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Cathryn H. Greenberg; Daniel G. Neary; Lawrence D. Harris; Steven P. Linda

American Midland Naturalist, Volume 133, Issue 1 (Jan., 1995), 149-163.

Stable URL:
http://links.jstor.org/sici?sici=0003-0031%28199501%29133%3A1%3C149%3AVRFHWA%3E2.0.CO%3B2-Y

Am. Midl. Nat. 133:149–163

Vegetation Recovery Following High-intensity Wildfire and Silvicultural Treatments in Sand Pine Scrub

CATHRYN H. GREENBERG[1]
U.S. Forest Service Southeastern Forest Experiment Station, Gainesville, Florida 32611

DANIEL G. NEARY
U.S. Forest Service Rocky Mountain Station, 700 Knoles Drive, Flagstaff, Arizona 86001

LAWRENCE D. HARRIS
Department of Wildlife and Range Sciences, University of Florida, Gainesville, 32611

STEVEN P. LINDA
Florida Game and Fresh Water Fish Commission, Gainesville 32601

ABSTRACT.—We hypothesized that clear-cutting mimics natural high-intensity disturbance by wildfire followed by salvage logging in sand pine scrub, and tested whether vegetation adapted to recovery from fire would respond similarly to another type of biomass removal. We measured plant community composition and structural characteristics in three replicated disturbance treatments and in mature sand pine forest (MF). Treatments were: (1) high-intensity burn, salvage logged and naturally regenerated (HIBS); (2) clear-cut, roller-chopped, and broadcast-seeded (RC); and (3) clear-cut and bracke-seeded (BK). All treatments were sampled 5–7 yr postdisturbance. Nonwoody plant species richness and diversity were significantly lower in MF than in disturbance treatments. Ruderal species were more abundant in HIBS and RC, but not to the exclusion of the characteristic suite of native scrub species. Shrub richness and diversity did not differ, but some species responded differently among treatments. Differences may be due to season of disturbance or rhizome depth [*e.g.*, *Serenoa repens* (Bartr.) Small vs. *Sabal etonia* Swingle ex Nash.]. Oak stem density was significantly lower in HIBS and RC. Most structural characteristics were similar in HIBS, RC and BK but differed from MF. Results suggest that many scrub species responded similarly to aboveground biomass removal and the consequent structural and microclimatic conditions across these disturbance types. We suggest that plant resiliency traits, which evolved in response to the selective pressures of high-intensity disturbance and harsh environmental conditions, confer resiliency to human-caused disturbance as well. Mechanical biomass removal may be a suitable ecosystem management practice where burning is impractical. Due to the absence of a "virgin" (unsalvaged) burn treatment or pretreatment data and the short-term scope of this study, interpretation of results should be made with caution.

INTRODUCTION

Efforts to maintain the intergrity of natural community biodiversity are bringing ecosystem management to the forefront of conservation biology (Kessler, 1992). Special attention is directed toward national forests as potential sites for promoting ecosystem management and biodiversity (Harris, 1984). "New Forestry" emphasizes forest management on a "sustainable ecosystem," rather than a "sustainable yield," basis. Under such management, timber harvesting and regeneration should be designed to best mimic the natural disturbance regimes of each ecosystem (Franklin and Forman, 1987).

[1] Corresponding author

Sand pine scrub is a sclerophyllous shrub-dominated ecosystem occurring on infertile xeric sands mainly in Florida. Plant and animal endemism is high (Auffenberg, 1982; Christman and Judd, 1990). The Ocala National Forest contains the largest remaining area of sand pine scrub. Elsewhere, most of this ecosystem has been lost to citrus and urban development (Myers, 1990; Peroni and Abrahamson, 1986).

Community resilience to low-frequency (10–100 yr) (Myers, 1990), high-intensity disturbance such as stand-replacing fire suggests that the scrub biota has evolved under selective pressure from such a disturbance regime. Postfire recovery of preburn dominants is rapid (Abrahamson, 1984a, 1984b). Most shrub species resprout vigorously from underground roots or rhizomes. In peninsular scrub stands, sand pine [*Pinus clausa* var. *clausa* (Chapm. ex Engelm.) Vasey ex Sarg.] cones are moderately serotinous (Cooper *et al.,* 1959), resulting in even-aged stands following fire. Many herbaceous species invade or germinate from the seed bank (Johnson, 1982; Hartnett and Richardson, 1989) shortly after a burn and decrease as the forest matures.

Other sources of disturbance appear to have many of the same effects as fire in maintaining the structure and species composition of scrub communities. The uneven-aged stands and nonserotinous cones of Panhandle sand pine (*Pinus clausa* var. *immuginata* Ward) suggest that fire does not reliably occur within its lifespan, and that regeneration is maintained instead by hurricanes and associated windthrow (Myers, 1990). Rare scrub endemics and other characteristic postfire herbaceous species frequently proliferate in plow lines, sand roads (Abrahamson, 1984a; Myers, 1990; Menges, 1992; Hawkes and Menges, in press), and recent clear-cuts in scrub. Similar increases in species richness following human and natural high-intensity disturbance in other fire- or drought-adapted ecosystems have been observed (Shafi and Yarranton, 1973; Boerner, 1981; Kruger, 1983; Fox and Fox, 1986; Westman and O'Leary, 1986).

The effect of high-disturbance forest regeneration practices on scrub plant communities has not been adequately documented. Current management of sand pine in the Ocala National Forest is oriented toward pulpwood production. Because of the wood fiber value and the possibility of large-scale, uncontrolled burns, fires in sand pine stands are actively suppressed. Burned sites at the Ocala National Forest are normally salvage-logged. Campbell and Christman (1982) have suggested that even-aged management by clear-cutting may mimic the natural disturbance regime of this ecosystem type.

Sand pine harvest and regeneration entail clear-cutting commonly followed either by roller chopping and broadcast seeding or by bracke seeding. Heavy machinery used during the clear-cutting operation crushes and top-kills nearly all vegetation. Bracke seeding entails direct seeding on small, machine-created mounds (ca. 8 cm high) where approximately 14 seeds/patch are planted on 2300 patches/ha (approximately 32,200 seeds/ha). This method patch-scarifies approximately 30% of the soil surface (Outcalt, 1990). Roller chopping and broadcast seeding entail single-chopping of the soil surface with a double drum roller chopper followed by broadcast seeding of approximately 41,513 seeds/ha. Roller chopper blades penetrate the soil to a maximum depth of 15 cm, and soil surface disturbance with this method is nearly complete.

Here we test the hypothesis that clear-cutting mimics high-intensity burning-salvage logging, in that vegetation adapted to recovery from fire will respond similarly to another type of biomass removal. Results could have useful implications for ecosystem management of scrub existing as patches surrounded by urban development where burning is infeasible or unsafe or where timber management and ecosystem management are dual goals. Nomenclature follows Wunderlin (1982).

METHODS AND MATERIALS

Study area.—The Ocala National Forest covers approximately 180,000 ha in Marion, Lake and Putnam counties in central Florida. It is bounded by the Ocklawaha River to the W and N, the St. John's River to the E, and extensive wetlands to the S. Elevations range from 2–49 m above mean sea level. Major plant communities within the forest include sand pine scrub, longleaf pine (*Pinus palustris*)-turkey oak (*Quercus laevis*) sandhills, pine flatwoods and hardwood swamp (Mohlenbrock, 1976). Sand pine scrub occupies over 100,000 ha as a SSE-oriented strip, approximately 60 km long and 10–20 km wide. Soils supporting sand pine scrub are excessively drained aeolian or marine sands, classified as hyperthermic, uncoated families of Spodic (Paola series) and Typic Quartzipsamments (Astatula series) (Kalisz and Stone, 1984). This area receives approximately 1300 mm of rainfall annually, with over half falling between June and September. Average temperatures range from 20–32 C between April and October and 11–23 C between November and March (Aydelott *et al.*, 1975).

Early reports (Hill, 1916; Rawlings, 1933; Webber, 1935; Bartram, 1955; Cooper *et al.*, 1959) describe low scrub or note recent wildfire, suggesting a relatively high-frequency (5–20 yr), widespread fire regime. Fire suppression increased after the area came under the administration of the U.S. Forest Service in 1908. Large-scale sand pine harvesting became economically viable when a postwar boom in pulpwood began in 1946 (Cooper *et al.*, 1959).

Study sites and treatments.—Within selection criteria constraints, we randomly selected five replicate stands of each of three 5- to 7-yr-old disturbance treatments and mature forest: (1) high-intensity burn, salvage-logged for several months thereafter, and then naturally regenerated (HIBS); (2) clear-cut, mechanically single-chopped with a double drum roller chopper, and broadcast seeded (RC); and (3) clear-cut and bracke seeded (BK). Stands of mature virgin forest (≥55 yr) that naturally regenerated following a stand-replacing fire in 1935 (ignited by sparks from a land-clearing brushpile fire in nearby pine flatwoods and carried into the sand pine scrub) were used as a reference (MF).

Selection criteria were: (1) similar elevation, topography and soil characteristics; and (2) stand area ≥ 8.1 ha. Other criteria for all treatments were: (1) same time interval since treatment (within 1.5 yr); (2) same pretreatment age and (known) disturbance history (identical to MF); and (3) same harvesting method. All five HIBS stands were located in two large (>360 ha) spatially disparate, high-intensity burns (three sites in one burn and two sites in the other). Both stand-replacing fires were ignited in May 1985 by trees falling onto powerlines (fire records, Ocala National Forest, Fla.). Table 1 describes variations in the timing of treatment administration.

Sampling methodologies.—We randomly established five 10 × 10-m quadrats in each stand. All were located ≥20 m from stand edges to minimize edge effects. Sand pine density and height were sampled in these quadrats or in a 20-m^2 subplot if density was high. Stem density and percent cover of herbaceous and shrub species were sampled in two 4 × 4-m quadrats nested in diagonal corners and sharing two sides with the larger one. Percent cover was estimated ocularly by classes (<1%; 1–10%; 11–30%; 31–50%; 51–70%; 71–90%; 91–100%) (modified from Mueller-Dombois and Ellenberg, 1974). Only percent cover was estimated for lichens and mosses. Clumps were considered individuals for density estimates of graminoids. Only cover data are presented by species. We recorded the maximum height of clumps, number of stems (or leaf fronds for palmettos) ≥ 3 cm in height, and percent cover for all shrub species.

We randomly established three 10-m line transects within each 10 × 10-m quadrat to quantify percent cover of the vegetation and structural features by category, including non-

TABLE 1.—Dates of treatment administration and vegetation sampling in three treatments and mature forest in sand pine scrub

Treatment	Burn	Clear-cut or salvage	Site preparation	Sand pine seed	Sample
Burn-salvage (HIBS)	May 1985	June–Oct 1985	N/A	N/A	Summer 1991
Chop (RC)	N/A	Apr 1983–Feb 1985	June 1986	Winter 1986–1987	Summer 1991
Bracke (BK)	N/A	Fall 1986	Winter 1986–1987	Winter 1986–1987	Summer 1991
Mature (MF)	Spring 1935	N/A	N/A	N/A	Summer 1991

woody plants, shrub, pine, leaf litter, woody debris and bare ground using the line-intercept technique (Mueller-Dombois and Ellenberg, 1974). In MF, we estimated pine cover using a spherical densiometer at the midpoint of each line transect. All vegetation sampling was conducted in summer 1991.

Statistical analyses.—We used Analysis of Variance (ANOVA) to compare percent frequency, percent cover, density, species richness and Shannon's diversity indices (Brower and Zar, 1977) of shrubs and nonwoody plants as well as percent cover of structural features among treatments. Importance values (IVs) (relative frequency + relative density + relative dominance) for shrub species were compared among treatments using ANOVA. Pairwise contrasts between least squares means were performed when there was a significant treatment effect (SAS, 1985). Data were log-, square root-, or (for proportions only) arcsine square root-transformed where required to correct for nonnormality or heteroscedasticity. Horn's Index of Community Similarity (Horn, 1966) was computed for all possible treatment pairs. Index values closer to 1.0 indicate greater community similarity between treatment pairs. All results reported were significant at the $P < 0.05$ level unless otherwise indicated.

Data interpretation is limited by several factors. We were unable to obtain pretreatment data due to the unpredictability of wildfire occurrence. Hence, MF was used as a reference for inferring changes in density and cover of species within treatments. The HIBS sites did not precisely mimic natural (unsalvaged) wildfire since the salvage logging operations altered microsite conditions such as shade and moisture, as well as mode and timing of nutrient removal and recycling. Heavy machinery operation in the HIBS stands during salvage logging operations probably had similar effects as in RC and BK, top-killing most vegetation.

RESULTS

Nonwoody plants.—We recorded 67 nonwoody plant species in all three treatments and mature forest combined (Table 2). The highest number occurred in RC (58), an intermediate number in HIBS (46) and BK (43), and the lowest number in MF (23). Species richness and diversity were significantly lower in MF than in the disturbance treatments (Table 3).

Some species showed conspicuous differences in percent cover between MF and disturbance treatments (Table 2). In general, trends for density and frequency values were similar to those for cover. Several herbaceous species (*e.g., Bulbostylis ciliatifolia, Eupatorium compositifolium, Pityopsis graminifolia, Opuntia humifusa*) were virtually absent from MF. On the other hand, several nonvascular taxa (*Bryophyta* spp., *Cladina* spp., *Cladonia subradiata*) were more abundant in MF.

Several species increased in response to disturbance. This was especially apparent in ruderals, *Andropogon* spp. and *Eupatorium compositifolium.* Percent cover of *Andropogon* spp. was significantly higher in RC and HIBS than in BK or MF (Table 2). Percent cover of *Eupatorium compositifolium* was significantly greater in RC than in other treatments and was significantly higher in HIBS than in MF, where it was absent. *Opuntia humifusa,* and *Cyperus nashii* followed a similar pattern, with significantly greater percent cover in RC.

The patchy and infrequent occurrence of several species including rare taxa prevented generalizations regarding impacts from being drawn. However, there were no notable differences in occurrence of *Asclepias curtissii* among treatments. Neither burn site occurred within the highly discrete range of *Bonamia grandiflora.* This species is fairly common within its range. Its percent cover was similar in RC and BK but lower in MF. *Bonamia grandiflora*

TABLE 2.—Mean (±SE) percent cover of select nonwoody plants in three treatments and mature forest in sand pine scrub. (Readers interested in the complete plant list may write the corresponding author)

	Cover (%)*			
Herbaceous species**	Burn-salvage (HIBS)	Chop (RC)	Bracke (BK)	Mature (MF)
Andropogon spp.	9.1^{a} ± 3.6	17.1^{a} ± 4.6	1.8^{b} ± 1.2	0.2^{b} ± 0.1
Aristida spp.**	0.7 ± 0.6	1.9 ± 1.0	1.0 ± 0.6	<0.05 ± <0.05
Asclepias curtissii	<0.05 ± <0.05	<0.05 ± <0.05	0.1 ± <0.05	<0.05 ± <0.05
Bonamia grandiflora	0.0 ± 0.0	0.7 ± 0.4	1.3 ± 1.3	0.1 ± <0.05
Bryophyta spp.	0.1^{a} ± 0.1	0.06^{a} ± <0.05	0.3^{a} ± 0.1	1.5^{b} ± 0.8
Bulbostylis ciliatifolia	0.3^{a} ± <0.05	0.3^{a} ± 0.1	0.2^{a} ± 0.1	0.0^{b} ± 0.0
Cladina evansii	0.1^{a} ± 0.1	0.4^{a} ± 0.1	2.7^{b} ± 0.8	46.4^{c} ± 8.3
C. subtenuous	0.3^{a} ± 0.1	0.3^{a} ± 0.1	0.8^{a} ± 0.3	4.2^{b} ± 1.8
Cladonia spp.	<0.05 ± <0.05	0.3 ± 0.2	0.2 ± 0.1	0.1 ± 0.1
C. subradiata	0.1^{a} ± <0.05	$<0.05^{a}$ ± <0.05	$<0.05^{a}$ ± <0.05	0.2^{b} ± 0.1
Cyperus nashii	0.5^{a} ± 0.1	0.9^{b} ± 0.3	0.3^{a} ± 0.1	0.2^{a} ± 0.1
Eupatorium compositifolium	2.4^{a} ± 1.0	7.0^{b} ± 1.6	$0.7^{a,c}$ ± 0.4	0.0^{c} ± 0.0
Opuntia humifusa	0.1^{a} ± 0.1	1.2^{b} ± 0.4	$<0.05^{a}$ ± <0.05	0.0^{a} ± 0.0
Panicum spp.	1.0^{a} ± 0.2	$0.6^{a,b}$ ± 0.1	0.5^{b} ± 0.1	0.3^{b} ± 0.1
Pityopsis graminifolia	0.4 ± 0.3	0.3 ± 0.2	1.0 ± 0.5	0.0 ± 0.0
Polygala lewtonii	0.0 ± 0.0	0.0 ± 0.0	<0.05 ± <0.05	0.0 ± 0.0
Rhynchospora megalocarpa	2.8 ± 1.3	1.5 ± 0.6	5.3 ± 2.0	2.2 ± 0.8
Tephrosia chrysophylla	0.6^{a} ± 0.3	1.9^{b} ± 0.8	0.4^{a} ± 0.4	$<0.05^{a}$ ± <0.05

* Cover data log-transformed for ANOVA
** Different letters within a row denote significant differences among treatments (P < 0.05)
*** Includes *Aristida gyrans* and *A. purpurascens*

was never observed to flower in MF stands. *Polygala lewtonii* was observed in only one stand (BK) (Table 2), but subsequent populations were found in disturbed areas nearby.

Horn's Index of Community Similarity showed that among disturbance treatments the greatest community overlap was between HIBS and RC and the lowest was between BK and RC (Table 4). Mature forest had low similarity with any disturbance treatment, having its greatest overlap with BK. The prevalence of lichens in MF became obvious when nonvas-

TABLE 3.—Mean site species richness and diversity (H′) (±SE) of herbaceous plants in three treatments and mature forest in sand pine scrub

Treatment*	Richness	Diversity
Burn-salvage (HIBS)	23.6^{a} ± 1.9	2.29^{a} ± 0.08
Chop (RC)	30.6^{a} ± 3.3	2.21^{a} ± 0.23
Bracke (BK)	22.4^{a} ± 4.4	2.16^{a} ± 0.22
Mature (MF)	13.0^{b} ± 0.5	0.79^{b} ± 0.15
P-value	0.0055	0.0001

* Different letters within a column denote significant differences among treatments (P < 0.05)
Note: H′ calculated based on percent cover

TABLE 4.—Horn's Index of Community Similarity (R_0) for nonwoody species including and excluding nonvascular (NV) plants in three treatments and mature forest in sand pine scrub

	Including NV plants			Excluding NV plants		
	Burn-salvage (HIBS)	Chop (RC)	Bracke (BK)	Burn-salvage (HIBS)	Chop (RC)	Bracke (BK)
Burn-salvage (HIBS)						
Chop (RC)	0.855			0.855		
Bracke (BK)	0.720	0.657		0.757	0.683	
Mature (MF)	0.215	0.174	0.487	0.678	0.543	0.792

Note: Calculations are based on percent cover
Note: Values closer to 1.0 indicate greater community similarity between treatments

cular plants were excluded from community comparisons (Table 4). Community overlap values between HIBS, RC, and BK pairs did not change markedly, but overlap between MF and all disturbance treatments increased substantially.

Shrubs.—We recorded 23 shrub species in all study sites combined. Eighteen species occurred in HIBS, RC and MF, and 17 occurred in BK (Table 5). There were no significant differences in shrub species richness or diversity among disturbance treatments or MF (Table 6).

Community dominance by a few shrub species was apparent (Table 5). Only two oak species (*Quercus myrtifolia* and *Q. geminata*) and one palmetto species (*Sabal etonia*) had IVs > 50 in any single treatment. Only five additional species, including *Q. chapmanii, Serenoa repens, Lyonia ferruginea, Ceratiola ericoides* and *Vaccinium darrowii,* had IVs > 10. When IVs were combined for all oak species, this group dominated the shrub class in all treatments and MF, composing over half of total shrub "importance" in RC, BK and MF

TABLE 5.—Mean importance values (±SE) of select shrub species in three treatments and mature forest in sand pine scrub. (Readers interested in the complete plant list can write the corresponding author)

	Importance value**			
Shrub species*	Burn-salvage (HIBS)	Chop (RC)	Bracke (BK)	Mature (MF)
Ceratiola ericoides	12.2 ± 5.1	13.8 ± 3.0	3.1 ± 1.5	18.2 ± 8.7
Garberia heterophylla	2.5 ± 0.7	11.6 ± 5.8	2.6 ± 1.8	7.8 ± 4.3
Ilex opaca var. *arenicola*	5.9 ± 3.6	0.5 ± 0.5	2.0 ± 2.0	2.3 ± 1.6
Lyonia ferruginea	37.3[a] ± 8.2	11.2[b] ± 4.4	10.2[b] ± 5.2	10.0[b] ± 3.2
Quercus chapmanii	16.3 ± 3.0	20.6 ± 9.6	6.3 ± 4.1	8.4 ± 4.1
Q. geminata	25.3[a] ± 4.8	56.3[b] ± 6.9	43.8[a,b] ± 9.7	38.4[a,b] ± 5.6
Q. laevis	0.0 ± 0.0	3.5 ± 2.5	6.7 ± 2.9	3.3 ± 2.1
Q. myrtifolia	53.9[a] ± 16.6	81.2[a,b] ± 14.8	120.1[b] ± 15.6	116.8[b] ± 12.7
Sabal etonia	60.6 ± 22.6	67.3 ± 2.6	64.3[b] ± 6.8	46.9 ± 4.4
Serenoa repens	34.7[a] ± 11.1	5.1[b] ± 2.6	15.2[b] ± 4.7	15.7[a,b] ± 3.2
Vaccinium darrowii	12.6 ± 4.2	8.2 ± 2.2	9.8 ± 5.8	8.7 ± 2.4

* Different letters within a row denote significant differences among treatments (P < 0.05)
** Relative frequency + relative density + relative dominance (maximum value per treatment = 300)

TABLE 6.—Mean site species richness and diversity (H')* (±SE) of shrubs in three treatments and mature forest in sand pine scrub

Treatment	Richness	Diversity
Burn-salvage (HIBS)	12.2 ± 1.2	1.87 ± 0.16
Chop (RC)	11.2 ± 1.0	1.72 ± 0.08
Bracke (BK)	10.0 ± 0.7	1.46 ± 0.15
Mature (MF)	12.6 ± 1.4	1.68 ± 0.15
P-value	0.3730	0.2590

* H' calculated based on percent cover

and nearly a third in HIBS (Table 7). *Quercus myrtifolia* and *Q. geminata* were most important in all treatments and MF (Table 5).

Stem density of oaks was significantly lower in HIBS and RC than in BK or MF (Table 7). Percent cover also decreased from MF and BK to RC and HIBS. Oak height did not significantly differ among treatments or MF.

Quercus myrtifolia recovered most slowly in HIBS, followed by RC, then BK (Table 5). *Quercus geminata* recovered more slowly in HIBS than in RC (Table 5). *Serenoa repens* recovered significantly more rapidly in HIBS than in RC or BK. Data suggest that roller-chopping was detrimental to *Serenoa repens* recovery, but in the absence of pretreatment data this cannot be confirmed (Table 5). Interestingly, this trend was not apparent in *Sabal etonia,* a similar life form. Significantly higher IV and stem density of *Lyonia ferruginea* in HIBS suggest that resprouting or seeding of this species was stimulated by HIBS.

In contrast, *Ceratiola ericoides* responded similarly in all disturbance treatments (Table 5). Importance values in MF suggest that *C. ericoides* persists ≥55 yr or slowly increases in sand pine stands regenerated by fire.

Pine.—Pine density was significantly lower and height significantly greater in MF than in disturbance treatments (Table 8). Variability in pine dispersion or clumping was significantly lower in MF but did not differ among disturbance treatments.

Structural characteristics.—Total nonwoody plant cover was greater in RC than BK but highest in MF (Fig. 1). Lichens were dominant in MF whereas vascular plants dominated the groundcover in disturbance treatments (Table 4). Total shrub cover was lowest in RC

TABLE 7.—Mean stem density, height, percent cover, and importance values* (±SE) of oaks (species combined) in three treatments and mature forest in sand pine scrub

Treatment**	Stem density*** (#/ha)	Height*** (m)	Cover*** (%)	Importance value
Burn-salvage (HIBS)	9478.8[a] ± 2549.5	0.9 ± 0.1	26.5[a] ± 7.3	95.5[a] ± 22.8
Chop (RC)	14,468.8[a] ± 747.5	1.1 ± 0.2	38.2[a,b] ± 3.7	161.6[b] ± 10.3
Bracke (BK)	25,975.0[b] ± 5315.4	0.9 ± 0.1	50.2[b,c] ± 6.8	176.8[b] ± 15.3
Mature (MF)	26,480.0[b] ± 2898.4	1.1 ± 0.1	61.7[c] ± 9.3	167.3[b] ± 12.5
P-value	0.0030	0.7875	0.0175	0.0093

* Relative frequency + relative density + relative dominance (maximum value per treatment = 300)

** Data square root-transformed for ANOVA

*** Different letters within a column denote significant differences among treatments ($P < 0.05$)

TABLE 8.—Mean density and height of sand pine stems (±SE) (excluding seedlings <1 m) in three treatments and mature forest in sand pine scrub

Treatment*	Stem density** (#/ha)	Height** (m)
Salvage-burn (HIBS)	4076.0[a] ± 653.0	2.7[a] ± 0.1
Chop (RC)	3496.0[a] ± 270.1	2.8[a] ± 0.1
Bracke (BK)	3080.0[a] ± 388.4	1.9[b] ± 0.1
Mature (MF)	641.7[b] ± 65.8	16.7[c] ± 0.6
P-value	0.0001	0.0001

* Data were log-transformed for ANOVA

** Different letters within a column denote significant differences among treatments ($P < 0.05$)

and highest in MF. Mean percent pine cover was significantly lower in BK than MF or RC and significantly greater in MF than in all disturbance treatments.

MF had significantly higher leaf litter cover and less bare ground than did disturbance treatments. Litter cover was significantly higher in RC than BK, but cover in HIBS was no different than either of these. Percent bare ground ranged from 16.8% (HIBS) to 22.9% (RC), with no differences among HIBS, RC and BK. There was significantly less woody debris in RC than in the other treatments followed by MF; both had significantly less than BK or HIBS.

DISCUSSION

Many scrub species responded similarly to both HIBS and mechanical disturbance as indicated by an absence of significant differences in species diversity and richness, similarity in species composition, and relatively high community overlap among HIBS, RC and BK treatments. Lower species richness and diversity in MF further suggests that some nonwoody species require high-intensity disturbance, such as wildfire or soil disturbance, for germination or establishment.

Domination of the understory by native ruderal species, such as *Eupatorium compositifolium* and *Andropogon* spp. in RC and HIBS, did not detract from the suite of nonwoody plant species expected in sand pine scrub of this region. An increase in abundance of these ruderal species following mechanical disturbance is common (Grelen, 1962; Schultz and Wilhite, 1974; Conde *et al.*, 1986), but is not commonly reported following fire-only in scrub (Abrahamson, 1984a, 1984b; Schmalzer and Hinkle, 1992). This suggests that postfire salvage logging differs in its effect from fire-only.

Increased flowering and seeding following growing season burns (Robbins and Myers, 1989) or biomass removal (Partch, 1950) have been observed in many Florida grasses. Increased numbers of ramets per clone following fire have been reported for several composites (Hartnett, 1987; Platt *et al.*, 1988). Increases in perennial grasses such as *Andropogon* spp. and *Panicum* spp. following disturbance may be at least partly attributable to resprouting (Schmalzer and Hinkle, 1992). Such responses may contribute to observed higher levels of ruderal species in disturbance treatments.

Creation of suitable site conditions, such as increased light, bare mineral soil, soil heating, soil temperature fluctuations, or reduced competition, may promote colonization or germination of several species which were absent from MF. These conditions may be enhanced or prolonged in RC and HIBS relative to BK by reduction in oak stem density and consequent reductions in competition and shade.

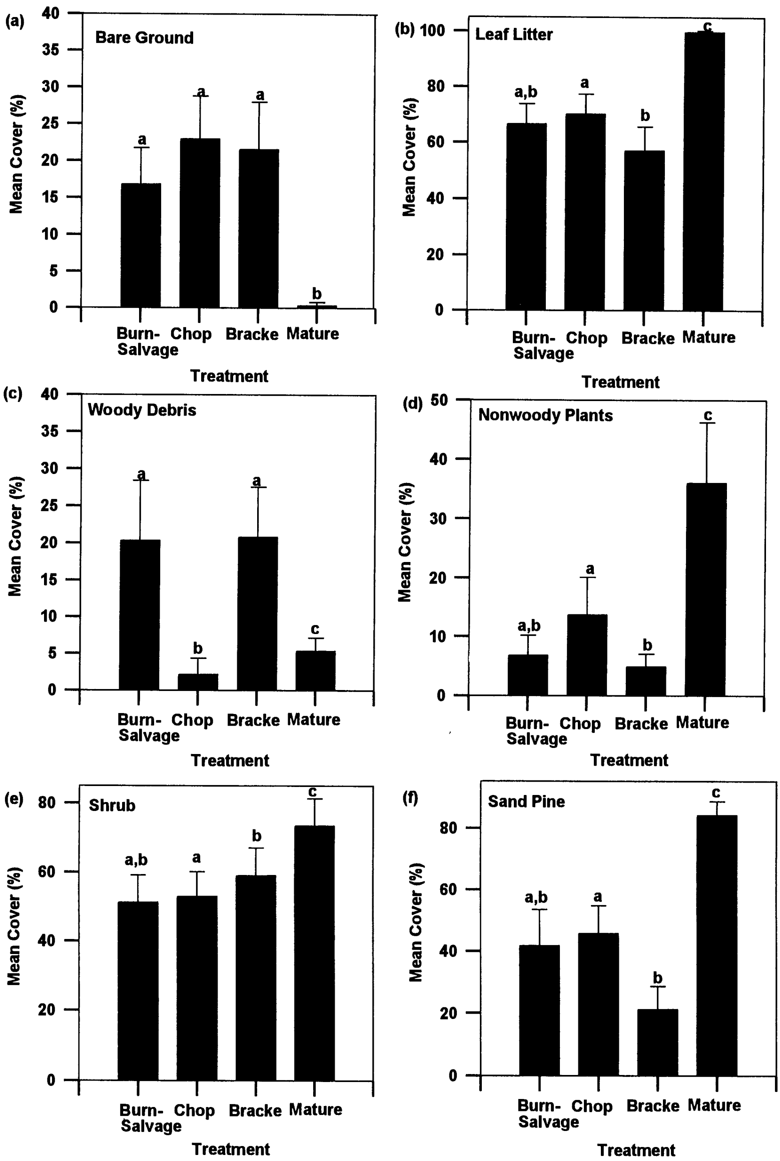

FIG. 1.—Mean percent cover (±SE) of (a) bare ground; (b) leaf litter; (c) woody debris; (d) nonwoody plants; (e) shrub, and (f) sand pine in three treatments and a reference on the Ocala National Forest, Florida. Means are for five replicate sites each, and significant differences within categories are denoted by different letters among treatments

Reduced levels of *Quercus* in HIBS and RC treatments may be due to season and/or intensity of disturbance. Several studies report that scrub oaks (*Q. laevis* and *Q. incana*) were nearly eliminated from NW Florida sandhills for several years following late spring roller chopping (Grelen, 1962; Hebb, 1971). Burns conducted during the growing season are most effective in top-killing scrub oaks and reducing resprouts (Robbins and Myers, 1989). In contrast, Abrahamson (1984a) reported that oaks in scrubby flatwoods regained preburn cover levels within 2–3 yr of a winter burn. Schmalzer and Hinkle (1992), however, reported that oak cover (>0.5-m in height) was less than preburn levels 3 yr following a December fire in oak-saw palmetto scrub.

Differences in preburn *Quercus* species dominance could affect postburn oak recovery, since not all species recover with equal rapidity. The faster recovery of *Q. geminata* relative to *Q. myrtifolia* seen in this study is similar to findings by Schmalzer and Hinkle (1992).

Carbohydrate reserves are lowest in *Serenoa repens* rhizome tissue in early summer (Hough, 1968). Both the wildfire and roller chopping occurred in late spring with different responses. These differences suggest that roller chopping, which destroys aboveground and near-surface belowground biomass, is detrimental to *S. repens* recovery (Schultz and Wilhite, 1974; Conde *et al.*, 1986). Conversely, occasional burning which destroys aboveground biomass may actually stimulate frond production. In xeric scrub, rhizomes are rarely aboveground, rendering them less vulnerable to fire damage (and desiccation) than to roller chopping. Rapid postburn recovery of *S. repens* has been reported in other studies (Abrahamson, 1984a, 1984b; Breininger and Schmalzer, 1990; Schmalzer and Hinkle, 1992). Greater rhizome depth and/or position of the apical meristem of *Sabal etonia* could render it less vulnerable to damage from mechanical disturbance than *Serenoa repens*.

Serenoa repens provides a volatile fuel source. Even where it is sparse, it is important in maintaining and carrying fire across the landscape or upward into tree crowns. In addition, rhizomes may function as important nutrient reserves in the scrub ecosystem (Schmalzer and Hinkle, 1987). Substantial reductions in *Serenoa repens* abundance could interfere with fire management and should be further investigated before implementing management strategies based on mechanical disturbance.

Density and IV of *Lyonia ferruginea* were significantly higher in HIBS than in other treatments and 2–4 times higher in HIBS than in MF. This suggests that burning may actually stimulate resprouting and/or germination of this species.

Ceratiola ericoides exhibited yet a different response, germinating in all three disturbance treatments (although notably less so in BK). This species is commonly found on plow lines and along road shoulders as well. This contrasts with Johnson's (1982) suggestion that *C. ericoides* germinates in response to fire and suggests that other disturbance types such as roller chopping or the consequent conditions may also stimulate seed germination. Gibson and Menges (in press) report recruitment in response to continuous sand movement in coastal populations of *C. ericoides*.

Significantly less woody debris in RC is due to pine slash fragmentation and partial burial during roller chopping, resulting in accelerated rates of decomposition. In contrast, scattered piles of logging debris remain in HIBS and BK stands. Natural limb- and tree-falls contribute to woody debris scattered about in MF.

Delayed oak recovery and consequent leaf litter in both HIBS and RC may account for similar levels of bare ground observed in this study. Although there was significantly more litter in RC than BK, means ranged from only ca. 57.0–70.0% (with HIBS not different from either). Relatively lower levels of woody debris in RC resulted in similar values for bare ground as in HIBS and BK despite higher litter levels.

The results of this study agree with Denslow's (1980) hypothesis that selective pressure on plant life history strategies should lead to higher species richness in the most common patch types of a given ecosystem (historically early successional in sand pine scrub). Similar species richness, composition and abundance levels in both postclear-cut (RC or BK) and postburn (HIBS) treatments suggest that many nonwoody plants respond similarly to both high-intensity silvicultural disturbance and high-intensity wildfire.

Clearly, both silvicultural treatments and HIBS differ in many regards from fire-only. Tree boles remain standing or fallen as dead biomass following high-intensity natural disturbance whereas whey are removed during clear-cutting or salvage operations. This could result in differences in microsites ("safe sites" for plant establishment) and nutrient cycling.

Differences in timing and mechanisms of nutrient cycling exist between high-intensity wildfire and silvicultural disturbance. Based on estimates from loblolly pine (*Pinus taeda*), only a small fraction of nutrients ($<5\%$ of N, $<4\%$ of P, and $<14\%$ of total N) are transported offsite by bole-only removal (Jorgensen and Wells, 1986). This is probably small relative to nutrient losses by volatilization or subsequent erosion and soil leaching following wildfire (DeBano and Conrad, 1978; Rundel, 1983; Schmalzer and Hinkle, 1987). Besides creating a flush of nutrients in available form, high-intensity fire also differs from clear-cutting by providing a sudden, temporary "heat treatment."

However, a similar response of many scrub species to both high-intensity burning-salvage logging, burn-only (Abrahamson, 1984a, 1984b; Schmalzer and Hinkle, 1992), and silvicultural disturbance suggests that clear-cutting followed by mechanical disturbance mimics the natural disturbance process in aspects relevant to plant response. We suggest that, in scrub: (a) many fire-selected traits that facilitate high resiliency to fire, such as postdisturbance resprouting, increase ramet production or seed germination (Keeley and Zedler, 1978), and may coincidentally function similarly in response to specific nonfire disturbance conditions (Fox and Fox, 1986); and/or (b) plant characteristics evolved in response to selective pressures of disturbance types, including but not limited to fire, and therefore are not dependent upon properties unique to fire for their persistence through time.

Coastal scrub currently occurs on stabilized dunes (behind foredunes). This environment subjects plants to constant sand erosion, deposition and movement by wind and water. Periodic hurricanes result in widespread windthrow and sand movement via blow-outs or overwash plains (Johnson and Barbour, 1990; Myers, 1990). Several typical scrub species occur in both high-disturbance dunal zones of coastal scrubs and inland peninsular scrub (Johnson and Barbour, 1990). Inland scrubs also occurred on coastal dunes and on barrier islands during higher sea levels (Laessle, 1967; Watts, 1971) and would have been exposed to similar selective pressures.

Such disturbances, depending upon type and intensity, disturb the soil in a manner not unlike soil movement caused by mechanical disturbance. Resulting site conditions include: bare ground exposure and consequent increases in soil temperature or soil temperature fluctuation thought to be required by some species to break dormancy; greater soil surface texture; and reduced shade, competition and transpiration with consequent changes in water, light and nutrient availability (Bazzaz, 1979). Some or all of these are necessary conditions for seed establishment and/or germination of many species.

Clonal reproduction from roots and rhizomes, as well as growth and production patterns by ramets, are common traits of coastal dune species, probably as adaptive responses to sand movement and migration by wind, wave and sand burial (Johnson and Barbour, 1990). Seed germination also may be initiated by sand movement (Gibson and Menges, in press). Such responses may be stimulated by and adaptive in a number of disturbance situations including fires, mechanical treatment, or during hurricanes as well as in continually unstable soils.

Data presented in this study support the hypothesis that, at least in the short term, high-intensity silvicultural disturbance mimics natural disturbance by high-intensity wildfire-salvage logging in sand pine scrub, and that vegetation adapted to rapid recovery from high-intensity wildfire responds similarly to another type of biomass removal. The importance of disturbance and consequent changes in microclimate and microsite conditions required by many scrub plant species is clear. Clear-cutting may be a viable approach to ecosystem management of sand pine scrub vegetation where a natural disturbance regime is impractical. This may by suitably applied in small patches of scrub surrounded by urban development, or where timber harvesting and ecosystem management for vegetation are dual management objectives.

Due to the limited temporal and spatial scope of this study, interpretation and implementation of results should be made with caution. This study addressed only one moment in seral time. Long-term effects of high-intensity silvicultural practices within and spanning several rotations are unknown. Landscape patterns created by silvicultural practices such as clear-cut size and arrangement differ from landscape patterns commonly imposed by natural, high-intensity disturbance and could have important long-term effects on sand pine scrub plant communities. Absence of pretreatment data could obscure important treatment differences. Salvage logging in HIBS sites could have affected vegetation recovery through snag removal (hence alteration of microsites and nutrient cycling) or impacts of heavy machinery during the early postfire recovery period.

In addition, although roller chopping and high-intensity burning/salvage logging have similar gross effects on vegetation recovery, responses to treatments varied among some species. Such differences, such as reductions in *Serenoa repens,* could affect ecosystem processes by changing fuel availability or structure. Other studies of burned-only scrub suggest that disturbance by postfire salvage logging may affect plant response as well (such as increasing the abundance of native ruderals).

Results of this study raise several intriguing questions warranting further study: What are the components of "disturbance" to which plants respond? Can they be identified for different disturbance types such that mechanisms behind plant responses can be determined? Is there something unique to fire such as the associated heat or nutrient flush which is required to elicit response by some scrub species? Alternatively, are some species' responses triggered by more generalized effects of fire, such as exposure of bare mineral soil and temporary reduction of competition, evapotranspiration, and associated changes in microclimate? If the latter is true, which of these characteristics can be achieved by disturbance types other than fire? Further exploration of these questions may enhance our understanding of disturbance ecology and improve ecosystem management.

LITERATURE CITED

ABRAHAMSON, W. G. 1984a. Species responses to fire on Florida Lake Wales Ridge. *Am. J. Bot.,* **71**:35–43.

———. 1984b. Post-fire recovery of Florida Lake Wales Ridge vegetation. *Am. J. Bot.,* **71**:9–21.

AUFFENBERG, W. 1982. Florida environments and their herpetofaunas part III. Herpetogeography. *Fla. Herpetol.,* **4**:1–35.

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.

BARTRAM, W. 1955. The travels of William Bartram. 1791, edited by M. Van Doren. Dover Publications, Inc., New York. 414 p.

BAZZAZ, F. A. 1979. The physiological ecology of plant succession. *Annu. Rev. Ecol. Syst.,* **10**:351–371.

BOERNER, R. E. J. 1981. Forest structure dynamics following wildfire and prescribed burning in the New Jersey pine barrens. *Am. Midl. Natl.,* **105**:321–333.

BREININGER, D. R. AND P. A. SCHMALZER. 1990. Effects of fire and disturbance of plants and birds in a Florida oak/palmetto scrub community. *Am. Midl. Nat.*, **123**:64–74.

BROWER, J. E. AND J. H. ZAR. 1977. Field and laboratory methods for general ecology. W. C. Brown Company, Dubuque, Iowa. 226 p.

CAMPBELL, M. W. AND S. P. CHRISTMAN. 1982. The herpetological components of Florida sandhill and sand pine scrub associations, p. 163–171. *In:* N. J. Scott (ed.). Herpetological communities. *U.S. Fish Wildl. Serv. Wildl. Res. Rep.* **13.**

CHRISTMAN, S. P. AND W. S. JUDD. 1990. Notes on plants endemic to Florida scrub. *Biol. Sci.*, **53**:52–73.

CONDE, L. F., B. F. SWINDEL AND J. E. SMITH. 1986. Five years of vegetation changes following conversion of pine flatwoods to *Pinus elliottii* plantations. *For. Ecol. Manage.*, **15**:295–300.

COOPER, R. W., C. S. SCHOPMEYER AND W. H. DAVIS MCGREGOR. 1959. Sand pine regeneration on the Ocala National Forest. *U.S. For. Serv. Prod. Res. Rep.* **30**. 37 p.

DEBANO, L. F. AND C. E. CONRAD. 1978. The effect of fire on nutrients in a chaparral ecosystem. *Ecology*, **59**:489–497.

DENSLOW, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia (Berl.)*, **46**:18–21.

FOX, B. J. AND M. D. FOX. 1986. Resilience of animal and plant communities to human disturbance, p. 39–64. *In:* B. Dell, A. J. M. Hopkins and B. B. Lamont (eds.). Resilience in Mediterranean-type ecosystems. Dr. W. Junk Publishers, Boston, Mass.

FRANKLIN, J. F. AND R. T. T. FORMAN. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecol.*, **1**:5–18.

GIBSON, D. J. AND E. S. MENGES. 1994. Population structure and spatial patterns in the dioecious shrub *Ceratiola ericoides. J. Veg. Sci.* **5**:337–346.

GRELEN, H. E. 1962. Plant succession on cleared sandhills in northwest Florida. *Am. Midl. Nat.*, **67**: 36–44.

HARRIS, L. D. 1984. The fragmented forest: island biogeographic theory and the preservation of biotic diversity. University of Chicago Press, Chicago, Ill. 211 p.

HARTNETT, D. C. 1987. Effects of fire on clonal growth and dynamics of *Pityopsis graminifolia* (*Asteraceae*). *Am. J. Bot.*, **74**:1737–1743.

——— AND D. R. RICHARDSON. 1989. Population biology of *Bonamia grandiflora* (*Convolvulaceae*): effects of fire on plant and seed dynamics. *Am. J. Bot.*, **76**:361–369.

HAWKES, C. V. AND E. S. MENGES. 1995. Density of seed production of a Florida endemic, *Polygonella basiramia,* in relation to time since fire and open sand. *Am. Midl. Nat.* (in press).

HEBB, E. A. 1971. Site preparation decreases game food plants in Florida sandhills. *J. Wildl. Manage.*, **35**:155–162.

HILL, W. F. 1916. Land classification of the Florida national forest, Florida. Unpubl. Rep. to the Secretary of Agriculture, Florida. 83 p.

HORN, H. S. 1966. Measurements of overlap in comparative ecological studies. *Am. Nat.*, **100**:419–424.

HOUGH, W. A. 1968. Carbohydrate reserves of saw-palmetto: seasonal variation and effects of burning. *For. Sci.*, **14**:399–405.

JOHNSON, A. F. 1982. Some demographic characteristics of the Florida rosemary *Ceratiola ericoides* Michx. *Am. Midl. Nat.*, **108**:170–174.

——— AND M. G. BARBOUR. 1990. Dunes and maritime forests, p. 429–480. *In:* R. L. Myers and J. J. Ewel (eds.). Ecosystems of Florida. University of Central Florida Press, Orlando.

JORGENSEN, J. R. AND C. G. WELLS. 1986. Foresters' primer in nutrient cycling. *U.S. For. Serv. Gen. Tech. Rep. SE-37.* 42 p.

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.

KEELEY, J. E. AND P. H. ZEDLER. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. *Am. Midl. Nat.*, **99**:142–161.

KESSLER, W. B. 1992. A tale of two paradigms: multiple use of ecosystem management. *The George Wright Forum,* **8**:13–20.

KRUGER, F. J. 1983. Plant community diversity and dynamics in relation to fire, p. 446–472. *In:* F. J. Kruger, D. T. Mitchell and J. U. M. Jarvis (eds.). Mediterranean-type ecosystems: the role of nutrients, Vol. 43. Springer-Verlag, New York.

LAESSLE, A. M. 1967. Relation of sand pine scrub to former shorelines. *Quart. J. Fla. Acad. Sci.,* **30**: 269–286.

MENGES, E. S. 1992. Habitat preferences and response to disturbance for *Dicerandra frutescens,* a Lake Wales Ridge (Florida) endemic plant. *Bull. Torrey Bot. Club,* **119**:308–313.

MOHLENBROCK, R. H. 1976. Woody plants of the Ocala National Forest. *Castanea,* **41**:309–319.

MUELLER-DOMBOIS, D. AND Y. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, Inc., New York. 547 p.

MYERS, R. S. 1990. Scrub and high pine, p. 150–193 *In:* R. L. Myers and J. J. Ewel (eds.). Ecosystems of Florida. University of Central Florida Press, Orlando.

OUTCALT, K. W. 1990. Operational trials of a scarifier-seeder for regenerating Ocala sand pine. *South. J. Appl. For.,* **14**:85–88.

PARTCH, M. L. 1950. Some factors affecting flower production in *Andropogon gerardi. Ecology,* **31**:488–489.

PERONI, P. A. AND W. G. ABRAHAMSON. 1986. Succession in Florida sandridge vegetation: a retrospective study. *Fla. Sci.,* **49**:176–191.

PLATT, W. J., G. W. EVANS AND M. M. DAVIS. 1988. Effects of fire season on flowering forbs and shrubs in longleaf pine forest. *Oecologia (Berl.),* **76**:353–363.

RAWLINGS, M. K. 1933. South moon under. Charles Scribner and Sons, New York. 334 p.

ROBBINS, L. E. AND R. L. MYERS. 1989. Seasonal effects of prescribed burning in Florida: a review. *Tall Timbers Res. Stn. Misc. Publ.* **8**. Tallahassee, Fla.

RUNDEL, P. W. 1983. Impact of fire on nutrient cycles in Mediterranean-type ecosystems, p. 192–207. *In:* F. J. Kruger, D. T. Mitchell and J. U. M. Jarvis (eds.). Mediterranean-type ecosystems: the role of nutrients, Vol. 43. Springer-Verlag, New York.

SAS INSTITUTE, INC. 1985. SAS User's Guide: statistics, version 5. SAS Institute, Cary, N.C.

SCHMALZER, P. A. AND C. R. HINKLE. 1987. Effects of fire on composition, biomass, and nutrients in oak scrub vegetation on John F. Kennedy Space Center, Florida. *NASA Tech. Mem.,* **100305.**

——— AND ———. 1992. Recovery of oak-saw palmetto scrub after fire. *Castanea,* **57**:158–173.

SCHULTZ, R. P. AND L. P. WILHITE. 1974. Changes in a flatwoods site following intensive preparation. *For. Sci.,* **20**:234–242.

SHAFI, M. I. AND G. A. YARRANTON. 1973. Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. *Ecology,* **54**:897–902.

WATTS, W. A. 1971. Postglacial and interglacial vegetation history of southern Georgia and central Florida. *Ecology,* **52**:676–690.

WEBBER, H. J. 1935. The Florida scrub, a fire fighting association. *Am. J. Bot.,* **22**:344–361.

WESTMAN, W. E. AND J. F. O'LEARY. 1986. Measures of resilience: the response of coastal sage scrub to fire. *Vegetatio,* **65**:179–189

WUNDERLIN, R. P. 1982. Guide to the vascular plants of central Florida. University Presses of Florida, Tampa. 472 p.

SUBMITTED 18 APRIL 1994 ACCEPTED 16 SEPTEMBER 1994