Effects of a Low-Intensity Winter Fire on Long-Unburned Florida Sand Pine Scrub

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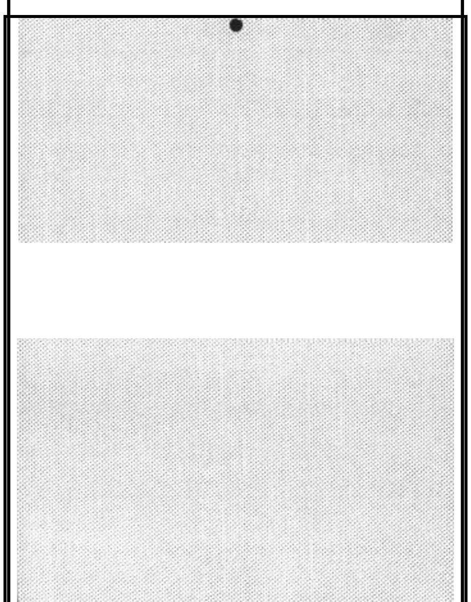

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ABSTRACT: Fire suppression and habitat fragmentation during the twentieth century have generated many long-unburned stands of relatively isolated sand pine scrub. Such stands often lose most of their endemic herbs as woody species come to dominate. A sand pine scrub stand last burned in 1926 or 1927 was prescription burned in February 1986 after a 1985 vegetation census and then was resampled five times over a 7-year recovery period. In spite of a wide variety of recovery strategies to the low-intensity bum, there was little change in the floristic makeup of postburn stands compared to the preburn stand. Detrended correspondence analyses suggested that floristic composition and community structure of postburn stands shifted away from those of the preburn stand. However, this shift did not restore the populations of narrowly endemic scrub herbs. Instead, the change was toward xeric hammock, characterized by the persistence of woody understory species, the unsuccessful restoration of sand pine *(Pinus clausa)* as a canopy dominant, and the near absence of most herbs. These results suggest that long-unburned sand pine scrub will not return to typical scrub through the reintroduction of a single low-intensity, winter burn. This study demonstrates the necessity of monitoring the consequences of the reintroduction of fire to long-unburned vegetation associations and of recognizing variation in vegetative responses to different fire regimes.

INTRODUCTION

Sand pine scrub is a unique, seasonally dry ecosystem containing xeromorphic shrubs and many narrowly endemic plant species growing on excessively well-drained, nutrient-poor sands (Abrahamson et al. 1984, Kalisz and Stone 1984, Martin 1993, Stap 1994). Sand pine scrub is restricted to Florida and Alabama, though it once occurred more commonly on the coastal dunes of the Atlantic and Gulf coasts, and on the Miocene- through Pleistocene-age inland dunes of central Florida (Laessle 1958, White 1970, Brooks 1972, Myers 1990). The occurrence of scrub species, and hence the scrub association, is strongly influenced not only by soil type and drainage, but by fire also (Abraham-son et al. 1984, Myers 1990). Scrub, like many shrub-dominated associations world-wide, is characterized by recurrent fire (Myers 1990, Menges 1993), rapid post-fire vegetation recovery (Abrahamson 1984a, 1984b, 1995; Johnson et al. 1986; Abrahamson and Hartnett 1990; Schmalzer and Hinkle 1992), and fire-stimulated flowering (Abrahamson 1984b, Ostertag and Menges 1994, Menges and Kohfeldt 1995).

The southeastern United States and, in particular, the Florida peninsula have one of the highest frequencies of lightning strikes (Goodman and Christian 1993) and lightning-origin fires in the world (Abraham-son et al. 1984). As a likely consequence of recurrent fire and seasonal drought during their evolutionary history, the plant species of sand pine scrub possess a variety of mechanisms that facilitate either resistance to damage from fire or recovery following fire. For example, although sand pine (P. *clausa)* is readily killed by fire, its fire-sensitive serotinous cones release large numbers of seeds that can generate dense stands of even-aged pines. (Nomenclature follows Wunderlin 1982.) Other woody species (e.g., *Quercus* spp., *Lyonia* spp.) and herbs use a variety of recovery strategies including obligate and facultative seeding, resprouting, clonal spread, and combinations of these strategies (Menges and Kohfeldt 1995).

During most of the twentieth century, wild-fires were actively suppressed in sand pine scrub and most other fire-prone North American plant associations. In addition, suburban sprawl has reduced not only the frequency but also the extent of wildfires (Pyne 1982). Power lines now ground lightning strikes that otherwise might have ignited trees, and roads, agricultural fields, and other development restrict the movement and extent of wildfires (Abrahamson et al. 1984).

Florida and other areas with pyrogenic vegetation presently contain substantial tracts of long-unburned native vegetation. Although fire is being aggressively reintroduced to some of these long-unburned tracts, little is known about the effects of fire reintroduction on long-unburned sand pine scrub. Depending on the fire intensity and season of burning, the reintroduction of fire to long-unburned scrub may not necessarily produce the desired effect of returning the association to a state typical under pre-Colonial fire regimes. For ex-ample, Myers (1985) suggested that the reintroduction of frequent, low-intensity fires in sand pine scrub may change scrub to sandhill (an open woodland of *P. elliottii* var. *densa*, xerophytic oaks, and *Carya floridana*, with an *Aristida stricta* and palmetto understory). On the other hand, a single, high-intensity fire in sand pine scrub may facilitate the persistence of the scrub stand (Myers 1985; Menges 1993; Meng-es and Hawkes, in press). Alternatively, a single low-intensity fire event could facilitate the shift of scrub toward xeric ham-mock (similar to sand pine scrub except that sand pine is uncommon to absent; understory xerophytic oaks become canopy dominants). The latter consequence would occur if a fire enhanced the abundance of the resprouting understory species (e.g., scrub hickory, clonal oaks), which subsequently suppress the regeneration of the obligate seeding species including sand pine and some herbs.

Unfortunately, few data currently are avail-able to test these hypotheses about the effects of the reintroduction of fire to long-unburned sand pine scrub. The purpose of the present study was to detail the effects of a single winter fire on species abundances and community structure in a sand pine scrub stand that had not been burned since 1926 or 1927 (a 60-year absence of fire). Opinions vary on the pre-Colonial range of fire-return intervals typical of sand pine scrub, but for the Florida peninsula, a range of once every 20 to 100 years is a reasonable approximation (Myers 1990, Menges et al. 1993). As far as we know, this study is the first detailed examination of species and community responses to the reintroduction of fire to long-unburned sand pine scrub. Its results offer insights into the appropriate and inappropriate use of fire as a tool in the management of sand pine scrub.

METHODS

Study Site

The study site is on the grounds of the Archbold Biological Station in Highlands County, Florida, 12 km south of the town of Lake Placid (27°11'N, 81°21'W). The Archbold property contains some of the largest and most representative tracts of remaining, undisturbed Lake Wales Ridge sand pine scrub (Abrahamson et al. 1984, Myers 1990). The Ridge's desert-like scrub contains one of the highest North American concentrations of narrowly endemic plants (Christman and Judd 1990, Wood 1994). The Lake Wales Ridge National Wildlife Refuge was recently established as the first federally designated refuge for endangered plants (Martin 1993, Stap 1994).

"Sand pine scrub" is used here in the restricted sense to designate the oak-understory phase of scrub (Abrahamson et al. 1984), a three-layered community characterized by a canopy of nearly even-aged sand pine (see Table 1 for endemic species). The second, lower canopy of very dense shrubs and small trees is composed of scrub hickory *(Carya floridana)*, myrtle

Table 1. Florida endemic or near-endemic plants mentioned in the text, listed by scientific name, common name, distribution, and status (according to Wood 1994). Abbreviations: AL=Alabama, CE=commercially exploited, FL=Florida, FC=candidate for federal listing, FE=federal endangered, FT=federal threatened, GA=Georgia, LWR=Lake Wales Ridge, pen=peninsula, NL=not listed, SE=state endangered, ST=state threatened.

Scientific Name	**Common Name**	Distribution	Status
Carya floridana	scrub hickory	FL pen	NL
Chapmannia floridana	alicia	FL	NL
Dicerandra frutescens	Lake Placid scrub mint	southern LWR	SE, FE
Eryngium cuneifolium	scrub celery	southern LWR	SE, FE
Garberia heterophylla	garberia	FL central and northern pen	ST
Ilex opaca var. *arenicola*	scrub holly	FL pen	CE
Lechea cernua	hoary pinweed	LWR, east coast of pen	SE, FC
Lechea deckertii	woody pinweed	FL pen and south GA	NL
Palafoxia feayi	palafoxia	FL	NL
Paronychia chartacea -	papery whitlow-wort	LWR	SE, FT
Persea humilis	silk bay	FL	NL
Pinus clausa	sand pine	FL to southern AL	NL
Pinus elliottii var. *densa*	south Florida slash pine	FL pen and keys	NL
Polygonella basiramia	hairy jointweed	LWR, Avon Park Air Force Range Ridge	SE, FE
Sabal etonia	scrub palmetto	FL pen	ST
Wtis *munsoniana*	muscadine grape	FL and GA	NL

oak *(Quern us myrtifolia),* rusty lyonia *(Lyonia ferruginea),* sand live oak *(Q. geminata),* **Chapman's oak *(Q. chapmanii),* silk** bay *(Persea humilis),* and scrub holly *(Ilex opaca* var. *arenicola).* A third, still lower canopy is created by saw palmetto *(Serenoa repens)* and scrub palmetto *(Sabal etonia).* The monitored stand occurs on excessively well-drained and strongly acidic, nutrient-poor Entisol soil (Abrahamson et al. 1984).

The scrub stand we studied is surrounded by approximately 430 ha of a 60-year-unburned mosaic of southern ridge sand-hills, sand pine scrub, scrubby flatwoods, flatwoods, and bayhead. More recently burned stands of sand pine scrub and scrub-by flatwoods occur approximately 1 km to the southwest, west, and northwest. These more recently burned stands do contain many of the narrow endemics noted for such sites on the Lake Wales Ridge (Abrahamson et al. 1984).

The climate of the study area is characterized by hot, wet summers and mild, dry winters (Chen and Gerber 1990). Mean annual rainfall recorded at Archbold for the 62-year period of 1932—1994 was 136 cm. The rainy season typically occurs from June through September, with over 60% of the annual precipitation falling during this 4-month period (Abrahamson et al. 1984).

Sampling Methods

Fire temperatures during the February 1986 prescription burn were determined by using blotches of 21 Tempil™ temperature-sensitive paints with melting points ranging from 66 to 1093 °C. All 21 paints were applied to each of 96 steel plates (7.7 x 12.8 x 0.3 cm; -240 g) suspended in 16 sets of 3 from steel wires to hang at either 0.5 m (48 plates) or 1.5 m (48 plates) above the ground. The mass of a steel plate allows a better approximation of the temperature experienced by woody twigs and trunks than do lighter aluminum plates of the same size. Plates were arbitrarily located throughout the vegetation sampling grid.

A series of 32 permanently marked, nested quadrats was established during January 1985. Basal diameter, crown height, and crown width were measured for emergent shoots (except mature sand pines) in 1 x 1 m (every shoot), 2 x 2 m (shoots > 30 cm but < 1 m tall), 4 x 4 m (shoots > 1 but < 3 m tall), and 8 x 10 m (shoots > 3 m tall) quadrats. Litter and lichen *(Cladonia spp.)* cover were estimated and litter depth was measured at three points within each 1 x 1 m quadrat and averaged. Basal diameters of all trees (shoots > 3 m) were measured at approximately 30 cm from ground level. Basal diameters of mature sand pines were measured in all 32 nested quadrats as well as in an interspersed set of forty-one 8 x 10 m quadrats. The cumulative number of sampled species did not change appreciably after fewer than 10 quadrats for all quadrat sizes. The sample area for mature sand pines totaled 5,840 m^2, 2,560 m^2 for all other shoots > 3 m, 512 m^2 for shrubs > 1 m but < 3 m, 128 m^2 for shoots > 30 cm but < 1 m, and 32 m^2 for shoots < 30 cm. This grid of nested quadrats was censused in January of 1985 (1 year prior to burning), 1987 (approximately 1 year post fire), 1988 (2 year), 1989 (3 year), 1991 (5 year), and 1993 (7 year). Even though all sampling occurred during January, most herbaceous scrub species can be censused during the dormant season, as shown by our studies at more recently burned sites (Abrahamson 1984a, 1984b). A 7.2-ha area containing the vegetation grid was prescription burned using a combination of back fires and head fires.

Raw vegetation data were summarized to include absolute and relative density, dominance (based on basal areas), frequency, and importance values (sum of the relative values of density, dominance, and frequency) by species and size class. To gain more insight into the structural and compositional changes in the postburn community, we calculated species richness, evenness, and diversity by size class for the preburn and all postburn samples of the sand pine scrub stand. Finally, we used Detrended Correspondence Analysis (DECORANA) to visualize the multivariate changes in species densities and dominances in the preburn and postburn samples over time. DECORANA calculates stand ordination scores as averages of the species ordination scores and, reciprocally, it computes the species ordination scores as the averages of stand ordination scores (Hill 1979, Hill and Gauch 1980). Ordinations were performed on both absolute and relative densities and dominances using PC-ORD (McCune 1993). Absolute values were relativized using standardization by the norm (Greig-Smith 1983).

RESULTS

Historical Vegetation Pattern

An aerial view of the Archbold Biological Station's original tract taken in 1984, prior to the reintroduction of fire, shows relatively high frequency of south Florida slash pine *(Pinus elliottii* var. *densa;* to the left and center in the photo) and sand pine (in portions of the foreground and to the right in the photo; Figure 1, top). However, an aerial photograph taken in 1933 of nearly the same northward view reveals a substantially lower frequency and density of both pine species (Figure 1, bottom; this stand was never logged). The absence of standing dead pine trunks in the 1933 photograph indicates that pine occurrence was low prior to the 1926 or 1927 wildfire. If mature pine density had been reduced substantially by a fire only 6 or 7 years prior to the 1933 photograph, the landscape would still be dotted with fire-killed pine trunks (especially the resin-rich trunks of south Florida slash pine, also known as "fatwood").

Characterization of the Prescription Burn

The drought index was 573 (scale of 0 to 800, with 800 the maximum possible, Keetch and Byram 1968) on the day of the prescription burn (February 3, 1986) and had been consistently over 500 since November 1985. The burn occurred under conditions of southeast winds at approximately 16 km/h with a temperature of 24°C and relative humidity of 69% at ignition time. Relative humidity reached a low of 41% during the burn and air temperatures increased to 29°C. The burn consumed a total of 7.2 ha of old-growth sand pine scrub and scrubby flatwoods.

The fire produced a patchy burn of the understory vegetation throughout the sam-

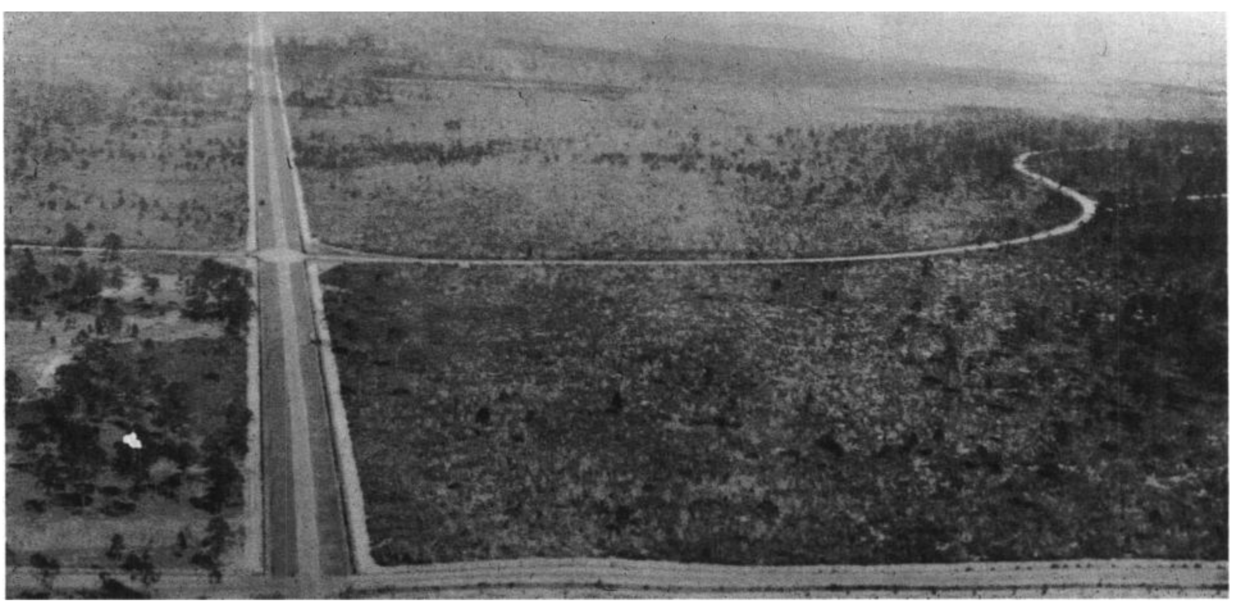

Figure 1. Top: Northward view of the original tract of the Archbold Biological Station taken In 1984 after nearly 60 years without fire. The road running northward Is State Road 8 and Lake Annie Is visible in the upper left corner of the photograph. Note the high density of sand pine and south Florida slash pine. Photograph taken by R.L. Myers. Bottom: Nearly the same northward view taken in 1933. Note the low density of pine species. The area illustrated had been burned 6 or 7 years earlier in 1926 or 1927. (Photograph from the Archbold Biological Station Archives.)

pling grid. In most places it was sufficiently hot that all woody shoots and leaves were killed. However, in many portions of the sampling grid, temperatures were in-sufficient to ignite the leaves of shrubs. At a few locations within the vegetation grid, the fire ignited and consumed all under-story leaves. The overstory was much less affected: approximately 55% of canopy sand pines survived the fire.

Overall, the temperatures recorded during the burn were low for oak scrub fires. The highest temperature we recorded was 316°C on one plate at the 0.5-m height and 232°C on one plate at the 1.5-m height (this can be compared to a mean tempera-ture at 1-m height of 405°C [individual fire means range from 261 to 546°C] for 15 subsequent burns at the Archbold Biolog-ical Station, E. Menges, unpubl. data). The mean (t s.e.) of plates with at least one melted paint was 102 ± 10°C (N = 33) at the 0.5-m height and 95 ± 10°C (N = 20) at 1.5 m. Approximately 31% of the plates at the 0.5-m height and 58% of the 1.5-m plates had no paint blotches melted. The prescription burn produced a mosaic of cool and warm temperatures within the vegetation grid (Figure 2).

The fire consumed only a portion of the litter. Litter depth significantly declined from a preburn depth of 5.8 ± 0.4 cm (t s.e., N = 32) to 4.2 ± 0.3 cm following the burn ($F_{5,186}$ = 11.4, P< 0.001). Litter depth had returned to preburn depths (6.2 ± 0.3 cm) by 7 years after the burn. A Tukey post-hoc test showed that litter depth was reduced significantly for the first three postburn years. Likewise, litter cover declined significantly following fire ($F_{5,186}$ = 4.8, P< 0.001) but only at the first postburn census (Tukey post-hoc test, P= 0.002). All sampled quadrats had 100% litter cover prior to the fire but dropped to a mean of 97 ± 0.9% (N = 32) after the fire. Litter cover returned to 99.9 ± 0.1% at 7 years post fire. The amount of ground covered by lichens varied considerably prior to the burn. Some relatively open 1 x 1 m quadrats had as much as 50% lichen cover, while well-shaded quadrats had no lichen cover prior to the fire. The mean preburn lichen cover for all 1 x 1 m quad-rats was 4 ± 2%. Lichen cover dropped significantly to < 0.1 ± 0.06% after the bum and recovered to only 0.2 ± 0.08% at 7 years after the fire (Kruskal-Wallis non-parametric statistic = 18.7, df = 5, P = 0.002).

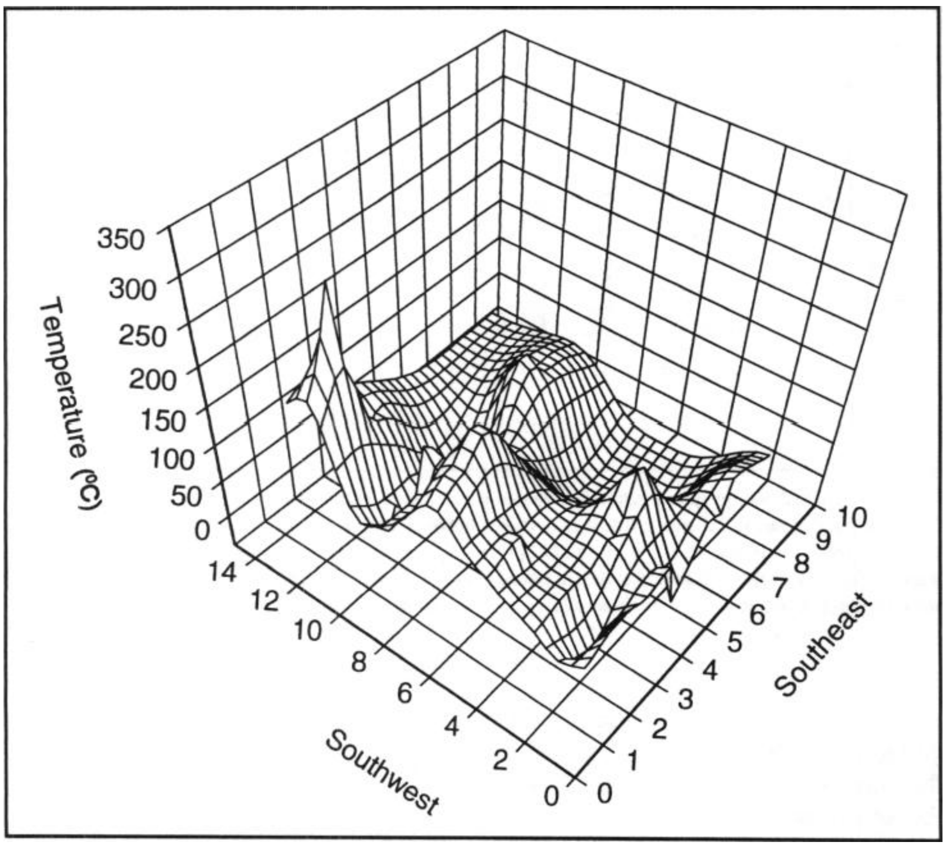

Figure 2. Three-dimensional mesh plot of fire temperatures measured by Tempil™ temperature-sensitive paints applied to steel plates (—240 g) located within the sampled vegetation grid. X axis represents the southeast side of the sampling grid, Y axis the southwest side, and the Z axis the measured temperatures at 0.5- and 1.5-m heights combined.

Species Responses of Seeders

The responses of shrub and tree species to the prescription burn varied considerably. For example, approximately 45% of the mature sand pines were killed by the fire, causing sand pine dominance to drop steeply. Subsequently, sand pine dominance increased as the surviving trees gained basal area (Figure 3, top right). In contrast, the density of the obligate seeding sand pine increased from < 300 to approximately 3,000 ramets per ha during the 3 years following fire as a direct result of seedling recruitment (Figure 3, top left). However, the growth and survival of these sand pine seedlings were apparently sup-pressed by the survival and continued presence of a mature sand pine canopy and the dense understory of rapidly resprouting oaks, lyonias, and palmettos. None of these sand pine seedlings survived to the 5-year postburn census and few ever topped 30 cm in height (Figure 3, top left).

Species such as palafoxia *(Palafoxia feayi),* garberia *(Garberia heterophylla),* saw pal-metto, and scrub palmetto usually respond to fire with a combination of seeding and resprouting (Menges and Kohfeldt 1995). For example, the density of palafoxia un-der the preburn, closed canopy scrub was < 20 ramets per ha (too few to show on Figure 3) and all of the sampled ramets were between 1 and 3 m in height. Howev-er, ramet density increased at every post-burn census, primarily owing to the recruitment of seedlings and secondarily to resprouting. Likewise dominance increased nearly 90 fold over the 7-year recovery period (Figure 3, middle). Garberia also recovered from the fire by resprouting and seeding (Figure 3, bottom). Prior to the fire, garberia was represented by fewer than 80 relatively large-diameter ramets per ha. Although garberia density and dominance were both low at 1 year post fire, density increased more than 16 times the preburn level at 2 years post fire and dominance regained approximately 45% of the preburn level at 7 years post fire.

Saw palmetto density fell during the 7-year postburn period, primarily owing to the loss of small palmettos (Figure 4, top left). However, the remaining saw palmettos had approximately the same dominance as in the prebum stand. Scrub palmetto had approximately the same density over the 9-year census period but somewhat lower dominance at 7 years post fire (Figure 4, middle). Dominance of both palmettos fluctuated over the recovery period, owing to the 2- to 3-year longevity of individual palmetto leaves and the rapid production of new leaves following fire (W. Abrahamson, unpubl. data).

Species Responses of Sprouters

Rusty lyonia, scrub hickory, and silk bay typify the range of responses for species recovering from fire primarily by resprouting. Rusty lyonia, for example, exhibited a strong resprouting response with ramet density nearly doubling after the fire (Figure 4, bottom left). However, the dominance of rusty lyonia dropped following the fire to only about 35% of the preburn level. In spite of the strong resprouting and subsequent thinning of smaller ramets, dominance was only about 55% of the prebum level at 7 years after the fire (Figure 4, bottom right). Scrub hickory vigorously resprouted following fire (Figure 5, top left). Its density at only 11 months after the bum was approximately 7 times greater than the prebum density. Hickory ramets thinned continuously after the initial resprouting as surviving ramets gained basal diameter. At 7 years post fire, scrub hickory density was 2.6 times greater than the preburn value, and its dominance was 1.3 times greater than the initial amount. On the other hand, silk bay not only lost ramets immediately after the fire, but thinning of its ramets has continued through-out the 7-year postburn period (Figure 5,

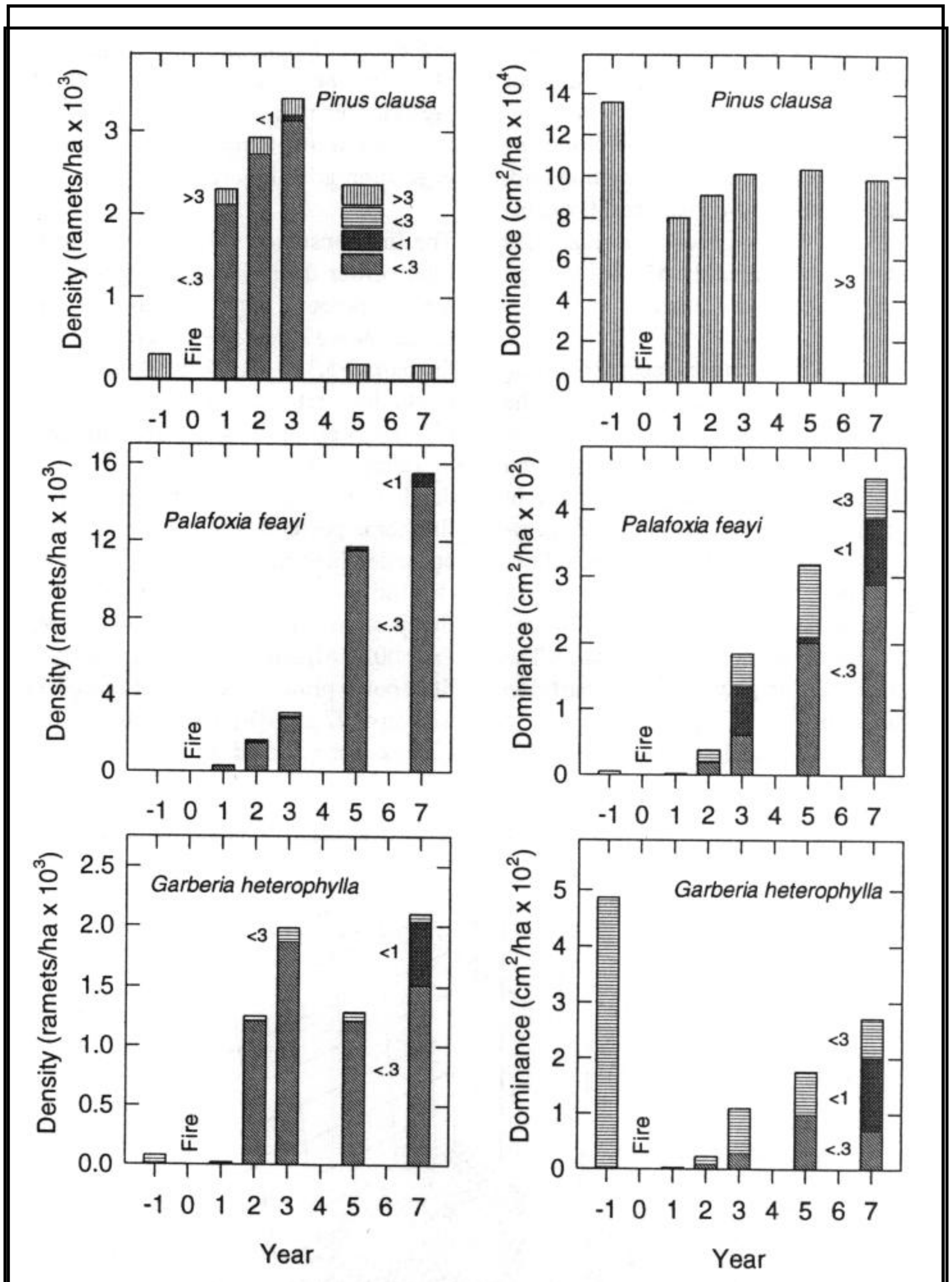

Figure 3. Stacked bar graphs Illustrating ramet density (left column) and dominance (right column) based on basal areas for shoots < 0.3 m tall, shoots between 0.3 m and 1 m tall (< 1 m), shoots between 1 and 3 m tall (< 3 m), and shoots over 3 m tall (> 3 m) by years prior to (-1 year) and after a prescription burn in February 1986. A legend for the fill patterns (size classes) is in the upper left graph. All censuses were conducted in January of each census year (no censuses were conducted in years 4 and 6).

middle left). Dominance of silk bay surpassed the preburn level at 3 years after the bum (Figure 5, middle right). This was the consequence of larger diameters of the postburn silk bay ramets (means of 6.6 cm at 7 years post fire versus 4 cm at the prebum census).

Species Responses of Clonal Sprouters

Other woody sub-shrubs and shrubs, including dwarf huckleberry *(Gaylussacia dumosa),* myrtle oak, sand live oak, and Chapman's oak, typically respond to fire through resprouting and clonal spread. For example, the density of dwarf **huckleberry**

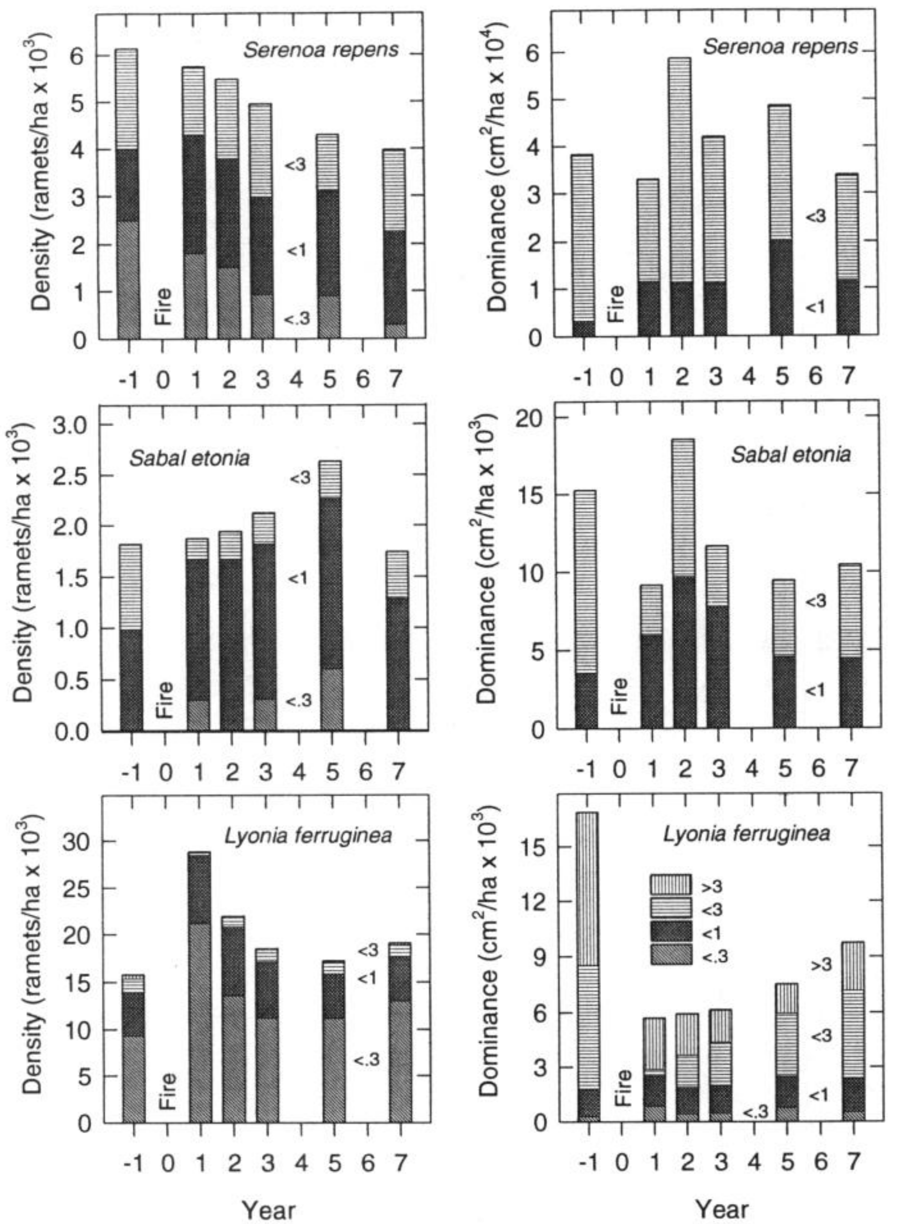

Figure 4. Stacked bar graphs as in Figure 3. A legend for the fill patterns (size classes) Is in the bottom right graph.

more than doubled during the first 11 months following the fire owing to re-sprouting and clonal spread (Figure 5, bottom left). Absolute dominance for dwarf huckleberry increased more slowly until 3 years post fire, when levels were more than double those in the long-unburned scrub (Figure 5, bottom right). Oaks strongly dominated both the preburn and post-burn understory. While clones of myrtle and sand live oak quickly resprouted, Chap-man's oak clones lost density in the post-burn period (Figure 6, bottom left). How-ever, Chapman's oak and sand live oak had appreciably higher dominances at 7 years after the fire than they did in the preburn stand (Figure 6, bottom and middle right, respectively).

Species Importance

Importance values for many species (e.g., myrtle and sand live oaks, saw palmetto) were stable during the postburn recovery period. These species neither appreciably gained nor lost in importance value during any of the census intervals. However, several species made substantial gains in calculated importance values over the duration of the recovery period, including palafoxia (30 fold due to seeding and re-sprouting), muscadine grape *(Vtis munsoniana)* (5 fold due to extensive resprouting and some seeding; data not illustrated), large-seeded **beak** rush ***(Rhynchospora** megalocarpa)* (3.7 fold because of re-sprouting and seeding, data not illustrated), garberia (2.7 fold due to resprouting and seeding), and scrub hickory (2.5 fold due to resprouting). A few species lost importance value over the course of the recovery period, including scrub palmetto (–60% of its preburn importance value due to reduced dominance), rusty lyonia (–75% of its original value because of loss of dominance), and Chapman's oak (–80% of its prebum value because of reduced ramet density).

Community Structure

Species richness (number of species present) of the smallest size class increased appreciably following the fire (Table 2). Only 15 species with shoots less than 30 cm tall were sampled in the prebum stand. However, at least 23 and as many as 26 species were identified in this size class in the postburn stands. However, most of the increase in richness for shoots less than 30 cm was the result of sprouts of sub-shrubs, shrubs, and trees. Most important, given the typical occurrence of herbs within the gaps of recently burned sand pine scrub (Menges and Hawkes, in press), few herbaceous species were added to the stand.

Evenness (es) of all size classes except trees (> 3 m height) was relatively low, indicating the predominance of several species and the limited occurrence of most species (Table 2). Species diversity (Shannon-Wiener H') showed significant changes in all size classes (Table 2). The smallest size class (< 30 cm tall) had elevated diversity from the second year through the seventh year post fire as a result of three factors. First, the postburn environment encouraged plants that typically recover from fire, at least in part, by seeding (e.g., sand pine, palafoxia) and several forbs, including a few, scattered individuals of **tread-softly** ***(Cnidosculus*** *stimulosus),* fire weed *(Erechtites hieracifolia),* and the legumes partridge-pea *(Chamaecrista fasciculata),* alicia *(Chapmannia floridana),* and milk pea *(Galactia regularis). Sec*ond, the relative densities of shoots < 30 cm became more even among species in the postburn stands as the three most dense species temporarily declined in relative density. Third, as scrub hickory resprouted it added many sprouts in the smallest size class. Before the burn, scrub hickory was not represented in this size class. The remaining three larger size classes exhibited reduced species diversity for at least some portion of the monitored postburn period.

Community Responses

DECORANA analyses based on absolute ramet densities and dominances (emphasizing structural shifts) showed that this sand pine scrub stand was relatively stable following fire, even when the community had been unburned for 60 year (Figures 7 and 8). Eigenvalues based on absolute density and absolute dominance data were small, indicating little variance along the ordination axes (Table 3). However, DECORANAs based on relativized (using standardization of the norm) density and dominance data (emphasizing compositional shifts) produced higher eigenvalues, indicating more variance. The r^2 coefficients of determination (correlations between Euclidean ordination distances and Euclidean distances in the original n-dimensional space) were relatively high for stands over time (Table 3). Except in the case of absolute density, the first axes had much higher coefficients of determination than the second or third axes.

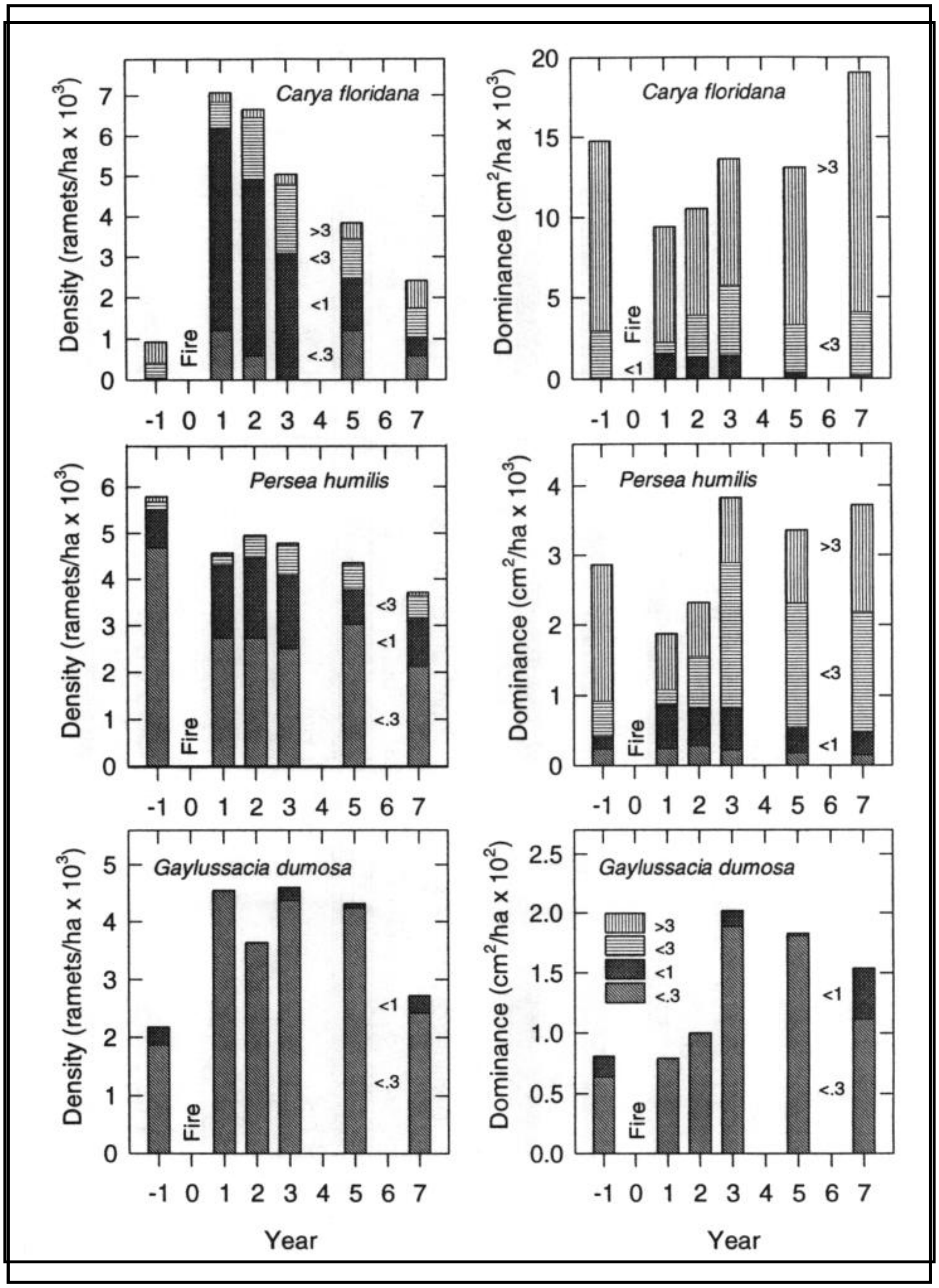

Figure 5. Stacked bar graphs as In Figure 3. A legend for the nu patterns (size classes) is in the bottom right graph.

The greatest amount of structural and compositional change occurred immediately after the fire, between the prebum and 1-year postburn censuses (Figures 7 and 8). However, changes between the 1-year and 2-year censuses after fire were primarily compositional; little structural change was measured. The larger shifts and greater variance in the relativized rather than the absolute data indicate that compositional shifts were greater than structural shifts (Figures 7 and 8). The species/stand ordinations based on density illustrate that the principal shift has been toward species that are able to quickly resprout, clonally spread, and seed after fire. Such species include palafoxia, garberia, dwarf huckleberry, shiny blueberry *(Vaccinium myrsinites),* greenbrier *(Smilax auriculata),* large-seeded beak rush, scrub hickory, and muscadine grape. The species/stand ordinations based on dominance further suggest a shift away from sand pine (an obligate seeder) and rusty lyonia (which was slow to regain dominance) and toward strong resprouters like oaks and scrub hickory.

DISCUSSION

Species Responses

The recovery responses of scrub species were highly specific even among species with similar life-history strategies (e.g., resprouters, seeders). Strong resprouters

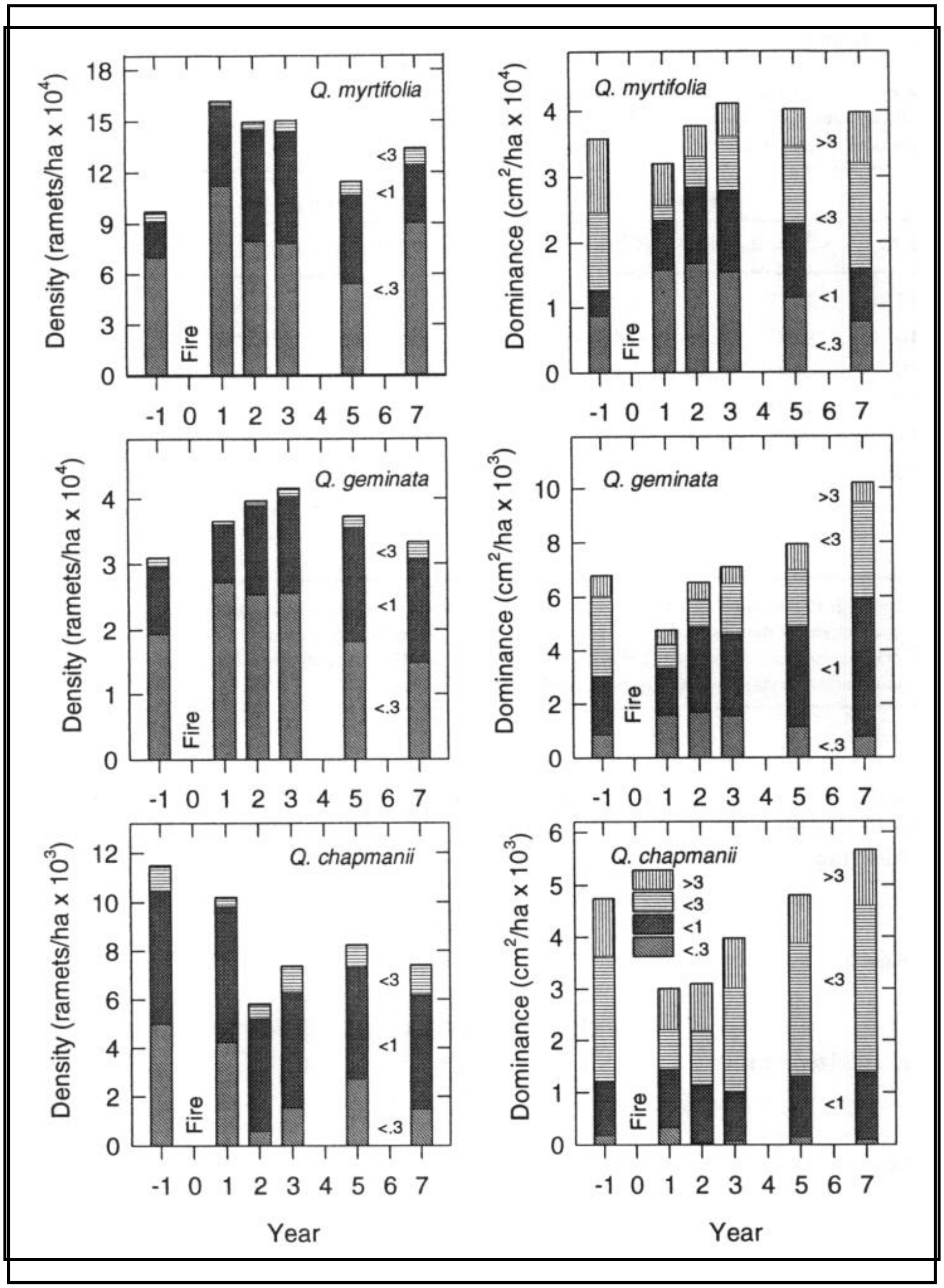

Figure 6. Stacked bar graphs as in Figure 3. A legend for the fill patterns (size classes) is in the bottom right graph.

like rusty lyonia and scrub hickory, for example, differed markedly in the number of sprouts produced and in the rate at which they regained dominance during postburn recovery. Species such as palafoxia and garberia that use a combination of seeding and resprouting differed considerably in seedling success and growth. Yet even in an association with a number of species that at least partially recover from fire via seeding, there were limited changes in herb occurrence. Only a few, scattered herbs including tread-softly, fire weed, and the legumes partridge-pea, alicia, and milk pea sporadically occurred in the postburn samples. None of these species were sampled in the preburn stand. Missing from both preburn and postburn samples were typical scrub species, including *Dicerandra frutescens, Eryngium cuneifolium, Lechea cernua, Paronychia chartacea,* and *Polygonella basiramia.* Unfortunately, we do not know if these species were ever common in the specific scrub stand we studied. However, the 1933 photograph (Figure 1, bottom) suggests that conditions were once suitable to support populations of such herbs at our study site. Herbaceous species typical of sand pine scrub are well represented in more recently burned scrub stands located only 1–2 km west of our study site. Unfortunately, we know little about the dispersal of these species or the time necessary for their re-invasion of previously long-unburned sites.

Many of the herbaceous plants of sand pine scrub are specialists for gaps among the dominant shrubs (Hawkes and Menges 1995; Abrahamson and Abrahamson, in press; Menges and Hawkes, in press). Fire has the effect of creating or enlarging gaps, making the occurrence of gap specialists sensitive to time-since-fire. For gap specialists, long periods without fire may be detrimental because gaps can rapidly disappear in sand pine scrub, and scrub stands are becoming increasingly fragmented. Time-since-fire likely influences both the availability and the viability of seeds in scrub soils. Years of shading by sand pines and shrubs reduce herb populations in long-unburned stands and may limit the addition of fresh, viable seeds to the stand's seed bank. While the loss of locally added seeds may not have had serious consequences prior to suburban sprawl, the present isolation of long-unburned stands due to fragmentation may virtually eliminate seed dispersal among stands.

In spite of marked differences in the recovery responses of individual species, the overall effect of a low-intensity, winter fire on this long-unburned scrub was subtle change in the structure and composition of the stand. For example, the only appreciable change in species richness occurred among ramets in the smallest size class. This increase was primarily caused by species formerly represented only in the shrub and tree size classes entering the < 30-cm-tall size class through resprouting and seeding. Smaller gains in richness came from the clonal spread of a few species and seed germination of several others. The significant changes in community structure as measured by species diversity were relatively small.

Table 2. Richness (number of species), evenness (e_s), and species diversity (Shannon-Wiener H') for the preburn and all postburn communities based on number of shoots for each size lass in 32 permanently marked, nested quadrats. Size classes (height) were structured to Include those shoots less than 30 cm tall (sampled in 1 x 1 m quadrats), shoots between 30 cm and 1 m (In 2 x 2 m quadrats), shoots between 1 and 3 m (in 4 x 4 m quadrats), and shoots over 3 m (in 8 x 10 m quadrats). The significance of differences In H' within a size class Is shown by different letter superscripts in columns, according to Hutcheson's (1970) t-test method. All censuses were done during January of sample years.

	Richness				Evenness				Diversity			
Census	**<30 cm**	**<1 m**	**an**	**>3 m**	**<30 cm**	**<1 m**	**<3 m**	**>3 m**	**<30 cm**	**<1 m**	**<3 m**	**>3 m**
Preburn	15	17	15	11	0.27	0.21	0.28	0.47	1.75[a]	1.67[a•d]	1.79[a,b]	1.72[a•c]
1 yr post burn	26	15	10	10	0.20	0.19	0.44	0.47	1.82[a]	1.47[b•e]	136[a•b,c]	1.73[a•c]
2 yr post bum	25	15	12	10	0.30	0.16	0.37	0.51	**2.00**[b•c]	1.33[c]	**1.81**[a,b]	1 72[a•c]
3 yr post burn	26	20	13	10	0.30	0.13	0.33	0.50	2.06	1.37[c]	**1.83**[b]	1.71["0]
5 yr post burn	23	17	13	10	0.35	0.15	0.26	0.41	234[d]	1.42[b•c]	1.71[a•O]	1.55[b]
7 yr post burn	23	17	14	10	0.21	0.18	0.25	0.45	**1.99**[b•c]	1.57[d•e]	1.64[c]	1.59[c]

Ordination based on absolute and relativized density and dominance showed that the postburn samples have shifted away from the prebum sample in both structural and compositional components. Further-more, the greater lengths of the ordination vectors between stand representations over time, based on relativized data compared to those using absolute data, suggest that fire had its greatest impact on the relative abundances of species within the stand. Postburn samples showed consistent, directional change after the initial postburn census, although the change was not to-ward or away from the preburn sample. To the contrary, a 45- to 65-year unburned sand pine scrub stand did not change con-sistently over a 20-year period; many quad-rats in this long-unburned scrub changed little or shifted erratically (Givens et al. 1984, Menges et al. 1993).

Table 3. Eigenvalues (measures of the amount of variance along a given ordination axis) and r^2 coefficients of determination (correlations between ordination distances and the distances in the original n-dimensional space) resulting from Detrended Correspondence Analyses of the preburn and postburn stands of a long-unburned sand pine scrub.

			R^2	
Data	**Axis**	**Eigenvalue**	**Increment**	**Cumulative**
Absolute density	1	0.04	0.20	0.20
	2	0.01	0.30	0.50
	3	0.0003	-0.02	0.48
Absolute dominance	1	0.03	0.73	0.73
	2	0.001	-0.06	0.67
	3	0.00001	0.04	0.71
Relativized density	1	0.29	0.79	0.79
	2	0.08	-0.17	0.61
	3	0.01	0.08	0.70
Relativized dominance	1	0.36	0.75	0.75
	2	0.10	-0.13	0.62
	3	0.02	-0.16	0.47

Fire Suppression and Species Persistence

Fire suppression in plant associations such as sand pine scrub endangers the persis-tence of some species (Johnson and Abra-hamson 1990; Menges and Kohfeldt 1995; Menges and Kimmich 1996; Abrahamson and Abrahamson, in press). For example, the populations of several narrow-endemic scrub herbs (e.g., *Eryngium cuneifolium, Paronychia chartacea, Lechea cernua)* decline markedly with time-since-fire, yet these species can strongly increase after fire if viable seeds are available (Johnson and Abrahamson 1990, Menges and Kim-mich 1996). Previously, scrub herbs may have persisted because of gene flow from adjacent, more recently burned stands or from nearby rosemary scrubs where gaps are much longer lived (Menges and Hawkes, in press). A long fire-free interval in a given stand may have greater con-sequences today, given that for many long-unburned stands, there are no nearby, recently burned stands.

In the absence of fire, scrub species on the southern Lake Wales Ridge are not re-placed by invading, late-successional spe-cies, in part owing to the absence of near-by seed sources for mesic hammock species (Abrahamson et al. 1984; Givens et al. 1984; Myers 1985, 1990; Peroni and Abrahamson 1986; Menges et al. 1993; but see Veno 1976). Instead, in the absence of fire, Lake Wales Ridge sand pine scrub shifts toward xeric hammock characterized by the persistence of understory oaks, the loss of canopy sand pine, and the absence of most endemic herbs. In this context it is important to note that the introduction of a

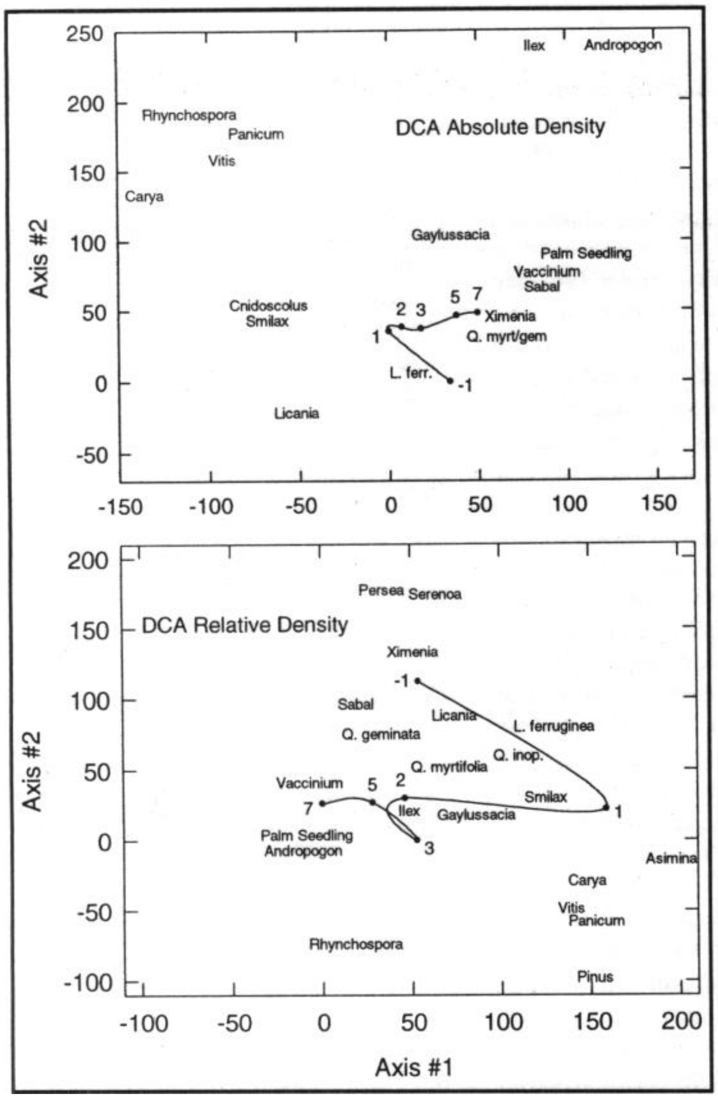

Figure 7. **Stand and species ordination based on absolute (top) and relativized (bottom) densities of each species according to a Detrended Correspondence Analysis. Absolute densities were relativized using standardization by the norm (Greig-Smith 1983). Each point represents the stand's position on the first two axes of the ordination at a given time (indicated in years) prior to or after a February 1986 prescription burn. Lines connecting the points create vectors showing the direction and amount of change from census to census. Names of species appear as symbols for species ordination coordinates. Only species located near the stand ordination coordinates are illustrated. Figures are shown at the same scale but origins differ.**

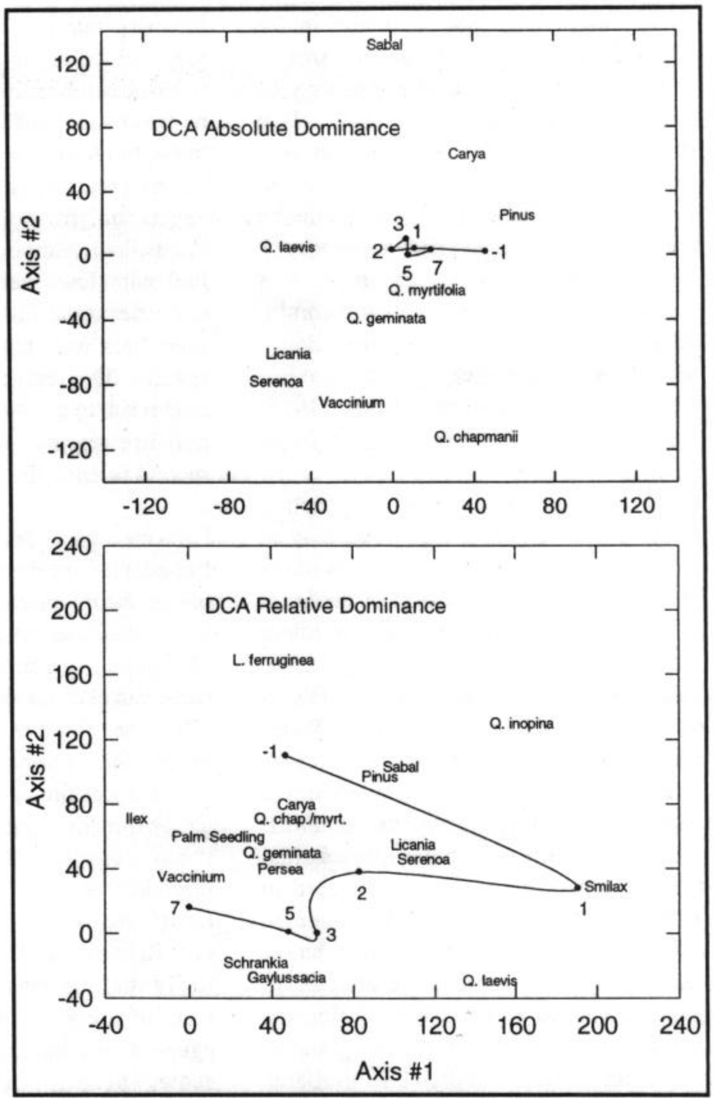

Figure 8. Stand and species ordination based on absolute (top) and relativized (bottom) dominance according to basal areas as determined by a Detrended Correspondence Analysis. Absolute dominances were relativized using standardization of the norm (Greig-Smith 1983). Other information as in Figure 7.

low-intensity winter fire to a 60-year unburned sand pine scrub hastened the shift toward xeric hammock. The February prescription burn resulted in limited mortality among the mature sand pines and a lack of recruitment of replacement sand pines. Furthermore, the low-intensity winter burn reinvigorated the rapidly resprouting oak, scrub hickory, and rusty lyonia understory, creating unfavorable, shady conditions for scrub herbs.

Consequences of Introducing Low-Intensity Winter Fires to Long-Unburned Scrub

Our winter prescription bum initiated a shift of the scrub stand toward a xeric hammock community in which oaks, hickory, and lyonia, but not sand pine, are dominant. This outcome was a striking contrast to the desired result. One objective of the prescription burn had been to restore the stand to a state that contained populations of many of the narrowly endemic scrub herbs. These narrow endemics are characteristically ephemeral and infrequently occur in long-unburned scrub. An adjacent stand of sand pine scrub that had been burned in the same 1926 or 1927 fire as our prescription-burned stand contained relatively few of the narrow endemics in 1969 when it was first censused (some 42 or 43 years after fire). Furthermore, those herbs that did occur in the 1969 census (e.g., *Balduina angustifolia* and *Lechea deckertii)* declined during the next decade (Givens et al. 1984). That stand continued to lose sand pine at each subsequent 10-year census (in 1979 and 1989), and few new species have entered the stand (Givens et al. 1984, Menges et al. 1993). It appears that in the absence of fire, this long-unburned stand will continue to shift toward xeric hammock dominated by a mixture of myrtle oak, sand live oak, and Chapman's oak (Myers 1985) and will contain few typical scrub herbs.

Clearly the objective of our prescription burn was not achieved. This result may be the consequence of the low intensity of the prescription burn, the season of the bum, or some combination of these or other factors. We know, for instance, that the vast majority of lightning strikes and lightning-origin fires occur on the Lake Wales Ridge between May and the end of September (Abrahamson et al. 1984) and that winter-burned and growing-season burned individuals of the same plant species often respond very differently (Abrahamson 1984b, Platt et al. 1988, Abrahamson 1995). This latter point suggests that at least some scrub species are adapted to particular kinds of fires (e.g., during the growing season rather than during winter dormancy), and the limited data available suggest that herbs and grasses (e.g., *Aristida stricta,* Lemon 1967) may be especially sensitive.

Implications for Management

Our results should be interpreted with caution because they are based on a single fire. However, these results do offer an important lesson about the need to monitor the consequences of the reintroduction of fire to long-unburned vegetative associations. Although in our case the single burn invigorated the populations of many of the dominant and more persistent woody species (e.g., *Quercus myrtifolia, Q. geminata, Carya floridana),* this fire did not enhance the richness and diversity of the narrowly endemic herbs. Sand pine scrub ignites infrequently, but when it does burn, it often burns with a high-intensity, catastrophic fire. Our findings suggest that low-intensity burning and/or winter burning may not be an appropriate management tool for scrub unless humidities and fuel moistures are sufficiently low that an in-tense, hot burn is possible (portions of the 7.2-ha prescription burn area outside the vegetation grid did experience higher fire intensities). Although the removal of some fuel with low-intensity, winter fire may seem desirable for fire-control purposes, such fires may hasten the loss of scrub species. The return of this stand of sand pine scrub to a state more typical of recur-rent fire regimes will require at least a second intense fire.

Land managers dealing with associations of fire-adapted species such as scrub must recognize the importance of variation in vegetative responses to different fire regimes. The timing of reintroduction of fire to a stand can alter the directional changes that fire causes (Platt et al. 1988, Robbins and Myers 1992). Furthermore, the intensity and frequency of fire once reintroduced can al-ter the direction and amount of these shifts because scrub plants vary widely in their reproductive patterns with time-since-lastfire (Ostertag and Menges 1994, Menges and Kohfeldt 1995). These observations imply that the most appropriate management of fire-adapted associations is management that integrates the evolution and ecology of the life histories of the complete range of species. For scrub this means avoiding extremely short intervals between fires that could occur prior to the onset of seed reproduction in obligate seeders like sand pine. It also means avoiding such long intervals between fires that seed sources for the ephemeral, obligate-seeding species are lost and resprouters such as oaks accumulate large amounts of underground resources. Fragmentation of scrub habitats due to suburban sprawl makes the maintenance of seed sources critical. Management should include use of variable fire-return intervals, because no single interval explains the diversity of fire-recovery strategies observed among scrub species (Ostertag and Menges 1994, Menges and Kohfeldt 1995). Finally, the results for this stand of sand pine scrub argue against excessively cautious prescription burning of sand pine scrub under conditions that are too mild. 10/12 97%width

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