EFFECTS OF TIME-SINCE-FIRE ON SOIL NUTRIENT DYNAMICS IN FLORIDA SCRUBBY FLATWOODS

Jennifer L. Schafer(1,2)* and Michelle C. Mack(1)

(1)Department of Biology, 220 Bartram Hall, University of Florida, P. O. Box 118525, Gainesville, FL 32611-8525
(2)Present address: Department of Plant and Microbial Biology, North Carolina State University, 2115 Gardner Hall, Box 7612, Raleigh, NC 27606

Abstract: *Differences in the volatilization temperatures and sources of inputs of nitrogen (N) and phosphorus (P) suggest that fire will decrease N relative to P over the short term and that N will increase relative to P over the long term after fire. In Florida scrubby flatwoods—a pyrogenic ecosystem that occurs on sandy nutrient-poor soils—we tested the hypotheses that N availability increases with time-since-fire, that P availability decreases with time-since-fire, and that the ratio of available N to P increases with time-since-fire. We measured nutrient availability and soil characteristics in scrubby flatwoods sites along a time-since-fire chronosequence (1, 4, 6, 8, and 10 yr since fire). Resin-exchangeable and* K_2SO_4*-extractable N, soil N and C pools, potential net N mineralization, chloroform-labile microbial N, resin-exchangeable* PO_4^{3-}*, and resin-exchangeable N:P ratios did not differ significantly with time-since-fire. Turnover of organic matter likely controls nutrient availability in scrubby flatwoods; and low organic matter in sandy scrubby flatwoods soils, coupled with sequestration of nutrients in plant biomass, appears to limit accumulation of soil N with time-since-fire. In contrast to many other fire-influenced ecosystems, we did not detect a long-term effect of fire on nutrient availability in scrubby flatwoods.*

Key Words: Carbon pools, nitrogen availability, nitrogen mineralization, nitrogen pools, phosphorus availability, soil pH

Fire consumes plant biomass, litter, and soil organic matter, converting organically bound nitrogen (N) and phosphorus (P) into inorganic forms (Certini, 2005) that might be lost to the atmosphere or returned to the ecosystem in ash. The fate of these elements is likely to differ with fire intensity. Nitrogen volatilization occurs at temperatures as low as 200°C (White et al., 1973), which are commonly reached in fires (Gibson et al., 1990), whereas P is volatilized at temperatures above 774°C (Raison et al., 1985a), which occur rarely and instantaneously (E. Menges, unpublished data). Thus, although soil N (Wilbur and Christensen, 1983; Wan et al., 2001; Turner et al., 2007) and P (Lewis, 1974; Wilbur and Christensen, 1983; Giardina et al., 2000) often increase immediately after fire, the ratio of available N to P might decrease after fire (Schafer and Mack, 2010); approximately twice as much N as P is lost to the atmosphere during fire (Gillon and Rapp, 1989; Cook, 1994). Within several years after fire, P might become relatively less available as it is

---

* Corresponding author. E-mail: jlschafe@ncsu.edu

immobilized by plants and microbes or fixed via geochemical reactions, while soil N might increase as N inputs accumulate (Carter and Foster, 2004).

Previous studies of time-since-fire chronosequences have found that ammonium (NH_4^+), nitrate (NO_3^-), or P can increase (MacKenzie et al., 2004; Durán et al., 2008) or decrease with time-since-fire (Marion and Black, 1988; Wan et al., 2001; DeLuca et al., 2002; Bloom and Mallik, 2006). As a result, soil N:P ratios can increase (Bloom and Mallik, 2006) or decrease (Durán et al., 2008) with time-since-fire. Inconsistent patterns of N and P availability over time might be due to respective differences in controls over nutrient availability. Nitrogen availability is controlled by microbial biomass (Smithwick et al., 2005) and through mineralization and nitrification rates, which might increase or decrease over time-since-fire (Pérez et al., 2004; MacKenzie et al., 2006; Yermakov and Rothstein, 2006) and are positively correlated with soil percent N (Marion and Black, 1988). Phosphorus availability, on the other hand, is correlated with soil pH (Jaggi et al., 2005) and is influenced by phosphatase activity (DeForest and Scott, 2010), soil sorption capacity, and microbial activity (Olander and Vitousek, 2004). Investigation of the effects of fire on controls over nutrient availability can provide insight into the mechanisms affecting N and P availability over time-since-fire.

Florida scrub ecosystems occur on sandy ridges along the Atlantic and Gulf coasts and in the central peninsula (Myers, 1990). Scrub soils are well-drained nutrient-poor quartz sands with low clay content and few weatherable nutrients (Myers, 1990) such that the amount and type of dead organic matter are primary controls on nutrient availability and storage; and high leaching, due to low clay content, contributes to low amounts of soil organic matter (Gholz and Fisher, 1982). Florida scrub is a pyrogenic ecosystem that experiences infrequent high-intensity fires, and scrub species have adapted to fire (Myers, 1990). Most dominant woody species are able to resprout after fire, which allows for rapid post-fire recovery, while some species recruit from seed and have abundant recruitment after fire (Myers, 1990).

In coastal Florida scrub-oak woodlands, soil organic matter is an important supply of inorganic N (McKinley et al., 2009). Plants can take up N from the water table (McKinley et al., 2009), and N mineralization rates are highest in surface soils (Langley et al., 2009). In relation to fire, N fixation by a leguminous vine is an important source of post-fire N inputs (Hungate et al., 1999, 2004), and litter N inputs increase over 7 yr after fire (Hungate et al., 2006). Furthermore, ecosystem N pools are consistent over the first 5 yr after fire due to a decrease in soil N concomitant with an increase in plant and organic N (Johnson et al., 2003). In palmetto flatwoods, a more mesic ecosystem that can occur within the Florida scrub matrix, post-fire pulses of N and P persisted for 3 mo after fire (Schafer and Mack, 2010). Little is known, however, about the effects of fire on nutrient availability in Florida scrub communities such as scrubby flatwoods, which occur along the Lake Wales Ridge in central peninsular Florida. The dominant species in scrubby flatwoods—shrubby oaks, palmettos, and ericaceous shrubs—all resprout within weeks after fire and might utilize nutrients made available by fire. The infertile nature of scrubby flatwoods suggests that a post-fire flux in nutrient availability is likely to be an important source of plant nutrition and that nutrients might be conserved after fire.

Our main objective was to determine how soil nutrients vary from 1 to 10 yr after fire in scrubby flatwoods ecosystems. Specifically, we tested the hypotheses that: N availability and N pools increase with time-since-fire; P availability decreases with time-since-fire; and the ratio of available N to P increases with time-since-fire. We also measured soil carbon pools, soil pH, microbial N, and N mineralization and nitrification rates to gain a better understanding of the factors that might influence fire effects on nutrient availability.

MATERIALS AND METHODS—*Study site*—This study was conducted at Archbold Biological Station (ABS) in Highlands County, Florida (27° 10′ 50″ N, 81° 21′ 0″ W), which is near the southern tip of the Lake Wales Ridge (Fig. 1). Archbold Biological Station typically has warm wet summers and cool dry winters (Abrahamson et al., 1984). Mean annual precipitation is 136.5 cm (ABS weather records, 1932–2004), and mean annual temperature is 22.3°C (ABS weather records, 1952–2004). Archbold Biological Station is divided into burn units, which have been managed with prescribed fires for over 35 yr.

Our research focused on scrubby flatwoods, a distinctive plant community of Florida scrub. Scrubby flatwoods are dominated by shrubby oaks (Fagaceae), palmettos (Arecaceae), and ericaceous shrubs (Ericaceae). The shrubs are primarily evergreen with an average height of 1–2 m, and herbaceous species are sparse (Abrahamson et al., 1984). Scrubby flatwoods experience fire return intervals of 8–16 yr (Menges, 2007), and the dominant vegetation resprouts after fire (Menges and Kohfeldt, 1995). Sustained maximal fire temperatures at the soil surface reach 352°C, and instantaneous maximal temperatures can reach 865°C (E. Menges, unpublished data). Soils are entisols derived from paleo dunes (Abrahamson et al., 1984) that have no horizon development, little organic matter, and low exchange capacity and base saturation (Brown et al., 1990).

Field and laboratory sampling—In May 2005, we established fifteen 30 × 30-m plots in scrubby flatwoods communities, three each in sites 1, 4, 6, 8, and 10 yr since fire (hereafter referred to as 1-, 4-, 6-, 8-, and 10-yr plots or sites). All plots were established in scrubby flatwoods dominated by scrub oak (*Quercus inopina* ASHE) on flat or gently sloped sites. The 1-, 6-, 8-, and 10-yr sites were burned in prescribed summer fires (i.e., in May, June, or July), while the 4-yr sites were burned in a February wildfire. All fires were of moderate to high intensity (ABS fire records); above-ground vegetation was consumed by fire, and the dominant vegetation (i.e., shrubs) resprouted from below ground after fire. In each plot, we established 30-m transects across each plot that were initiated at 5, 10, 15, 20, and 25 m (Fig. 1).

The constraints of prescribed burning and the large scale of wildfires make it difficult to replicate fires (van Mantgem et al., 2001) and limited our ability to establish plots that were true replicates (Hurlbert, 1984). Within a time-since-fire treatment, however, we located the three plots in different burn units when possible (Fig. 1). When plots were located in the same burn unit, they were separated by at least 150 m, a distance deemed great enough to minimize bias from lack of independence (Parsons and Gosper, 2011). Furthermore, post-fire conditions exhibit high patch-scale heterogeneity (van Mantgem and Schwilk, 2009), indicating that plots within the same burn scar might be considered to be spatially independent. We considered each of our plots to represent an independent replicate of the time-since-fire treatment, but we acknowledge that our results should be extrapolated beyond our study area with caution. We did not include unburned control plots because scrubby flatwoods in our study region are managed with fire; at the time of our site selection, the maximal age of sites across the landscape that met our site requirements was 10 yr.

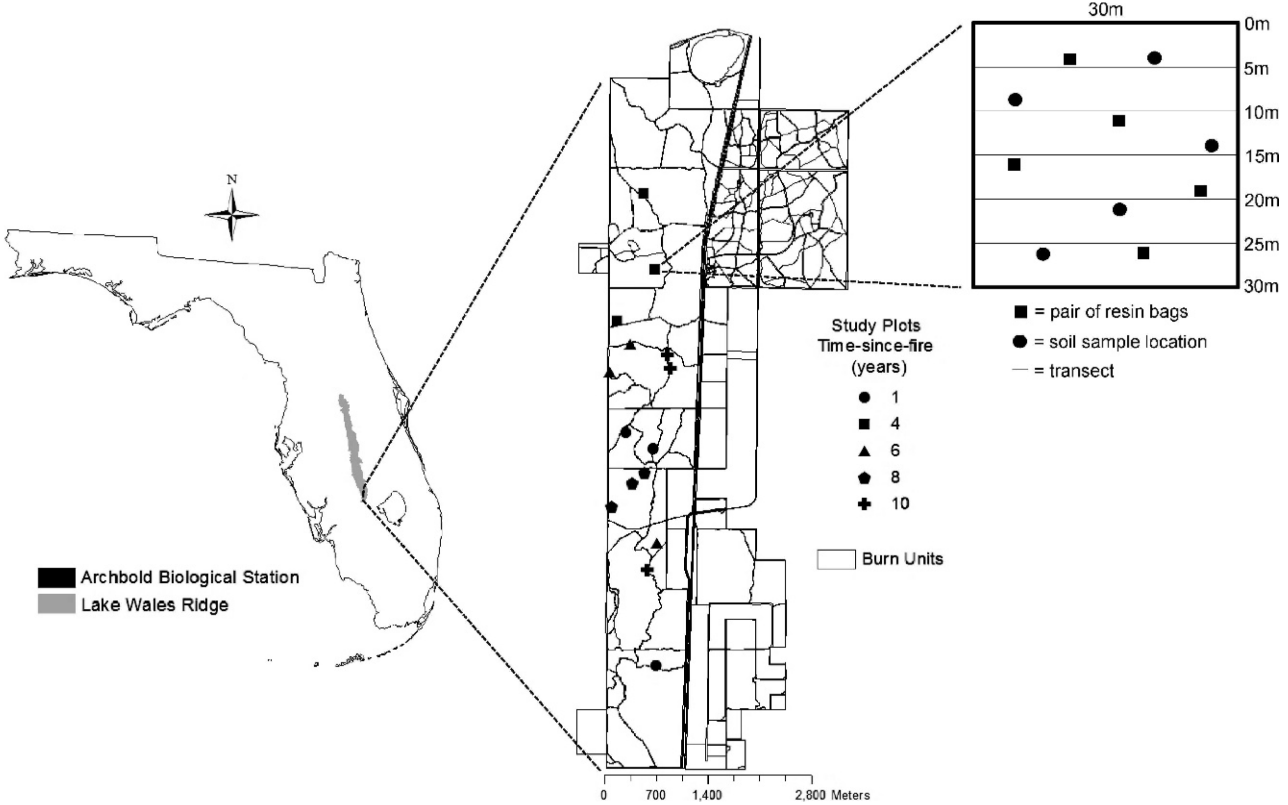

FIG. 1. Map of study site showing the location of Archbold Biological Station in Florida, the location of study plots at Archbold Biological Station, and an example of the soil-sampling design in a study plot.

In all plots, we used ion-exchange resins (anion [AG 1-8X chloride form] and cation [AG 50W-X8 hydrogen form]; Bio-Rad, Hercules, CA) to measure soil ammonium (NH_4^+), nitrate (NO_3^-), and phosphate (PO_4^{3-}). At a random location on each transect, separate anion and cation exchange resin bags (5 × 5 cm) were placed in the top 5 cm of the soil. Resin bags were in the field for 3-mo intervals (new resin bags buried adjacent to removed bags) for 1 yr continuously (June 2005–June 2006). Before being buried in the field, anion and cation resin bags were charged with 2 M HCl and 2 M NaCl, respectively. After anion and cation bags were removed from the field, they were rinsed and extracted with 50 mL of 0.5 M HCl and 0.5 M NaCl, respectively, and shaken for 6 h. Resin extracts were frozen and taken to the University of Florida (UF) where NO_3^-, NH_4^+, and PO_4^{3-} concentrations were measured colorimetrically on a continuous-flow autoanalyzer (Astoria-Pacific, Inc., Clackamas, OR). We averaged values for each plot, so that the plot was the statistical unit, and we calculated total resin-exchangeable nutrients over 1 yr by summing NH_4^+, NO_3^-, total inorganic N, and PO_4^{3-} in each sample period. Resin-exchangeable N:P ratios were calculated from 1-yr sums of total inorganic N and total PO_4^{3-} for each plot.

In two plots for each time-since-fire treatment (10 plots total; time constraints preventing us from sampling all plots), we collected soil from a random location on each transect. During June and July 2005, one soil core (diameter = 8 cm) was taken at each location (five per plot) and divided into 0–5-, 5–10-, 10–15-, and 15–20-cm depths for a total of 20 soil samples per plot. Within 24 h of collection, soil samples were passed through a 2 mm-mesh sieve. Soils were sub-sampled for measurement of gravimetric soil moisture, pH, total percentages of N and C, inorganic and organic N concentrations, N mineralization and nitrification rates, and microbial N. Soil pH was measured on a slurry of 10 g of air-dried soil and 10 mL of de-ionized (DI) water (Thomas, 1996) with an electronic pH meter (Thermo Orion 250A+, Orion Research, Inc., Boston, MA). A subsample of soil was dried at 60°C for 48 h, hand ground with a mortar and pestle, and analyzed for percentages of N and C at UF on an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA). We used the mean bulk density for each depth for each time-since-fire treatment to calculate N and C pools.

To measure inorganic (NH_4^+ and NO_3^-) and organic N concentrations, a sub-sample (~10 g) of field moist soil was extracted with 50 mL of 0.5 M K_2SO_4, filtered through Whatman no. 1 filter paper that was pre-leached with 0.5 M K_2SO_4. Extracts were kept frozen until measurement of N concentrations. Concentrations of NH_4^+ and NO_3^- were measured colorimetrically on a continuous-flow autoanalyzer at UF. We measured K_2SO_4-extractable organic N using the persulfate oxidation digestion method (Sollins et al., 1999). All N was converted into NO_3^-, the concentration of which was measured colorimetrically on a continuous-flow autoanalyzer. To measure the concentration of organic N, the K_2SO_4-extractable inorganic N measured in the undigested samples was subtracted from the NO_3^- concentration of the digested samples.

We used an aerobic laboratory incubation at field capacity to measure potential N mineralization rates. Soil extractions performed immediately after collection (described above) were used to measure initial NH_4^+ and NO_3^- concentrations. A second sub-sample of 10 g of field moist soil was contained in a specimen cup and stored in a refrigerator (~4°C) for 2 d until gravimetric moisture content was measured. The average gravimetric moisture content was measured from all soils within each plot, and the same amount of DI water was added (169–226 μL) to bring the soils to field capacity. Specimen cups were then stored in the dark at room temperature (~23°C) for 1 wk, after which 50 mL of 0.5 M K_2SO_4 was added to the soil. Extracts were filtered, stored, and analyzed for NO_3^- and NH_4^+ as described above to measure final N concentrations after 1 wk of incubation. Net rates of N mineralization and nitrification were calculated from the difference in NH_4^+ and NO_3^- concentrations in the one initial and one final extraction.

The fumigation extraction method was used to measure microbial N (Horwath and Paul, 1994). A 10-g sample of field moist soil was contained in a glass beaker and fumigated with chloroform in a desiccator for 24 h. Soil samples were then transferred to a specimen cup, extracted with 50 mL of 0.5M K_2SO_4, and processed the same as K_2SO_4-extractable organic N; i.e., all N was converted to NO_3^- using the persulfate oxidation digestion method. The NO_3^- concentration of the fumigated digested sample was measured colorimetrically on a continuous-flow autoanalyzer.

The concentration of chloroform-labile microbial N was calculated as the difference between the NO_3^- concentration of the fumigated and unfumigated samples.

In 2006, when plots were 2, 5, 7, 9, and 11 yr post-fire, we assessed cover of shrubs, palmettos, sub-shrubs, and suffrutescent species (Table 1) in the 12 plots where we collected soil samples. We established five equally spaced 30-m line transects in each plot (Fig. 1) and measured the length of each transect intersected by each non-herbaceous species. In addition, we measured the height of the tallest plant every 5 m along each transect.

Statistical analyses—We fit models with time-since-fire as a fixed effect and with plot nested within time-since-fire as a random effect to determine the effect of time-since-fire on resin-exchangeable nutrients and soil properties (listed in Table 2) separately for each soil depth (0–5, 5–10, 10–15, and 15–20 cm). These models were fit using the standard-least-squares/expected-mean-squares method in JMP Pro 9 (SAS Institute Inc., Cary, NC). Data were ln-transformed before analyses to meet the assumption of normality when necessary.

We calculated the total length of line transects (maximum = 15,000 cm) intersected by non-herbaceous species (i.e., cover). Changes in plant cover and height with time-since-fire were analyzed with linear regression. We also calculated the percent of the total cover made up by each functional group (Table 1; oaks, palmettos, ericaceous shrubs, other shrubs, ericaceous sub-shrubs, and other sub-shrubs/suffrutescents). Changes in the percent of total cover of each functional group with time-since-fire were analyzed with one-way ANOVAs. Cover and height data were analyzed using SPSS version 19.0 (IBM Corporation, Armonk, NY).

RESULTS—Resin-exchangeable NH_4^+, NO_3^-, total N, PO_4^{3-}, and N:P ratios did not differ significantly across the time-since-fire chronosequence (Table 2; Fig. 2). Time-since-fire had no effect on K_2SO_4-extractable inorganic N for any soil depth (Fig. 3A), while K_2SO_4-extractable organic N was higher in 4-yr sites than in 1-yr sites in 5–10-cm soils (Fig. 3B). Across all times-since-fire and depths, mean K_2SO_4-extractable inorganic N ranged from 0.49 to 1.55 μg N/g soil, and mean K_2SO_4-extractable organic N ranged from 1.22 to 2.99 μg N/g soil. Across all times-since-fire, K_2SO_4-extractable inorganic N was 2.0–2.9 times greater in surface soils (0–5 cm) than in deep soils (15–20 cm). The ratio of K_2SO_4-extractable inorganic N to organic N did not vary with time-since-fire (Table 2) and was always less than 1.0 (Fig. 3C).

Time-since-fire had no effect on soil percent N or N pools (Table 2). Soil percent N (Fig. 3D) and N pools (Fig. 4A) decreased with depth. Total N pools (per 20-cm depth) ranged from 45.6 g N/m^2 in 6-yr sites to 70.1 g N/m^2 in 1-yr sites. Soil percent C (Fig. 3E) and C pools (Fig. 4B) followed similar patterns with time-since-fire as soil percent N and N pools. Total C pools (per 20-cm depth) ranged from 1285.3 g C/m^2 in 6-yr sites to 1793.9 g C/m^2 in 1-yr sites. Time-since-fire had no effect on soil C:N (Fig. 3F).

Chloroform-labile microbial N (CLMN) did not differ with time-since-fire (Table 2). CLMN, on average, was 2.5–5.6 times greater in surface soils than in deep soils (Fig. 3G). Across all times-since-fire and depths, mean CLMN ranged from 0.94 to 6.90 μg N/g soil. Time-since-fire also had no effect on soil pH (Fig. 3H).

Potential N mineralization and nitrification rates did not vary with time-since-fire (Table 2). In surface soils (0–5 cm), N immobilization occurred in 1-yr sites, while N mineralization (μg N/g soil d) occurred at all other

TABLE 1. Species composition in 2006 of the 10 plots where soil samples were collected in 2005. Values are the number of plots in which a species occurred. Cover of the first six functional groups (oaks, palmettos, ericaceous shrubs, other shrubs, ericaceous sub-shrubs, other sub-shrubs/suffrutescents) was assessed, and only species that were encountered along line transects are included. For all other functional groups, only species present in at least three plots are included. Nomenclature follows Wunderlin and Hansen (2003).

			Years after Fire in 2005 (in 2006)				
Functional Group	Family	Species	1 (2)	4 (5)	6 (7)	8 (9)	10 (11)
Oaks	Fagaceae	*Quercus champanii*	2	2	2	2	2
	Fagaceae	*Quercus geminata*	2	2	2	2	2
	Fagaceae	*Quercus inopina**	2	2	2	2	2
Palmettos	Arecaceae	*Sabal etonia**	2	2	2	1	2
	Arecaceae	*Serenoa repens*	2	2	2	2	2
Ericaceous Shrubs	Ericaceae	*Bejaria racemosa*	1	0	0	0	2
	Ericaceae	*Lyonia ferruginea*	0	0	1	1	0
	Ericaceae	*Lyonia fruticosa*	2	2	2	2	2
	Ericaceae	*Lyonia lucida*	2	2	1	2	2
Other Shrubs	Annonaceae	*Asimina obovata**	0	0	1	1	0
	Asteraceae	*Palafoxia feayi**	1	2	2	2	2
	Lauraceae	*Persea humilis*	0	0	0	1	0
	Olacaceae	*Ximenia americana*	2	2	2	1	1
Ericaceous Sub-shrubs	Ericaceae	*Gaylussacia dumosa*	1	2	2	0	2
	Ericaceae	*Vaccinium darrowii*	1	0	1	0	1
	Ericaceae	*Vaccinium myrsinities*	2	2	2	2	2
Other Sub-shrubs/ Suffrutescent	Chrysobalanaceae	*Licania michauxii*	1	2	2	1	1
	Cistaceae	*Helianthemum nashii**	0	1	1	1	0
	Cistaceae	*Lechea deckertii*	1	2	2	2	1
	Polygalaceae	*Polygala polygama*	2	1	2	1	0
N-fixers	Fabaceae	*Chapmanii floridana**	1	1	2	1	0
	Fabaceae	*Galactia regularis/ elliottii*	1	2	1	1	0
	Fabaceae	*Mimosa quadrivalvis**	0	1	0	0	1
Graminoids	Cyperaceae	*Rhynchospora megalocarpa*	2	2	2	1	2
	Poaceae	*Andropogon floridanus**	2	0	0	0	1
	Poaceae	*Aristida beyrichiana*	2	2	2	2	2
	Poaceae	*Dicanthelium* sp.	2	0	1	0	0
Herbs	Asteraceae	*Ambrosia artemisiifolia*	1	0	1	1	0
	Asteraceae	*Balduina angustifolia*	0	0	1	1	1
	Asteraceae	*Liatris ohlingerae**	0	1	1	1	0
	Caryophyllaceae	*Paronychia chartacea**	1	1	0	1	0
	Commelinaceae	*Commelina* sp.	1	1	1	1	1
	Euphorbiaceae	*Cnidoscolus stimulosus*	0	1	1	1	1
Other	Cactaceae	*Opuntia humifusa*	1	1	2	2	1
	Selaginellaceae	*Selaginella arenicola*	1	2	2	2	2
	Smilacaceae	*Smilax auriculata*	2	1	2	2	2
	Cladoniaceae	*Cladonia* sp.	0	0	0	1	2

* endemic to Florida.

TABLE 2. Results of models with time-since-fire (TSF) as a fixed effect and plot nested within time-since-fire (Plot(TSF)) as a random effect for soil variables at each depth. N and P were measured with ion-exchange resins only in surface soils (0–5 cm). For ion-exchange resins, *df* = 4,60 for TSF and 10,60 for Plot(TSF). For soil samples, *df* = 4,39 for TSF and 5,39 for Plot(TSF). *, data ln-transformed before analysis.

			Soil Depth (cm)							
			0–5		5–10		10–15		15–20	
Sampling Method	Soil Variable	Factor	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Ion-exchange Resins	NH_4^+	TSF	2.84	0.082						
		Plot(TSF)	2.37	0.020						
	NO_3^- *	TSF	2.75	0.089						
		Plot(TSF)	1.39	0.206						
	Total N	TSF	2.94	0.076						
		Plot(TSF)	2.37	0.019						
	PO_4^{3-} *	TSF	2.08	0.159						
		Plot(TSF)	1.95	0.055						
	N:P*	TSF	2.54	0.106						
		Plot(TSF)	1.20	0.312						
Soil Samples	Inorganic N (NH_4^+ + NO_3^-)* (µg N/g soil)	TSF	0.36	0.831	0.60	0.681	0.70	0.623	2.19	0.206
		Plot(TSF)	1.64	0.173	0.86	0.500	2.36	0.058	1.48	0.219
	Organic N* (µg N/g soil)	TSF	0.25	0.900	6.91	0.029	3.80	0.088	1.48	0.333
		Plot(TSF)	1.68	0.163	0.87	0.509	1.92	0.114	1.77	0.141
	Inorganic N:Organic N*	TSF	0.64	0.660	1.58	0.312	0.74	0.601	1.34	0.370
		Plot(TSF)	1.35	0.263	1.08	0.388	1.66	0.168	1.30	0.284
	%N*	TSF	1.17	0.423	0.15	0.958	0.23	0.910	0.40	0.803
		Plot(TSF)	1.80	0.135	4.30	0.003	5.30	<0.001	1.95	0.108
	%C*	TSF	1.61	0.304	0.06	0.991	0.10	0.977	0.34	0.839
		Plot(TSF)	1.06	0.400	2.88	0.026	5.54	<0.001	2.66	0.037
	C:N*	TSF	0.75	0.600	0.44	0.776	0.02	0.998	0.29	0.873
		Plot(TSF)	1.17	0.341	1.31	0.281	4.50	0.003	2.57	0.042
	N (g/m^2)*	TSF	1.28	0.390	0.46	0.762	0.47	0.759	0.48	0.759
		Plot(TSF)	1.77	0.140	2.28	0.065	3.50	0.010	1.71	0.155

TABLE 2. Continued.

			Soil Depth (cm)							
			0–5		5–10		10–15		15–20	
Sampling Method	Soil Variable	Factor	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
	C (g/m^2)*	TSF	1.67	0.291	0.27	0.883	0.15	0.957	0.34	0.841
		Plot(TSF)	1.01	0.427	1.71	0.154	3.98	0.005	2.39	0.054
	Chloroform-labile microbial N* (µg N/g soil)	TSF	0.54	0.713	0.17	0.947	0.39	0.806	1.05	0.465
		Plot(TSF)	1.42	0.238	8.95	<0.001	10.98	<0.001	4.69	0.002
	pH	TSF	1.27	0.391	0.50	0.738	0.81	0.571	0.47	0.759
		Plot(TSF)	2.00	0.100	3.14	0.018	4.25	0.004	4.97	0.001
	N mineralization* (µg N/g soil d)	TSF	1.02	0.479	0.19	0.934	1.37	0.364	1.31	0.381
		Plot(TSF)	0.84	0.523	3.37	0.013	1.45	0.227	1.15	0.351
	N mineralization (µg N/g N d)	TSF	0.47	0.760	0.14	0.960	0.90	0.530	1.03	0.476
		Plot(TSF)	1.20	0.327	3.74	0.007	3.45	0.011	2.08	0.089
	Nitrification* (µg N/g soil d)	TSF	2.03	0.228	1.14	0.434	3.16	0.120	1.14	0.433
		Plot(TSF)	0.80	0.557	3.05	0.021	0.94	0.467	1.00	0.432

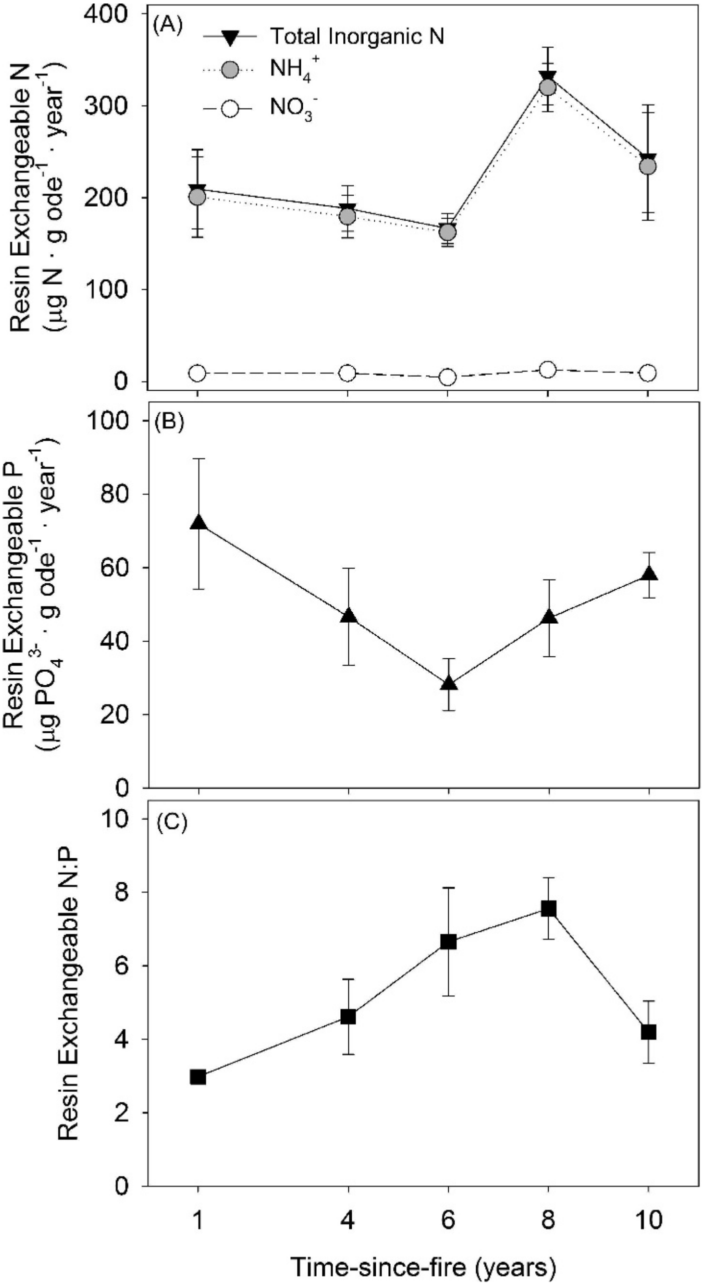

FIG. 2. Mean ± standard error (SE) of resin-exchangeable NH_4^+, NO_3^-, and total inorganic N (A), PO_4^{3-} (B), and N:P ratios (C) over 1 yr at each time-since-fire. Units in A and B are µg of nutrient exchanged per oven-dry equivalent (ode; i.e., dry mass) of ion-exchange resin beads per year.

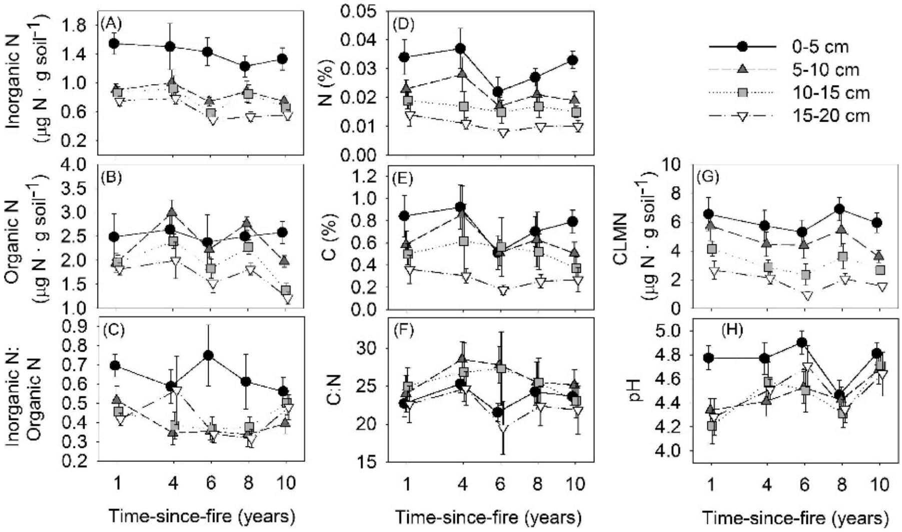

FIG. 3. Mean ± SE K$_2$SO$_4$-extractable inorganic N (A), K$_2$SO$_4$-extractable organic N (B), K$_2$SO$_4$-extractable inorganic N-to-organic N ratio (C), soil percent N (D), soil percent C (E), soil C-to-N ratio (F), chloroform-labile microbial N (G), and soil pH (H) at each sampling depth and time-since-fire.

times-since-fire (Fig. 5A). Nitrification rates were highest in surface soils in 4-yr and 8-yr sites (Fig. 5B).

Cover of shrubs, palmettos, sub-shrubs, and suffrutescents increased with time-since-fire (Fig. 6A). Similarly, plant height increased with time-since-fire (Fig. 6B). Oaks accounted for the greatest proportion of total cover (Fig. 6C). The percent of total cover made up by oaks ($F_{4,5} = 0.58$, $P = 0.690$), palmettos ($F_{4,5} = 0.95$, $P = 0.506$), ericaceous shrubs ($F_{4,5} = 0.83$, $P = 0.558$), ericaceous sub-shrubs ($F_{4,5} = 1.37$, $P = 0.362$), and other sub-shrubs/suffrutescents ($F_{4,5} = 0.748$, $P = 0.599$) did not change with time-since-fire. Other shrubs made up a greater percent of total cover 9 yr after fire than 11 yr after fire ($F_{4,5} = 5.61$, $P = 0.043$).

DISCUSSION—Contrary to our hypotheses, N availability, measured as either resin-exchangeable N or K$_2$SO$_4$-extractable N, soil N pools, resin-exchangeable PO_4^{3-}, and resin-exchangeable N:P ratios did not vary significantly with time-since-fire in scrubby flatwoods. In palmetto flatwoods, a more mesic ecosystem with some of the same species as scrubby flatwoods, the post-fire pulse of NH_4^+ and PO_4^{3-} persisted for only 3 mo after fire (Schafer and Mack, 2010). Thus, by sampling 1 yr after fire, we might have missed a period of elevated N and P availability in the current study. Net N immobilization occurred in surface soils (0–5 cm) of 1-yr sites, suggesting that N made available by fire might have been incorporated into microbial biomass. Furthermore, all dominant scrubby flatwoods species (including oaks, palmettos, and ericaceous shrubs and sub-shrubs) resprout within weeks after

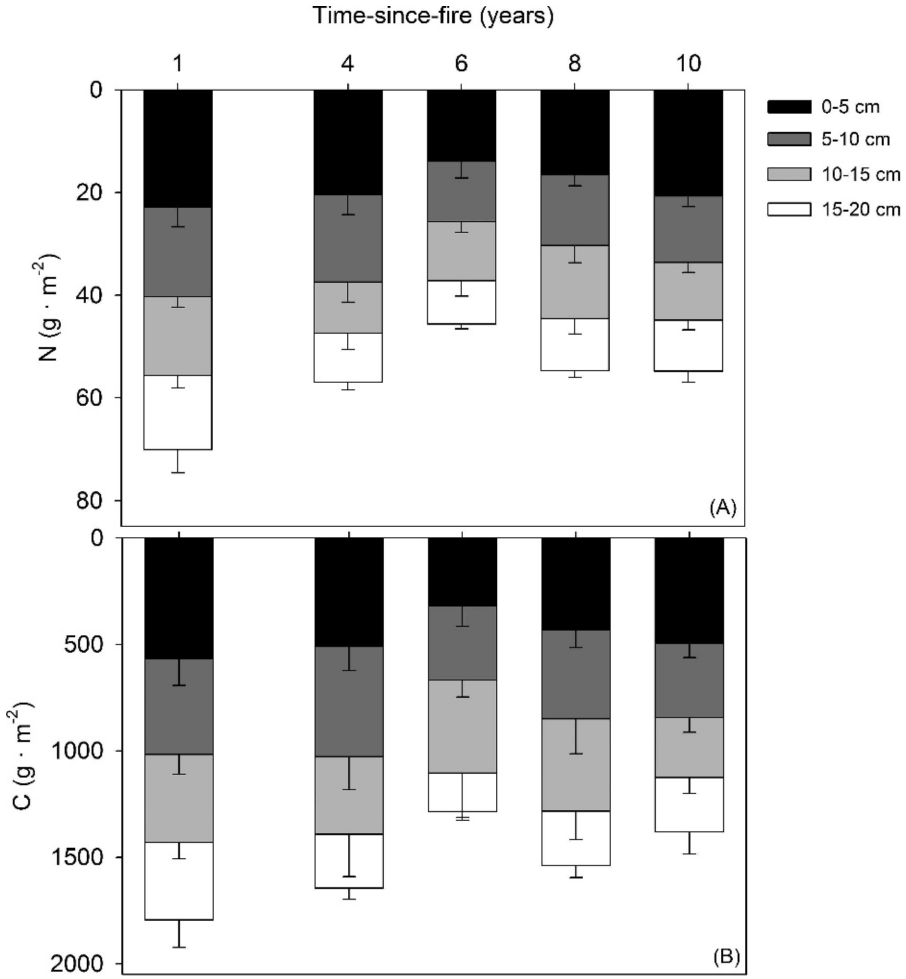

FIG. 4. Mean ± SE soil N (A) and C (B) pools (g/m^2) with depth at each time-since-fire.

fire and might be able to use nutrients made available by fire. PO_4^{3-} availability in recently burned sites could be influenced by high concentrations of P in ash post-fire (Wilbur and Christensen, 1983; Raison et al., 1985b). The consistency in soil nutrient availability and N:P ratios with time-since-fire was surprising and indicates that soil nutrient dynamics in Florida scrubby flatwoods are resilient to fire.

We expected soil N availability and pools to increase over time-after-fire as a result of N inputs via N fixation. In a coastal Florida scrub-oak woodland, *Galactia elliottii*, a N-fixing vine, accounts for 66% of litterfall (Hungate et al., 2006) and fixes ~0.2–0.7 g N/m^2 yr over the first 7 yr after fire (Hungate et al., 2004). N-fixing species in our scrubby flatwoods sites, however, were not present in all plots (Table 2) and were not abundant; and, thus, they likely had

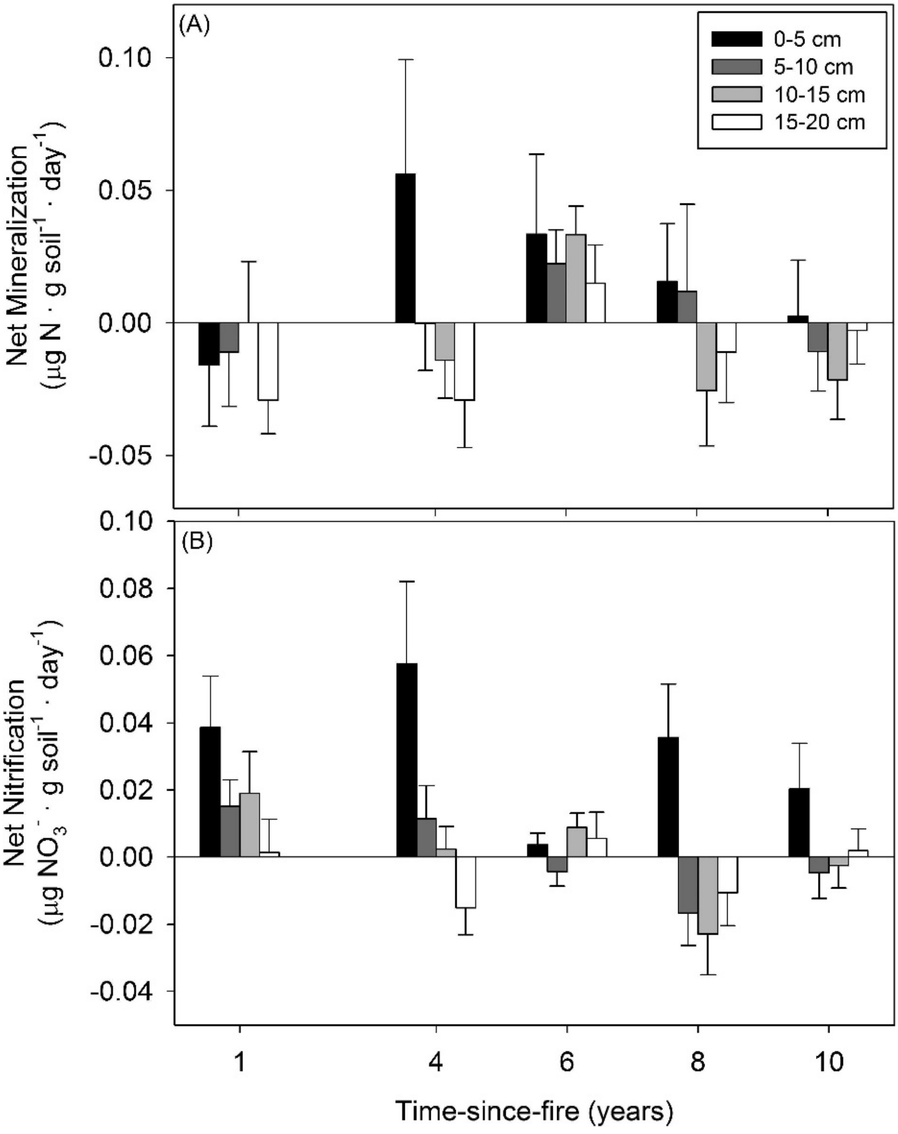

FIG. 5. Mean ± SE potential net N-mineralization rates (A) and nitrification rates (B) in soils at field capacity at each sampling depth and time-since-fire.

lower N inputs than in coastal Florida scrub. In Florida rosemary scrub and, likely, scrubby flatwoods, N fixation by soil crusts is an important N input, but it is reduced after fire (Hawkes, 2003). Nitrogenase activity—an indicator of soil crust N-fixing ability—is very low in the first 8 yr after fire in Florida rosemary scrub and increases 55-fold by 10–15 yr after fire (Hawkes, 2003). Low abundance of N-fixing plants and low N fixation by soil crusts in sites less

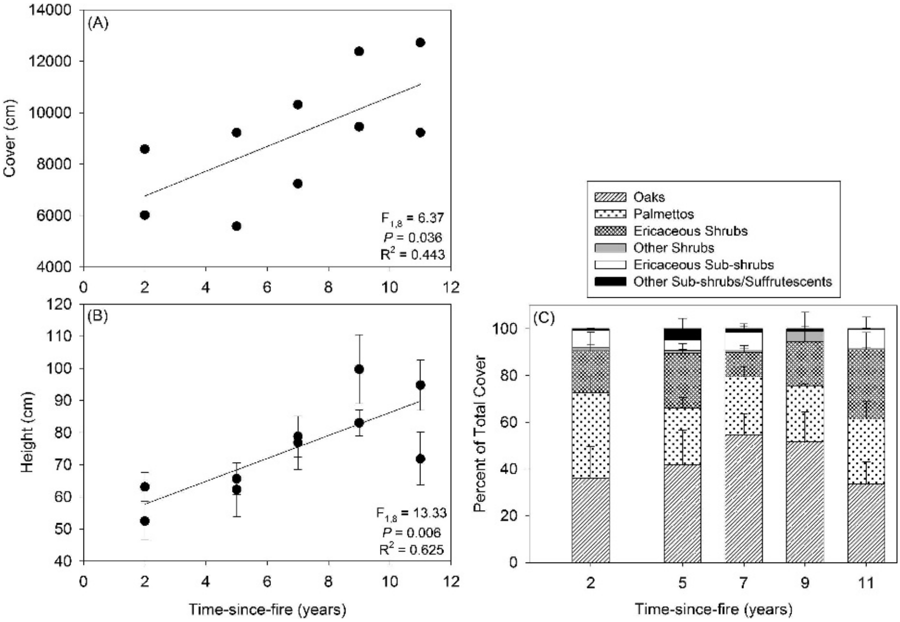

FIG. 6. Relationships between time-since-fire and total cover of shrubs, palmettos, sub-shrubs, and suffrutescent species on line transects (A) and mean ± SE vegetation height (B) in each plot, and the mean ± SE percent of total cover made up by each functional group (C).

than 10 yr post-fire suggest that N inputs were not high enough to increase soil N pools or availability in our chronosequence.

Soil percent N and percent C and N and C pools in our study sites are within the range of or lower than comparable measurements in coastal Florida scrub ecosystems of similar times-since-fire (Schmalzer and Hinkle, 1992, 1996; Hungate et al., 2006; Langley et al., 2009; McKinley et al., 2009). In contrast to coastal Florida scrub-oak woodlands (Johnson et al., 2003), our scrubby flatwoods sites did not have a distinguishable organic horizon, which suggests that nutrient dynamics might differ between these scrub communities. For example, N-mineralization rates are approximately twice as high in coastal Florida scrub (Langley et al., 2009) as in our scrubby flatwoods sites (Fig. 5). Similar patterns of soil percent N and soil percent C with time-since-fire in scrubby flatwoods suggest that soil N is related to the accumulation of organic matter. Sandy soils with low clay content are prone to high leaching, which limits accumulation of organic matter in Florida scrub soils (Gholz and Fisher, 1982; Myers, 1990). Considering that N and C do not increase over the first 10 yr after fire in scrubby flatwoods, it is unlikely that organic matter and N will accumulate in scrubby flatwoods that are burned frequently and at the short end (i.e., 8–10 yr) of the fire return interval (Menges, 2007).

The consistency in nutrient availability across our time-since-fire chronosequence might be a consequence of accumulation of nutrients in plant biomass rather than in the soil. Although woody plant cover and height increased with time-since-fire (Fig. 6), estimates of shrub biomass are similar in scrubby flatwoods 1 yr (mean = 361 g/m^2, range = 194–513 g/m^2) and 8 yr (mean = 334 g/m^2, range = 146–631 g/m^2) post-fire (Schafer, 2010). We are not able to assess differences in above-ground nutrient pools with time-since-fire, but scrubby flatwoods species differ in patterns of foliar percent N with time-since-fire such that community-level foliar percent N is similar 1 and 12 yr post-fire (J. Schafer, unpublished data). Nutrient storage in above-ground living plant tissue might, therefore, be relatively consistent across our time-since-fire chronosequence as a result of similar biomass and foliar nutrients. Inputs of N via fixation, however, might have been sequestered into litter or root biomass. Litterfall in scrubby flatwoods was higher during the eighth year after fire than during the first year after fire (Schafer, 2010), and litter N inputs in coastal Florida scrub increase over 7 yr after fire (Hungate et al., 2006). Furthermore, in coastal Florida scrub, fine root biomass increases after fire (Day et al., 2013). This indicates that leaf-litter and root nutrient pools might accumulate with time-since-fire. Johnson et al. (2003) measured decreases in soil N over the first 5 yr after fire in coastal Florida scrub; the decreases were offset by increases in vegetation and organic soil N such that total ecosystem N pools did not change. In scrubby flatwoods, total ecosystem N pools might have increased slightly with time-since-fire.

Nutrient partitioning and similar species abundances might also contribute to the lack of change in nutrient availability with time-since-fire. Oaks, palmettos, and ericaceous species have associations with ectomycorrhizae (Langley et al., 2002), arbuscular mycorrhizae (Fisher and Jayachandran, 1999), and ericoid mycorrhizae (Pearson and Read, 1973), respectively, which might contribute to differences among species in efficiency of N versus P acquisition (Schafer, 2010). Because proportional cover of oaks, palmettos, and ericaceous shrubs does not change with time-since-fire, relative plant acquisition of both N and P is likely consistent across the time-since-fire chronosequence.

Time-since-fire chronosequences are commonly used to examine changes in soil nutrients (DeLuca et al., 2002; Bloom and Mallik, 2006; Durán et al., 2008), but there are limitations of chronosequence studies (Walker et al., 2010). For example, fire intensity (Gimeno-García et al., 2000; Kennard and Gholz, 2001) and fire frequency (Hernández and Hobbie, 2008; Wanthongchai et al., 2008) have direct effects on nutrient availability and losses, which could contribute to differences in nutrient availability between plots with the same time-since-fire treatment (Table 2) and affect patterns of nutrient availability over time-since-fire. In addition, spatial heterogeneity in fire characteristics such as burn severity can affect post-fire species' cover and density (Turner et al., 2003). Our scrubby flatwoods study sites had burned one to four times in the 35 yr previous to our study, and all fires were of moderate to high intensity (ABS fire records). Plots within a time-since-fire treatment differed in fire frequency and intensity such that effects of fire frequency and intensity on soil nutrients should not have been more important at any time-since-fire. Although plant cover increased with time-since-fire (Fig. 6A), the percent frequency of species occurrences (Menges and Kohfeldt, 1995) and the proportional cover of dominant functional groups (Fig. 6C) do not change with time-since-fire. This suggests that pre-fire species composition and species-specific effects on nutrient availability were likely consistent across our study sites. Thus, limitations of chronosequence studies should be relatively minimal and should not be reason to discount the results of this study.

Nutrient availability in scrubby flatwoods soils was low overall, and we were unable to detect effects of time-since-fire on soil nutrients. Availability of N and P and N:P ratios did not change as predicted based on fundamental differences in the biogeochemical cycles of N and P and the effects of fire on these elements over time. Low sorption capacity and high leaching of sandy scrubby flatwoods soils likely contribute to low retention of post-fire pulses of N and P, limit accumulation of organic matter over 10 yr post-fire, and contribute to the lack of change in nutrient pools or availability with time-since-fire. Consistency in both proportional woody plant cover and N and P availability with time-since-fire suggests that Florida scrubby flatwoods are relatively resilient to fire.

ACKNOWLEDGMENTS—We thank Jeremy Ash, Craig Beatty, and Josh Picotte for help processing samples in the laboratory and Catherine Cardelús, Grace Crummer, and Jennie DeMarco for help with laboratory methods. We thank Kevin Main and all others who have contributed to fire management at ABS. This research was supported by Hilary Swain, Eric Menges, Carl Weekley, and the Plant Ecology Program at ABS. Comments from Silvia Alvarez-Clare, Doria Gordon, and several anonymous reviewers improved this manuscript.

LITERATURE CITED

ABRAHAMSON, W. G., A. F. JOHNSON, J. N. LAYNE, AND P. A. PERONI. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. Fla. Scient. 47:209–250.

BLOOM, R. G. AND A. U. MALLIK. 2006. Relationships between ericaceous vegetation and soil nutrient status in a post-fire *Kalmia angustifolia*-black spruce chronosequence. Plant Soil 289:211–226.

BROWN, R. B., E. L. STONE, AND V. W. CARLISLE. 1990. Soils. Pp. 35–69. *In*: MYERS, R. L. AND J. J. EWEL (eds.), Ecosystems of Florida. University Presses of Florida, Gainesville, FL.

CARTER, M. C. AND C. D. FOSTER. 2004. Prescribed burning and productivity in southern pine forests: a review. Forest Ecol. Manag. 191:93–109.

CERTINI, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia 143:1–10.

COOK, G. D. 1994. The fate of nutrients during fires in a tropical savanna. Aust. J. Ecol. 19:359–365.

DAY, F. P., R. E. SCHROEDER, D. B. STOVER, A. L. P. BROWN, J. R. BUTNOR, J. DILUSTRO, B. A. HUNGATE, P. DIJKSTRA, B. D. DUVAL, T. J. SIELER, B. G. DRAKE, AND C. R. HINKLE. 2013. The effects of 11 yr of CO_2 enrichment on roots in a Florida scrub-oak ecosystem. New Phytol. [doi: 10.1111/nph.12246]

DEFOREST, J. L. AND L. G. SCOTT. 2010. Available organic soil phosphorus has an important influence on microbial community composition. Soil Sci. Soc. Am. J. 74:2059–2066.

DeLuca, T. H., M.-C. Nilsson, and O. Zackrisson. 2002. Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. Oecologia 133:206–214.

Durán, J., A. Rodríguez, J. M. Fernández-Palacios, and A. Gallardo. 2008. Changes in soil N and P availability in a *Pinus canariensis* fire chronosequence. Forest Ecol. Manag. 256:384–387.

Fisher, J. B. and K. Jayachandran. 1999. Root structure and arbuscular mycorrhizal colonization of the palm *Serenoa repens* under field conditions. Plant Soil 217:229–241.

Gholz, H. L. and R. F. Fisher. 1982. Organic matter production and distribution in slash pine (*Pinus elliottii*) plantations. Ecology 63:1827–1839.

Giardina, C. P., R. L. Sanford, Jr., and I. C. Døckersmith. 2000. Changes in soil phosphorus and nitrogen during slash-and-burn clearing of a dry tropical forest. Soil Sci. Soc. Am. J. 64:399–405.

Gibson, D. J., D. C. Hartnett, and G. L. S. Merrill. 1990. Fire temperature heterogeneity in contrasting fire prone habitats: Kansas tall grass prairie and Florida sandhill. Bull. Torrey Bot. Club 177:349–356.

Gillon, D. and M. Rapp. 1989. Nutrient losses during a winter low-intensity prescribed fire in a Mediterranean forest. Plant Soil 120:69–77.

Gimeno-García, E., V. Andreu, and J. L. Rubio. 2000. Changes in organic matter, nitrogen, phosphorus and cations in soil as a result of fire and water erosion in a Mediterranean landscape. Eur. J. Soil Sci. 51:201–210.

Hawkes, C. V. 2003. Nitrogen cycling mediated by biological soil crusts and arbuscular mycorrhizal fungi. Ecology 84:1553–1562.

Hernández, D. L. and S. E. Hobbie. 2008. Effects of fire frequency on oak litter decomposition and nitrogen dynamics. Oecologia 158:535–543.

Horwath, W. R. and E. A. Paul. 1994. Microbial biomass. Pp. 753–773. *In*: Weaver, R. W., S. Angle, P. Bottomley, D. Bezdicek, S. Smith, A. Tabatabai, and A. Wollum (eds.), Methods of Soil Analysis, part 2, Microbiological and Biochemical Properties. Soil Science Society of America, Inc., Madison, WI.

Hungate, B. A., P. Dijkstra, D. W. Johnson, C. R. Hinkle, and B. G. Drake. 1999. Elevated CO_2 increases nitrogen fixation and decreases soil nitrogen mineralization in Florida scrub oak. Global Change Biol. 5:781–789.

———, D. W. Johnson, P. Dijkstra, G. Hymus, P. Stilling, J. P. Megonigal, A. L. Pagel, J. L. Moan, F. Day, J. Li, R. Hinkle, and B. G. Drake. 2006. Nitrogen cycling during seven years of atmospheric CO_2 enrichment in a scrub oak woodland. Ecology 87:26–40.

———, P. D. Stiling, P. Dijkstra, D. W. Johnson, M. E. Ketterer, G. J. Hymus, C. R. Hinkle, and B. G. Drake. 2004. CO_2 elicits long-term decline in nitrogen fixation. Science 304:1291.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187–211.

Jaggi, R. C., M. S. Aulakh, and R. Sharma. 2005. Impacts of elemental S applied under various temperature and moisture regimes on pH and available P in acidic, neutral and alkaline soils. Biol. Fert. Soils 41:52–58.

Johnson, D. W., B. A. Hungate, P. Dijkstra, G. Hymus, C. R. Hinkle, P. Stiling, and B. G. Drake. 2003. The effects of elevated CO_2 on nutrient distribution in a fire-adapted scrub oak forest. Ecol. Appl. 13:1388–1399.

Kennard, D. K. and H. L. Gholz. 2001. Effects of high- and low-intensity fires on soil properties and plant growth in a Bolivian dry forest. Plant Soil 234:119–129.

Langley, J. A., B. G. Drake, and B. A. Hungate. 2002. Extensive belowground carbon storage supports roots and mycorrhizae in regenerating scrub oaks. Oecologia 131:542–548.

———, D. C. McKinley, A. A. Wolf, B. A. Hungate, B. G. Drake, and J. P. Megonigal. 2009. Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed to elevated CO_2. Soil Biol. Biochem. 41:54–60.

Lewis, W. M., Jr. 1974. Effects of fire on nutrient movement in a South Carolina pine forest. Ecology 55:1120–1127.

MacKenzie, M. D., T. H. DeLuca, and A. Sala. 2004. Forest structure and organic horizon analysis along a fire chronosequence in the low elevation forests of western Montana. Forest Ecol. Manag. 203:331–343.

———, ———, and ———. 2006. Fire exclusion and nitrogen mineralization in low elevation forests of western Montana. Soil Biol. Biochem. 38:952–961.

Marion, G. M. and C. H. Black. 1988. Potentially available nitrogen and phosphorus along a Chaparral fire cycle chronosequence. Soil Sci. Soc. Am. J. 52:1155–1162.

McKinley, D. C., J. C. Romero, B. A. Hungate, B. G. Drake, and J. P. Megonigal. 2009. Does deep soil N availability sustain long-term ecosystem responses to elevated CO_2? Global Change Biol. 15:2035–2048.

Menges, E. S. 2007. Integrating demography and fire management: an example from Florida scrub. Aust. J. Bot. 55:261–272.

——— and N. Kohfeldt. 1995. Life history strategies of Florida scrub plants in relation to fire. Bull. Torrey Bot. Club 122:282–297.

Myers, R. L. 1990. Scrub and high pine. Pp. 150–193. *In*: Myers, R. L. and J. J. Ewel (eds.), Ecosystems of Florida. University Presses of Florida, Gainesville, FL.

Olander, L. P. and P. M. Vitousek. 2004. Biological and geochemical sinks for phosphorus in soil from a wet tropical forest. Ecosystems 7:404–419.

Parsons, B. C. and C. R. Gosper. 2011. Contemporary fire regimes in a fragmented and an unfragmented landscape: implications for vegetation structure and persistence of the fire-sensitive malleefowl. Int. J. Wildland Fire 20:184–194.

Pearson, V. and D. J. Read. 1973. The biology of mycorrhiza in the Ericaceae. I. The isolation of the endophyte and synthesis of mycorrhizas in aspect culture. New Phytol. 72:371–379.

Pérez, C. A., M. R. Carmona, J. C. Aravena, and J. J. Armesto. 2004. Successional changes in soil nitrogen availability, non-symbiotic nitrogen fixation and carbon/nitrogen ratios in southern Chilean forest ecosystems. Oecologia 140:617–625.

Raison, R. J., P. K. Khanna, and P. V. Woods. 1985a. Mechanisms of element transfer to the atmosphere during vegetation fires. Can. J. Forest Res. 15:132–140.

———, ———, and ———. 1985b. Transfer of elements to the atmosphere during low-intensity prescribed fires in three Australian subalpine eucalypt forests. Can. J. Forest Res. 15:657–664.

Schafer, J. L. 2010. Effects of Fire on Nutrient Availability and Limitation in Florida Scrub Ecosystems. Ph. D. dissert. University of Florida, Gainesville, FL.

——— and M. C Mack. 2010. Short-term effects of fire on soil and plant nutrients in palmetto flatwoods. Plant Soil 334:433–447.

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

——— and ———. 1996. Biomass and nutrients in aboveground vegetation and soils of Florida oak-saw palmetto scrub. Castanea 61:168–193.

Smithwick, E. A. H., M. G. Turner, K. L. Metzger, and T. C. Balser. 2005. Variation in NH_4^+ mineralization and microbial communities with stand age in lodgepole pine (*Pinus contorta*) forests, Yellowstone National Park (USA). Soil Biol. Biochem. 37:1546–1559.

Sollins, P., C. Glassman, E. A. Paul, C. Swanston, K. Lajtha, J. W. Heil, and E. T. Elliott. 1999. Soil carbon and nitrogen: pools and fractions. Pp. 89–105. *In*: Robertson, G. P., D. C. Coleman, C. S. Bledsoe, and P. Sollins (eds.), Standard Soil Methods for Long-term Ecological Research. Oxford University Press, Inc., New York, NY.

Thomas, G. W. 1996. Soil pH and soil acidity. Pp. 475–490. *In*: Sparks, D. L., A. L. Page, P. A. Helmke, R. H. Loeppert, P. N. Soltanpour, M. A. Tabatabai, C. T. Johnston, and M. E. Sumner (eds.), Methods of Soil Analysis, part 3 Chemical Methods. Soil Science Society of America, Inc., Madison, WI.

Turner, M. G., W. H. Romme, and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. Front. Ecol. Environ. 1:351–358.

———, E. A. H. Smithwick, K. L. Metzger, D. B. Tinker, and W. H. Romme. 2007. Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. Proc. Natl. Acad. Sci. U. S. A. 104:4782–4789.

van Mantgem, P. J., M. Schwartz, and M. B. Keifer. 2001. Monitoring fire effects for managed burns and wildfires: coming to terms with pseudoreplication. Nat. Area. J. 21:266–273.

——— and D. W. Schwilk. 2009. Negligible influence of spatial autocorrelation in the assessment of fire effects in mixed conifer forest. Fire Ecol. 5:116–125.

Walker, L. R., D. A. Wardle, R. D. Bardgett, and B. D. Clarkson. 2010. The use of chronosequences in studies of ecological succession and soil development. J. Ecol. 98:725–736.

Wan, S., D. Hui, and Y. Luo. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol. Appl. 11:1349–1365.

Wanthongchai, K., J. Bauhus, and J. G. Goldammer. 2008. Nutrient losses through prescribed burning of aboveground litter and understorey in dry dipterocarp forests of different fire history. Catena 74:321–332.

White, E. M., W. W. Thompson, and F. R. Gartner. 1973. Heat effects on nutrient release from soils under Ponderosa pine. J. Range Manag. 26:22–24.

Wilbur, R. B. and N. L. Christensen. 1983. Effects of fire on nutrient availability in a North Carolina coastal plain pocosin. Am. Midl. Nat. 110:54–61.

Wunderlin, R. P. and B. F. Hanson. 2003. Guide to the Vascular Plants of Florida, 2nd ed. University Press of Florida, Gainesville, FL.

Yermakov, Z. and D. E. Rothstein. 2006. Changes in soil carbon and nitrogen cycling along a 72-year wildfire chronosequence in Michigan jack pine forests. Oecologia 149:690–700.

Florida Scient. 76(3-4): 417–435. 2013
Accepted: July 13, 2013