spearman's rho = -0.807, p < 0.001, n = 576) and was therefore not analyzed with ANOVAs. In the pre-treatment survey, there was a modest but significant positive relationship between lichen cover and percent bare sand (Spearman's rho = 0.455, p < 0.001, n = 576).

Appendix Table 1. Summary of transformations and procedures used for analyses of five key parameters of sandhill vegetation structure. For epsilon > 0.7, univariate repeated measures ANOVA was used; for epsilon < 0.7, Pillai's Trace statistic in multivariate repeated measures ANOVA was used (SPSS Vers. 11.5, 2002).

| Parameter | Normality Transformation | Epsilon | Analysis |
|------------------------|--------------------------|---------|--------------|
| | | Value | |
| Subcanopy stem density | Square root | 0.448 | Multivariate |
| Shrub stem density | Natural log | 0.546 | Multivariate |
| Forb stem density | Natural log | 0.74 | Univariate |
| Graminoid cover | Arcsin-square root | 0.726 | Univariate |
| Bare sand cover | Arcsin-square root | 0.849 | Univariate |

212 Natural Areas Journal Volume 33 (2), 2013

Percent frequency of vegetation plot occupancy for shrub dominants, characteristic sandhill species, and graminoids contributing fine fuels. Among the characteristic sandhill species, Prunus geniculata is a shrub; the other four species are forbs. Changes in percent frequency are shown for the three treatments from pre-treatment through the fourth post-treatment survey (2001-2005). If the p-value in logistic regression for treatment (T), year (Y), or their interaction (X) is significant with a sequential Bonferroni-corrected alpha, the corresponding letter(s) is (are) shown. Signif. Of T.Y.X** . [\] Ε ĭ 50 ¥ 50 75 α Saw & burn 2 yr 54 96 92 yr 92 87 96 Pre-50 50 100 8 57 GRAMINOIDS CONTRIBUTING FINE FUEL CHARACTERISTIC SANDHILL SPECIES 4 yr 77 ∞ ∞ 3 yr 77 SHRUB DOMINANTS Burn-only ∞ 1 yr ∞ ∞ Pre- ∞ ĭ Appendix Table 2. Treatment Responses of Selected Sandhill Species 3 yr 87 87 71 92 Control 2 yr 87 87 54 ĭ Pre-83 96 58 75 58 Prunus geniculata* Dichanthelium spp. Quercus chapmanii Polygala lewtonii * Quercus myrtifolia Stillingia sylvatica Quercus geminata Andropogon spp. Lupinus diffusus Serenoa repens Quercus laevis Aristida stricta **Piptochaetium** longifolium* Sabal etonia Eriongonum Aristida spp. avenacoides Species

Volume 33 (2), 2013 Natural Areas Journal 213

* federally listed species