RESEARCH ARTICLE

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Effects of Reintroduction of Fire into Fire Suppressed Coastal Scrub and Longleaf Pine Communities Along the Lower Gulf Coastal Plain

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ABSTRACT: The Northwest Florida coastal landscape consists of a mosaic of sand pine scrub, longleaf pine, and ecotonal communities. Fire suppression has altered the structure and composition of these communities. The effects of environmental variation and the recent reintroduction of fire on plant distribution and abundance across this landscape were investigated. Relative cover of herbaceous and woody ground cover species and density of sapling and canopy trees along with elevation, percent bare ground, percent canopy cover, and litter depth were determined in burned and long-unburned treatments for all community types. Canonical correspondence analysis (CCA) identified elevation and time since fire as the most influential environmental variables for species distribution and abundance. Species most closely associated with lower sites included *Gaylussacia mosieri* Small, *Ilex glabra* (L.) Gray, *Kalmia hirsuta* Walt., *Magnolia virginiana* L., *Pinus palustrus* P. Mill., *Vaccinium myrsinites* Lam., *Aristida* L. species, *and Calamovilfa curtissii* (Vasey) Schribn.. Species associated most closely with higher sites included *Ilex vomitoria* Ait., *Quercus chapmanii* Sarg., *Quercus geminata* Small, *Quercus myrtifolia* Willd., *Vaccinium stamineum* L., *Baptisia lanceolata* (Walt.) Ell., *Cladonia* Hill ex P. Browne species, *Eriogonum tomentosum* Michx., *Rhynchospora megalocarpa* Gray, and *Yucca filamentosa* L. Eight months post fire, burned sites had lower density of woody overstory and saplings compared to long-unburned sites. Herbaceous species richness did not differ between burned and long-unburned sites. Repeated prescribed fires during the growing season and direct seeding may be needed to promote flowering and establishment of additional herbaceous species.

Index terms: fire reintroduction, longleaf, panhandle sand pine scrub

INTRODUCTION

Historically, fire was a dominant force shaping the vegetation communities of the Southeastern Coastal Plain (Frost et al. 1986). Long-term fire suppression negatively impacts fire adapted species and alters the composition and structure of these communities. The reintroduction of fire serves several purposes, including hazardous fuel reduction and the conservation of fire-dependent plants and animals; however, the return of fire alone may not lead to complete vegetation recovery if ecosystem thresholds have been crossed (Suding et al. 2004).

Sand pine scrub and longleaf pine communities differ not only in vegetation composition and species diversity, but also in the manner in which fire acts in and upon their flora (Abrahamson and Harnett 1990; Greenburg et al. 1995). Longleaf pine communities consist of an open overstory of longleaf pine (*Pinus palustris* P. Mill.) and/or slash pine (*P. elliottii* Engelm.) and an understory of deciduous oaks and/or evergreen oaks (*Quercus* spp.), gallberry (*Ilex glabra* (L.) Gray), and saw palmetto (*Serenoa repens* (Bartr.) Small) with or without a well-developed herbaceous component. They are found on various soil types throughout the southeast (Myers 1990). Sand pine scrub occupies droughty, infertile upland sites. Where sand pine scrub and longleaf association are contiguous, extended changes in fire frequency may cause a gradual shift from one community type to the other (Kalisz and Stone 1984).

Historically, fires in the longleaf pine communities were of low intensity and occurred every 1-10 years (Glitzenstein et al. 1995; Maliakal et al. 2000). These frequent ground fires facilitated longleaf seedling establishment through the reduction of the litter layer and mid-story shrubs, both of which hinder seed, rain, and sunlight penetration to mineral soil. The herbaceous component also benefits from regular fires through the reduction of understory vegetation (Brockway and Lewis 1997). In contrast, the sparse herbaceous ground cover in sand pine scrub does not carry frequent ground fires; therefore, sand pine scrub fires are infrequent (every 10-60 years) but intense and stand-replacing canopy fires (Webber 1935; Menges et al. 1993). In general, the aboveground parts of midstory and overstory sand pine scrub species are killed. Though resprouting is a common post-fire recovery mechanism for many sand pine scrub perennials, others have demonstrated the close link between fire and seedling recruitment in scrub for a variety of perennial species (Abrahamson and Abrahamson 1996; Carrington 1999). In addition, periodic fire also prevents the succession of mainland scrub to xeric hammock and facilitates the recruitment of serotinous sand pine (*Pinus clausa* var. *clausa* D.B. Ward) seedlings.

Panhandle sand pine scrub communities are restricted to a narrow strip on the Gulf coast and barrier islands and may differ floristically from the geographically larger central mainland Florida scrub (Myers 1990). The role fire plays in maintenance of composition and structure of Panhandle sand pine scrub is not clear. The uneven-aged stands and nonserotinous cones of Panhandle sand pine (*Pinus clausa var immuginata* Ward) suggest regeneration of these stands may be associated with hurricanes and wind throw more so than fire (Greenberg et al. 1995). Although recent studies have quantified the effect of fire on geologically older and geographically larger Florida central ridge scrub (Menges and Hawkes 1998), no studies have addressed the effects of reintroduction of fire into the more isolated panhandle sand pine scrub. Also, longleaf pine communities of this region are transitional between the more thoroughly studied wiregrass/longleaf association (*Aristida beyrichiana* Trin. & Rupr./ *P. palustris)* and the less well-studied bluestem/longleaf association (*Schizachyrium scoparium* (Michx.) Nash/ *P. palustris),* and they have unique ground cover assemblages, including the occurrence of the rare endemic grass, Florida sandreed (*Calamovilfa curtssii* (Vasey) Scribn.) (Peet 1995). This study examined: (1) the differences in vegetation composition and structure between long-unburned longleaf pine, ecotone, and panhandle sand pine scrub communities, and (2) the effects of reintroduction of burning on vegetation composition and structure in each of these three communities.

MATERIALS AND METHODS

Study Site

This study was conducted on the 558-hectare Naval Live Oaks area (NLO) of the Gulf Islands National Seashore in Santa Rosa County Florida (30° 22'N, 87° 07'W). NLO includes wetlands, xeric hammocks, sand pine scrub, and longleaf pine flatwoods and sandhills. Topography ranges from flat land to gently rolling relict sand dunes with elevations peaking at 15 meters above sea level.

The study was concentrated in assemblages of longleaf pine flatwoods, sand pine scrub, and an ecotone separating the longleaf and sand pine scrub communities. Description of longleaf pine flatwoods, sand pine scrub, and sandhills are given elsewhere (Abrahamson and Harnett 1990; Myers

Table 1. Soil profile description for the three vegetation communities at Naval Live Oaks.

Site	Depth (cm)	Horizon	Water Table (cm)	Matrix Color	Texture	Consistency	Structure
Longleaf	0-20	A		10 YR 4/1	sand	loose	single grain
	20-46	A		10 YR 5/1	sand	loose	single grain
	46-53	Bh	46[a]	10 YR 4/4	sand	loose	single grain
	53-58	Bh[c]		10 YR 3/3	sand	loose	single grain
	58-86	Bh		10 YR 5/1	sandy loam	friable	granular
	86-203	Bh	152[b]	2.5 Y 8/1	sand	loose	single grain
Ecotone	0-15	A		10 YR 5/2	sand	loose	single grain
	15-89	C_1		10 YR 7/6	sand	loose	single grain
	89-147	C_2		10 YR 6/6	sand	loose	single grain
	147-152	C_3	152[a]	10 YR 7/2	sand	loose	single grain
	152-165	C_4		10 YR 7/2	sand	loose	single grain
	165-178	C_5		2.5 YR 8/2	sand	loose	single grain
	178-203	C_6		2.5 YR 8/1	sand	loose	single grain
Sand	0-5	A		10 YR 7/2	sand	loose	single grain
Pine Scrub	May-64	C_1		10 YR 6/6	sand	loose	single grain
	64-203	C_2	>203[a]	10 Y/R 7/6	sand	loose	single grain

[a] Seasonally high water table

[b] Free water

[c] Spodic layer

1990). Sand pine scrub on NLO is part of the panhandle mainland scrub group, which is restricted to a narrow strip along the northern Gulf coast and on barrier islands. This scrub community consists of a dense shrub layer dominated by *Quercus geminata*, *Quercus myrtifolia,* and *Quercus chapmanii* with a sparse overstory of sand pine. Ecotonal sites consist of an open-sand pine dominated canopy with turkey oak (*Quercus laevis* Walter) and patches of schlerophyllous oaks, including sand live oak (*Quercus* geminata) and myrtle oak (*Quercus* myrtifolia) occupying the midstory. Longleaf pine occurs rarely in the overstory. Flora nomenclature follows the Integrated Taxonomic Information System on-line database (2004).

The climate of NLO is subtropical with annual rainfall amounts of 152-162 cm (Wolfe et al. 1988). The NLO communities are found on the most recent Pleistocene terraces (Pamlico and Silver Bluff) (Myers 1990). See Table 1 for detailed soil profile description of sand pine scrub, longleaf pine, and ecotonal sites.

Aside from small-acreage wildfires, the entire park was fire-suppressed for at least 50 years until February 1999. About 22% of the park (~121 hectares) has been burned in prescribed fires ignited by the National Park Service in the early springs of 1999, 2000, and 2002.

Plot Establishment

Sampling was conducted utilizing a nested plot design. Within each community type (sand pine scrub, longleaf pine, and ecotone), 20 long-unburned main plots were established randomly and permanently marked with rebar within areas fire-suppressed for >50 years. Ten plots were established randomly and permanently marked in each of the 2000 burn areas of the longleaf pine and ecotonal communities and in each of the 2002 burn areas of the longleaf pine and sand pine scrub communities. Because of the dense midstory of sand pine scrub, plot size was adjusted for this community type.

Vegetation Sampling

Woody individuals >10 cm dbh and woody/suffrutescent individuals 1 cm≤dbh≤10 cm were termed overstory and saplings, respectively. In the sand pine scrub, density and dbh of all woody non-oak species >10 cm dbh and all oak species >10 cm dbh were recorded in the 15-m x 25-m main-plot and a 5-m x 25-m sub-plot, respectively. All woody species 1cm ≤dbh ≤ 10 cm were tallied for density only within a 5-m x 10-m sub-plot. In the longleaf pine and ecotone, density and dbh of all woody non-oak species >10 cm dbh and all oak species >10 cm dbh were recorded in the 50-m x 10-m main-plot and the 5-m x 25-m sub-plot, respectively. All woody species 1 cm≤dbh≤10 cm were tallied for density only within the 5-m x 10-m subplot. Relative density (density of a species/total density of all species in a plot) was calculated for both sapling and overstory species. Sampling of woody overstory and saplings was conducted in early November 2000 for plots situated within long-unburned and 2000 burn areas and in late June 2002 for plots situated within 2002 burn areas.

The density of all woody/suffrutescent species <1 cm dbh (from here on termed woody ground cover) and aerial cover of individual herbaceous were repeatedly sampled within three 0.5-m^2 permanently marked quadrats established near the center of all main plots in November 2000, August 2001, March 2002, and November 2002. Percent cover was estimated using the midpoint of modified Daubenmire classes (Daubenmire 1959). Mean values calculated across sample dates for ground cover were used in all analysis. Relative cover was computed for the herbaceous

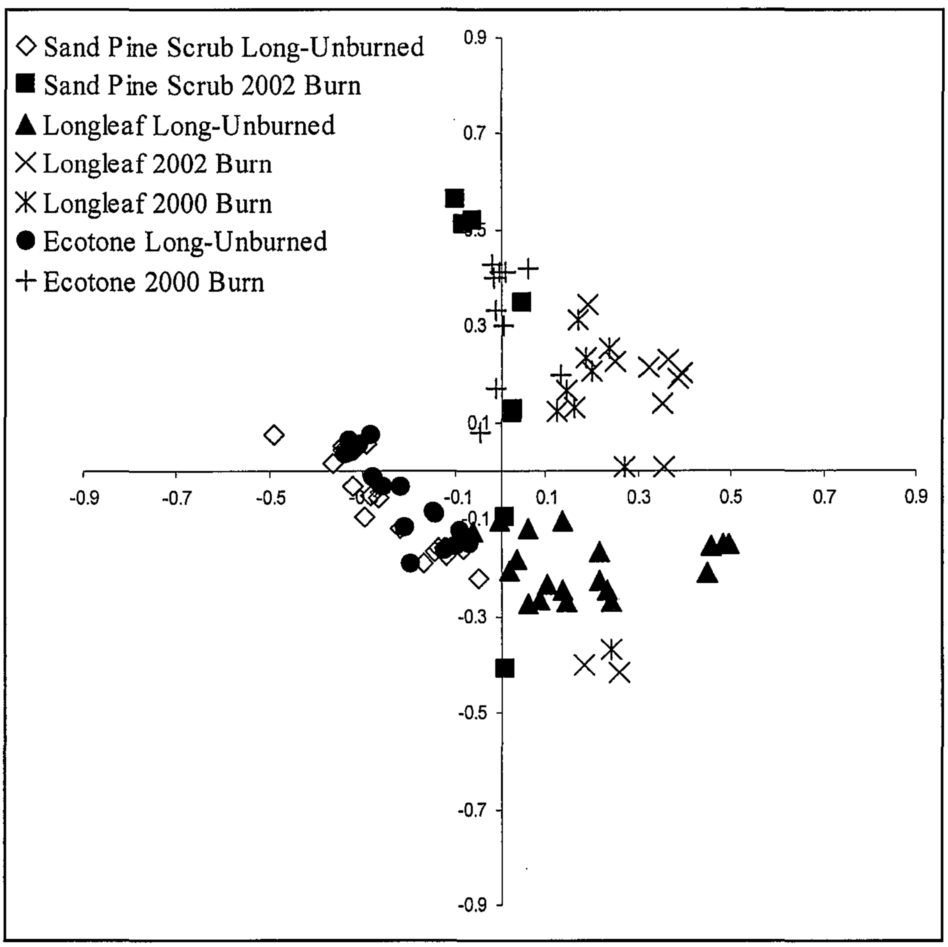

Figure 1. Canonical correspondence analysis (CCA) for herbaceous species at Naval Live Oaks with ordination of sample plots displayed. The first CCA axis was most highly correlated with elevation. The second CCA axis was most highly correlated with time since fire.

species, and relative density was calculated for the seedlings and vegetative sprouts of each woody species.

Environmental Variables

Percent bare ground was estimated and litter depth (cm) (subplot center) was recorded within the permanently marked 0.5-m^2 subplots for all treatments. Canopy cover was measured in four cardinal directions with a densiometer at the center of all main plots. The mean of the four measurements was used in all analyses. Elevation to the nearest 0.76 m was estimated from a USGS topographic map of the Naval Live Oaks area. A soil profile measured to 203 cm in each community was characterized (Table 1).

Data Analysis

Canonical Correspondence Analysis (CCA) reveals correlations between environmental gradients and species distributions (Palmer 1993). Distribution of woody ground cover species (all woody and suffrutescent species < 1cm dbh), herbaceous species, and sapling-overstory species (all woody species >1cm dbh) were analyzed using CCA. Relative cover was utilized in the herbaceous ordination analysis and relative density was utilized for the regeneration and sapling-overstory ordination analysis. Environmental variables incorporated into CCA were litter depth, percent canopy cover, percent bare ground, elevation, and time since last fire. All ordination analyses were completed using CANOCO 4.0 (Ter Braak and Šmilauer 1998). Monte Carlo permutation (randomization) tests available in CCA were used to evaluate the significance of each CCA axis (testing the relationship between matrices).

Diameter class density differences for species in burned and long-unburned sites were analyzed using a two-way ANOVA (PROC GLM) within the framework of a completely randomized design. These analyses were performed using SAS Version 8.0 (SAS 2000). Statistical significance is set at $\alpha = 0.05$. Shannon-Weiner diversity indices (H'), using richness and evenness, were calculated for: (1) herbaceous and (2) woody/suffrutescent species in all community/treatment combinations. Log_e was used in diversity calculations.

RESULTS

Herbaceous Ordination Analysis

CCA ordination and Monte Carlo permutation tests identified elevation (p=0.005)

Table 2. Mean relative cover (%)[a] for herbaceous species occurring in the seven community/treatment combinations (SC: Sand Pine Scrub Control, S02: Sand Pine Scrub 2002 Burn, LLC: Longleaf Control, LL00: Longleaf 2000 Burn, LL02: Longleaf 2002 Burn, EC: Ecotone Control, E00: Ecotone 2000 Burn). Longleaf sites are found at lower elevation and sand pine sites at higher elevation.

	Relative Cover						
Species Name	SC	S02	LLC	LL00	LL02	EC	E00
Andropogon gyrans Ashe	0	0	0	0.78	0	0	0
Andropogon spp. L.	0	0	0	0	0	0	0.89
Andropogon ternarius Michx.	0	0	0	0.1	0	0	0.38
Andropogon virginicus var. *glaucus* Hack.	0	0	0	0	0	0	0.91
Andropogon virginicus var. *virginicus* L.	0	0	0	0	0	0.41	0
Aristida beyrichiana Trin.& Rupr.	0	0	4.04	0	3.61	0.03	0
Aristida purpurascens var. *Tenuispica* (A.S. Hitchc.) Allred	0	0	0.21	0	0	0	0.10
Aristida spp. L.	0	0	2.44	0	0	0	0.07
Baptisia lanceolata (Walt.) Ell.	0.07	0	0	0	0	2.76	0
Bulbostylis ciliatifolia (Ell.) Fern.	0	0	0	0	0	0	0.38
Calamovilfa curtissii (Vasey) Schribn.	0	0	10.85	0	17.68	0	0
Cladonia spp. Hill ex P.Browne	59.43	0	2.41	1.39	5.22	23.47	7.73
Conradina canescens Gray	0	0	0	1.71	0	0	0
Crotalaria rotundifolia Walt. ex J.F. Gmel.	0	0	0.24	0	0	0	0

continued

[a] Relative cover means are calculated from the four sampling periods.

Table 2. Continued.

Species Name	Relative Cover SC	S02	LLC	LL00	LL02	EC	E00
Cyperaceae Family	0	0	0	0.23	0	0.01	0
Dichanthelium oligosanthes var. *oligosanthes* (J.A.Schultes) Gould	0	0	0.19	3.02	0.05	0.48	1.43
Dichanthelium ovale var. *ovale* (Ell.) Gould & C.A. Clark	0	0	0.16	1.95	0	3.97	5.25
Dichanthelium strigosum var. *leucoblepharis* (Trin.) Freckmann	0	0	0.88	1.02	4.09	3.91	2.07
Eriogonum tomentosum Michx.	0	0.09	0	0	0	0.51	0
Eupatorium capillifolium (Lam.) Small	0	0	0	1.75	0	0.01	1.91
Euphorbia inundata Torr. ex. Chapman.	0	0.82	0.82	0.23	0.57	0.94	1.10
Euphorbia spp. L.	0	6.98	0.21	0	4.55	0	0
Galactia regularis (L.) B.S.P.	0	0	0	0.36	0	0	1.85
Gaylussacia frondosa (L.) Torr. & Gray ex Torr.	0	0	0.21	0	0	0	0
Gelsemium sempevirens (L.) St. Hill	0	0	0	0	0	0.11	0
Gnaphalium falcatum Lam.	0	0	0	1.13	0	0	0
Liatris spp. Gaenrtn. ex Schreb.	0	0	0	0	0	0	3.64
Ludwigia maritima Harper	0	0	0	0.43	0	0	0
Lupinus diffusus Nutt.	0	0	0	0.40	0	0	0
Mimosa quadrivalvis L.	0	0	0	4.13	0	0	0
Panicum rigidulum Bosc ex Nees	0	0	0	0	0	0.34	0
Panicum virgatum L.	0	0	1.93	6.58	6.23	0	0
Pityopsis graminifolia (Michx.) Nutt.	0.06	0	0.08	2.57	0	0.04	0.50
Pluchea spp. Cass.	0	0	0	0.57	0	0	0
Poaceae Family	0.06	0	0.64	0	0	0.2	0
Polygonella polygama (Vent.) Engelm. & Gray	0	0	0.21	0	0.91	1.17	0.03
Pteridium aquilinum (L.) Kuhn	0	0	0.7	0	3.27	0	0
Rhexia alifanus Walter	0	0	1.01	6.32	0.06	0	0
Rhexia mariana L.	0	0	0	0	0	0.01	0
Rhynchospora megalocarpa Gray	12.43	28.02	0.24	0	0	15.61	23.07
Schizachyrium scoparium (Michx.) Nash	0.19	0	1.12	2.58	5	0.14	3.96
Serenoa repens (Bartr.) Small	17.16	44.09	63.23	50.67	38.08	39.64	40.84
Seymeria cassioides (G.F. Gmel.) Blake	0	0	0	0	0	0.05	0
Solidago odora Ait.	0	0	1.54	0	0	0.17	0.02
Stylisma patens (Desr.) Myint	0	0	0	0.23	0.91	0.34	0.98
Tradescantia ohiensis Raf.	0	0	0	0	0	0.5	0
Tragia urens L.	0	0	0	0.17	0	0	1.11
Vitis rotundifolia Michx.	0.01	0	0	0	0	0	0
Xyris caroliniana Walt.	0	0	0	1.65	0.17	0	1.42
Yucca filamentosa L.	10.59	0	1.65	0.06	5.47	0.16	0

and time since last fire (p=0.005) as the most influential environmental variables in determining the distribution of herbaceous species. The first species axis was most highly correlated with elevation (r^2 =0.3071) and the second species axis with time since fire (r^2=0.1359). The first two axes accounted for approximately 68% of the variation that could be described by all measured environmental variables. For all CCA analysis, little additional variation was explained with more than two species axes.

The plot ordination segregated lower plots dominated by longleaf pine (the right side of the diagram) from higher sites (ecotone and sand pine scrub plots on the left) (Figure 1). Species most closely associated with lower sites included *Aristida* L. species, *Calamovilfa curtissii*, and *Panicum virgatum L.*, *Rhexia alifanus* Walter, *Gnaphalium falcatum* Lam. (Table 2), while *Baptisia lanceolata* (Walt.) Ell., *Cladonia* Hill ex P. Browne species, *Eriogonum tomentosum* Michx., *Rhynchospora megalocarpa* Gray, and *Yucca filamentosa* L. were closely associated with higher sites. Depth to water table was not assessed for every plot, but personal field observations and soil profile description (Table 1) indicate the elevation gradient was linked to a subsurface water gradient.

Burned sites were also separated from their respective long-unburned sites along the time since last fire gradient (Figure 1). Species most closely associated with sites long unburned included *B. lanceolata*, *Cladonia* species, and *Crotalaria rotundifolia* Walt. ex J.F. Gmel. (Table 2), while *Andropogon* L. *and Schizachyrium* Nees species, *Galactia regularis* (L.) B.S.P., *Eupatorium capillifolium* (Lam.) Small, *Euphorbia* L. species, *Liatris* Gaertn. ex Schreb. species, and *Xyris caroliniana* Walt. were associated with burned sites.

Shannon Weiner diversity indices indicated longleaf pine and ecotonal long-unburned sites were equally diverse for the herbaceous layer (H'=2.80 and 2.86, respectively), while fire-suppressed sand pine scrub sites were considerably less diverse (H'=1.29) (Table 3). *Calamovilfa curtissii*, an endemic Florida grass listed as threatened by the State of Florida and restricted to four coastal Florida counties (Wunderlain and Hansen 2004), represented a higher proportion of relative cover in fire suppressed longleaf pine sites, but did not occur in either long-unburned sand pine scrub or ecotonal sites (Table 2).

Table 3. Shannon Weiner's diversity indices (H'), richness, and evenness for herbaceous and woody species occurring in the seven community/treatment combinations (SC: Sand Pine Scrub Control, S02: Sand Pine Scrub 2002 Burn, LLC: Longleaf Control, LL00: Longleaf 2000 Burn, LL02: Longleaf 2002 Burn, EC: Ecotone Control, E00: Ecotone Burn). Longleaf sites are found at lower elevation and sand pine sites at higher elevation.

	Site	H'	Richness	Evenness
Herbaceous	SC	1.29	7	0.66
	S02	1.15	4	0.83
	LLC	2.80	20	0.94
	LL00	3.04	24	0.96
	LL02	2.38	14	0.90
	EC	2.86	24	0.90
	E00	2.85	21	0.94
Woody	SC	2.90	28	0.87
	S02	2.08	12	0.84
	LLC	2.69	21	0.88
	LL00	2.41	13	0.94
	LL02	2.38	13	0.93
	EC	2.74	24	0.86
	E00	2.69	18	0.93

Woody Ground Cover Ordination Analysis

Elevation and time since last fire also influenced the distribution of woody ground cover. The first CCA species axis was most highly correlated with elevation (r^2 = 0.4698) and the second with time since fire (r^2 = 0.0983). Litter depth was also significant (p=0.0200). The first two axes accounted for approximately 82% of the variation that could be described by all measured environmental variables.

Species most closely associated with lower sites included *Gaylussacia mosieri* Small, *I. glabra*, *Kalmia hirsuta* Walt., *P. palustris*, and *Vaccinium myrsinites* Lam. Species associated most closely with higher sites included *Ilex vomitoria* Ait., *Q. chapmanii*, *Q. geminata*, and *Q. myrtifolia* (Table 4).

Burned sites (top portion of ordination diagram) are segregated from respective long-unburned sites (lower portion of diagram) in ordination space (Figure 2). Woody ground cover species associated most closely with burned sites included *P. clausa* and *Polygonella polygama* (Vent.) Engelm. & Gray., while *Ceratiola ericoides* Michx., *G. mosieri*, *Kalmia hirsute*, *Vaccinium elliottii* Chapman, and *Viburnum* L. species were associated with sites long unburned (Table 4).

Sapling-Overstory Ordination Analysis

The first species axis of the sapling-overstory ordination plot was most highly correlated with elevation (r^2= 0. 5162) and the second axis with litter depth (r^2=0.1930), though time since fire also exhibited high correlation with the second axis. However, as with the herbaceous and woody ground cover ordinations, elevation (p=0.005) and time since last fire (p=0.005) were the most highly significant variables. Litter

Table 4. Mean relative density for woody groundcover species (dbh<1cm) for the seven community/treatment combinations (SC: Sand Pine Scrub Control, S02: Sand Pine Scrub 2002 Burn, LLC: Longleaf Control, LL00: Longleaf 2000 Burn, LL02: Longleaf 2002 Burn, EC: Ecotone Control, E00: Ecotone 2000 Burn). Longleaf sites are found at lower elevation and sand pine sites at higher elevation.

	Relative Density						
Species Name	SC	S02	LLC	LL00	LL02	EC	E00
Asimina parviflora (Michx.) Dunal	0.02	0	0	0	0	0	0
Ceratiola ericoides Michx.	0	0	0	0	0	0.76	0
Chrysoma pauciflosculosa (Michx.) Greene	0	0	0	0	0	0	0.67
Clinopodium coccineum (Nutt. ex Hook.) Kuntze	0.05	0	0	0	0	0.28	5.22
Conradina canescens Gray	0.26	0	3.86	10.10	0	0.66	10.11
Crataegus spp. L.	0	0	0	0	0	0	0
Gaylussacia mosieri Small	0	0	1.74	0	0	0	0
Hypericum spp L.	0	0	0	0	0	0	0
Ilex glabra (L.) Gray	0	0	36.04	30.01	47.79	0	0
Ilex vomitoria Ait.	4.69	1.38	0.22	0.86	0.61	1.11	0
Kalmia hirsuta Walt.	0	0	1.23	0	0	0	0
Licania michauxii Prance	2.60	0.15	26.77	33.93	32.12	15.55	19.95
Magnolia grandiflora L.	0	0	0	0	0	0	0
Magnolia virginiana L.	0.04	0	0	0	0	0	0
Morella cerifera (L.) Small	0	0	0	0	0	0	0
Osmanthus americanus (L.) Benth. & Hook. f. ex Gray	0.23	0	0	0	0	0	0
Pinus clausa (Chapm. Ex Engelm.) Vasey ex Sarg.	0.89	0	0.15	1.62	0	9.70	18.57
Pinus elliottii Engelm.	0	0	0	0	0	0	0
Pinus palustris P. Mill.	0	0	0.12	0	1.30	0	0
Polygonella polygama (Vent.) Engelm. & Gray	0	0	0.20	0	0	2.46	5.69
Prunus umbellata Ell.	0.17	0	0	0	0	0	1.67
Quercus chapmanii Sarg.	4.22	0	0	0	0	4.8	1.14
Quercus geminata Small	17.09	13.40	18.92	7.72	3.54	13.15	11.87
Quercus incana W. Bartr.	0.06	0	0	0	0	0	0
Quercus laevis Walt.	0	0	1.25	0	0	0.41	2.87
Quercus laurifolia Michx.	0.73	0	0.40	0	0	0.61	1.33
Quercus myrtifolia Willd.	65.37	83.25	3.37	0	12.63	47.06	16.25
Quercus pumila Walt.	0	0	0	0	0	0	0
Quercus virginiana P. Mill	0.28	0	0	0	0	0	0
Unknown *Quercus* spp L.	0.11	0	0	0	0	0	0
Vaccinium arboreum Marsh.	1.64	1.15	0	1.79	2.02	3.02	4.66
Vaccinium corymbosum L.	1.04	0.65	0	0	0	0.22	0
Vaccinium myrsinites Lam.	0	0	5.71	13.97	0	0	0
Vaccinium stamineum L.	0.44	0	0	0	0	0.09	0
Viburnum spp. L.	0.05	0	0	0	0	0	0
Yucca filamentosa L.	0	0	0	0	0	0.15	0

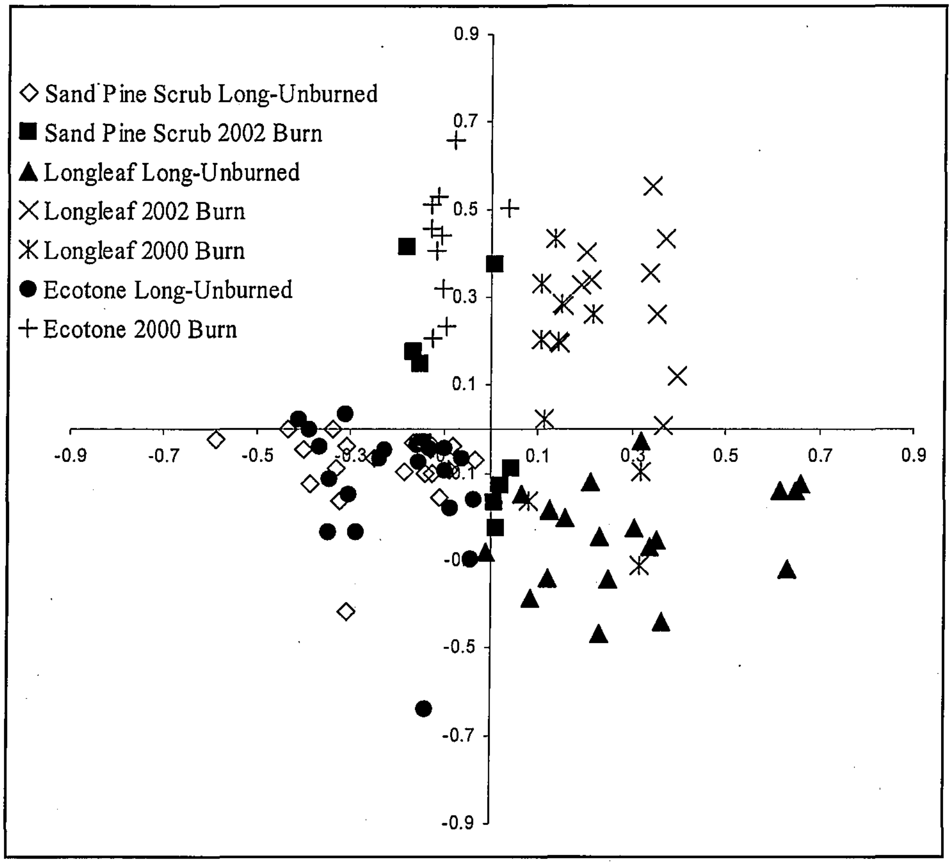

Figure 2. Canonical correspondence analysis (CCA) for woody groundcover species at Naval Live Oaks with ordination of sample plots displayed. The first CCA axis was most highly correlated with elevation. The second CCA axis was most highly correlated with time since fires.

depth and percent closed canopy were also significant. The first two axes explained approximately 83% of the variation that could be described by all measured environmental variables.

Ilex glabra, *Magnolia virginiana* L., *P. elliottii*, and *P. palustris* were species associated with elevationally depressed sites (left of the diagram) (Figure 3). Sites on higher ground included *Hypericum* L. species, *Osmanthus americanus*, *Vaccinium stamineum* L., *Q. chapmanii*, and *Q. myrtifolia* (right of the diagram).

Recently burned and long-unburned sites were differentiated along a time since fire gradient for sapling-overstory species. *Ceratiola ericoides*, *I. glabra*, *I. vomitoria*, *M. virginiana*, and *Viburnum* species were most commonly associated within long-unburned sites (top of diagram) (Figure 3), while *Crataegus* L. species, *P. elliottii*, *P. palustris*, and *Prunus umbellata* Ell. were associated with burned sites (Tables 5 and 6).

Effects of Burning

Cladonia species were abundant in long-unburned sand pine scrub sites absent from recently burned sand pine scrub, and were lower in relative frequency in burned ecotonal sites compared to long-unburned ecotonal sites. Also, burned sand pine scrub and ecotonal sites had greater relative cover of *Rynchospora meglocarpa* by 125 and 48%, respectively, compared to long-unburned sites (Table 2). Sand pine seedlings were not found in burned sand pine scrub two years and eight months after burning. However, the frequency of sand pine seedlings was 200% greater in burned 2000 longleaf sites compared to long-unburned longleaf sites.

While herbaceous species composition differed little among longleaf sites, relative cover of species such as *Aristida spp.*, *Calamovilfa curtissii* and *Dicanthelium strigosum* (Muhl.Ex Ell.) Freckmann and *Andropogon gyrans* Ashe, *A. ternarious* Michx., *Euphorbia inundata* Torr. ex Chapman were higher in the 2002 and 2000 burn, respectfully, compared to long-unburned sites. However, relative frequency for these herbaceous species was less than 17% for burned and long-unburned longleaf sites.

Absolute density of woody ground cover in burned sand pine scrub sites was significantly greater than long-unburned sand pine scrub sites within eight months after burning (Table 7). Absolute density was 53% less in longleaf pine sites burned in 2000, while 2002 burn and long-unburned sites did not differ significantly. Absolute density was significantly less by 52% in recently-burned ecotonal sites compared to long-unburned sites.

Fire reduced the number of sapling-sized species within all of the communities (Table 7). Sapling absolute density in burned sites was 99, 80, 94, and 72% less for sand pine scrub, 2000 longleaf, 2002 longleaf, and ecotone, respectively, compared to long-unburned sites. Overstory density in burned sites was 78, 50, and 55% less for sand pine scrub, 2000 longleaf and ecotone, respectively, compared to long-unburned sites. However, overstory density in burned 2002 longleaf sites was similar to long-unburned longleaf sites.

DISCUSSION

Fire-Suppressed Communities

All communities in this study endured more than 50 years of fire suppression and appear structurally different from their pre-Colonial fire-maintained counterparts. However, they retained much of their respective species composition. Sand pine scrub sites occurred on the highest elevations of NLO, and no water table was evident at depths of 203 cm. Longleaf pine sites best described as flatwoods were lowest in elevation with some plots occasionally flooded. Ecotone topography and, therefore, depth to water table varied. Similar to some central Florida scrub communities, the fire-suppressed sand pine scrub consisted of a midstory

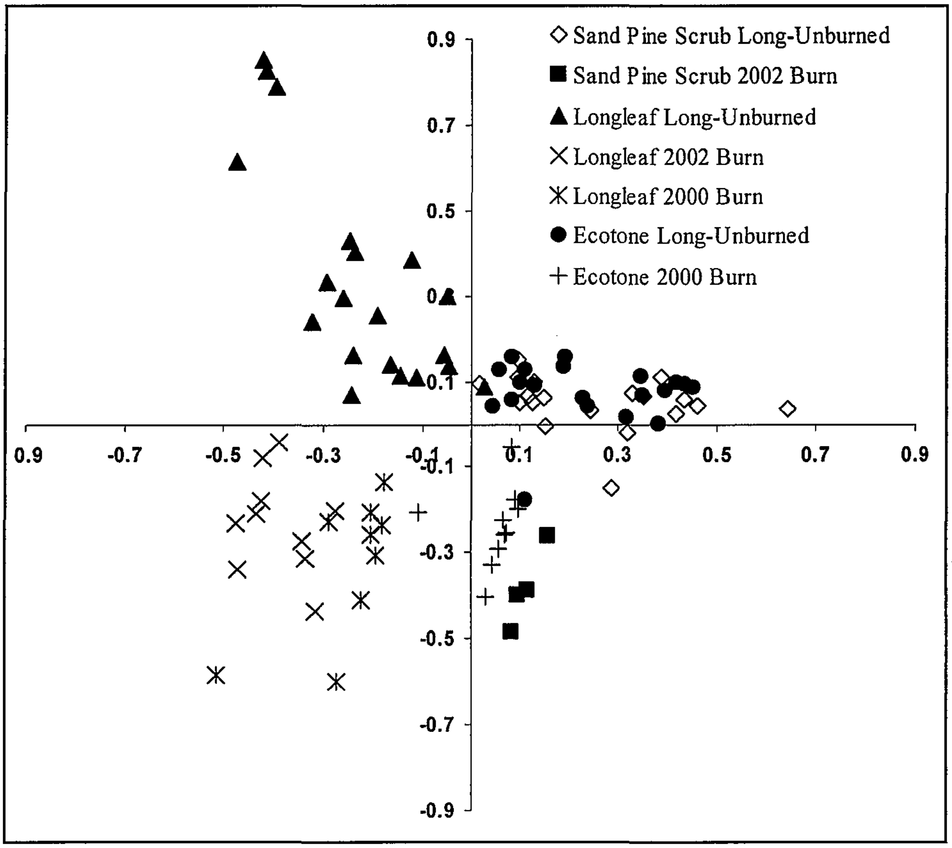

Figure 3. Canonical correspondence analysis (CCA) for sapling and overstory species at Naval Live Oaks with ordination of sample plots displayed. The first CCA axis was most highly correlated with elevation. The second CCA axis was most highly correlated with litter depth and time since fire.

dominated by xerophytic oaks with a scattered canopy of *P. clausa* and woody seedlings and reindeer lichens (*Cladonia* spp.) dominating the ground cover. Ground cover dominated by lichens also occurs in similar evergreen scrub forest of Georgia and Alabama (Menges and Hawkes 1998). However, the relative preponderance of evergreen oaks, especially *Q. geminata* in the overstory and the mortality of *P. clausa* individuals in the canopy (pers. observation), suggest fire-suppressed sand pine scrub sites are succeeding towards a xeric hammock community at NLO (Veno 1976; Myers 1985, 1990; Menges et al. 1993).

Compared to long-unburned central Florida scrub communities (Greenberg et al. 1995), herbaceous species richness was lower in NLO sand pine scrub. Panhandle sand pine scrub may be lower in herbaceous richness compared to central Florida scrub because of their relatively younger geologic age, smaller area, and isolation from larger scrub communities. Also, competition with fire-intolerant *Cladonia* species (Johnson and Abrahamson 1990) and the lack of gaps in the shrub-dominated matrix may have limited the presence of herbaceous species (Menges and Hawkes 1998). Woody shrub (1 cm≤dbh≤10 cm) richness in NLO long-unburned sand pine scrub was comparable to shrub richness in other long-term fire suppressed scrub areas (Greenburg et al. 1995; Abrahamson and Abrahamson 1996).

Numerous studies have documented the structural and compositional vegetation changes, which occur within long-unburned longleaf pine sites (Myers 1985; Peroni and Abrahamson 1986; Menges et al. 1993; Brockway and Lewis 1997; Maliakal et al. 2000; McCay 2000). *Pinus clausa*, which is intolerant of frequent fire, was present in relative abundance within the fire suppressed longleaf pine communities of NLO. Many studies report the development of a midstory of fire-intolerant species within long-unburned longleaf sites (Myers 1985; Brockway and Lewis 1997; Gilliam and Platt 1999; McCay 2000). Relative frequency and cover of herbaceous species characteristically prolific in fire-maintained longleaf were noticeably low in longleaf sites of NLO. However, species richness (richness=36) and diversity (H'=3.2) of understory plants (woody and herbaceous ground cover) was appreciably greater than that found in other studies of fire-suppressed longleaf pine sites (Brockway and Lewis 1997; Maliakal et al. 2000). The longleaf pine regeneration at NLO was essentially absent. The proliferation of a midstory component and accumulation of litter caused by lack of recurrent fire ultimately results in the diminution of the herbaceous layer (Brockway and Lewis 1997; Maliakal et al. 2000) and reduction in longleaf pine recruitment (Gilliam and Platt 1999).

Effects of Fire

Succession in the fire-maintained communities of NLO can be classified as inhibitory succession because the species, which comprise these communities, are present immediately following fire either as sprouts or in-site seedlings and exclude or suppress subsequent colonization of other species (Connell and Slayter 1977; Abrahamson 1984a). CCA determined that burning was the second most important variable in determining species distribution among communities.

The 2002 burn in NLO sand pine scrub was a typical stand-replacing scrub fire with a large portion of the above ground plant tissue destroyed. Except for *Q. geminata*, all sapling species found in long-unburned sand pine scrub were absent from burned sand pine scrub. Vigorous sprouts of *Q. myrtifolia*, *Q. geminata*, and *S. repens* blanketed the burned sand pine scrub site within months after the fire. Lake Wales Ridge, Florida, plant communities dominated by sprouting species recover their pre-burn aspect within 2-4 years (Abrahamson 1984a) as opposed to rosemary scrub, which require 10-12 years to recover to pre-burn levels (Johnson and Abraha-

Table 5. Relative density for woody species (1 cm<dbh<10 cm) for the seven community/treatment combinations (SC: Sand Pine Scrub Control, S02: Sand Pine Scrub 2002 Burn, LLC: Longleaf Control, LL00: Longleaf 2000 Burn, LL02: Longleaf 2002 Burn, EC: Ecotone Control, E00: Ecotone 2000 Burn). Longleaf sites are found at lower elevation and sand pine sites at higher elevation.

	Relative Density						
Species Name	**SC**	**S02**	**LLC**	**LL00**	**LL02**	**EC**	**E00**
Ceratiola ericoides Michx.	0.62	0	0	0	0	1.43	0.71
Chamaecyparis thyoides (L.) B.S.P.	0.08	0	0	0	0	0	0
Chrysoma pauciflosculosa (Michx.) Greene	0	0	0	0	0	0.78	0
Conradina canescens Gray	0.15	0	0.42	0	0	1.09	0
Crataegus spp L.	0	0	0.71	0	0	0.25	1.67
Hypericum spp L.	0	0	0	0	0	0.18	0
Ilex glabra (L.) Gray	0	0	34.38	0	0	0	0
Ilex vomitoria Ait.	0.59	0	3.16	0	0	1.06	0
Magnolia virginiana L.	0.14	0	0.42	0	0	0.24	0
Morella cerifera (L.) Small	0.87	0	0	0	0	0	0
Osmanthus americanus (L.) Benth. & Hook. f. ex Gray	1.49	0	0	0	0	0	0
Pinus clausa (Chapman ex Engelm) Vasey ex Sarg.	1.94	0	6.65	0	40.00	22.53	10.83
Pinus elliottii Engelm.	0	0	2.42	0	20.00	0	0
Pinus palustris Mill.	0	0	1.67	0	40.00	0	0
Prunus spp L.	1.07	0	0	0	0	0	0
Prunus umbellata Ell.	0.17	0	0	0	0	0.06	1.25
Quercus chapmanii Sarg.	11.16	0	0.71	0	0	1.25	0
Quercus geminata Small	12.43	100	31.76	47.83	0	14.39	16.57
Quercus incana Bartr.	0.45	0	0	0	0	0	0
Quercus laevis Walt.	0.76	0	6.05	0	0	10.95	36.20
Quercus laurifolia Michx.	0	0	0.42	0	0	2.34	4.82
Quercus myrtifolia Willd.	47.92	0	6.89	0	0	35.87	22.53
Vaccinium arboreum Marsh.	12.17	0	1.84	52.17	0	7.28	2.08
Vaccinium corymbosum L.	5.23	0	2.50	0	0	0.31	0
Vaccinium stamineum L.	2.63	0	0	0	0	0	3.33

mson 1990). Fire at 5-10 year intervals does not change the dominant species in oak-saw palmetto scrub in central Florida (Schmalzer 2003). *P. clausa* seedling appearance reportedly is delayed three years post burning (Abrahamson 1984b). At NLO, *P. clausa* seedlings were absent eight months to two years after burning from sand pine scrub and longleaf sites but increased in frequency by 200% three years after burning in longleaf sites. Thus suggesting that in the absence of frequent fire, *P. clausa* can rapidly reinvade longleaf sites contiguous to sand pine scrub.

Apart from *R. megalocarpa*, the herbaceous response to burning sand pine scrub was limited and species richness declined. Nevertheless, species not present in long-unburned sites were noted in burned areas. An increase in *R. megalocarpa* after fire also occurs in central Florida scrub (Carrington 1997). Abrahamson and Abrahamson (1996) reported a lack of herbaceous response in winter-burned scrub; however, they noted species in the burned areas not found in NLO's long-unburned sites.

Herbaceous cover and richness in longleaf pine communities reportedly increases one- to two years following burning (Christensen 1981; Gillam and Christensen 1986). Increases were attributed to elevated irradiance due to shrub removal and increased soil nutrient levels (Wells et al. 1973). Although the 2002 fire in the longleaf pine sites resulted in the removal of all midstory evergreen oaks, herbaceous species richness was lower in the 2002 sites than in that of the long-unburned plots. However, non-weedy species such as *Dichanthelium/Panicum* spp. and *Calamovilfa curtissii* had appreciably more cover in the 2002 burned sites compared to the long-unburned sites. A depauperate

Table 6. Mean Relative density (%) for woody species (>10cm dbh) for the seven community/treatment combinations (SC: Sand Pine Scrub Control, S02: Sand Pine Scrub 2002 Burn, LLC: Longleaf Control, LL00: Longleaf 2000 Burn, LL02: Longleaf 2002 Burn, EC: Ecotone Control, E00: Ecotone 2000 Burn). Longleaf sites are found at lower elevation and sand pine sites at higher elevation.

	Relative Density						
Species Name	SC	S02	LLC	LL00	LL02	EC	E00
Magnolia grandiflora L.	0.42	0	0	1.59	0	0	0
Pinus clausa (Chapman ex Engelm.) Vasey ex Sarg.	30.05	0.77	8.97	9.83	8.84	46.10	73.10
Pinus elliottii Engelm.	0	0	5.93	21.87	12.64	0	0
Pinus palustris Mill.	0	0	70.87	58.17	69.25	1.08	6.68
Quercus chapmanii Sarg.	4.77	0	0	0	0	0	0
Quercus geminata Small	51.88	70.99	8.89	8.54	4.44	20.96	6.53
Quercus laevis Walt.	6.47	8.33	4.89	0	4.83	31.55	13.69
Quercus laurifolia Michx.	3.12	0	0	0	0	0	0
Quercus myrtifolia Willd.	3.29	18.75	0.45	0	0	0	0

Table 7. Mean basal area[a] and densities (± 1 SE) for woody ground cover, sapling, and overstory[b] classes in the seven community/treatment combinations. Longleaf sites are found at lower elevation and sand pine sites at higher elevation.

Treatment	Basal area (m^2/ha)	Woody groundcover density[c] (stems/ha)	Sapling density (stems/ha)	Overstory density (stems/ha)
Sand Pine Scrub Control	21 (5)	287056 (24561)	9280 (683)	432 (56)
Sand Pine Scrub 2002 Burn	1 (1)	455333 (60968)	20 (20)	93 (42)
Longleaf Control	359 (63)	195083 (32690)	2670 (632)	500 (40)
Longleaf 2000 Burn	80 (17)	91500 (23878)	540 (458)	252 (62)
Longleaf 2002 Burn	166 (44)	228000 (50792)	160 (58)	566 (78)
Ecotone Control	170 (32)	176500 (34818)	6480 (749)	613 (49)
Ecotone 2000 Burn	124 (18)	85000 (13170)	1840 (380)	396 (47)

[a] Basal area of woody species > 10cm dbh

[b] All species were suffretescent or completely woody. Woody groundcover class (<1cm dbh), sapling class (1cm<dbh<10cm), and overstory class (>10cm dbh)

[c] Woody groundcover densities are means calculated from the four sampling periods

seed bank (Ruth 2003) and the lack of seed dispersal from adjacent sites may limit the potential for increased herbaceous richness with the reintroduction of fire for all of the communities.

There were no appreciable differences in the species richness or diversity for the herbaceous layer burned and unburned-ecotonal areas. Diversity for the woody/suffrutescent species also did not differ between burned and unburned areas of the ecotone; however, six fewer woody/suffrutescent species were noted in the burned ecotonal areas. Abrahamson (1984a) also showed that scrubby flatwoods sites similar to many of the NLO ecotonal sites did not reveal appreciable changes in diversity when burned.

CONCLUSIONS

The use of prescribed fire within the vegetation communities of NLO will benefit the restoration and maintenance of species structure and composition. Recurrent prescribed fires (every 1-10 years) in the pine flatwoods are needed to revert this community to a more open canopy with a diminished midstory. These fires will decrease litter levels and allow herbaceous species and longleaf pine to regenerate. However, levels of grazing and logging documented in historical aerial photography in the longleaf pine community has potentially resulted in degradation to the herbaceous layer that fire alone will not remedy. Additional restoration techniques, such as seeding, may be necessary to replace lost or sparse species. If the sand pine scrub at NLO is burned less frequently (every 10-60 years), succession towards xeric hammock can be halted, schlerophyllous oaks can be maintained as a midstory, and gaps can be created which are vital to the recruitment of herbaceous species. Burning on a recurrent basis (every 1-10 years) in ridge ecotone areas could potentially transform these scrub-like communities into longleaf communities.

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