RESEARCH ARTICLE

Vegetation Recovery and Stand Structure Following a Prescribed Stand-Replacement Burn in Sand Pine Scrub

Cathryn H. Greenberg[1]
U.S. Forest Service
Southern Research Station
Bent Creek Experimental Forest
1577 Brevard Road
Asheville, NC 28806 USA

ABSTRACT: Vegetation and stand structure of sand pine scrub in central Florida, USA, were measured before a prescribed stand-replacement bum and for > 8 y afterward. Herbaceous species richness peaked within 16 months postburn, then gradually declined, although significant differences were detected only between 16 months and > 8 y postburn. Twenty-two plant species were detected after the bum that were not recorded prior to the burn. Woody plant species richness recovered to preburn levels within 5 months. Myrtle oak (*Quercus myrtifolia* Willd.), the dominant species, regained its prebum cover within 16 months and preburn height within 40 months. Scrub palmetto (*Sabal etonia* Swingle ex Nash) regained its prebum cover and height within 5 months. After > 8 y sand pine (*Pinus clausa clausa* [Chapm. Ex Engelm.] Vasey ex Sarg.) had regained 29% cover and 2.3 m height. Litter layer thickness was reduced by the fire but was subsequently stable. Bare ground increased postburn but was similar to prebum levels within 64 months. Light at breast height peaked at 28-64 months postburn, and light at ground level increased postburn and remained high. Coarse woody debris cover and diameter increased beginning 28 months postburn as snags fell. Under the right conditions, prescribed stand-replacement fire can be used in sand pine scrub to enhance species richness, temporarily increase cover and reproduction by some endemic plant species, and temporarily eliminate the sand pine canopy to restore a historically common stand structure.

Recuperación de la Vegetación y Estructura Después de un Fuego Programado en un Sand Pine Scrub

RESUMEN: La estructura de la vegetación de sand pine scrub en Florida central, USA, fue medida antes de un fuego programado y a los 8 años posteriores. La riqueza de las especies herbáceas hizo un pico dentro de los 16 meses posteriores a la quema, luego gradualmente declinaron, aunque sólo se detectaron diferencias significativas entre los 16 meses y más de 8 años despues de la quema. Veintidds especies de plantas fueron detectadas despues de la quema que no fueron registradas previo a la misma. La riqueza de las plantas leñosas se recuperó a los niveles previos a la quema dentro de los 5 meses. La especie dominante (*Quercus myrtifolia* Willd.), recuperó su cobertura previa a la quema dentro de los 16 meses y la altura previa dentro de los 40 meses. *Sabal etonia* Swingle ex Nash recuperó su cobertura previa y altura dentro de los 5 meses. Después de más de 8 años el pino de la arena (*Pinus clausa clausa* [Chapm. Ex Engelm.] Vasey ex Sarg.) recuperó el 29% de su cobertura previa y 2,3 m de altura. El grosor de la hojarasca se redujo por el fuego pero estuvo estable posteriormente. El suelo desnudo aumentó despues del fuego pero fue similar a los niveles previos a la quema dentro de los 64 meses. La luz a la altura del pecho hizo un pico a los 28-64 meses posteriores a la quema, y la luz a nivel del suelo aumentó despues de la quema y se mantuvo alta. La cobertura de pedazos de troncos y el diámetro empezó a aumentar a los 28 meses cuando las ramas cmpezaron a caer. Bajo las condiciones correctas, cl fuego programado puede ser utilizado en sand pine scrub para aumentar la riqueza de especies, temporalmente aumentar la cobertura y la reproduccidn de algunas plantas endémicas, y temporahnente eliminar el dosel de pino de arena para restaurar la estructura histórica.

Index terms: fire ecology, prescribed fire. sand pine scrub, stand-replacement burn, stand structure

INTRODUCTION

The sand pine scrub ecosystem is rich in endemic species (Christman and Judd 1990), probably due to a unique interplay between harsh edaphic conditions and geologic and climatic history (Watts 1971, 1975, 1980; Zona and Judd 1986). This ecosystem is limited primarily to Florida, USA, where its distribution is patchy and restricted to relict beach ridges and bars (Stout and Marion 1993). The scrub ecosystem and associated endemic plant and animal species are threatened by conversion to citrus groves and urban development (Myers 1990).

There are four major "types" of scrub: scrubby flatwoods, rosemary scrub, oak-palmetto scrub, and sand pine scrub. Scrub types are differentiated based on stand structure, the relative abundance of common scrub species, and the composition of endemic species (Menges 1999). Factors influencing the development of different scrub types include the age of the scrub ridge, biogeography, fire history, distance from the water table, and soil type (Abra-

[1] Author e-mail: kgreenberg@fs.fed.us

Natural Areas Journal 23:141–151

hamson et al. 1984; Schmalzer and Hinkle 1992a, 1992b; Menges 1999; Schmalzer et al. 1999).

The largest remaining contiguous area of scrub is sand pine scrub type and occurs on the Ocala National Forest (ONF) in north-central peninsular Florida (Myers 1990). Sand pine scrub contains a high density of peninsular sand pine (*Pinus clausa* var. *clausa* [Chapm. Ex Engelm.] Vasey ex Sarg.) that forms a continuous tree canopy at maturity. Historically, widespread stand-replacement fires burned in sand pine scrub at relatively long intervals (IO-100 y) (e.g., Rawlings 1933, Webber 1935).

Scrub plants exhibit numerous adaptations that enable rapid recovery after high-intensity disturbance (Myers 1990). Most shrub species resprout vigorously from underground roots or rhizomes (Abrahamson 1984a, 1984b). Cones of peninsular sand pine are serotinous, resulting in high density, even-aged stands following fire (Cooper et al. 1959). Many herbaceous species germinate from the seed bank or resprout after fire (Menges and Kohfeldt 1995, Carrington 1997, Carrington and Keeley 1999). Some rare species, such as scrub morning glory (*Bonamia grandiflora* [A. Gray] Heller), persist inconspicuously in mature sand pine forest (pers. obs; this study) but flower and increase in cover after disturbance (Hartnett and Richardson 1989). Many species flower and fruit prolifically shortly (months to years) after fire (Abrahamson 1984b, Ostertag and Menges 1994, Carrington 1999). Several vertebrate species, including Florida scrub jay (*Aphelocoma coerulescens* Bosc) and several reptile species, also require recently burned or silviculturally disturbed scrub with abundant bare ground (Breininger et al. 1995, Greenberg et al. 1995).

A fire suppression policy was implemented under U.S. Forest Service administration in 1908. Currently, most of the sand pine scrub ecosystem in the ONF is managed for pulpwood production by clearcutting followed by site preparation and direct seeding of sand pine. If wildfire occurs, sand pine stems arc usually salvage-logged. Greenberg et al. (1995) reported few short-term differences in plant community response among stands that were clearcut and site-prepared or burned by wildfire and salvage-logged; species richness and diversity of herbaceous plants were significantly higher after both of these disturbances compared to mature sand pine forest.

Relatively few studies address issues related to the management and conservation of sand pine scrub at a community level, even though it is the predominant remaining type of scrub, contains endemic plant and animal species, and is heavily managed by the U.S. Forest Service. Laessle's (1958) classic description of soils, vegetation, and successional relationships between sandhill and scrub included sand pine scrub, but did not address postfire recovery except descriptively. Most studies have been in oak-palmetto (e.g., Schmalzer and Hinkle 1992a, 1992b; Schmalzer 2003), rosemary, and scrubby flatwoods scrub types (e.g., Abrahamson 1984a, 1984b; Menges and Kohfeldt 1995, Abrahamson and Abrahamson 1996a, Young and Menges 1999). Abrahamson and Abrahamson (1996b) reported on postfire recovery of sand pine scrub after a low-intensity winter burn.

Fire intensity probably differs in sand pine scrub relative to other scrub types because closely spaced sand pine trees create high-intensity crown fires. After fire, sand pine scrub also differs from other scrub types in that there is thick sand pine regeneration and a high density of snags. Fire intensity may affect the recovery dynamics of scrub vegetation; some species respond differently to winter (and usually lower-intensity) versus higher-intensity growing-season burns (Platt et al. 1988). The presence of a sand pine canopy presents a special challenge to managers wishing to prescribe burn under smoke and safety guidelines (Custer and Thorsen 1996). This paper examines vegetation recovery and structural dynamics of sand pine scrub during eight years after a prescribed, stand-replacement burn conducted during the growing season.

METHODS

Study Area

The Ocala National Forest encompasses approximately 180,000 ha in Marion, Lake, and Putnam Counties in central Florida. Over half of the forest is occupied by sand pine scrub in a south-southeast strip of ancient dune, approximately 60 km long and 1O-20 km wide. Soils supporting sand pine scrub are excessively drained aeolian or marine sands, classified as hypertheric, uncoated families of Spodic (Paola series) and Typic Quartzipsamments (Astatula series) (Kalisz and Stone 1984). The area receives approximately 130 cm of rainfall annually, with over half falling between June and September. Average temperatures range from 20°C to 32°C between April and October and 11°C to 23°C between November and March (Aydelott et al. 1975). The study site was a 12.2-ha portion of a 57-year-old sand pine forest stand that originated from a 1935 wildfire (G. Custer, U.S. Forest Service, Ocala National Forest, Fla., pers. corn.) within an area of the ONF that is high in endemic, threatened, and endangered plant species (Christman 1988).

Prescribed Burn

A prescribed, stand-replacement burn was conducted on 11 May 1993 (Outcalt and Greenberg 1998). Ambient temperature was 26°C, relative humidity was 50%, and the wind was from the southeast at 3 km/h. The Keetch/Bryam (Keetch and Bryam 1968) drought index was 457. of an 800 maximum (Custer and Thorsen 1996). Fire intensity differed among plots, but all aboveground biomass was killed (Outcalt and Greenberg 1998).

Vegetation Sampling

The study site was sampled prior to the burn on 8 May 1993, and again following the burn in June and October 1993, and July–early October of 1994, 1995, 1996, 1998, and 2001. Six 50-m permanent line transects were established at random locations throughout the stand. Percent cover (total distance intercepted by species divided by SO m and multiplied by 100) of all vascular plant species, bare ground, and coarse woody debris (CWD) (≥ 10 cm diameter at interception with transect) intercepting (above, below, or touching) transects was measured. The diameter of CWD at interception with the transect also was measured except during 1994. Depth of the litter layer, height of the nearest myrtle oak (*Quercus myrtifolia* Willd.) and scrub palmetto (*Sabal etonia* Swingle ex Nash), and light availability were measured at the beginning, midpoint, and end of each transect. Light availability (percent open canopy) was measured at breast height (LBH) and at ground level (LGL) using a spherical densiometer. Because of time constraints some measurements (depth of litter layer and percent bare ground) were not measured before the burn; preburn measurements of those two features are from an adjacent control stand measured two weeks later. Sand pine height was measured in 1998 and 2001 only. Flowering and fruiting were not systematically surveyed but were recorded in field notes as encountered.

Statistical Analyses

Univariate analysis of variance (ANOVA) was performed with Tukey's Studentized Range Test for multiple comparisons of species richness, percent cover of selected species, and stand structural features among sample periods. Time was effectively the "treatment" in this experimental design; therefore, a repeated measures ANOVA, which requires two factors (treatment and time), could not be performed. Percentage data were square-root arcsine transformed prior to ANOVA. Transects were considered the replicate unit. Although technically within-stand replication is pseudoreplication, it was determined to be the most appropriate means for statistically describing the temporal dynamics of stand structure and species composition following a prescribed stand-replacement burn.

RESULTS

The fire scorched most of the sand pine crowns, except for a few along the edge of the stand. Pines retained their needles for a few weeks, but within 5 weeks most pines had lost about 50% of the needles from their crowns, and about half of the ground surface was littered with pine needles. Pine seed fell heavily from newly opened serotinous pine cones for about a month after the burn. Large flocks (5–50) of mourning doves (*Zenaida macroura*) were seen on the ground eating seeds during that period. By 16 June 1993 few pine seeds remained on the forest floor. In August 1993 apical meristems were torn from about 50% of scrub palmetto and saw palmetto (*Serenoa repens* [Bartr.] Small), and apparently consumed by black bear (*Ursus americanus* [Linnaeus] Pallus) (B. Simons, independent forester, Gainesville, Fla.; J. Buckner, Marion County public schools, Ocala, Fla., and C.H. Greenberg, pers. obs.). Bark beetles and woodborers could be heard throughout the stand within a few days of the fire (Outcalt and Greenberg 1998), and by 16 June 1993 the air was filled with sawdust falling from standing snags. All pine trees were dead within two months.

Prior to the prescribed burn a total of 25 species occurred on transects, including 15 species of shrubs, trees, and palmettos (referenced henceforth as "woody plants"), and 10 species of vines, grasses, and herbaceous plants (referenced as "herbaceous"). Sand pine density was about 670 trees ha-' (Outcalt, in press). After the burn a total of 47 plant species, including 18 woody species and 29 herbaceous species, occurred on transects (Table 1).

Herbaceous species richness did not significantly differ before and after the prescribed fire, although after > 8 years (2001) it was significantly lower than at 16 months postburn (df = 7; $F = 3.21$; $P = 0.0086$). However, a clear trend was apparent: herbaceous species richness increased within 5 months of the prescribed burn, peaked within 16 months, and began to decline by 40 months postburn (Figure 1). Nineteen herbaceous species and three woody species that were absent from transects prior to the burn occurred on transects during postburn samples (Table 1). Woody species richness also dropped immediately following the prescribed burn, but differences were only significant between 5 weeks and 16 months postburn and there-

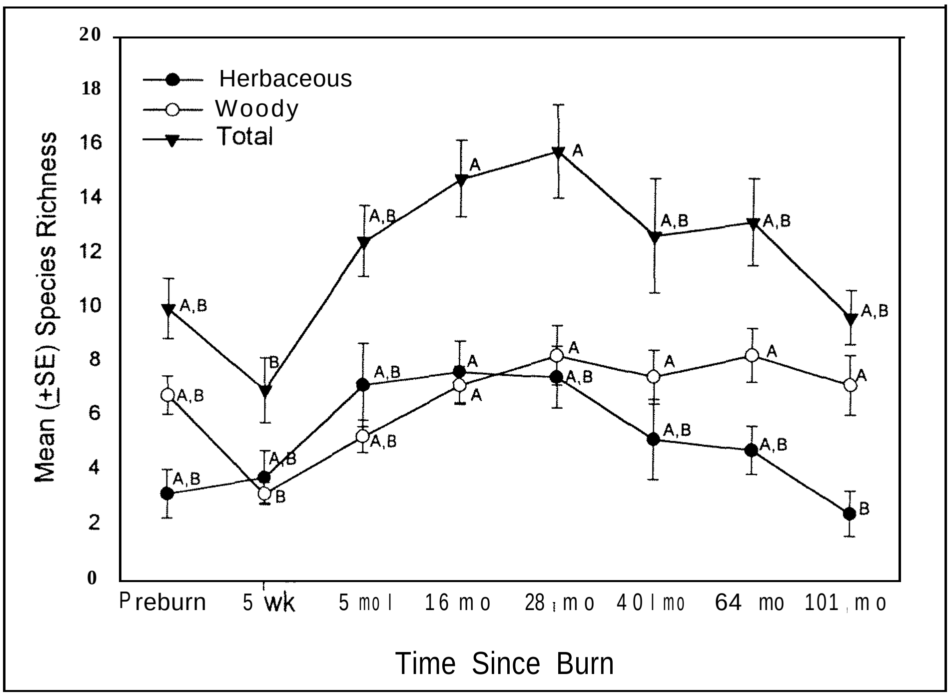

Figure 1. Mean (± SE) species richness of herbaceous, woody, and all vascular plants before and for > 8 y following a prescribed stand-replacement burn in sand pine scrub, Ocala National Forest, Florida. Different letters among data points for a given variable indicate significant differences among sample dates ($P < 0.05$).

Table 1. Mean (± SE) percent cover of plants before and for > 8 y following a prescribed stand-replacement burn (May 1993) in sand pine scrub, Ocala National Forest, Florida. Different letters within rows indicate significant differences (P < 0.05) among sample dates. Observed flowering or fruiting noted on second line of entry.

	Preburn	Postburn						
Species	May 1993	5 weeks	5 months	16 months	28 months	40 months	64 months	101 months
HERBACEOUS SPECIES								
Andropogon L. sp.	0.00±0.00	0.00±0.00	0.02±0.02	0.00±0.00	0.27±0.20	0.02±0.02	0.17±0.17	0.00±0.00
Aristolochin serpentaria L.	<0.01	0.00±0.00	<0.01	0.00±0.00	0.00±0.00	0.01±0.01	0.02±0.02	0.00±0.00
Arnoglossum floridanum (A. Gray) H. Rob.	0.03±0.03	0.06±0.06	0.03±0.03	0.02±0.02	0.10±0.10	0.10±0.10	0.10±0.10	0.00±0.00
Asclepias curtissii A. Gray	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.01±0.01	0.00±0.00	0.02±0.02	0.00±0.00
Baptisia lecontei Torr. & Gray	0.10±0.01	0.00±0.00	0.03±0.03	0.00±0.00	0.00+0.00	0.00±0.00	0.00±0.00	0.10±0.10
Bonamia grandiflora (A. Gray) Heller	0.12±0.10	0.11±0.07	0.37±0.23 (Fl, Fr)	0.30±0.19	0.17±0.11	0.10±0.10	0.10±0.10	0.02±0.02
Bulbostylis ciliatifolia (Ell.) Fem.	0.00±0.00	0.00±0.00	0.00±0.00 (Fl)	0.16±0.16	0.08±0.07	0.00±0.00	0.00±0.00	0.00±0.00
Chapmania floridana Torr. & Gray	0.00±0.00^{a}	0.01±0.01^{a,b}	0.15±0.06^{b}	0.06±0.06^{a,b}	0.07±0.05^{a,b}	0.02±0.02^{a,b}	0.05±0.03^{a,b}	0.00±0.00^{a}
Clitoria mnriana L.	0.00±0.00	0.01±0.01	0.45±0.41	0.80±0.58	0.16±0.11	0.01±0.01	0.47±0.43	0.07±0.04
Cyperus nashii L.	0.00±0.00^{a}	0.00±0.00^{a}	0.05±0.03^{a,b} (Fl)	0.21±0.10^{b}	0.02±0.0^{a}	0.04±0.03^{a,b}	0.03±0.02^{a}	0.00±0.00^{a}
Dalea faeyi (Chapm.) Barneby	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.05±0.05	0.12±0.07	0.00±0.00	0.00±0.00
Desmodium floridana Chapm.	0.00±0.00	0.00±0.00	0.07±0.07	0.034.03	0.23±0.23	0.00±0.00	0.00±0.00	0.07±0.07
Dichanthelium (Hitchc. & Chase) Gould, spp.	0.00±0.00	0.33±0.33	0.05±0.02 (Fr)	0.29±0.07	0.24±0.17	0.01±0.01	0.02±0.02	0.00±0.00
Eriogonum longifolium Nutt. var. *gnaphalifolium* Gand.	0.00±0.00	0.00±0.00	0.01±0.01 (Fl)	0.05±0.05	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Eupatorium compositofolium Walt.	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	<0.01	0.09±0.07	0.00±0.00	0.00±0.00
Galactia elliottii Nutt.	0.00+0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.02±0.02
Galactia volubilus (L.) Britt.	0.01±0.01^{a}	0.13±0.07^{a}	1.40±0.50^{b,c} (Fr)	1.53±0.63^{c}	0.17±0.10^{a,b}	0.07±0.06^{a}	0.09±0.04^{a}	0.02±0.02^{a}
Hedyotis procumbens (J.F. Gmel.) Fosberg	0.00±0.00	0.00±0.00	0.00±0.00	0.07±0.04	0.05±0.03	0.00±0.00	0.01±0.01	0.00±0.00

Table 1, *continued*

Species	Preburn	Postburn						
	May 1993	5 weeks	5 months	16 months	28 months	40 months	64 months	101 months
Opuntia humifusa (Raf.) Raf.	0.00±0.00	0.00±0.00	0.00±0.00	0.01±0.01	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00
Pityopsis graminifolia (Michx.) Nutt.	0.05±0.03	0.00±0.00	0.07±0.07 (Fl)	0.13±0.07	0.11±0.07	0.114.06	0.00±0.00	0.00±0.00
Polygala incarnata L.	0.00±0.00	0.00±0.00	0.10±0.08	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Rhynchosia reniformis DC.	0.00±0.00	0.01±0.01	0.08±0.05	0.04±0.03	0.00±0.00	0.03±0.03	0.02±0.02	0.07±0.07
Rynchospora megalocarpa A. Gray	1.84±0.55	0.43±0.17	0.73±0.29	1.91±0.47	1.22±0.36	3.79±2.66	1.78±0.55	0.42±0. 10
Sisyrinchium nashii Bickn.	0.00±0.00	0.00±0.00	0.00±0.00	0.02±0.02	0.13±0.12	0.14±0.10	0.10±0.07	0.039.03
Smilax auriculata Walt.	0.07±0.07	0.00±0.00	0.01±0.01	0.01±0.01	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Stillingia sylvatica L.	0.03±0.03	0.07±0.07(Fl)	0.02±0. 16 (Fr)	0.24±0.23	0.00±0.00	0.00±0.00	0.08±0.08	0.00±0.00
Tephrosia chrysophylla Pursh	0.00±0.00	0.00±0.00	0.00±0.00	0.01±0.01	0.17±0.17	0.10±0.10	0.05±0.05	0.00±0.00
Tragia urens L.	0.00±0.00	0.06±0.04	0.01±0.01 (Fr)	0.00±0.00	0.01±0.01	0.00±0.00	0.00±0.00	0.00±0.00
Zamia pumila L.	0.03±0.03	0.22±0.22	0.42±0.42	0.53±0.53	0.10±0.10	0.02±0.02	0.00±0.00	0.00±0.00
WOODY SPECIES								
Asimina obovata (Willd) Nash	<0.01	0.02±0.02	0.01±0.01	0.10±0.07	0.07±0.07	0.00±0.00	0.20±0.10	0.03±0.03
Calamintha ashei (Weatherby) Shinners	0.03±0.03[a]	0.00±0.00[a]	0.00±0.00[a]	0.01±0.01[a]	0.07±0.07[a,b]	0.23±0.12[a,b,c]	0.85±0.26[c]	0.73±0.30[b,c]
Ceratiola ericoides Michx.	2.37±1.08[a]	0.00±0.00[b]	0.00±0.00[b]	0.00±0.00[b]	0.00±0.00[b]	0.00±0.00[b]	0.00±0.00[b]	0.07±0.07[b]
Garberia heterophylla (Bartr.) Merr. & Harp.	0.67±0.37	0.03±0.03	0.00±0.00 (Fl)	0.05±0.03	1.02±0.62	0.45±0.34	0.13±0.11	0.27±0.18
Hypericum hypericoides (L.) Crantz	0.01±0.01	0.00±0.00	0.00±0.00	0.00±0.00	0.17±0.13	0.00±0.00	0.07±0.07	0.00±0.00
Lyonia ferruginea (Walt.) Nutt.	0.84±0.84	0.00±0.00	0.20±0.20	1.10±1.10	0.93±0.93	0.32±0.32	0.33±0.33	0.00±0.00
Persea humilis Nash	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00

Pr :n		Po ıurn						
	M 99				28 onth			
Pinus clausa clausa (Chapm. ex Engelm.) Vasey ex Sarg.	83.60±1.43[a]	0.00±0.00[b]	0.04±0.02[b]	0.38±0.15[b,c]	2.00±0.46[b,c]	4.64±1.33[c]	17.72±4.17[d]	29.17±6.52[d]
Quercus chapmanii Sarg.	0.98±0.43	0.00±0.00	0.33±0.17	0.93±0.34	1.27±0.42	1.27±0.47	2.03±0.89(Fr)	0.73±0.42
Q. geminata Small	2.67±0.75[a,b,c]	0.25±0.16[b]	1.14±0.31[b,c]	2.23±0.36[a,b,c]	4.30±0.87[a,c]	4.38±0.95[a,c]	7.97±3.16[a]	4.98±1.56[a,c]
Q. laevis Walt.	1.33±0.90	0.00±0.00	0.43±0.30	0.35±0.35	1.17±0.43	0.40±0.40	0.57±0.30	0.53±0.26
Q. myrtifolia Willd.	58.73±5.3[a]	18.11±2.79[b]	22.67±3.16[b]	39.59±5.01[a,b]	51.20±6.33[a]	49.05±5.80[a]	53.15±5.99[a](Fr)	62.93±5.74[a]
Rhus copallina L.	0.00±0.00	0.00±0.00	0.00±0.00	0.02±0.02	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Sabal etonia Swingle ex Nash	13.57±2.52[a]	1.02±0.34[b] (Fl)	7.73±1.86[a] (Fr)	11.93±2.65[a]	10.38±1.61[a]	8.10±2.33[a]	6.57±0.95[a]	7.13±1.86[a]
Serenoa repens (Bartr.) Small	0.40±0.33	0.00±0.00	0.33±0.33	0.30±0.30	0.57±0.25	0.22±0.14	0.45±0.34	0.13±0.13
Vaccinium darrowii Camp	0. ±0. 0	0.00±0. 8	0.07±0.04	0.07±0.07	0.13±0.10	0.32±0.16	0.08±0.06	0.40±0.29
V. stamineum L.	0.60±0.42	0.00±0.8	0.00±0.00	0.00±0.00	0.27±0.20	0.07±0.07	0.15±0. 0	0.07±0.07
Yucca filamentosa L.	0.8 ±0.8	0.00±0.00(Fl)	0.00±0.00	0.03±0.03	0.03±0.03	3.20±3.20	8 0 ±0.00	0.8 ±0.8

Note: Also seen in stand 1993–1994: *Cnidoscolus stimulosus* (Michx.) Engelm. & Gray (Fl 6/93); *Liatris tenuifolia* Nutt.; *Palafoxia faeyi* (A. Gray), Fl 5 mo postburn; *Bumelia tenax* (L.) Willd

after (df = 7; *F = 4.03; P = 0.0020)* (Figure I). Total species richness also differed significantly between measurements 5 weeks postburn and measurements 16 and 28 months postburn (df = 7; *F* = 3.99; *P* = 0.0021) (Figure 1).

Myrtle oak was the dominant shrub before the fire (mean ± SE; 58.7±5.3 percent cover) and recovered rapidly by sprouting. New sprouts composed 18.1% ± 2.8% cover after 5 weeks, and within 16 months of the fire myrtle oak had regained preburn cover levels (df = 7; *F* = 10.43; *P* = 0.0001) (Table 1). Percent cover of Chapman's oak (*Q. chupmanii* Sarg.) (df = 7; *F* = 1.72; *P* = 0.1328) and turkey oak (*Q. laevis* Walt.) (df = 7; *F = 1.04; P = 0.4201)* did not differ significantly before or after the prescribed burn (although they were not detected 5 weeks postburn) (Table 1). Sand live oak (Q. *geminata* Small) resprouted within 5 weeks, and regained preburn cover levels within 16 months postburn (df = 7; *F = 6; P* = 0.0001) (Table 1). Scrub palmetto also recovered quickly, regaining preburn cover levels in less than 5 months (df = 7; *F* = 6.57; *P* = 0.0001) (Table 1). Sand pine seedlings were established within 5 months of the fire; they had regained about 18% cover within 64 months (1998), and about 29% cover within 101 months postburn (2001) (Table 1).

Myrtle oak regained its preburn height within 40 months (df = 7; *F* = 16.1; *P* = 0.0001), and scrub palmetto regained its preburn height within 5 months of the fire (df = 7; *F = 5.2; P = 0.0003)* (Figure 2). Within 64 months of the prescribed burn mean (±SE) sand pine saplings were 0.8±0.06 m tall, and within 101 months they were 2.28±0.30 m tall. Several species flowered and fruited within a month to a year of the prescribed burn (Table 1).

Two endemic species were sufficiently frequent to statistically detect trends in cover. Scrub morning glory regained its preburn cover within 5 weeks of the burn (df = 7; *F = 0.53; P = 0.8089)* (Table 1); by October it bore fruit and continued to flower and form new fruits.

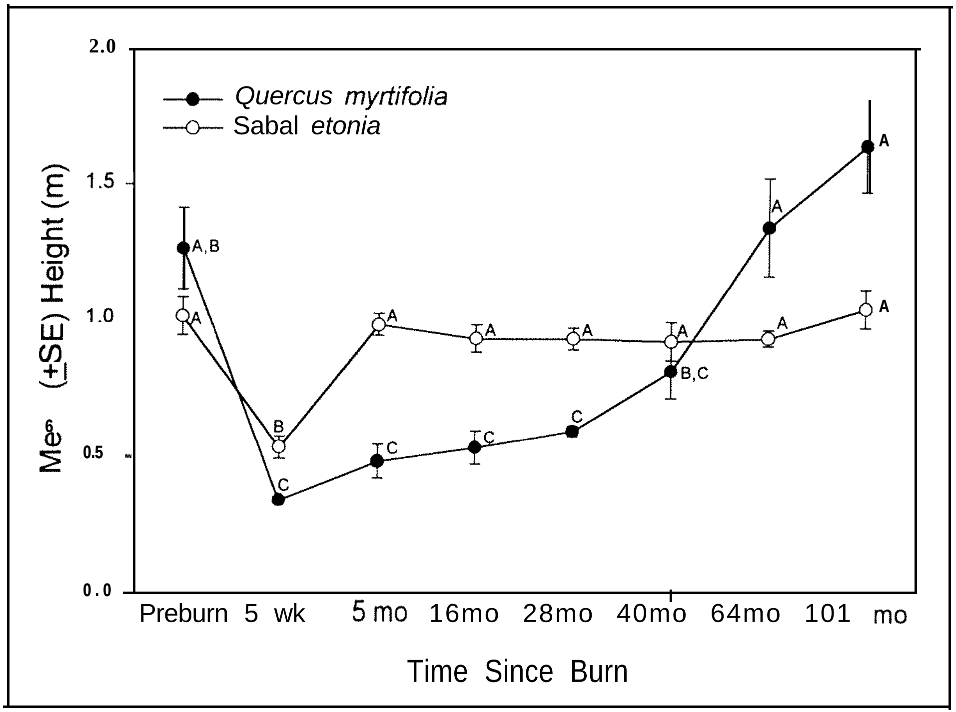

Figure 2. Mean (± SE) height of myrtle oak (Quercus *myrtifolia* Willd.) and scrub palmetto (*Sabal etonia* Swingle ex Nash) before and for > 8 y following a prescribed stand-replacement burn in sand pine scrub, Ocala National Forest, Florida. Different letters among data points for each species indicate significant differences among sample dates ($P < 0.05$).

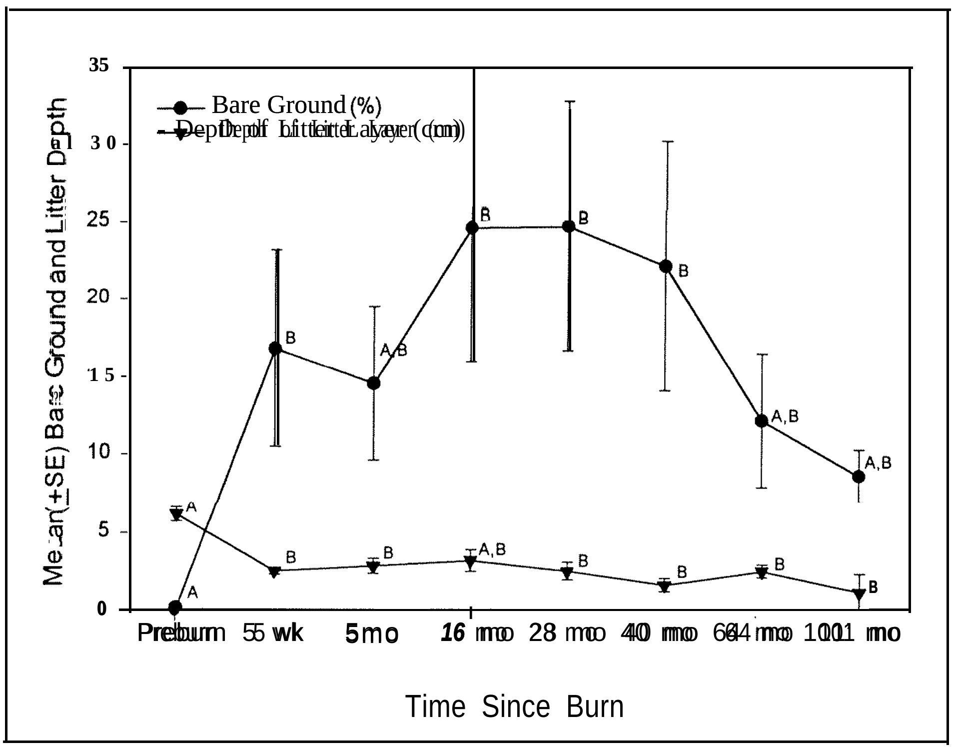

Figure 3. Mean (±SE) depth (cm) of litter layer and percent cover of bare ground before and for > 8 y following a prescribed stand-replacement burn in sand pine scrub, Ocala National Forest, Florida. Different letters among data points for each variable indicate significant differences among sample dates ($P < 0.05$).

Ashe's savory (*Calamintha ashei* [Weatherby] Shinners) was present in low levels before the fire. Aboveground stems disappeared after the fire, and were not detected by transects or during visual surveys until the following year. Within 64 months postburn, there was significantly more Ashe's savory in the stand than prior to the burn or other postburn samples (df = 7; F = 6.1 I; P = 0.0001) (Table 1).

The thickness of the litter layer was significantly reduced but not eliminated by burning, and thickness remained stable for at least 8 y postfire (df = 7; F = *38.3;* P = 0.0001) (Figure 3). The proportion of bare ground increased significantly following the burn, but by 64 months postburn did not significantly differ from pre- or other postburn levels (df = 7; F = 3.41; P = 0.0060) (Figure 3).

LBH did not increase significantly until 16 months after the prescribed fire (df = 7; F = 123.8; P = 0.0001). Immediately following the tire (June) pine trees still retained nearly full crowns of dead or dying needles. LBH peaked from 28 to 64 months postburn, but decreased significantly after 8 y as shrub height exceeded 1.6 m (Figure 4). LGL increased significantly immediately after the fire and remained high through 2001, although a slight decrease was apparent during 2001 (df = 7; F = 4.35; P = 0.001 I) (Figure 4).

CWD cover was minimal prior to the burn. Levels increased significantly beginning 28 months postburn when snags began falling, and continued to increase through 40 months postburn (by then about 35% of standing pine snags had fallen; Outcalt, in press) (df = 7; F = 19.6; P = 0.0001) (Figure 5). CWD diameter also increased significantly within 28 months after the burn, and remained high (df = 6; F = *4.55;* P = 0.0035) (Figure 5).

DISCUSSION

Recovery of stand structure and species composition after a high-intensity, stand-replacement burn was rapid. Within 16 months of the fire, shrub species composition and cover values were virtually identical to preburn values, and within 40

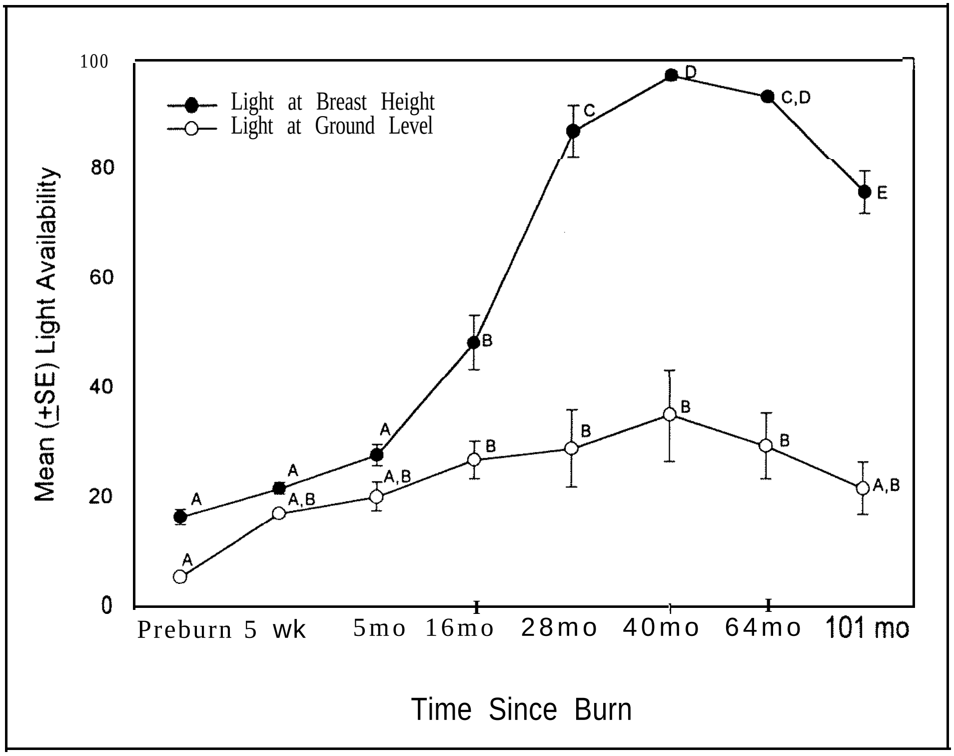

Figure 4. Mean (±SE) light at breast height and light at ground level before and for > 8 y following a prescribed stand-replacement burn in sand pine scrub, Ocala National Forest, Florida. Different letters among data points for each variable indicate significant differences among sample dates (P < 0.05).

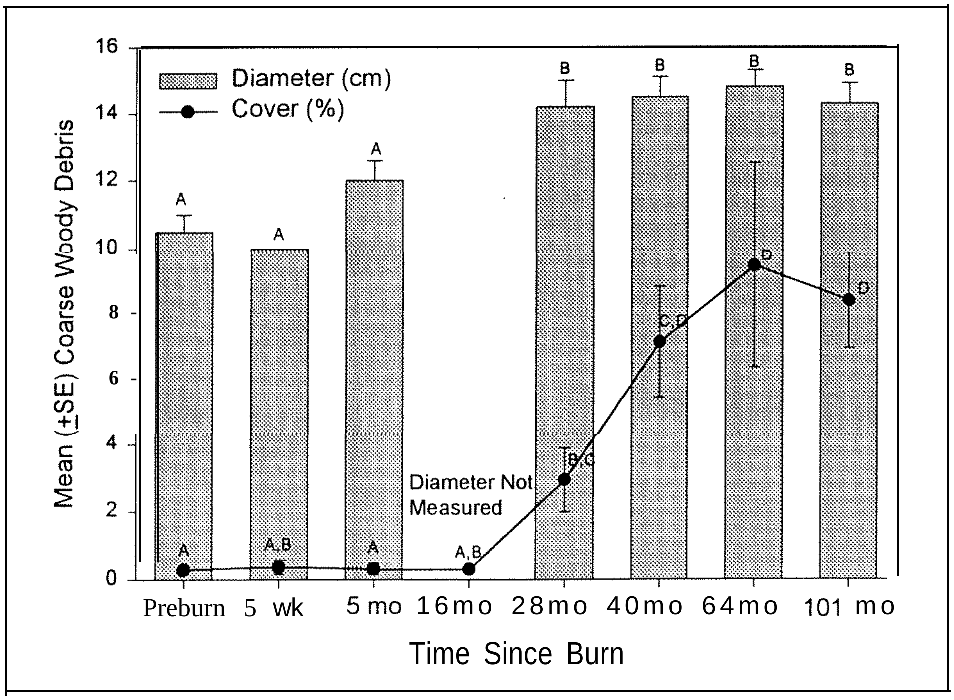

Figure 5. Mean (±SE) percent rover and diameter (at interception with the transect) of coarse woody debris (≥ 10 cm) before and for > 8 y following a prescribed stand-replacement burn in sand pine scrub, Ocala National Forest, Florida. Different letters among data points for each variable indicate significant differences among sample dates (P < 0.05).

months myrtle oak, the dominant shrub, had regained its preburn height. Abrahamson and Abrahamson (1996b) reported shifts toward xeric hammock following a low-intensity winter burn in sand pine scrub, primarily because sand pine was not successfully restored as a canopy dominant. They also found a paucity of herbaceous species and few shifts in the shrub composition. In contrast, Schmalzer and Hinkle (1992a, 1992b), working in an oak–saw palmetto scrub in Florida, reported shifts in oak-palmetto dominance after fire due to differences in recovery rates. In this study, scrub palmetto recovered its preburn cover levels faster (within 5 months) than myrtle oak, but myrtle oak was still dominant throughout, and regained its preburn cover levels within 16 months. Hence, in this study different recovery rates among species did not result in long-term shifts in species dominance.

Eight years after the fire only a few measured features still differed from the preburn stand structure. These included more and larger-diameter CWD from fallen snags, an absence of a sand pine canopy, and consequently higher LBH. LBH gradually increased postburn, as needles fell from tree crowns and snags fell, and began to decrease within 64 months as oaks approached breast height. LGL remained high for several years despite increasing shrub cover and height and decreasing numbers of snags; however, a declining trend in LGL began 64 months postburn. High variance in LGL among transects beginning 28 months postburn indicates that open areas were patchy.

Carrington and Keeley (1999) suggested that relatively low postfire seedling recruitment in sand pine scrub is probably due to the elimination of suitable microsites by resprouting shrubs. In this study, an increase followed by a gradual decline of herbaceous species richness appeared to correspond with gradual increases in shrub cover and decreases in bare ground availability over the > 8-y study period. Although the average number of herbaceous species differed significantly only between 16 and 101 months postburn, 22 total species of both woody (3) and herbaceous (19) plants occurred on transects after the burn that were not detected before. Clearly, the number of new species increased after the prescribed burn, even though the mean number of species per transect did not.

Menges and Hawkes (1998) suggested that many scrub endemics are "gap specialists" that increase in density and seed production in open, litter- and shrub-free areas created by fire (also see Johnson and Abrahamson 1990, Hawkes and Menges 1996, Young and Menges 1999). Greenberg et al. (1995) reported higher plant species richness in anthropogenically disturbed sand pine scrub with more bare ground than in forested controls. Several endemic vertebrate species, including Florida scrub jay (Breininger et al. 1995) and scrub lizards (*Sceloporus woodi* Stejneger) (Greenberg et al. 1994) also require recently burned or silviculturally disturbed scrub with abundant bare ground patches. Abrahamson and Abrahamson (1996a) found higher herbaceous species richness in recently winter-burned than in long-unburned scrubby flatwoods, and attributed this to more and larger gaps for gap-specialist herbs. Clearly, fire plays a primary role in maintaining or creating open, bare ground in the shrub-dominated sand pine scrub (Young and Menges 1999).

The addition of several new herbaceous species following the burn probably resulted from seed banks or seed dispersal from plants occurring along roadsides or in recently harvested stands near the study site. Schmalzer and Hinkle (1992a) reported no major changes in species richness with time-since-fire in an oak-saw palmetto association. Abrahamson and Abrahamson (1996b) reported few changes in the occurrence of herbaceous species following a low-intensity winter burn in 60-y-old sand pine scrub on the Lake Wales Ridge, Florida. Further, several rare species that are typical of more frequently burned Lake Wales Ridge scrub sites were absent both before and after the burn. They postulated that decades of shading by sand pines and shrubs eliminated most herbaceous plants from the stand, and consequently the addition of fresh, viable seeds to the soil seed bank. Although the suite of endemic species differs between the LWR and the ONF study areas, two endemics (scrub morning glory and Ashe's savory) persisted at low levels within the stand for five decades after the last wildfire and recovered rapidly following the prescribed wildfire. Factors affecting postburn species richness may include initial species richness of the stand, stand proximity to seed sources, stand history (e.g., past fire intensity and frequency), and season and intensity of burn.

The structural and compositional similarities between mature sand pine forest (preburn measurements) and young scrub just a few years after a stand-replacement fire indicate scrub's resilience and resistance to classic succession. Menges et al. (1993) reported few changes in species composition over 20 y in a long-unburned sand pine scrub, although the stand structure changed because of substantial sand pine tree mortality. High-intensity disturbance offers a brief opportunity for establishment or increased cover by "gap specialists," but not for long-term changes in species composition or major structural features of sand pine scrub.

Recovery trends of some less abundant species also corresponded with findings in other studies. Rosemary (*Ceratiola ericoides* Michx.) was present before the burn, but was not seen in the stand until 64 months postburn, or detected on transects until 101 months postburn. The slow recovery of rosemary probably was due to its delayed seed germination (Johnson 1982). Hartnett and Richardson (1989) reported a large increase in stem densities of scrub morning glory due to increased clonal stem production and new genet recruitment from seed. Results of this study confirm their findings; percent cover of scrub morning glory just 5 weeks after the fire did not differ from preburn levels. Results of this study correspond with Carrington's (1999) (working in the same study site) finding of a IO-month postfire delay in seedling establishment of Ashe's savory. Furthermore, after 5 y the percent cover of Ashe's savory significantly increased from preburn and earlier postburn measurements.

Although flowering and fruiting were not systematically surveyed, several species were noted as flowering or fruiting within 5 months of the fire. Scrub palmetto, an endemic scrub species and important fruit producer, flowered within 5 weeks and fruited within 5 months. In contrast, Abrahamson (1999) reported that scrub palmetto did not flower until spring the year following a February burn in scrub. This suggests that the season of burn, fire intensity, or both may be important cues for flowering and fruiting by some species.

Understanding the effects of prescribed stand-replacement fire is important for maintaining conditions required by endemic and characteristic species of sand pine scrub. Abrahamson and Abrahamson (1996b) suggested that low-intensity or winter burning may be inappropriate fire management for sand pine scrub, primarily because they found little herbaceous response and no endemic herb recovery in a winter-burned stand. Fire intensity clearly affects the amount of topkill, sand pine mortality (Abrahamson and Abrahamson 1996b) and structural changes, as well as plant response (Platt et al. 1988) and recovery time (Abrahamson 1984b). However, their results probably were due, in part, to the absence of endemic herbs prior to the burn and a low-intensity fire. Fire intensity, as opposed to season of burn per se, may be the primary determinant of plant response and has not been studied in sand pine scrub. Results of this study suggest that high-intensity prescribed fire promotes an increase in herbaceous richness for several years, and rapid recovery of endemic herbaceous species that were present prior to the fire. However, it is difficult to make generalizations about effects of fire intensity or season of burn without conducting replicated prescribed burns of varying intensity and season in stands with similar disturbance history and plant composition.

Some management questions remain unanswered: (1) How do plant species and communities respond to growing-season versus winter burns, or high-intensity versus low-intensity fire? (2) Is there a maximum fire interval beyond which endemic species cannot persist? (3) How does stand history (e.g., prior fire-return intervals and fire intensity) affect current plant composition, hence future postfire plant composition? (4) Is fire per se a critical cue for plant recovery (e.g., germination), or can microsites similar to those created by tire, such as light and abundant bare ground, be created by silvicultural or other high-intensity disturbance types? (5) Can the sand pine scrub ecosystem persist in the long term under a silvicultural disturbance regime in lieu of disturbance by stand-replacement fire? This study indicates that prescribed high-intensity, stand-replacement burns can be used in sand pine scrub to enhance species richness, temporarily increase cover and reproduction by some endemic and other herbaceous species, and temporarily eliminate the sand pine canopy to restore areas to a historically common stand structure (Hill 1916, Rawlings 1933, Webber 1935).

ACKNOWLEDGMENTS

I thank the staff of the Ocala National Forest, USDA Forest Service, especially Jim Thorsen and George Custer, for conducting the prescribed burn and for welcoming studies on postburn stand response. Bob Simons deserves a special thanks for donating his good company and assistance in the field. Bob Simons, Mary Carrington, Paul Schmalzer, Ken Outcalt, Ron Myers, Charles Williams, and Zoe Hoyle gave useful suggestions for improving the manuscript.

Cuthryn H. Greenberg is a Research Ecologist for the U.S. Forest Service, Southern Research Station. Her research interests include the ecology of natural and silvicultural disturbance, and plant-animal interactions at a landscape level.

LITERATURE CITED

Abrahamson, W.C. 1984a. Post-fire recovery of Florida Lake Wales Ridge vegetation. American Journal of Botany 71:9-21.

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

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

Abrahamson, W.G., and C.R. Abrahamson. 1996a. Effects of fire on long-unburned Florida uplands. Journal of Vegetation Science 7:565-574.

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

Abrahamson, WG., 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.

Aydelott, K.G., H.C. Bullock, A.L. Furman, H.O. White, and J.W. Spieth. 1975. Soil survey of Ocala National Forest, Florida. U.S. Government Printing Office, Washington, D.C. 64 pp.

Breininger, D.R., V.L. Larson, B.W. Duncan, R.B. Smith, D.M. Oddy, and M.F. Goodchild. 1995. Landscape patterns of Florida scrub jay habitat use and demographic success. Conservation Biology 9: 1442-1453.

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

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

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

Christman, S.P. 1988. Endemism and Florida's interior scrub. Final report to Florida Game and Fresh Water Fish Commission, Tallahassee (Contract No. GFC-84-101). 247 pp. + maps, tables, appendices.

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

Cooper, R.W., C.S. Schopmeyer, and W.H.D. McGregor. 1959. Sand pine regeneration on the Ocala National Forest. Research Paper SE-30, U.S. Department of Agriculture, Forest Service, Asheville, NC. 37 pp.

Custer, G., and J. Thorsen. 1996. Stand-replacement bum in the Ocala National Forest: a success. Fire Management Notes 56:7-12.

Greenberg, C.H., D.G. Neary, and L.D. Harris. 1994. Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand pine scrub. Conservation Biology 8:1047-1057.

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

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

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

Hill, W.F. 1916. Land Classification of the Florida National Forest, Florida. Unpubl. report to the Secretary of Agriculture, Washington, D.C. 83 pp.

Johnson, A.F. 1982. Some demographic characteristics of the Florida rosemary *Ceratiola ericoides* Michx. American Midland Naturalist 108:170-174.

Johnson, A.F., and W.G. Abrahamson. 1990. A note on the fire responses of species in rosemary scrubs on the southern Lake Wales Ridge. Florida Scientist 53:138-143.

Kalisz, P.J., and E.L. Stone. 1984. The longleaf pine islands of the Ocala National Forest, Florida: a soil study. Ecology 65: 1743- 1754.

Keetch, J.J., and G.M. Bryam. 1968. A drought index for forest fire control. Research Paper SE-38, U.S. Department of Agriculture, Forest Service, Asheville, N.C. 32 pp.

Laessle, A.M. 1958. The origin and successional relationship of sandhill vegetation and sand pine scrub. Ecological Monographs 28:361-387.

Menges, E.S. 1999. Ecology and conservation of Florida scrub. Pp. 7-22 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, UK.

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

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

Menges, E.S., W.G. Abrahamson, K.T. Givens, N.P. Gallo, and J.N. Layne. 1993. Twenty years of vegetation change in five long-unburned Florida plant communities. Journal of Vegetation Science 4:375-386.

Myers, R.L. 1990. Scrub and high pine. Pp. 150-193 *in* R.L. Myers and J.J. Ewel, eds., Ecosystems of Florida. University Presses of Florida, Gainesville.

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

Outcalt. K.W., and C.H. Greenberg. 1998. A stand-replacement prescribed burn in sand pine scrub. Tall Timbers Fire Ecology Conference Proceedings 20: 14 1- 145.

Outcalt, K.W. In press. Decay of fire caused snags in Ocala sand pine scrub. Tall Timbers Fire Conference 2000: The First National Congress on Fire Ecology, Prevention and Management. 27 November-I December 2000, San Diego, Calif.

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

Rawlings, M.K. 1933. South Moon Under. Charles Scribner and Sons, New York. 334 pp.

Schmalzer, P.A. 2003. Growth and recovery of oak-saw palmetto scrub through ten years after fire. Natural Areas Journal 23:5-13.

Schmalzer. P.A., and C.R. Hinkle. 1992a. Species composition and structure of oak-saw palmetto scrub vegetation. Castanea 57:220-251.

Schmalzer, P.A., and C.R. Hinkle. 1992b. Recovery of oak-saw palmetto scrub after fire. Castanea 57:158-193.

Schmalzer, P.A., S.R. Boyle, and H.M. Swain. 1999. Scrub ecosystems of Brevard County, Florida: a regional characterization. Florida Scientist 62: 13-47.

Stout, I.J., and W.R. Marion. 1993. Pine flatwoods and xeric pine forests of the southern (lower) coastal plain. Pp. 373-446 *in* W.H. Martin, S.G. Boyce, and A.C. Echternacht, eds., Biodiversity of the Southeastern United States. Lowland Terrestrial Communities. John Wiley and Sons, New York.

Watts, W.A. 1971. Post-glacial and interglacial vegetational history of southern Georgia and central Florida. Ecology 52:676-690.

Watts, W.A. 1975. A late Quaternary record of vegetation from Lake Annie, south-central Florida. Geology 3:344-346.

Watts, W.A. 1980. The late Quaternary vegetation history of the southeastern United States. Annual Review of Ecology and Systematics 1I :387-409.

Webber, H.J. 1935. The Florida scrub, a fire fighting association. American Journal of Botany 22:344-361.

Young, C.C., and E.S. Menges. 1999. Postfire gap-phase regeneration in scrubby flatwoods on the Lake Wales Ridge. Florida Scientist 62:1-12.

Zona, S., and W.S. Judd. 1986. *Sabal etonia* (Palmae): Systematics, distribution, ecology, and comparisons to other Florida scrub endemics. Sida 1 1:417-427.