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REGULAR ARTICLE

Short-term effects of fire on soil and plant nutrients in palmetto flatwoods

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Abstract Fire may have different effects on the relative availability of nitrogen (N) and phosphorus (P) because N volatilization occurs at lower temperatures than P volatilization, and fire-mediated changes in soil nutrient availability may affect foliar nutrient concentrations. We assessed the short-term effects of fire on soil and plant nutrients and ^{15}N isotopic signatures in a palmetto flatwoods ecosystem in central Florida. Fire caused a short-term increase in extractable ammonium (NH_4^+) and phosphate (PO_4^{3-}). The increase in PO_4^{3-} was greater than the increase in NH_4^+, resulting in a decrease in the soil extractable N:P ratio shortly after fire. Similarly, foliar %P of the palmetto *Serenoa repens* (W. Bartram) Small increased more than foliar %N, resulting in a decrease in foliar N:P ratios shortly after fire. Soil δ^{15}N and the difference between foliar and soil δ^{15}N did not vary with time since fire; however, foliar δ^{15}N of *S. repens* decreased after fire. Foliar %N of *Quercus geminata* Small and ericaceous shrubs was positively correlated with soil extractable inorganic N, while foliar %P of *S. repens* was positively correlated with soil extractable PO_4^{3-}. Variation in foliar δ^{15}N after fire and the positive relationship between soil and foliar nutrients suggest that both increased soil nutrient availability and reallocation of nutrients from below- to aboveground can be important for plant nutrient status after fire in palmetto flatwoods.

Keywords Ericaceae · Florida · N:P ratios · δ^{15}N · *Quercus geminata* · *Serenoa repens*

Introduction

Fire, a natural disturbance in many shrubland ecosystems (Little 1979; Abrahamson et al. 1984; Christensen 1985; Keeley and Keeley 1988; Moreno and Oechel 1994; Bradstock et al. 2001), has profound impacts on nutrient cycling and availability. Fire consumes plant biomass, litter, and soil organic matter, converting organic nutrients into inorganic forms (Certini 2005) that may be lost to the atmosphere or returned to the ecosystem in ash. Although fire often has no detectable effects on total soil nitrogen (N) (Christensen and Muller 1975; Jensen et al. 2001; Wan et al. 2001; Britton et al. 2008; Boerner et al. 2009) or phosphorus (P) pools (Kauffman et al. 1993), numerous studies have measured increases in concentrations of soil ammonium (NH_4^+), nitrate (NO_3^-), and/or phosphate (PO_4^{3-}) after fire (e.g., Lewis 1974; Wilbur and Christensen 1983; Stock and Lewis 1986; Schmidt and Stewart 1997; Giardina et al. 2000; Grogan et al.

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2000; Wan et al. 2001; Smithwick et al. 2005; Turner et al. 2007).

Fire can have different effects on the relative availability of N and P because N volatilization occurs at temperatures as low as 200°C (White et al. 1973), whereas P is volatilized at temperatures above 774°C (Raison et al. 1985a). Regardless of ecosystem type or fire intensity, approximately twice as much N as P is lost to the atmosphere during fire (Gillon and Rapp 1989; Pivello and Coutinho 1992; Cook 1994; Mackensen et al. 1996). Thus, ash on the soil surface contains high concentrations of P and low concentrations of N (DeBano and Conrad 1978; Raison et al. 1985b), suggesting that fire affects both the absolute and relative availability of soil N and P.

Plant species in pyrogenic habitats have evolved a variety of mechanisms that allow them to persist and recover after fire (Sousa 1984; Christensen 1985). While some species are killed by fire and recolonize via seedling recruitment, other species are resilient and resprout after burning (Keeley 1977; Keeley and Zedler 1978; Menges and Kohfeldt 1995; Weekley and Menges 2003). Plant species that recruit from seed after fire rely on nutrients made available by fire; whereas, plant species that resprout after fire may similarly utilize nutrients made available by fire or reallocate nutrients from below- to aboveground tissues (El Omari et al. 2003). The effect of fire-induced changes in soil nutrient availability on plant nutrition, however, remains unclear. Several studies have found increases in foliar N and P after fire (Gilliam 1988; Franco-Vizcaíno and Sosa-Ramirez 1997), while others have found no effect of fire on foliar nutrients (Bennett et al. 2002; Ferran et al. 2005). Understanding the effects of fire on foliar nutrient concentrations is important because variation in foliar N:P ratios with time after fire may indicate changes in plant nutrient status and nutrient limitation, as foliar N:P ratios have been used to indicate N limitation, P limitation, or co-limitation by N and P (Koerselman and Meuleman 1996; Güsewell 2004).

Soil and plant $\delta^{15}N$ values have been used as indicators of ecosystem nitrogen cycling (Martinelli et al. 1999). Fire consumes surface soil layers and volatilizes N, which can leave post-fire soils enriched in ^{15}N (Högberg 1997) because soil $\delta^{15}N$ tends to increase with depth (Nadelhoffer et al. 1996; Frank and Evans 1997). Foliar $\delta^{15}N$ signatures are related to plant N sources, mycorrhizal status, rooting depth, N assimilation, and within-plant N reallocation (Högberg 1997; Evans 2001). Thus, taken together, soil and plant $\delta^{15}N$ values may provide insight into integrated fire effects on plant and soil N dynamics and the causes of increased foliar N concentrations after fire.

We examined the effects of fire on plant and soil nutrient dynamics in flatwoods ecosystems of the Lake Wales Ridge in central peninsular Florida, where fire has historically maintained shrub-dominated habitats (Abrahamson et al. 1984; Menges 1999). Although N and P are essential plant nutrients that limit plant growth in most, if not all, terrestrial ecosystems (Vitousek and Howarth 1991), few studies have investigated the effects of fire on both soil and plant N, P, and N:P ratios. Understanding nutrient dynamics in flatwoods ecosystems is important because nutrient availability is low and fires occur relatively frequently. We assessed the short-term effects of fire on soil and plant nutrients and ^{15}N isotopic signatures. We hypothesized that soil extractable N and P would increase immediately post-fire, but that the ratio of soil extractable N:P would decrease immediately post-fire due to the differential effects of fire on N and P. Furthermore, we hypothesized that foliar N and P concentrations of resprouting plants would increase after fire. We investigated ^{15}N isotopic signatures to differentiate among mechanisms that can cause increased foliar N concentrations.

Materials and methods

This study was conducted at Archbold Biological Station (ABS) in Highlands County, Florida, USA (27º10′50″N, 81º21′0″ W), near the southern tip of the Lake Wales Ridge. The Lake Wales Ridge supports fire adapted Florida scrub ecosystems characterized by deep sandy soils derived from paleo dunes (Abrahamson et al. 1984), and high endemism, with many endangered and threatened species (Menges 1999). 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). The ABS preserve is divided into burn units that have been managed with prescribed fires for over 35 years. Archbold Biological Station comprises a mosaic of plant communities including seasonal ponds, flatwoods, scrubby flatwoods, oak-hickory scrub, and sand pine scrub.

Our research focused on the palmetto flatwoods plant community. Palmetto flatwoods are dominated by saw palmetto (*Serenoa repens* (W. Bartram) Small), a repent shrub that reaches heights of 1–2 m, and scattered shrubs with occasional to dense slash pines (*Pinus elliottii* Engelm.). Palmetto flatwoods often occur as a distinct zone around seasonal ponds on entisols, inceptisols, and spodosols that are poorly drained and can have standing water during times of high rainfall (Abrahamson et al. 1984). Flatwoods typically burn every 2–9 years (Main and Menges 1997). Palmettos and other dominant shrubs resprout after fire, while slash pines survive by resisting fire and recruit from seed after fire (Menges and Kohfeldt 1995). Fires are intense and leave few areas unburned due to the high flammability of palmettos and pine duff (Abrahamson et al. 1984). Maximum sustained fire temperatures in flatwoods range from 373°C to 688°C, while absolute maximum temperatures have been measured as high as 796°C (E. Menges, unpublished data).

On 4 August 2006, we randomly selected five sampling locations within the palmetto flatwoods vegetation association in a 19 acre burn unit that had previously burned in 2003, 1996, 1993, and 1972. At all sampling locations, which were separated by at least 5 m, we marked a soil sampling site and the nearest individual of five common flatwoods species (when present within 1 m of the soil sampling location). Our focal species, all of which resprout after fire, were the palmetto *S. repens*, the shrubby oak *Quercus geminata* Small, and the ericaceous shrubs *Lyonia fruticosa* (Michx.) G.S. Torr., *Lyonia lucida* (Lam.) K. Koch, and *Vaccinium myrsinities* Lam. (Wunderlin and Hanson 2003). On 4 August 2006, several hours before ignition of a prescribed fire, we collected five soil samples (0–15 cm depth, 8 cm diameter core), one at each sampling location, and thirteen foliar samples, two to four at each sampling location depending on the species present. *Serenoa repens* was present at all sampling locations, while *Q. geminata* was present at four of the five sampling locations. Eleven of the thirteen plants sampled were completely consumed by the fire. The first post-fire soil samples (n=5) were collected on the afternoon of 4 August 2006, within 3 h after the fire had burned through the unit. Subsequent post-fire soil samples (n=5) were collected on 24 August, 5 October, and 11 December 2006 and 11 December 2007. We collected post-fire foliar samples (n=13) on 6 October 2006, 12 December 2006, and 10 December 2007. At all sampling times, we collected the newest leaves from the upper portion of shrub stems. To collect foliar samples of the palmetto *S. repens*, we clipped a small portion of the newest leaves (1 to 3 depending on total leaf number), thereby permanently marking the leaves. Thus, at all sampling times post-fire, we collected a portion of only the new leaves that had been produced after the previous sampling event.

Within 24 h of collection, we passed soil samples through a 2-mm sieve and sub-sampled for determination of gravimetric soil moisture, pH, total percentages of N and C, inorganic P concentration, inorganic N concentration, N mineralization rates, and soil δ^{15}N. Gravimetric moisture content was determined on samples dried at 105°C for 48 h. For soil pH, 10 g of air dried soil was added to 10 mL of deionized water, shaken for 30 s, allowed to stand for 10 min (Thomas 1996), then pH was determined with an electronic pH meter (Thermo Orion 250A+, Orion Research, Inc., Boston, Massachusetts, USA). A subsample of soil was dried at 60°C for 48 h, ground to a fine powder on a spex mill (8000D dual mixer/mill, Spex Certiprep Inc., Metuchen, New Jersey) at the MacArthur Agro-Ecology Research Center (MAERC), and analyzed for percentages of N, C, and ^{15}N natural abundance at the University of Florida on an elemental analyzer (ECS 4010, Costech Analytical, Valencia, California, USA) coupled with an isotope ratio mass spectrometer (Delta Plus XL, ThermoFinnigan, Brenen, Germany). Abundances of ^{15}N were measured using delta (δ) notation with atmospheric N_2 as the standard.

To measure inorganic P concentrations, 30 mL of 0.05 M hydrochloric acid (HCl) and 0.0125 M hydrogen sulfate (H_2SO_4) was added to 15 g of field moist soil, shaken for 5 min, then filtered through Whatman #42 filter paper. We stored filtered samples in a refrigerator for up to three weeks before analysis for phosphate (PO_4^{3-}) concentrations on a spectrophotometer microplate reader (μQuant Microplate Spectrophotometer, Bio-Tek Instruments, Inc., Winooski, Vermont, USA) using the malachite green method (D'Angelo et al. 2001) at the MAERC.

To measure inorganic N concentrations, 50 mL of 0.5 M potassium sulfate (K_2SO_4) was added to 10 g of field moist soil, shaken for 30 s, and allowed to stand overnight. We filtered solutions through Whatman #42 filter paper that was pre-leached with 0.5 M K_2SO_4. Filtered samples were frozen then taken to the University of Florida where ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were determined colorimetrically on a segmented flow autoanalyzer (Astoria-Pacific, Inc., Clackamas, Oregon, USA). For N mineralization rates, 10 g of field moist soil was contained in a specimen cup and stored in the dark at room temperature (~ 24°C). After one week, 50 mL of 0.5 M K_2SO_4 was added to the soil, shaken for 30 s, and allowed to stand overnight. We filtered, stored, and analyzed solutions as described above. Net rates of N mineralization were calculated from the difference in μg N-(NH_4^+ + NO_3^-)·g soil^{-1} of initial and one week extractions.

Leaf samples were dried at 60°C for 48 h and ground on a spex mill (8000D dual mixer/mill, Spex Certiprep Inc., Metuchen, New Jersey) at the MAERC. All foliar samples were analyzed for percentages of N and C and ^{15}N natural abundance at the University of Florida on an elemental analyzer (ECS 4010, Costech Analytical, Valencia, California, USA) coupled with an isotope ratio mass spectrometer (Delta Plus XL, ThermoFinnigan, Brenen, Germany). Abundances of ^{15}N were measured using delta (δ) notation with atmospheric N_2 as the standard. We determined foliar phosphorus for all samples of *Serenoa repens*. Subsamples of 0.2–0.5 g were weighed into crucibles, ashed in a muffle furnace at 500°C for 5 h, extracted with 6 M HCl, then brought to volume so that the solution was 0.6 M. Extracts were stored in the refrigerator for several days then analyzed colorimetrically on a spectrophotometer microplate reader (PowerWave XS Microplate Reader, Bio-Tek Instruments, Inc., Winooski, Vermont, USA) at the University of Florida using the ascorbic acid molybdenum-blue method (Murphy and Riley 1962). Standard NIST peach leaves were used to determine the efficiency of the digestion.

Statistical analyses

To examine changes in soil variables over time after fire, we used a one-way mixed analysis of variance model with repeated measures with time as the within-subjects factor (SAS 9.1 2003; Littell et al. 2006). Differences in soil variables among times were determined with post-hoc pairwise comparisons with Bonferroni confidence interval adjustments. Soil NH_4^+ concentrations, total inorganic N, PO_4^{3-} concentrations, N:P ratios, soil $\delta^{15}N$, and soil %C were natural log transformed before analyses. Soil %N was square root transformed before analysis. Soil NO_3^- concentrations could not be transformed to fit normality because of many zeros and were analyzed using Friedman's analysis of variance (SPSS 11.5 for Windows 2000).

To examine changes in foliar nutrients (%N, %P, and N:P ratios) and foliar $\delta^{15}N$ over time after fire, we used one-way repeated measures analysis of variance with time as the within-subjects factor (SPSS 11.5 for Windows 2000; Field 2009). Differences in foliar nutrients and foliar $\delta^{15}N$ among times were determined with post-hoc pairwise comparisons with Bonferroni confidence interval adjustments. In addition, we calculated the absolute difference between foliar $\delta^{15}N$ and soil $\delta^{15}N$ (Chang and Handley 2000; Schuur and Matson 2001) for each plant at each soil sampling location and analyzed differences over time after fire with a one-way repeated measures analysis of variance. Foliar nutrient variables were analyzed separately for each species/family (*Serenoa repens*, *Quercus geminata*, and Ericaceae (ericaceous shrubs include *Lyonia lucida*, *Lyonia fruticosa*, and *Vaccinium myrsinities*)).

We used linear regression to assess the relationship between soil and foliar nutrients (Sigma Plot for Windows 11.0 2008). We correlated the foliar %N of each individual at each site with total soil extractable inorganic N at each site. Analyses were conducted separately for each species/family. We correlated foliar %P of *S. repens* with soil extractable PO_4^{3-}, which was natural log transformed. Because the first post-fire foliar sample collection corresponded with the third post-fire soil sample collection, data from only four time points (pre-fire and 62/63, 129/130, and 493/494 days post-fire) were used in the regression analyses.

Results

Three hours post-fire, NH_4^+ concentrations were 5.5 times higher than pre-fire values, and NH_4^+ remained higher through at least 20 days after fire ($F_{5,20}$=6.16, p=0.001; Fig. 1a). Soil extractable NO_3^- was undetectable pre-fire, but was greater than zero 3 h, 20 days, and 62 days after fire ($\chi_{(5)}{}^2$=9.81, p=0.081; Fig. 1a).

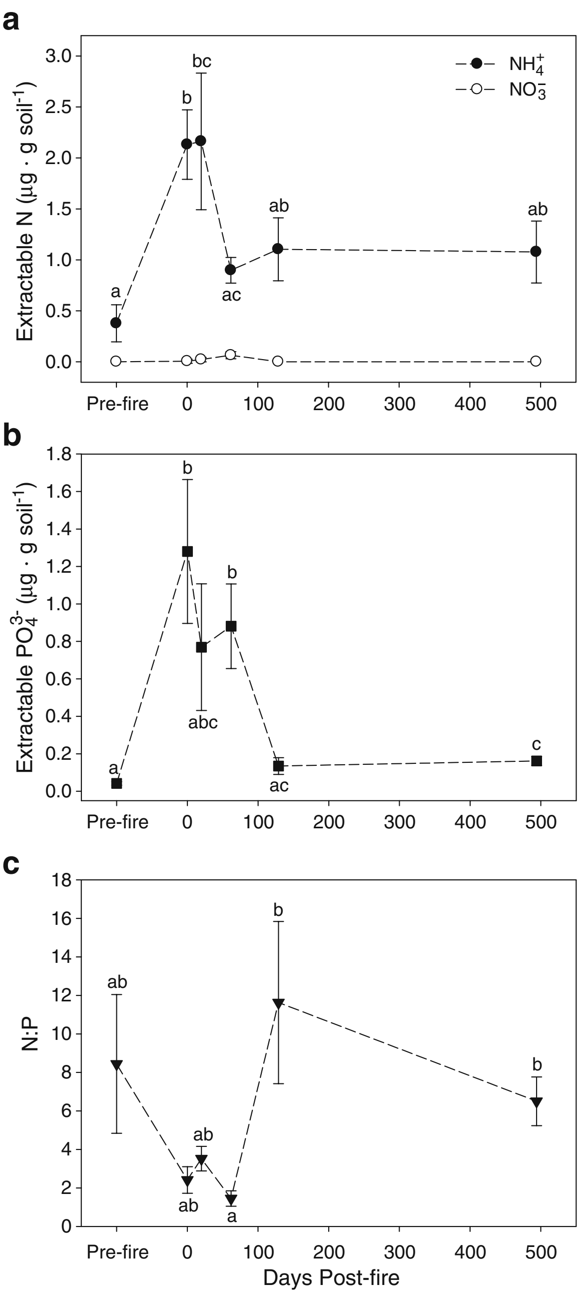

Fig. 1 Mean (± SE) soil extractable NH_4^+ and NO_3^- (**a**), soil extractable PO_4^{3-} (**b**), and soil extractable N:P ratios (**c**) in palmetto flatwoods pre-fire and 0.125, 20, 62, 129, and 494 days post-fire. Different letters represent significantly different means at α=0.05 determined by repeated measures analysis of variance with post-hoc pairwise comparisons with Bonferroni confidence interval adjustments

Three hours post-fire, PO_4^{3-} concentrations were 30 times higher than pre-fire values, and 62 days after fire, PO_4^{3-} concentrations were 21 times higher than pre-fire values ($F_{5,20}$=15.45, $p<0.001$; Fig. 1b). Soil extractable N:P ratios were significantly lower 62 days after fire than 129 and 494 days after fire ($F_{5,20}$=5.85, p=0.001, Fig. 1c). Soil pH increased over time after fire, and by 494 days, was significantly higher than pre-fire values (Table 1). There were no differences in soil %N, %C, C:N ratios, or soil $\delta^{15}N$ over time after fire (Table 1).

Foliar %N of *Serenoa repens* was higher 63 days after fire than 493 days after fire (Fig. 2a), and foliar %P of *S. repens* increased after fire (Fig. 2b). Foliar N:P ratios decreased after fire because of the larger increase in %P (1.39 times pre-fire values) than %N (1.15 times pre-fire values). Foliar %P and N:P ratios of *S. repens* were similar to pre-fire values by 493 days post-fire (Fig. 2). Foliar %N of *Quercus geminata* and ericaceous species increased shortly after fire then decreased to pre-fire values by 493 days post-fire (Fig. 3).

Foliar $\delta^{15}N$ of *S. repens* decreased significantly over time after fire, while foliar $\delta^{15}N$ of *Q. geminata* increased then decreased after fire (Fig. 3), although this change was only marginally significant (Table 2). Foliar $\delta^{15}N$ of ericaceous species did not change with time since fire (Table 2). The absolute difference between foliar $\delta^{15}N$ and soil $\delta^{15}N$ did not vary over time after fire for any plant species/family (Table 2). Over the entire study period, the mean (+ SE) difference between foliar and soil $\delta^{15}N$ was −3.06 (+ 0.29) for *S. repens*, −5.14 (+ 0.27) for *Q. geminata*, and −5.83 (+ 0.15) for ericaceous shrubs.

Total extractable inorganic N was positively correlated with foliar %N of *Q. geminata* ($F_{1,14}$=3.77, p=0.073, R^2=0.21) and ericaceous shrubs ($F_{1,14}$=5.49, p=0.034, R^2=0.28) (Fig. 4). Total extractable inorganic N was not correlated with foliar %N of *S. repens* ($F_{1,18}$=0.85, p=0.368, R^2=0.04). Foliar %P of *S. repens* was positively correlated with soil extractable PO_4^{3-} ($F_{1,18}$=10.57, p=0.004, R^2=0.37; Fig. 5).

Discussion

Fire caused a short-term increase in soil extractable nutrients in the palmetto flatwoods ecosystem investigated in our study. While soil N concentrations

Table 1 Results of repeated measures analysis of variance for soil variables, and means (+ SE) of soil variables pre-fire and 0.125, 20, 62, 129, and 494 days (d) post-fire. Different letters represent significantly different means at α=0.05 determined by post-hoc pairwise comparisons with Bonferroni confidence interval adjustments

Variable	$F_{5,20}$	*p*	Pre-Fire	0.125 d post-fire	20 d post-fire	62 d post-fire	129 d post-fire	494 d post-fire
pH	3.27	0.026	4.09+0.05 a	4.23+0.08 ab	4.38+0.14 ab	4.34+0.11 ab	4.39+0.12 ab	4.41 + 0.08 b
% N[a]	0.16	0.975	0.092+0.016	0.102+0.007	0.094+0.009	0.096+0.007	0.099+0.024	0.110+0.034
% C[b]	0.18	0.968	2.85+0.54	3.30+0.39	2.98+0.42	2.99+0.27	3.04+0.90	3.23+0.91
C:N	0.54	0.747	30.79+0.64	32.08+1.58	31.38+1.41	31.09+0.73	29.67+1.31	29.95+0.85
Total Inorganic N[b] ($\mu g \cdot g\ soil^{-1}$)	6.01	0.001	0.377+0.182 a	2.135+0.345 b	2.183+0.678 bc	0.962+0.096 ac	1.104+0.309 ac	1.077+0.304 ac
N mineralization ($\mu g \cdot g\ soil^{-1} \cdot day^{-1}$)	12.55	<0.001	−0.009+0.004 a	−0.144+0.025 b	−0.110+0.081 ab	−0.062+0.017 ab	−0.060+0.007 b	−0.049+0.040 ab
Soil $\delta^{15}N$[b]	0.49	0.777	2.77+0.16	2.47+0.32	2.77+0.32	3.03+0.30	2.51+0.52	2.50+0.59

[a] analysis performed on square root transformed data

[b] analysis performed on natural log transformed data

remained elevated above pre-fire levels for at least 1 month after fire, soil P, in contrast, remained elevated above pre-fire levels for at least 2 months after fire (Fig. 1). Thus, flatwoods shrubs, which resprouted within a month after fire, experienced a sustained increase in P availability, but only a short pulse of N availability. Regardless, both foliar %N and %P increased over the short-term after fire. The relative magnitude of the soil P increase was greater than that of soil N, leading to a decrease in the soil extractable N:P ratio shortly after fire (Fig. 1). Similarly, for the palmetto *Serenoa repens*, the relative increase in foliar %P was greater than the increase in foliar %N, causing a decrease in the foliar N:P ratio shortly after fire (Fig. 2). Soil $\delta^{15}N$ did not vary with time since fire (Table 1), and only *S. repens* showed significant variation in foliar $\delta^{15}N$ with time after fire (Table 2).

Soil ammonium (NH_4^+) concentrations increased immediately after fire and decreased to pre-fire levels within 2 months after fire (Fig. 1). High concentrations of NH_4^+ and NO_3^- in burned sites may be related to high N mineralization and nitrification rates (DeLuca et al. 2002; DeLuca and Sala 2006); however, Turner et al. (2007) found that NH_4^+ increased during the first year after severe stand-replacing fire in pine forests, while net N mineralization rates were negative. Although net N mineralization rates were affected by fire in our study (Table 1), they were negative throughout the study, indicating that post-fire increases in inorganic N availability are not due to increased mineralization, but rather due to microbial or ash derived N. Increased soil temperatures associated with fire (Ewel et al. 1981) kill soil microbes, indicated by a decrease in microbial C and N after fire (Prieto-Fernández et al. 1998), which causes the release of N from ruptured microbial cells (Dunn et al. 1985; Serrasolsas and Khanna 1995). In addition, ash can contain high concentrations of N (Ewel et al. 1981; Kauffman et al. 1993), which can cause an increase in soil N after fire.

Similarly to NH_4^+, soil extractable phosphate (PO_4^{3-}) increased immediately after fire; however, in contrast to NH_4^+, PO_4^{3-} decreased to pre-fire levels within 4 months after fire (Fig. 1). High concentrations of PO_4^{3-} post-fire are related to high concentrations of P in ash (Raison et al. 1985b; Kauffman et al. 1993). Loss of high nutrient ash can occur by wind (Giardina et al. 2000) or water (Ewel et al. 1981), suggesting that post-fire weather contributes to variation in PO_4^{3-} concentrations. In our

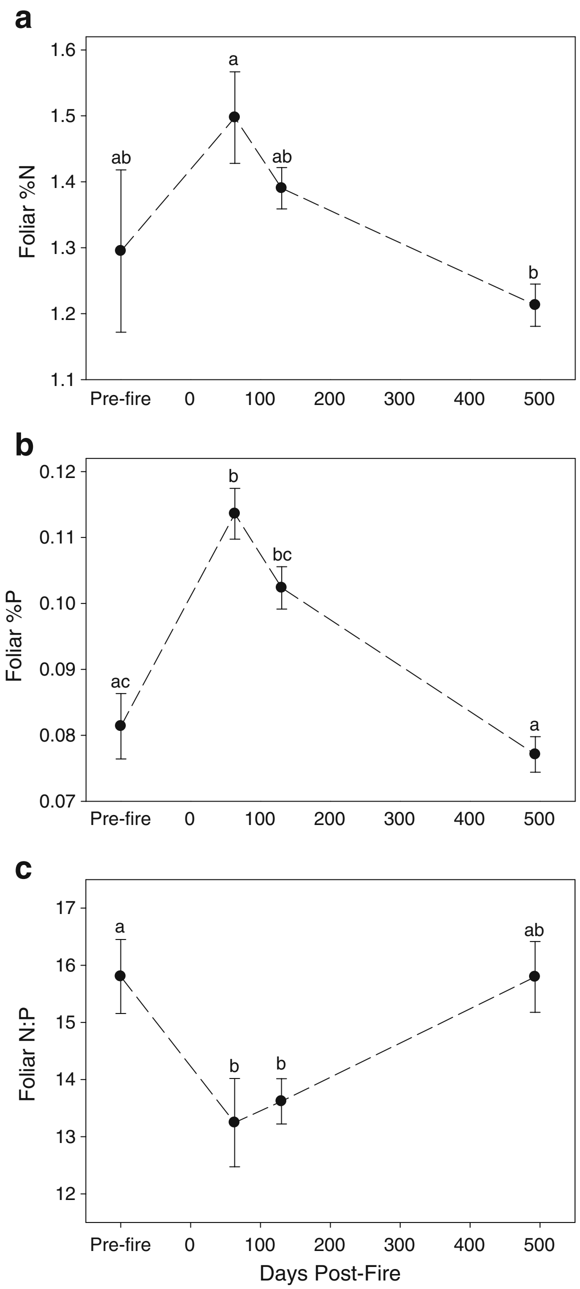

Fig. 2 Mean (± SE) foliar %N (**a**), foliar %P (**b**), and foliar N:P ratios (**c**) for *Serenoa repens* (n=5) in palmetto flatwoods pre-fire and 63, 130, and 493 days post-fire. Different letters represent significantly different means at α=0.05 determined by repeated measures analysis of variance with post-hoc pairwise comparisons with Bonferroni confidence interval adjustments

study, the first rain event occurred 2 days after fire, and 25.9 cm of rain fell between the first and second post-fire sampling dates (ABS weather records), which likely limited loss of wind blown ash and could have contributed to high concentrations of soil PO_4^{3-} after fire (Tomkins et al. 1991).

Soil extractable PO_4^{3-} increased more than total inorganic N after fire, causing a decrease in soil extractable N:P ratios (Fig. 1). This result is consistent

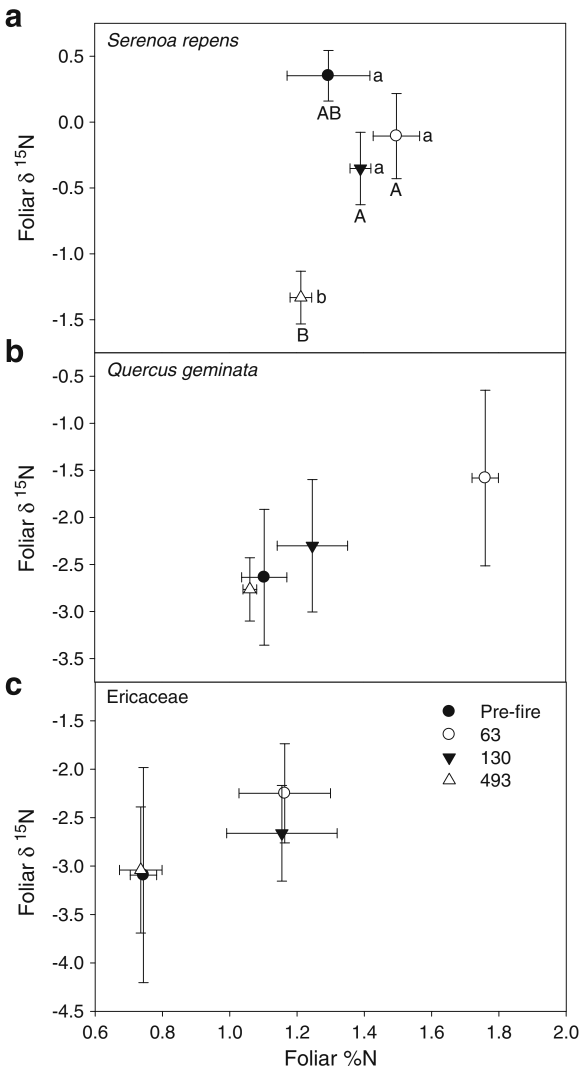

Fig. 3 Mean (± SE) foliar %N and $\delta^{15}N$ for *Serenoa repens* (n=5) (**a**), *Quercus geminata* (n=4) (**b**), and three ericaceous species (*Lyonia fruticosa*, *Lyonia lucida*, and *Vaccinium myrsinities*; n=4) (**c**) pre-fire and 63, 130, and 493 days post-fire in palmetto flatwoods. Uppercase letters represent significant differences in foliar %N and lowercase letters represent significant differences in foliar $\delta^{15}N$ at α=0.05 determined by repeated measures analysis of variance with post-hoc pairwise comparisons with Bonferroni confidence interval adjustments. There were no post-hoc differences in foliar %N or foliar $\delta^{15}N$ among times after fire for *Q. geminata* or ericaceous species

Table 2 Results of repeated measures analysis of variance for foliar %N, foliar δ^{15}N, the absolute difference in foliar δ^{15}N and soil δ^{15}N, foliar %P, and foliar N:P ratios of *Serenoa repens*, *Quercus geminata*, and three ericaceous shrubs (*Lyonia fruticosa*, *Lyonia lucida*, and *Vaccinium myrsinities*)

	%N			δ^{15}N			Foliar δ^{15}N–Soil δ^{15}N			%P			N:P		
Species or Family	F	$df_{n,d}$	p	F	$df_{n,d}$	p	F	$df_{n,d}$	p	F	$df_{n,d}$	P	F	$df_{n,d}$	p
S. repens	5.71	3,12	0.012	13.27	3,12	< 0.001	1.38	3,12	0.296	31.07	3,12	< 0.001	12.48	3,12	0.001
Q. geminata	5.63	3,9	0.019	3.55	3,9	0.061	0.87	3,9	0.492						
Ericaceae	7.44	3,9	0.008	1.31	3,9	0.329	0.24	3,9	0.863						

with the findings that more N than P is volatilized by fire (Gillon and Rapp 1989; Pivello and Coutinho 1992; Cook 1994; Mackensen et al. 1996) and that ash has higher concentrations of P than N (Raison et al. 1985b; Marcos et al. 2009). In a wetland with acidic, sandy soils, the soil extractable N:P ratio after fire was similar to our flatwoods site, but the pre-fire soil extractable N:P ratio was greater than in our site, so the magnitude of the decline was greater (Wilbur and Christensen 1983). While post-fire soil extractable N:P ratios may be similar across sites, differences in soil properties such as organic matter quantity or differences in fire temperature may affect the magnitude of fire-induced changes in soil extractable N:P ratios.

The post-fire pulse of PO_4^{3-} persisted twice as long as the post-fire pulse of NH_4^+ (Fig. 1). Although fire can kill soil microbes, the effects of fire on soil temperature decrease with depth (Ewel et al. 1981; Giardina et al. 2000; Jensen et al. 2001), so growth of microbes below the soil surface may be stimulated by post-fire increases in nutrient availability (Singh et al. 1991) or root exudates (Blagodatskaya et al. 2009) from damaged roots (Scott-Denton et al. 2006). Considering that soil microbial biomass N:P ratios average 7:1 at the global scale (Cleveland and Liptzin 2007), increased microbial growth would cause a faster decrease in soil N than soil P. Alternatively, sandy soils have lower sorption capacity than clayey soils (Villani et al. 1998), and high concentrations of potassium (K^+), calcium (Ca^{2+}) (Ewel et al. 1981; Kauffman et al. 1993), and chloride (Cl^-) (Khanna and Raison 1986) in ash may affect the mobility of NH_4^+ and PO_4^{3-} after fire. Leaching of Cl^- may be accompanied by leaching of NH_4^+ (Khanna and Raison 1986), and K^+ can compete with NH_4^+ for surface exchange sites (Chappell and Evangelou 2000); both of these interactions may contribute to

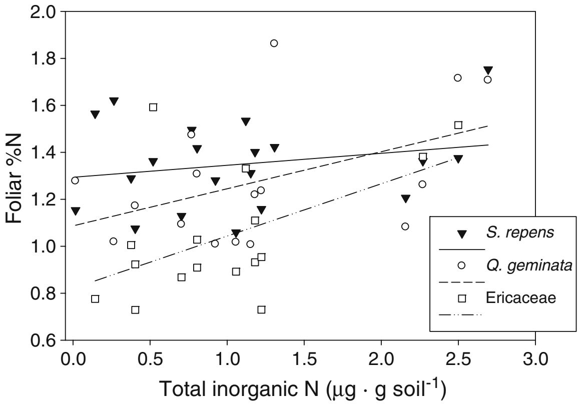

Fig. 4 Relationship between total extractable inorganic N and foliar %N of *Serenoa repens* (p=0.368, R^2=0.04; foliar %N= 1.29+(0.05 * inorganic N)), *Quercus geminata* (p=0.073, R^2= 0.21; foliar %N=1.09+(0.16 * inorganic N)), and ericaceous shrubs (p=0.034, R^2=0.28; foliar %N=0.82+(0.22 * inorganic N))

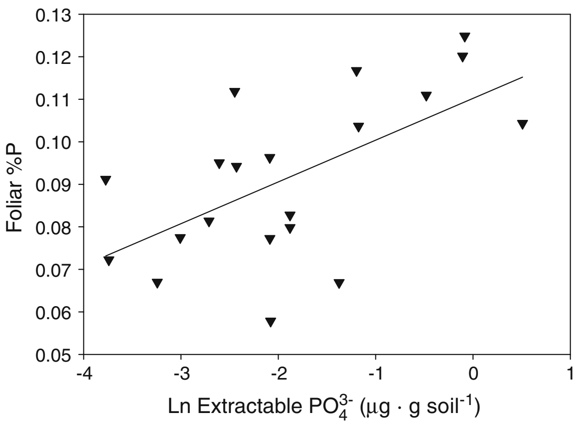

Fig. 5 Relationship between soil extractable PO_4^{3-} (natural log transformed) and foliar %P of *Serenoa repens* (p=0.004, R^2=0.37; foliar %P=0.11+(0.01 * ln PO_4^{3-}))

high leaching losses of NH_4^+ after fire. Phosphate (PO_4^{3-}) can form minerals with Ca^{2+}, and limited leaching of Ca^{2+} after fire (Khanna and Raison 1986) suggests that leaching losses of PO_4^{3-} may be low after fire. Regardless of the mechanism that leads to a shorter pulse of NH_4^+ than PO_4^{3-}, plants experience a greater period of elevated P; however, if microbial uptake, rather than leaching, reduces extractable NH_4^+, N is retained in the ecosystem, rather than lost from the ecosystem, which may prevent or slow N limitation of primary productivity.

In contrast to the effects of fire on inorganic nutrients, fire had no effect on total soil N, C, or C:N ratios (Table 1). DeBano and Conrad (1978) reported decreases in total N in the top 2 cm of soil after fire, which was associated with high soil surface temperatures and a loss of soil organic matter; however, any change in soil N or C in the top 0–2 cm of soil would likely be small relative to the total amount of N and C in the 0–15 cm of soil collected in our study. Other studies have found no effect of fire on total soil N (Christensen and Muller 1975; Jensen et al. 2001; Wan et al. 2001; Britton et al. 2008; Boerner et al. 2009), C, or C:N ratios (Boerner et al. 2009). Although fire often has limited effects on bulk soil properties, soil organic matter content and fire severity may mediate fire effects on total soil N and C.

Soil pH increased over time after fire in our study (Table 1). The presence of ash may increase soil pH (Grogan et al. 2000; Badía and Martí 2003; Molina et al. 2007) due to the high pH of ash (Jensen et al. 2001; Goforth et al. 2005; Molina et al. 2007; Marcos et al. 2009) and the high concentration of cations, such as Ca^{2+} and K^+, in ash (Raison et al. 1985b; Arocena and Opio 2003). The majority of aboveground biomass in our flatwoods site was consumed by fire, leaving large amounts of ash on the soil surface. Soil pH increases with % base saturation (Magdoff and Bartlett 1985), and leaching of ash covered soils increases soil pH (Molina et al. 2007), so integration of cation rich ash through the top 15 cm of soil after rain events likely contributed to the increase in soil pH over time. Soils are not well buffered between pH 4 and 7 (Magdoff and Bartlett 1985; James and Riha 1986), so even a small increase in sorption of Ca^{2+} and K^+ could have caused an increase in soil pH (Skyllberg et al. 2001). In addition, microbial biomass N, total microbial respiration, and total phospholipid fatty acids are lower in soils at pH 4.17 than at pH 4.65 (Aciego Pietri and Brookes 2009), suggesting that the increase in pH over time after fire in our study, from 4.09 to 4.41, could have significant effects on the microbial community.

Foliar %N and %P of the dominant flatwoods species, *Serenoa repens*, increased shortly after fire, and were similar to pre-fire values within 4 months after fire (Fig. 2). The increase in foliar %N occurred after soil extractable N was similar to pre-fire levels; whereas, the increase in foliar %P persisted over the same time scale as the increase in soil extractable P. Foliar %N of *Quercus geminata* and ericaceous shrubs also tended to be higher shortly after fire than pre-fire (Fig. 3). Several hypotheses could explain the increase in foliar %N and %P after fire. First, plants may be increasing foliar nutrients post-fire due to increased availability of N and P. Increases in foliar nutrients in our study tended to mirror changes in extractable N and P. Foliar %N of *Q. geminata* and ericaceous shrubs was positively correlated with soil extractable N (Fig. 4), and foliar %P of *S. repens* was positively correlated with soil extractable P. Similarly, other studies have found that foliar nutrients of resprouting species are correlated with soils nutrients after fire (Gilliam 1988; Franco-Vizcaíno and Sosa-Ramirez 1997). Second, N and P stored in belowground tissues of resprouting plants may be retranslocated to aboveground tissues. For example, to support new shoot growth, the resprouting shrub *Quercus ilex* first remobilizes N from belowground reserves then uses available N resources (El Omari et al. 2003). Decreases in retranslocation over time are suggested to occur as resource supply and root biomass increase (Salifu and Timmer 2001); however, for species that resprout after fire, an extensive root system already exists. Percent nonsoluble sugars in belowground structures of *Q. geminata* and *Vaccinium myrsinities* increase and decrease, respectively, with time after fire (Olano et al. 2006), suggesting that these species vary in their capacity to resprout after fire and that time after fire may affect the ability of shrubs to reallocate nutrients to aboveground tissues. In our study, foliar %N of *S. repens* was not correlated with soil extractable N, suggesting that retranslocation of N from below to aboveground may be more important for *S. repens* than for other species. Third, higher foliar nutrient concentrations after fire could be related to leaf age, increased leaf:shoot ratios, or the concentration of nutrients in a smaller amount of aboveground biomass post-fire.

New leaves tend to have higher N concentrations than old leaves (Hikosaka et al. 1994; Anten et al. 1998, Han et al. 2008). Although we have not investigated the effects of age on foliar %N of flatwoods species, we collected the newest leaves at each sampling time to minimize the effects of ontogeny on foliar nutrient concentrations. A decline in foliar N concentrations with leaf age can result from dilution of N (Han et al. 2008), but when plants are grow at high soil NO_3^- concentrations, there is less difference in foliar N content with leaf age (Hikosaka et al. 1994), suggesting that an increase in extractable N and P after fire may contribute to more similar nutrient concentrations among leaves of different ages. In a study of savanna grasses, Van de Vijver et al. (1999) determined that higher foliar N concentrations after fire were due to higher leaf:stem ratios after fire, higher N concentrations in young rather than old leaves, and the distribution of N over the lower amount of post-fire biomass; however, higher foliar P concentrations after fire were not easily explained. In our study, the number of palmetto leaves and the size of resprouting shrubs increased over the sampling period, so dilution of nutrients through more biomass could have occurred. Van de Vijver et al. (1999), however, did not find an effect of fire on soil nutrient availability, so their results do not rule out the possibility that higher foliar nutrient concentrations could be related to higher soil nutrient concentrations post-fire when they occur.

In our study, the relative increase in foliar %P was greater than the relative increase in foliar %N, so foliar N:P ratios of *Serenoa repens* decreased 20% from 15.8 pre-fire to 13.2 two months post-fire (Fig. 2). Over the same time period, soil N:P ratios decreased 83% from 8.4 pre-fire to 1.4 two months post-fire, suggesting that changes in plant nutrition post-fire are related to changes in soil extractable nutrients; however, since foliar N:P ratios did not decrease as much as soil extractable N:P ratios, reallocation of nutrients, particularly N, to aboveground tissue, increased leaf:shoot ratios, and concentration of nutrients in a smaller amount of aboveground biomass post-fire also likely contribute to the post-fire increase in foliar %N and %P. In addition, the foliar N:P ratios of *S. repens* suggests that flatwoods species are co-limited by N and P, because across habitats, N limitation occurs at foliar N:P ratios of 6.7 to 16 and P limitation occurs at foliar N:P ratios of 12.5 to 26.3 (Tessier and Raynal 2003).

Fire had no effect on soil $\delta^{15}N$ (Table 1). Saito et al. (2007) found that soils had to be burned at 400°C for at least 5 min to cause a significant enrichment of soil $\delta^{15}N$, suggesting that high, sustained fire temperatures cause a greater loss of ^{14}N compared to ^{15}N. In addition, if fire consumes surface soils, volatilization of N may cause soils to become enriched in ^{15}N (Högberg 1997). Temperatures recorded throughout a flatwoods fire usually exceeded 400°C for only 1 or 2 min (E. Menges, unpublished data). Thus, low sustained fire temperatures in flatwoods concomitant with low soil organic matter could explain the lack of an effect of fire on soil $\delta^{15}N$. Flatwoods plants were depleted in ^{15}N compared to the soil, which is common in ecosystems with mycorrhizal species (Michelsen et al. 1998; Schmidt and Stewart 2003); however, there was no change in the absolute difference between foliar $\delta^{15}N$ and soil $\delta^{15}N$ over time after fire (Table 2). Fire did, however, affect the foliar $\delta^{15}N$ signatures of flatwoods species; *Quercus geminata* tended to be more enriched in ^{15}N 63 and 130 days post-fire compared to pre-fire and 493 days post-fire, while *Serenoa repens* became more depleted in ^{15}N over time (Fig. 3). Grogan et al. (2000) found that all species in a pine forest were enriched in ^{15}N after fire, but this corresponded with an enrichment of soil $\delta^{15}N$ after fire (Grogan et al. 2000). Considering that we found no change in soil $\delta^{15}N$ after fire, changes in foliar $\delta^{15}N$ signatures post-fire could be caused by: (1) use of a different N source or change in discrimination of the same N source, (2) a change in the soil depth at which nutrient uptake occurs, (3) increased or decreased dependence on mycorrhizae for nutrient acquisition, and/or (4) within plant reallocation of N (Högberg 1997, Evans 2001).

Nitrogen sources (e.g. NH_4^+ versus NO_3^-) vary in their isotopic signatures (Dawson et al. 2002), which can affect foliar $\delta^{15}N$ signatures (Evans 2001); however, extractable NO_3^- was low throughout our study, suggesting that use of NO_3^- as a N source did not change with time after fire. Discrimination against ^{15}N during N uptake can occur at high concentrations of NO_3^- and NH_4^+ (Kolb and Evans 2003); however, even the increased concentrations of NH_4^+ after fire were likely not high enough to cause discrimination against ^{15}N. In addition, the lack of change in the difference in foliar and soil $\delta^{15}N$ over time suggests that neither a change in N sources nor greater discrimination occurred in our study.

Soil $\delta^{15}N$ values tend to increase with depth (Nadelhoffer et al. 1996), and can increase 3‰ over 0–50 cm (Frank and Evans 1997). A shift in N uptake from surface (0–15 cm) to deeper (>15 cm) roots could explain the increase in foliar $\delta^{15}N$ of *Q. geminata* immediately after fire, while a shift in uptake from deeper to surface roots could cause the foliar $\delta^{15}N$ of *S. repens* to become more depleted over time. In a coastal Florida scrub-oak ecosystem, where CO_2 enrichment caused a decrease in soil extractable inorganic N, both *Q. geminata* and *S. repens* took up N from the water table, but *S. repens* showed a greater use of deep soil N (McKinley et al. 2009). Thus, *S. repens* may shift uptake of N from deep soil to surface soil in response to an increase in extractable N in surface soils after fire.

Fire causes an increase in temperature (Ewel et al. 1981; Giardina et al. 2000; Jensen et al. 2001) and a decrease in moisture (Tomkins et al. 1991) of surface soils, which likely affects nutrient uptake by surface roots. Little is known about the root distribution of *Q. geminata* and *S. repens* in palmetto flatwoods, but root biomass has been investigated in other ecosystems where these species occur. In a coastal Florida scrub-oak ecosystem, where *Q. geminata* and *S. repens* comprise approximately 20% of the plant community, slightly less than half of roots <0.25 mm in diameter occur in the top 10 cm of soil (Brown et al. 2007). In scrubby flatwoods, a less mesic shrubland ecosystem often occurring at slightly higher elevations than palmetto flatwoods, approximately 85% of palmetto roots and 60% of oak roots in the top 50 cm of soil are ≤2 mm in diameter (Saha et al. in review). Thus, it seems unlikely that *Q. geminata* and *S. repens* would differ in fire-related root damage, suggesting that a shift in uptake from surface to deeper roots, or vice versa, could occur in response to changes in availability of or competition for soil nutrients.

Quercus geminata has associations with ectomycorrhizae (Langely et al. 2002), ericaceous species have associations with ericoid mycorrhizae (Pearson and Read 1973), and *S. repens* has associations with arbuscular mycorrhizae (Fisher and Jayachandran 1999); fractionation during the transfer of N from mycorrhizal fungi to a host plant results in plant tissue depleted in ^{15}N relative to the N source (Evans 2001; Hobbie and Colpaert 2003). Foliar $\delta^{15}N$ of *Q. geminata* could be more enriched shortly after fire if species reduced nutrient uptake through mycorrhizae, while foliar $\delta^{15}N$ of *S. repens* of could become more depleted over time if nutrient uptake through AM increased. Soil $\delta^{15}N$ and the difference between foliar and soil $\delta^{15}N$ did not change over time for any species, however, suggesting that dependence on mycorrhizae for N uptake did not change after fire. In addition, Anderson and Menges (1997) and Eom et al. (1999) found that fire had no effect on colonization of roots by arbuscular mycorrhizae. Schmidt and Stewart (1997) found that plant $\delta^{15}N$ signatures were more similar among species with the same mycorrhizal status than among species with the same post-fire response (e.g. resprouter vs. seeder species), so mycorrhizal status may play at least a small role in affecting changes in foliar $\delta^{15}N$ after fire.

Foliar $\delta^{15}N$ signatures decrease over time after leaf initiation (Bergersen et al. 1988), suggesting that reallocation of N within a plant can affect foliar $\delta^{15}N$ signatures (Evans 2001). Although we sampled the newest leaves, as leaf number increased, we were more likely to sample leaves of varying ages, which could cause a decline in foliar $\delta^{15}N$ over time after fire. In addition, leaves may be enriched in ^{15}N compared to roots (Evans et al. 1996), and the foliar $\delta^{15}N$ of *S. repens* could have decreased over time due to reallocation of N depleted in ^{15}N from belowground to aboveground tissues. We hypothesize that changes in foliar ^{15}N signatures after fire are influenced by N reallocation and leaf age and that a change in N uptake from roots at different levels in the soil may also contribute to variation in foliar $\delta^{15}N$.

One limitation of our experimental design is that we did not measure soil or plant nutrients in an unburned control site over the same time period that we measured soil and plant nutrients after fire in our flatwoods site; however, fire effects are the most likely explanation for our results for several reasons. First, across a scrubby flatwoods time-since-fire chronosequence, resin exchangeable NH_4^+ and PO_4^{3-} was 2.7 and 1.5 times higher, respectively, during September through December compared to June through September (J. Schafer, unpublished manuscript). In our flatwoods site, extractable NH_4^+ and PO_4^{3-} were 5.5 and 30 times higher, respectively, 3 h after fire than before fire. This change is much greater, and occurred over a much shorter time period, than seasonal variation in nutrient availability; thus, it is unlikely that the increases in extractable nutrients measured in this study are due to seasonal variation. Second, in the same palmetto flatwoods site used in this study, soil pH did not vary between September and November 2009 (J. Schafer, unpublished data). In addition, in oak and saw palmetto scrub, an ecosystem similar to flatwoods, Schmalzer and Hinkle (1991) found that in the first year after fire, soil pH was greater in December (12 months after fire) than in June (6 months after fire); whereas, in the second year after fire, soil pH was greater in June (18 months after fire) than in December (24 months after fire). Thus, changes in soil pH are likely due to fire effects rather than seasonal variation. Third, foliar %N and %P of oaks, ericaceous shrubs, and palmettos is higher six weeks after fire than before fire or one year after fire in scrubby flatwoods sites burned in March and July (J. Schafer, unpublished data), suggesting that the pattern of increased foliar nutrients after fire is consistent across sites and does not depend on burn season. We did not measure foliar nutrient concentrations of clipped plants over the same time scale that we measured foliar nutrient concentrations of burned plants, but burning and clipping can have similar effects on plant nutrient concentrations (Van de Vijver et al. 1999).

In our study, fire caused a short-term increase in soil extractable NH_4^+ and PO_4^{3-} in a palmetto flatwoods ecosystem (Fig. 1); PO_4^{3-} remained elevated above pre-fire levels twice as long as NH_4^+, possibly due to differences in microbial uptake and mobility of NH_4^+ and PO_4^{3-}. Both foliar %N and %P of resprouting plants increased over the short-term after fire (Table 2). The relative increase in soil extractable P and foliar P was greater than that of soil extractable N and foliar N, leading to a decrease in the soil extractable N:P ratio (Fig. 1) and the foliar N:P ratio of the palmetto *Serenoa repens* (Fig. 2) shortly after fire. The relationships between soil and foliar nutrients coupled with measurements of soil and foliar $\delta^{15}N$ suggest that both an increase in soil extractable nutrients and reallocation of nutrients from belowground to aboveground tissue contribute to the increase in foliar %N and %P shortly after fire. Previous research in Florida scrub ecosystems has found limited effects of fire on soil nutrient availability (Abrahamson 1984, Schmalzer and Hinkle 1991). We found that a pulse of nutrients is detectable if soils are sampled soon enough after fire. Furthermore, our results suggest that even a short-term increase in soil extractable nutrients can be important for plant nutrient status, especially in ecosystems with low nutrient availability.

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