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Nutrient limitation of plant productivity in scrubby flatwoods: does fire shift nitrogen versus phosphorus limitation?

Jennifer L. Schafer · **Michelle C. Mack**

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Abstract Differences in the biogeochemistry of nitrogen (N) and phosphorus (P) lead to differential losses and inputs during and over time after fire such that fire may affect nutrient limitation of primary productivity. We conducted a nutrient addition experiment in scrubby flatwoods, a Florida scrub community type, to test the hypothesis that nutrient limitation of primary productivity shifts from N limitation in recently burned sites to P limitation in longer unburned sites. We added three levels of N, P, and N and P together to sites 6 weeks, 8 years, and 20 years postfire and assessed the effects of nutrient addition on above- and belowground productivity and nutrient concentrations. At the community level, nutrient addition did not affect aboveground biomass, but root productivity increased with high N + P addition in sites 8 and 20 years after fire. At the species level, N addition increased leaf biomass of saw palmetto (*Serenoa repens*) in sites 6 weeks and 20 years postfire, while P addition increased foliar %P and apical shoot growth of scrub oak (*Quercus inopina*) in sites 8 and 20 years postfire, respectively. Contrary to our hypothesis, nutrient limitation does not appear to shift with time after fire; recently burned sites show little evidence of nutrient limitation, while increased belowground productivity indicates that scrubby flatwoods are co-limited by N and P at intermediate and longer times after fire.

Keywords Florida · Foliar nutrients · *Quercus inopina* · Root ingrowth cores · *Serenoa repens* · Soil nutrients

Introduction

The availability of essential plant nutrients is a primary control over plant productivity (Seastedt and Vaccaro 2001; Niinemets and Kull 2005). Nutrient limitation is defined as an increase in plant productivity with an increase in nutrient availability (Chapin et al. 1986; Vitousek and Howarth 1991), and nitrogen

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J. L. Schafer · M. C. Mack
Department of Biology, University of Florida,
Gainesville, FL 32611, USA

Present Address:
J. L. Schafer (✉)
Department of Biology, Winthrop University, 202 Dalton Hall,
Rock Hill, SC 29733, USA
e-mail: schaferj@winthrop.edu

Present Address:
M. C. Mack
Center for Ecosystem Science and Society, Northern Arizona
University, PO Box 5620, Flagstaff, AZ 86011, USA

(N) and/or phosphorus (P) limit plant productivity in the majority of terrestrial ecosystems (Vitousek and Howarth 1991; Elser et al. 2007; Vitousek et al. 2010). Co-limitation of plant productivity by N and P exists when N and P added together increase biomass or when N and P additions both increase biomass independently (Harpole et al. 2011). Fire, a common disturbance in many ecosystems, has differential effects on N and P due to fundamental differences in their biogeochemistry. Understanding the effects of fire on nutrient limitation is important because nutrient limitation of plant productivity has consequences for biomass accumulation (Wieder et al. 2015), nutrient retention and loss (Brookshire et al. 2012), and biodiversity (Wassen et al. 2005; Pekin et al. 2012).

During fire, nutrients in organic forms in consumed plant biomass, litter, and soil organic matter are converted to inorganic forms (Certini 2005), which can be returned to the ecosystem in ash or lost to the atmosphere through volatilization or transport of ash. Numerous studies have measured the effect of fire on nutrient volatilization and found that approximately twice as much N as P is lost to the atmosphere, on a mass basis (Gillon and Rapp 1989; Pivello and Coutinho 1992; Cook 1994; Wittkuhn et al. 2017), which occurs because of differences in volatilization temperatures. Nitrogen volatilization occurs at 200 °C (White et al. 1973), a temperature typically reached in fires (e.g., Iverson and Hutchinson 2002; Boring et al. 2004), and complete loss of organic N via volatilization can occur at 450 °C (Qian et al. 2009). In contrast, P only volatilizes above 774 °C (Raison et al. 1985a), a temperature reached rarely and instantaneously in fires (Wotton et al. 2012; E. Menges, unpublished data). Because more volatilization of N than P occurs during fire, ash on the soil surface contains higher concentrations of P than N (Debano and Conrad 1978; Raison et al. 1985b; Marcos et al. 2009). Furthermore, N retained in ash after fire is in mobile forms (NH_4^+, NO_3^-, or NO_2^-), which are susceptible to leaching, while P is in the form of PO_4^{3-} or bound with calcium or magnesium (Qian et al. 2009), which are less mobile and thus, less susceptible to leaching. Thus, differential losses of N and P during and shortly after fire can cause N to be relatively less available than P (Schafer and Mack 2010).

Over time after fire, the balance of inputs versus losses is likely to differ between N and P. Nitrogen lost during fire can be replaced via N-fixation and deposition. With frequent fire, N inputs are not high enough to replace volatilization losses (Cook 1994), leading to a decline in soil N pools (Pellegrini et al. 2015) and relatively low N availability (Hernández and Hobbie 2008). However, without subsequent fire for years to decades to centuries, depending on the ecosystem, N inputs via biological fixation and deposition can replace fire-induced N losses (Boring et al. 2004; Giesen et al. 2008; Chen et al. 2010) and increase soil N (Johnson and Curtis 2001). In contrast, inputs of P over time, via weathering and deposition, are likely to be low and not balance losses of P, leading to a decline in soil P over time after fire (Seaman et al. 2015). Inputs of P via weathering of parent material are dependent on soil age and likely to be negligible in highly weathered soils (Walker and Syers 1976). Atmospheric deposition of P is over 100 times lower than ash P inputs (Resende et al. 2011) and N deposition (Grimshaw and Dolske 2002), and P inputs from dust depend on proximity to deserts (Okin et al. 2004). Thus, decomposition of litterfall is likely to be the largest input to soil P (Resende et al. 2011), which reflects internal P cycling rather than an external P input to an ecosystem. Losses of N and P can occur via leaching. Although N leaching losses can be orders of magnitude greater than P leaching losses (Radulovich and Sollins 1991; Hedin et al. 2003), N losses are positively correlated with N mineralization (Hedin et al. 2003) and deposition (Hedin et al. 1995), indicating that increased N losses correspond with increased N availability. Losses of P from the available P pool also occur via sorption of P to soil surfaces and fixation via geochemical reactions (Walker and Syers 1976), which are affected by soil texture (Villani et al. 1998) and redox potential (Miller et al. 2001); in contrast, N does not become occluded in forms unavailable to plants. Thus, differential inputs and losses of N and P over the long-term after fire may cause P to become relatively less available than N (Wardle et al. 2004).

Because fire has the potential to alter the relative availability of N versus P both immediately following fire and over inter-fire cycles, a fundamental question about nutrient limitation is whether fire causes shifts in N versus P limitation. Fire-mediated differences in nutrient supply suggest that nutrient limitation may change with time after fire, with recently burned sites being N-limited due to high N losses during fire and long unburned sites being P-limited, particularly where soils are old and highly weathered, because most of the P is in organic matter. Research on the effects of time after fire on nutrient limitation, however, is scarce and has focused on more recently burned sites, with inconsistent results, or indirect measures of nutrient limitation. From 1 to 4 years after fire in heathlands, high N addition maintained high shoot N concentrations in *Calluna vulgaris* (Britton et al. 2008). However, in lodgepole pine forests 3–5 years postfire, three of the four understory species studied were not N-limited (Romme et al. 2009). And in a shrubland 5 years postfire, *Pinus halepensis* and *Quercus ilex* showed a greater response to P than N fertilization (Sardans et al. 2004). In a meta-analysis, Maynard et al. (2014) found that boreal forest tree species increase growth in response to N, P, or N and P addition together, but N versus P limitation was not assessed in relation to time postfire. Measurements of foliar N:P ratios are commonly used as an indirect measure of nutrient limitation (Koerselman and Meuleman 1996; Güsewell 2004). Foliar N:P ratios have been measured over longer times after fire and suggest that ecosystems experience N limitation (Durán et al. 2010), P limitation (Seaman et al. 2015), or co-limitation by N and P (Schafer and Mack 2014) across postfire chronosequences. However, foliar N:P ratios are not always indicative of plant responses to fertilization, and thus, nutrient limitation (Craine et al. 2008; Alvarez-Clare and Mack 2015). Therefore, direct tests of nutrient limitation over longer time-since-fire chronosequences are needed.

Fire-dependent Florida scrub ecosystems occur on quartz sand soils (Myers 1990) with little capacity for nutrient exchange or fixation (Brown et al. 1990). Scrubby flatwoods, a distinct Florida scrub community, are dominated by woody shrubs that resprout within weeks after fire, and over half of scrubby flatwoods species do not change in abundance over time after fire (Menges and Kohfeldt 1995). Scrubby flatwoods are an ideal community to investigate nutrient limitation over time after fire because any change in nutrient limitation is not likely to be driven by a change in species composition. We conducted a nutrient addition experiment to test the hypothesis that nutrient limitation of plant productivity in scrubby flatwoods changes with time after fire because of fundamental differences in the biogeochemistry of N and P. We predicted that (1) plant productivity in recently burned scrubby flatwoods is N-limited due to relatively higher losses of N than P during fire; (2) plant productivity in scrubby flatwoods at intermediate times after fire is co-limited by N and P; and (3) plant productivity in long unburned scrubby flatwoods is P-limited due to relatively lower inputs of P than N. We measured soil nutrient availability to determine if availability of N and P vary with time after fire as expected and if our nutrient addition increased the availability of N and P. Plants can allocate an increase in nutrients to increasing growth and/or tissue nutrient concentrations (D'Antonio and Mack 2006; Britton et al. 2008; Alvarez-Clare and Mack 2015). Thus, we measured the effects of nutrient addition on multiple components of productivity (aboveground biomass, leaf biomass, root production, and litterfall) and plant growth (basal diameter, height, and apical shoots) as well as foliar and root N and P concentrations.

Methods

Study site

Our study was conducted at Archbold Biological Station (ABS) in Highlands County, Florida, USA. Mean annual precipitation is 135.6 cm (ABS weather records, 1932–2014). Our research focused on the scrub oak (*Quercus inopina* Ashe) phase of scrubby flatwoods, which is dominated by shrubby oaks (Fagaceae), palmettos (Arecaceae), and ericaceous shrubs (Ericaceae) that resprout after fire (Menges and Kohfeldt 1995). Specifically, *Q. inopina* and saw palmetto (*Serenoa repens* (W. Bartram) Small) are the two most dominant species in this scrubby flatwoods community (Abrahamson et al. 1984; Online Resource 1). Soils are classified as entisols (Abrahamson et al. 1984) and have low exchange capacity, little organic matter, and low nutrient availability (Brown et al. 1990; Schafer and Mack 2013). Soil organic matter is an important supply of inorganic N (McKinley et al. 2009), and likely inorganic P, and is thus a primary control of nutrient availability and storage. The fire return interval of scrubby flatwoods is 8–16 years (Menges 2007), and scientists have documented fires at ABS for the last 50 years.

Experimental design

In July 2007, we selected three burn units located in the southern portion of ABS (Fig. 1); one was 6 weeks postfire (recently burned), one was 8 years postfire (intermediate), and one was 20 years postfire (long unburned; hereafter referred to as 6 weeks, 8 years, and 20 years sites). All burn units contained scrubby flatwoods communities classified as the *Q. inopina* phase. The size of the burn units ranged from 27 to 239 acres. The fires in all burn units were prescribed fires of moderate to high intensity (ABS fire records) that killed aboveground stems; the dominant species resprouted after fire.

We established three blocks in each burn unit (Fig. 1). Because of the constraints of prescribed burning and conducting a time-since-fire study, we were not able to establish blocks in different burn units for each time after fire to create true replicates (Hurlbert 1984). Nevertheless, inferential statistics can be used in this situation (Oksanen 2001), so we applied a replicated fertilization experiment within each of the burn units.

Within each block, we established ten 3 × 3 m plots with a buffer of 2–4.5 m between plots (Fig. 1), for a total of 30 plots for each time after fire. Plots were established to include at least three individuals of *Q. inopina* and *S. repens*. Blocks ranged in size from approximately 575–1100 m^2 to account for variation in the distribution of *Q. inopina* and *S. repens* across the landscape.

Within a block, each plot was randomly assigned one of the following treatments: control, low N (2 g m^{-2}), intermediate N (5 g m^{-2}), high N (10 g m^{-2}), low P (1 g m^{-2}), intermediate P (2.5 g m^{-2}), high P (5 g m^{-2}), low N + P (2 g N + 1 g P m^{-2}), intermediate N + P (5 g N + 2.5 g P m^{-2}), or high N + P (10 g N + 5 g P m^{-2}). Because sandy soils in Florida scrub have low sorption capacity, the annual dose of fertilizer was divided into equal amounts and added four times during the year: July 2007 (middle of the wet season), October 2007 (beginning of the early dry season), January 2008 (end of the early dry season), and April 2008 (end of the late dry season). Nitrogen was added as ammonium urea and ammonium nitrate (half of each) and P was added as triple superphosphate.

Soil nutrients

To monitor N and P availabilities in control plots during our experiment, we used ion exchange resins

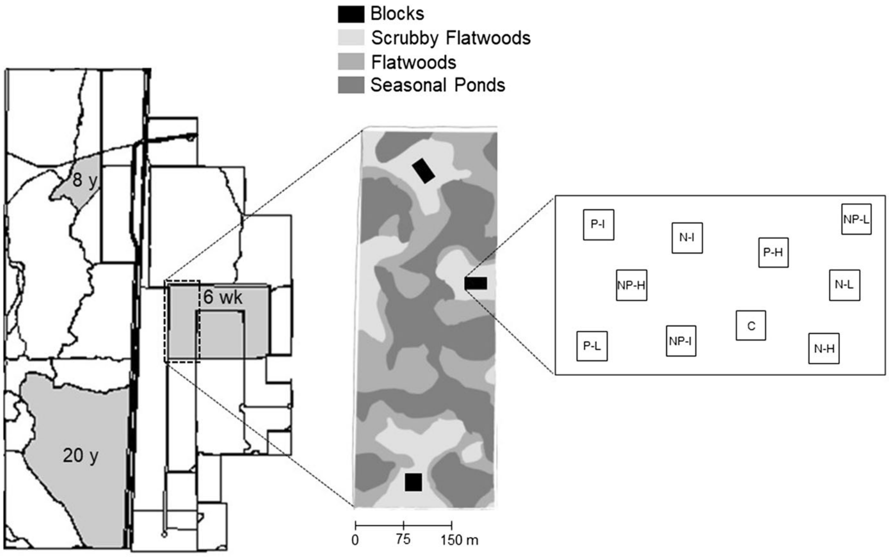


Fig. 1 Left: Map of burn units (outlined in black) at the southern end of Archbold Biological Station. Burn units used in this study are shaded gray and labeled with the time after fire (6 weeks, 8 years, and 20 years) at the beginning of the study. Center: Portion of the 6 week since fire burn unit with study blocks and vegetation types (scrubby flatwoods are the scrub oak (*Q. inopina*) phase). Right: Block showing ten 3 × 3 m study plots; *N* nitrogen, *P* phosphorus, *L* low, *I* intermediate, *H* high, and *C* control

(anion (AG 1-8X chloride form), cation (AG 50W-X8 hydrogen form); Bio-Rad, Hercules, CA, USA). We buried an anion and a cation exchange resin bag in the top 5 cm of soil near each corner of each control plot in July 2007. Subsequently, resin bags were removed and new bags were buried every three months for one year. Anion bags were charged with 2 M HCl before burial and extracted with 50 mL of 0.5 M HCl after removal, while cation bags were charged and extracted with 2 M NaCl and 50 mL of 0.5 M NaCl, respectively. Resin bags were shaken for 6 h during extraction, and extracts were frozen. Concentrations of NO_3^-, NH_4^+, and PO_4^{3-} were determined colorimetrically on a continuous flow autoanalyzer (Astoria-Pacific, Inc., Clackamas, Oregon) at the University of Florida. We summed resin-exchangeable N and P over 1 year for each sample location (four per control plot) and calculated the mean resin-exchangeable N, P, and N:P ratio for each control plot. Thus, we had only one replicate per block, so we used one-way ANOVAs with post hoc Tukey tests to analyze differences in resin-exchangeable N, P, and N:P ratios among times after fire.

In August 2008, after 1 year of nutrient addition, we collected soil from three random locations in all plots to assess the effect of nutrient addition on nutrient availability. Soil cores (2.5 cm diameter) were separated by depth (0–10 and 10–20 cm), and the three cores from each depth were bulked. Within 24 h of collection, soil samples were passed through a 2 mm sieve and subsampled for determination of gravimetric soil moisture and inorganic N and P concentrations. Gravimetric moisture content was determined on samples dried at 105 °C for 48 h. Soils from all times after fire had similar concentrations of total nonlimiting macro- and micronutrients (Online Resource 1).

To measure inorganic N concentrations, 50 mL of 0.5 M K_2SO_4 was added to 10 g of field moist soil, shaken for 30 s, and allowed to stand overnight. Solutions were filtered through Whatman #42 filter paper that was pre-leached with 0.5 M K_2SO_4, and filtered extracts were frozen. Dissolved inorganic N ($NH_4^+ + NO_3^-$) concentrations were determined colorimetrically on a continuous flow autoanalyzer at the University of Florida.

To measure inorganic P concentrations, 30 mL of 0.05 M hydrochloric acid (HCl) and 0.0125 M hydrogen sulfate (H_2SO_4) were 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 3 weeks before analysis of 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 MacArthur Agro-Ecology Research Center (Highlands Co., Florida).

Aboveground biomass and growth and foliar nutrients

In each plot before nutrient addition, we marked and measured three individuals of *Q. inopina* and *S. repens* and three individuals (if present) of *Lyonia lucida* (Lam.) K. Koch, *Lyonia fruticosa* (Michx.) G. S. Torr, *Quercus chapmanii* Sarg., *Quercus geminata* Small, and *Sabal etonia* Swingle ex Nash [nomenclature follows Wunderlin and Hansen (2011)] and estimated percent cover of each species. These species account for over 97% of shrub cover in our plots (Online Resource 1). The oaks (*Quercus* spp.) and ericaceous shrubs (*Lyonia* spp.) are clonal, multistemmed species; we measured crown length and width of each individual (defined by stems within a 10 cm diameter circle centered on the tallest stem) and height and basal diameter of each stem. For the palmettos *S. etonia* and *S. repens*, we measured maximum and minimum crown length and height. In July 2008, after 1 year of nutrient addition, we made the same measurements listed above. In addition, in the control and high nutrient addition plots, we measured apical shoot growth on a randomly selected subset of *Q. inopina* stems of each individual. For many stems, we measured a subset of the new apical shoot growth increments, estimated the proportion of increments that we measured, and scaled up to calculate total apical shoot growth per stem.

We used age specific allometric equations for each time after fire (Online Resource 1) to estimate total shoot biomass of each marked shrub stem and leaf biomass of each marked palmetto individual at each time point. For *Quercus* and *Lyonia* species, we summed shoot biomasses to determine the biomass of each individual. We calculated the area (maximum × minimum crown length) of each individual. We calculated the total measured biomass and total area covered by each species in each plot. If there were more than three individuals of a species, we used estimates of percent cover and the area covered by measured individuals to scale biomass to the entire plot. We calculated the percent change in total aboveground shrub biomass in each plot [((posttreatment total shrub biomass − pretreatment total shrub biomass)/pretreatment total shrub biomass) × 100%], and we used a one-way ANOVA to analyze the effect of time after fire on percent change in biomass in control plots. In the control and high nutrient addition plots, we calculated the percent change in total biomass of each individual of *Q. inopina* and *S. repens*, the percent change in basal diameter and height of each stem of *Q. inopina*, and total apical shoot growth of *Q. inopina* (mean of stems per individual).

We collected foliar samples of all marked *Q. inopina* and *S. repens* individuals pretreatment and from individuals in control and high nutrient plots in July 2008, after nutrient addition. Samples were dried at 65 °C for 48 h and ground. Percent N was determined at the University of Florida on an elemental analyzer (ECS 4010, Costech Analytical, Valencia, California). To measure foliar P, subsamples of 0.05–0.5 g were weighed into crucibles, ashed in a muffle furnace at 500 °C for 5 h, and extracted with 6 M HCl. Extracts were stored in the refrigerator then analyzed colorimetrically on a spectrophotometer microplate reader (PowerWave XS Microplate Reader, Bio-Tek Instruments, Inc., Winooski, Vermont, USA) using the ascorbic acid molybdenum-blue method (Murphy and Riley 1962). Standard NIST peach leaves were used to determine the efficiency of the extraction. To analyze differences in all measures of pre-fertilization foliar nutrients (%N, %P, and N:P ratios), we fit a model with species and time after fire and their interaction as main effects. Differences among species and times after fire were determined with post hoc Tukey HSD tests (JMP 8.0).

Litterfall

We measured litterfall by placing four litter traps in a cross formation on the ground of each plot. Each litter trap was 0.09 m^2, 10 cm deep, made of 2 mm hardware cloth, and established in July 2007. Litter was collected in December 2007 (the first time there was litter to collect) and March, May, and July 2008. Litter was pooled at the plot level, sorted to fractions (leaf, twig, and reproductive), dried at 65 °C for 48 h, and weighed. We calculated total leaf litterfall (g m^{-2} $year^{-1}$) for each plot. We used a one-way ANOVA to analyze the effect of time after fire on total leaf litterfall in control plots.

Root productivity and nutrient concentrations

We used root ingrowth cores (Cuevas and Medina 1988) to measure root productivity. In each plot before nutrient addition (July 2007), we randomly established three cylindrical, closed-bottom root ingrowth cores (2 mm mesh, 20 cm deep, 8 cm diameter). We collected soil cores, passed the soil through 2 mm and 1 mm sieves to remove roots and underground stems, placed the ingrowth cores in the ground, and then filled the cores with the root free soil. We weighed belowground biomass after drying at 65 °C for 48 h. Root ingrowth cores were removed from the ground in August 2008, and each core was immediately put into a plastic bag. We hand-picked roots from the inside of each core and sieved all sand from inside each core through 2 and 1 mm sieves. Long thin roots that passed through the sieve were picked out by hand. Roots were dried at 65 °C for 48 h then weighed. We used a one-way ANOVA to analyze the effect of time after fire on root productivity (g m^{-2} $year^{-1}$) in control plots. Roots from control and high nutrient plots were ground and percent N and P was determined as described above for foliar samples.

Analysis of nutrient addition effects

For all response variables, we analyzed the effects of nutrient addition separately for each time after fire. To analyze the effect of nutrient addition on soil extractable N and P (measured after 1 year of nutrient addition), we used general linear mixed-effect models with treatment as a fixed effect and block as a random effect; separate models were used for each soil depth (0–10 and 10–20 cm). We used general linear mixed-effect models with treatment as a fixed effect and block as a random effect to analyze the effect of nutrient addition on the percent change in total aboveground shrub biomass in each plot. To analyze the effect of nutrient addition on leaf litterfall, we used general linear mixed-effect models with treatment as a fixed effect, block as a random effect, and mean (of pre- and post-fertilization) total percent shrub cover as a covariate. We used general linear mixed-effect models with treatment as a fixed effect, block as a random effect, and pre-fertilization root biomass (> 2 mm + 2 mm fraction; g m^{-2}) as a covariate to analyze the effects of nutrient addition on root productivity. Data were transformed when necessary to meet the assumptions of normality.

To analyze the effect of high nutrient addition on root nutrient concentrations (community level) and percent change in foliar N and P concentrations and N:P ratios of *Q. inopina* and *S. repens* [e.g., ((post-treatment *Q. inopina* foliar %N − pretreatment *Q. inopina* foliar %N)/pretreatment *Q. inopina* foliar %N) × 100%] we used general linear mixed-effect models with treatment as a fixed effect and block as a random effect. To analyze the effect of high nutrient addition on percent change in biomass of *Q. inopina* and *S. repens* [e.g., ((posttreatment *Q. inopina* biomass − pretreatment *Q. inopina* biomass)/pretreatment *Q. inopina* biomass) × 100%] and percent change in height and basal diameter of *Q. inopina* stems we used general linear mixed-effect models with treatment as a fixed effect and block as a random effect. For the analyses of percent changes in biomass, height, and diameter of *Q. inopina*, extreme outliers (> 3 standard deviations from the mean) were removed from analyses if the percent change for a measure was negative, as this was likely a result of stem loss. To analyze the effect of high nutrient addition on apical shoot growth of *Q. inopina*, we used general linear mixed-effect models with treatment as a fixed effect and block as a random effect. Data were transformed when necessary to meet the assumptions of normality.

For all models that had a significant treatment effect, we used post hoc Dunnett's tests to determine if the response variable was higher (or lower) in nutrient addition treatments than the control. Because all blocks for a time after fire are within the same burn unit, our study design lacks true replication; thus, all analyses are inferential statistics. All analyses were conducted in SPSS version 11.5.

Results

In control plots, annual resin-exchangeable N and P tended to be highest during the first year after fire (Fig. 2). Total resin-exchangeable N was 3.2 and 2.6 times higher during the first year after fire than in the 8 years site and 20 years site, respectively. Both NH_4^+ and NO_3^- concentrations followed this pattern, but NH_4^+ concentrations were 5.7–15.2 times higher than NO_3^- concentrations (Fig. 2a). Resin exchangeable PO_4^{3-} was 5.1 and 3.8 times higher during the first year after fire than in the 8 years site and 20 years site, respectively (Fig. 2b). There was no significant difference, however, in resin-exchangeable N:P ratios with time after fire (Fig. 2c).

Nutrient addition did not significantly increase K_2SO_4-extractable N (measured after one of nutrient addition) in the 6 weeks or 8 years site (Fig. 3). In the 20 years site, absolute increases in mean K_2SO_4-extractable N with intermediate and high N addition (compared to control plots) were greater in surface (0–10 cm) soils (0.68 and 0.51 µg N g soil^{-1}, respectively) than in deep (10–20 cm) soils (0.34 and 0.45 µg N g soil^{-1}, respectively), but the increase was significant only in deep soils. Phosphorus addition significantly increased acid-extractable P in the 6 weeks site only when added with N at low levels. In the 8 years site, all levels of P addition increased acid-extractable P. In both the 8 and 20 years sites, high P addition increased acid-extractable P tenfold in surface and deep soils (Fig. 3).

Before nutrient addition, aboveground biomass (g m^{-2}) of dominant shrubs (mean ± SE) was 71 ± 5 in the 6 weeks site, 334 ± 20 in the 8 years site, and 377 ± 25 in the 20 years site. Shrub biomass in the 6 weeks site was only approximately 20% of biomass in the 8 and 20 years sites because fire removed all aboveground biomass and only new resprouts were present. Percent change in shrub biomass in the control plots was higher in the 6 weeks site than in the 8 years and 20 years sites ($F_{2,6} = 72.0$, $P < 0.001$). Nutrient addition did not affect the percent change in total shrub biomass at any time after fire (Fig. 4).

Time after fire did not have a significant effect on total leaf litterfall in control plots ($F_{2,6} = 0.72$, $P = 0.526$); total leaf litterfall (mean ± SE; g m^{-2} year^{-1}) was 86.0 ± 30.3, 138.3 ± 27.9, and 151.8 ± 58.0 in the 6 weeks, 8 years, and 20 years sites, respectively. Total leaf litterfall was not affected by nutrient addition at any time after fire (Fig. 4).

Time after fire did not have a significant effect on root productivity in control plots ($F_{2,6} = 2.34$, $P = 0.178$); root productivity (mean ± SE;

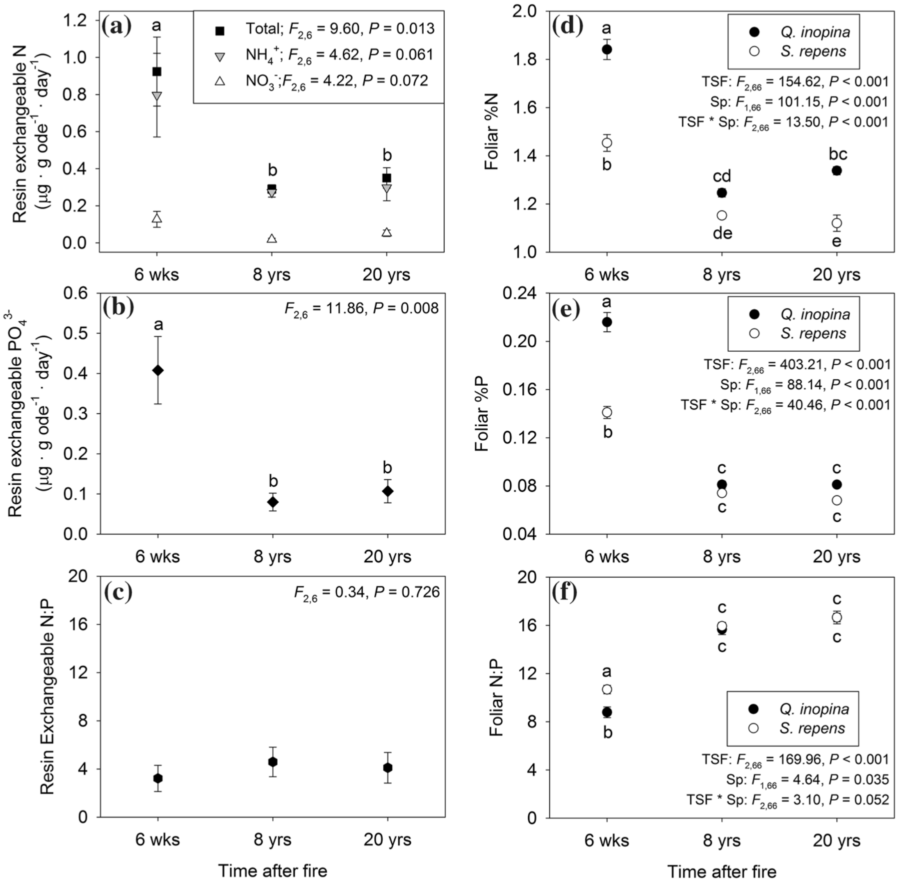


Fig. 2 Mean (± SE) resin-exchangeable soil N (**a**), P (**b**), and N:P (**c**), and pre-fertilization foliar %N (**d**), %P (**e**), and N:P (**f**) of *Quercus inopina* and *Serenoa repens* in sites 6 weeks, 8 years, and 20 years postfire. Different letters represent significant differences at $\alpha = 0.05$. *ode* oven dry equivalent

g m^{-2} year^{-1}) was 193.7 ± 50.7 in the 6 weeks site, 128.8 ± 10.7 in the 8 years site, and 145.4 ± 41.1 in the 20 years site. In the 6 weeks site, nutrient addition did not increase root productivity compared to control plots. In the 8 and 20 years sites, only high addition of N and P together increased root productivity (Fig. 4). Compared to control plots, root productivity was 3.6 and 2.4 times higher in high N + P addition plots in the 8 years site and the 20 years site, respectively (Fig. 4). High nutrient addition had no effect on root N concentrations in the 6 weeks ($F_{3,6} = 3.09$, $P = 0.111$), 8 years ($F_{3,6} = 1.96$, $P = 0.222$), or 20 years ($F_{3,6} = 1.03$, $P = 0.445$) sites (Fig. 5a). High P and N + P addition increased root P concentrations in the 6 weeks ($F_{3,6} = 31.53$, $P < 0.001$), 8 years ($F_{3,6} = 109.73$, $P < 0.001$), and 20 years ($F_{3,6} = 28.46$, $P = 0.001$) sites (Fig. 5b).

At the species level, high nutrient addition had no effect on the percent change in total aboveground biomass (Fig. 6a), basal diameter (Fig. 6b), or height (Fig. 6c) of *Quercus inopina* regardless of time after fire. In the 20 years site, high P addition increased *Q. inopina* apical shoot growth (Fig. 6d). The percent change in *Serenoa repens* leaf biomass was approximately 1.5 and 12 times greater in high N addition plots than in control plots in the 6 weeks site and the 20 years site, respectively (Fig. 7a); high nutrient addition did not increase *S. repens* leaf biomass in the 8 years site (Table 1).

Pre-fertilization, foliar %N and %P were higher in *Q. inopina* than in *S. repens*. Proportionally, the decrease in foliar %N of *Q. inopina* and *S. repens* from the 6 weeks to 8 years site (Fig. 2d) was less than the decrease in foliar %P (Fig. 2e). Foliar N:P ratios of *Q. inopina* and *S. repens* increased 8 and 6 units,

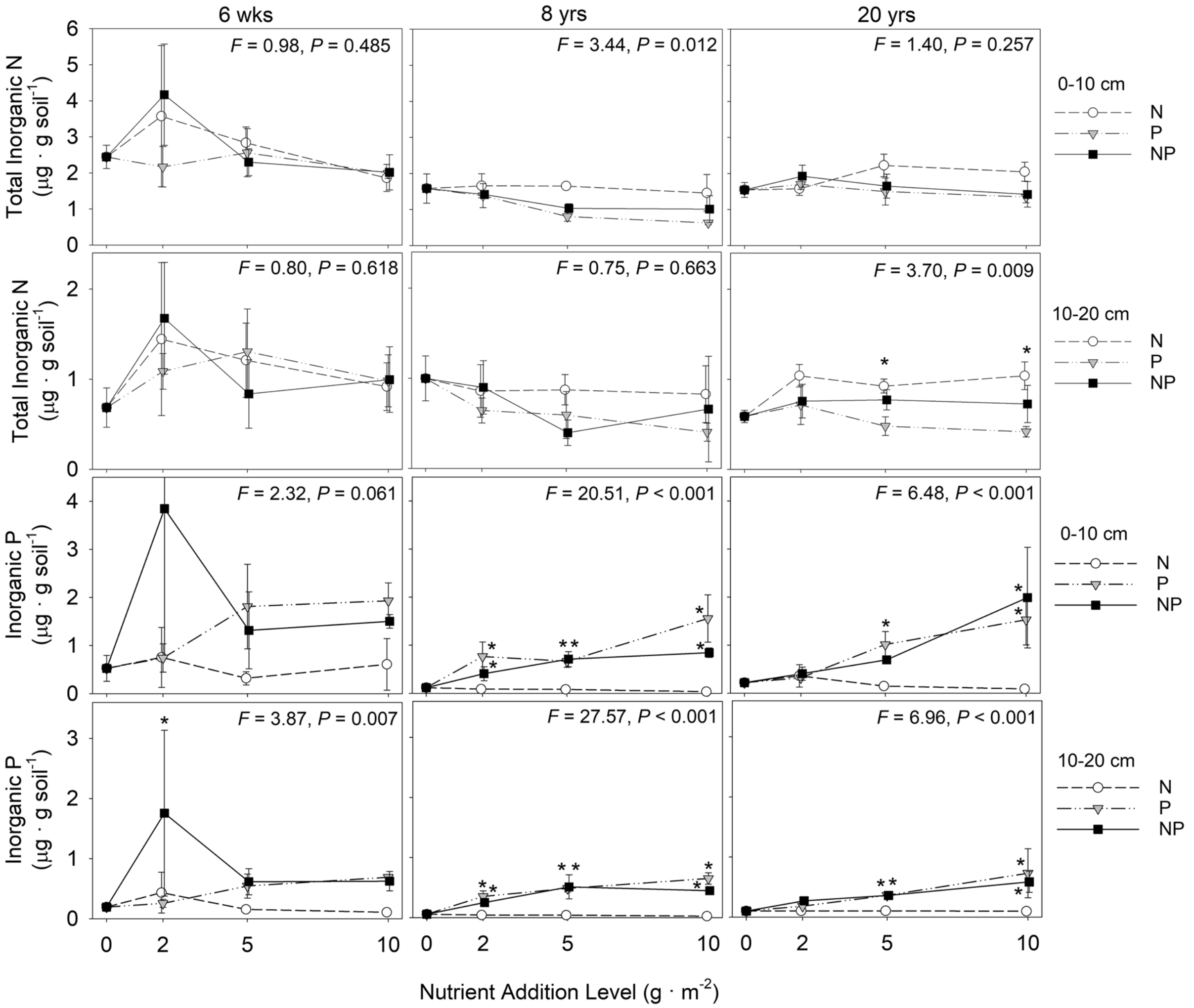


Fig. 3 Mean (± SE) inorganic N and P in 0–10 and 10–20 cm soils after nutrient addition in sites 6 weeks, 8 years, and 20 years postfire. Degrees of freedom (numerator, denominator) are 9, 18 for the treatment effect. Single asterisk (*) indicates a treatment is significantly greater than the control at α = 0.05. Note that the upper standard error bar (6.89 µg g soil^{-1}) for inorganic P in 0–10 cm soils in the N + P treatment in the 6 weeks postfire site is not shown

respectively, from the 6 weeks to 20 years site (Fig. 2f). High nutrient addition did not affect the percent change in foliar %N of *Q. inopina* at any time after fire (Fig. 6e). In the 8 years site, high P addition increased foliar %P of *Q. inopina* (Fig. 6f), which led to a decrease in the foliar N:P ratio (Fig. 6g). Although the percent change in foliar %N of *S. repens* was positive in high N and N + P addition plots in the 8 years and 20 years sites (Fig. 7b), the effect of nutrient addition was not significant (Table 1). In the 6 weeks site, where foliar %N and %P were higher pre-fertilization than post-fertilization, foliar %P of *S. repens* decreased less with high P addition than in control plots (Fig. 7c). Both high P and N + P addition led to less of an increase in foliar N:P ratios of *S. repens* (Fig. 7d).

Discussion

The effects of nutrient addition on plant productivity in scrubby flatwoods depended on time after fire and the level of analysis. At the community level, high N + P addition increased belowground productivity in the 8 and 20 years sites, but nutrient addition had no effect on aboveground productivity at any time after

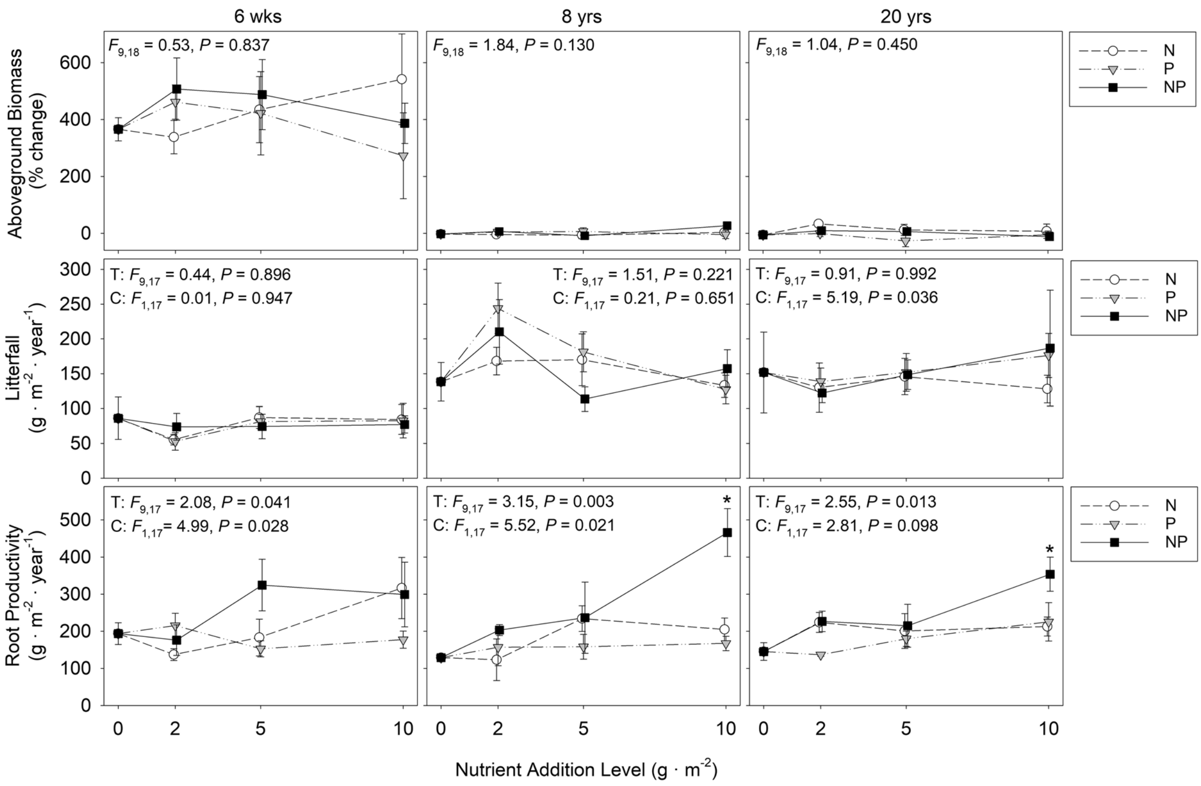


Fig. 4 Mean (± SE) percent change in aboveground shrub biomass (calculated as ((1 year posttreatment biomass − pretreatment biomass)/pretreatment biomass) × 100%), litterfall, and root productivity after nutrient addition in sites 6 weeks, 8 years, and 20 years postfire. Treatment (T) and covariate (C; for litterfall, mean of pre- and posttreatment shrub cover; for root productivity, pretreatment root biomass) effects are shown. Single asterisk (*) indicates a treatment is significantly greater than the control at α = 0.05

fire. At the species level, *Quercus inopina* responded to P addition, while *Serenoa repens* responded to N addition. Contrary to our hypothesis, the nutrient most limiting to productivity does not appear to change with time after fire. Postfire nutrient pulses seem to alleviate nutrient limitation in recently burned sites, while scrubby flatwoods are co-limited by N and P at intermediate and longer times after fire.

Despite adding N at levels similar to studies in other ecosystems with larger total N pools (e.g., Bret-Harte et al. 2004), our N addition did not saturate N demand; N addition increased soil N availability only in the 20 years site. Other studies from a variety of ecosystems, however, have found that N addition increases soil NO_3^- and NH_4^+ (Bret-Harte et al. 2004; Caffrey et al. 2007; Iversen and Norby 2008). In coastal Florida scrub-oak ecosystems, soil microbial communities are primarily N-limited with a secondary P limitation (Brown et al. 2009); thus, added N may have been incorporated into microbial biomass. If microbes and plants were not able to use the added N quickly, leaching could have occurred because scrubby flatwoods have sandy soils with low exchange capacity. The lack of sensitivity of soil inorganic N availability to N addition may also be related to the offset in times of nutrient addition and soil collection or use of a fast release fertilizer. Phosphorus addition led to a significant increase in soil extractable P in the 8 and 20 years sites, indicating that we saturated P demand and that the effect of added P was greater in sites with lower background P availability.

Nutrient addition had no effect on community-level productivity in the first year after fire. In the recently burned site, fire removed all aboveground biomass. Thus, the low shrub biomass 6 weeks after fire was due to the lack of large stems and presence of smaller resprouts, and the high percent change in biomass was due to postfire recovery; palmettos and oaks have

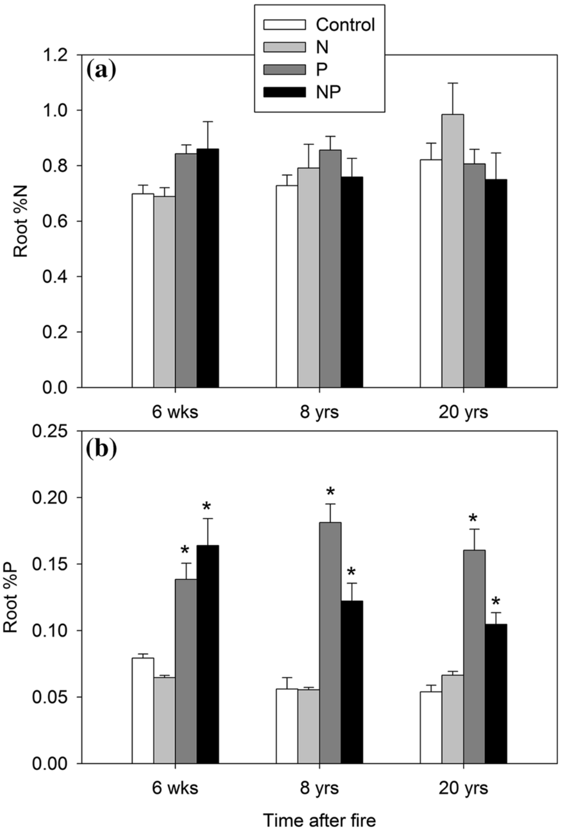


Fig. 5 Mean (± SE) root N (**a**) and P (**b**) concentrations in control and high nutrient addition treatments in sites 6 weeks, 8 years, and 20 years postfire. Single asterisk (*) indicates a treatment is significantly greater than the control at $\alpha = 0.05$

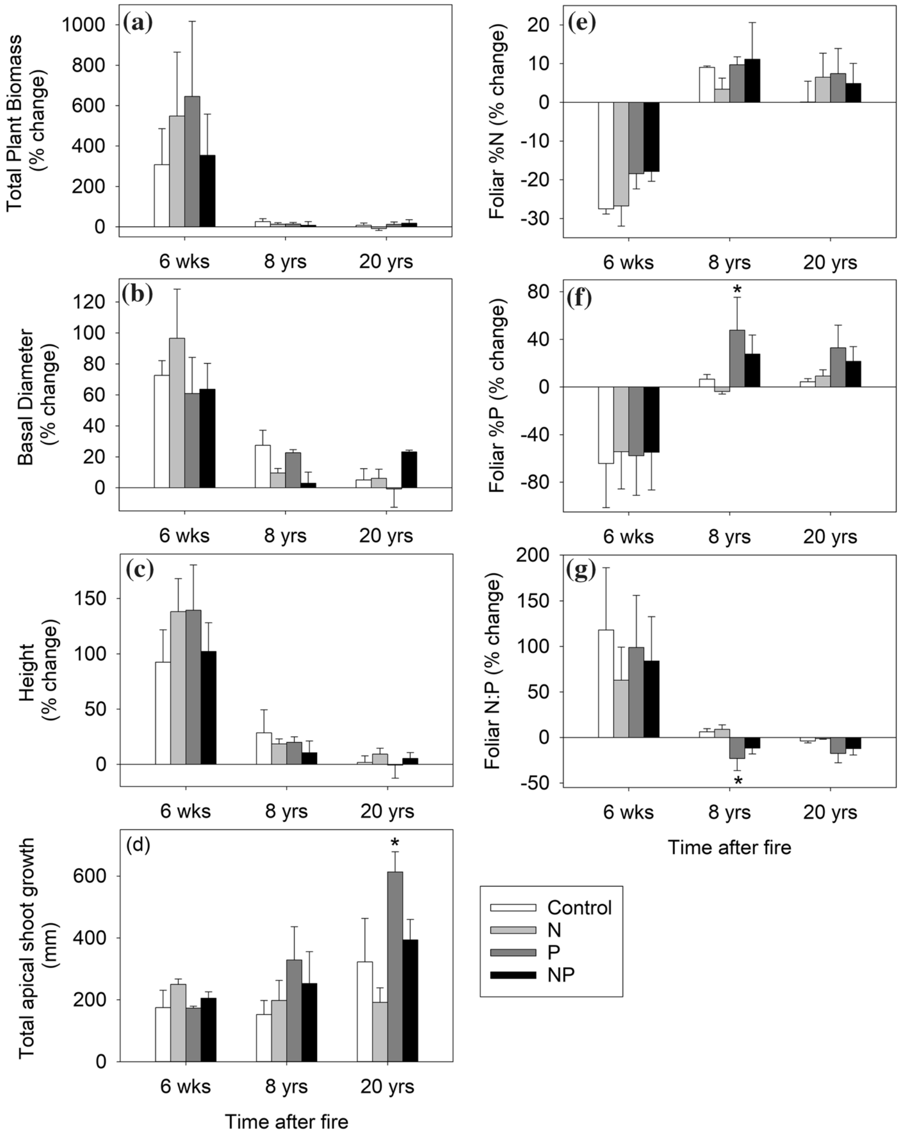
faster postfire growth rates than most other scrubby flatwoods species (Maguire and Menges 2011). There are two factors that likely contributed to the lack of an effect of nutrient addition on productivity in recently burned sites. First, short-term increases in N and P availability after fire (Schafer and Mack 2010) could have met plant nutrient demand and limited plant use of added nutrients. Second, resprout growth could have been supported by reallocation of nutrients from belowground reserves; the resprouting shrub *Q. ilex* remobilizes N from belowground reserves before using available N (El Omari et al. 2003).

At the community level, nutrient addition increased belowground productivity, but not aboveground productivity, in sites 8 and 20 years postfire. Although nutrient addition often increases aboveground biomass and litterfall (e.g., Tanner et al. 1992; Herbert and Fownes 1995; D'Antonio and Mack 2006; Iversen and Norby 2008) and causes a decrease in allocation to belowground biomass (e.g., Nadelhoffer 2000; Darby and Turner 2008), multiple studies have found that nutrient addition can increase belowground productivity (Cuevas and Medina 1988; Gross et al. 1993; Ostertag 2001). Allocation to belowground biomass is proportionally greater in drier and lower nutrient ecosystems (Chapin et al. 2002), including shrublands (Mokany et al. 2006), which are often dominated by resprouting species (e.g., Menges and Kohfeldt 1995). In Florida scrub ecosystems, eighty percent of biomass may be belowground (Saha et al. 2010).

There are several possible explanations for the increase in root productivity in scrubby flatwoods. First, an increase in root productivity may have occurred if nutrient addition did not alleviate limitation by N and P or if fertilization induced deficiency (Teng and Timmer 1995) in another nutrient such as potassium (K) or calcium (Ca) (Bigelow and Canham 2007; Wright et al. 2001). Biomass of *S. repens* and *Sabal etonia* increased with addition of N, P, K, Ca, and magnesium in combination (Abrahamson 1999), suggesting that increased growth of scrubby flatwoods species in response to one nutrient may depend on the presence of others. Although triple superphosphate contains Ca in addition to P, background levels of Ca in scrubby flatwoods range from 12.6 to 25.2 g m^{-2} (Abrahamson et al. 1984), and our rate of P addition corresponds to only 0.66–3.31 g Ca m^{-2}. Thus, our rate of Ca addition was likely not high enough to significantly increase Ca availability.

Second, scrubby flatwoods species may have increased root productivity to alleviate water limitation. Ladwig et al. (2012) suggested that water is more limiting than N in a semiarid grassland. Scrubby flatwoods soils have low water holding capacity (Abrahamson et al. 1984), and the biomass increment (Seiler et al. 2009) and radial growth (Foster et al. 2014, 2015) of oaks is correlated with precipitation in coastal Florida scrub. Lack of variation in leaf water potential and stomatal conductance with time after fire (K. Adams and S. Saha, unpublished data) suggests that water limitation could occur at any time postfire, regardless of plant size. Florida sandhill species, including *Q. geminata*, shift their water uptake from shallow to deep soils during the dry season (Ellsworth and Sternberg 2015); however, *Q. inopina*, the dominant scrubby flatwoods species, has a shallower depth of water uptake than other oaks (Saha et al. 2008),

Fig. 6 Mean (± SE) percent change in plant biomass (**a**), percent change in basal diameter (**b**), percent change in height (**c**), total apical shoot growth (**d**), percent change in foliar %N (**e**), percent change in foliar %P (**f**), and percent change in foliar N:P (g) of *Quercus inopina* in control and high nutrient addition treatments. Percent change was calculated as [(1 year posttreatment value − pretreatment value)/pretreatment value] × 100%. Total apical shoot growth was measured 1 year after nutrient addition. Single asterisk (*) indicates a treatment is significantly greater or less than the control at $\alpha = 0.05$



which may facilitate greater water limitation and drought stress during months with low rainfall. Across seasons, soil moisture is generally lower in surface soils than deeper soils (Weekley et al. 2007), so increasing root productivity in response to nutrient addition should allow scrubby flatwoods species to increase access to water in surface soils.

Third, resource allocation patterns associated with the resprouting life history strategy could explain the increase in root productivity of scrubby flatwoods species. Resprouting species allocate more resources to belowground biomass than species that recruit from seed after fire (Knox and Clarke 2005), and resprouting species have relatively low shoot:root ratios, indicating that allocation to belowground biomass is favored over allocation to aboveground biomass (Pate et al. 1990; Bowen and Pate 1993). Allocation to belowground biomass is necessary to maintain carbohydrate reserves for resprouting after fire. Reduced survival after short fire return intervals is likely due to limited reserves of nonstructural carbohydrates (Enright et al. 2011), and species that are good at resprouting appear to increase belowground storage at the cost of aboveground growth (Nzunda et al. 2014). Dominant scrubby flatwoods shrubs, including the focal species in this study, resprout after

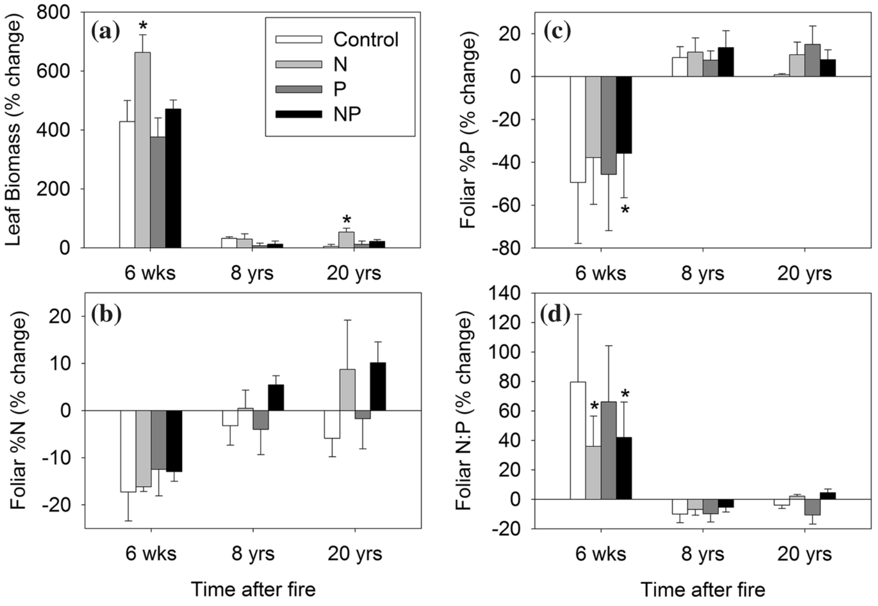


Fig. 7 Mean (± SE) percent change in leaf biomass (**a**), foliar %N (**b**), foliar %P (**c**), and foliar N:P (**d**) of *Serenoa repens* in control and high nutrient addition treatments. Percent change was calculated as: [(1 year posttreatment value − pretreatment value)/pretreatment value] × 100%. Single asterisk (*) indicates a treatment is significantly greater or less than the control at α = 0.05

Table 1 Effects of high nutrient addition on measures of growth and nutrient status of scrub oak (*Quercus inopina*) and saw palmetto (*Serenoa repens*) at each time after fire

Measure	*Q. inopina*						*S. repens*					
	6 weeks		8 years		20 years		6 weeks		8 years		20 years	
	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Aboveground biomass	2.06	0.207	0.56	0.661	0.66	0.607	10.92	0.008	1.15	0.403	3.51	0.089
Basal diameter	0.41	0.752	2.63	0.145	1.65	0.276						
Height	0.54	0.673	0.40	0.759	0.74	0.564						
Apical shoot growth (cm)	1.25	0.371	0.86	0.512	6.15	0.029						
Foliar %N	2.05	0.208	0.65	0.613	0.95	0.475	0.57	0.654	1.04	0.439	1.46	0.318
Foliar %P	2.22	0.186	8.37	0.015	3.19	0.106	3.63	0.084	0.21	0.888	1.52	0.302
Foliar N:P	1.57	0.292	7.31	0.020	1.19	0.389	13.25	0.005	0.13	0.938	0.66	0.606

The units for all measures of growth and nutrient status (except apical shoot growth of *Q. inopina*) are percent change. For *S. repens*, aboveground biomass is leaf biomass only. For each measure, the treatment effect degrees of freedom are 3 and 6 (numerator and denominator)

fire. The fire return interval in scrubby flatwoods is 8–16 years (Menges 2007) and fires consume aboveground biomass. Thus, in our 8 and 20 years sites, where the likelihood of fire is high, increasing belowground biomass may increase the probability of survival more than increasing aboveground biomass.

While there are multiple factors that could have contributed to the increase in belowground productivity at the expense of aboveground productivity at the community level, it is possible that we underestimated aboveground productivity because we did not measure biomass of subshrubs or herbaceous species, reproductive biomass, or leaf losses to herbivory. Subshrubs and herbaceous species may have been affected by nutrient addition because they may have most of their roots in surface soils, which could allow for greater access to added nutrients. Reproduction and leaf losses to herbivory are less likely to have been influenced by nutrient additions in our study. The majority of oak stems produced no acorns in our study, and precipitation may be a greater control over oak reproduction than nutrient availability (Abrahamson and Layne 2003). *Serenoa repens* does not increase flowering (Abrahamson 1999) or allocation to reproductive stems (J. Schafer, unpublished data) with nutrient addition. In addition, we did not observe differences in herbivory among our treatments (J. Schafer, personal observation).

At the species level, nutrient addition affected aboveground productivity in several cases. Nitrogen addition increased *S. repens* leaf biomass in the 6 weeks and 20 years sites, and P addition increased foliar %P and apical shoot growth of *Q. inopina* in the 8 years site and the 20 years site, respectively. Similarly, Berry and Menges (1997) found that N addition increased *S. repens* leaf production and P addition increased *Q. inopina* stem growth. These results indicate that the two dominant scrubby flatwoods species are limited by different nutrients—*S. repens* is more N-limited, while *Q. inopina* is more P-limited. There was no difference in foliar N:P ratios between *Q. inopina* and *S. repens* in either the 8 or 20 years site pre-fertilization, and the N:P ratios were approximately 16, which suggests that these species would both be P-limited or co-limited by N and P (Güsewell 2004). Thus, our study provides further evidence that foliar N:P ratios may not be representative of plant responses to fertilization or nutrient limitation (Craine et al. 2008; Alvarez-Clare and Mack 2015).

Limitation of the two dominant scrubby flatwoods species by different nutrients is indicative of heterogeneous nutrient limitation (Alvarez-Clare et al. 2013), which has also been observed in tropical forest trees (Mayor et al. 2014; Alvarez-Clare and Mack 2015) and grassland species (Wei et al. 2014). Differences in mycorrhizal status may contribute to species-specific differences in nutrient limitation (Diehl et al. 2008). Oaks have associations with ectomycorrhizae (Langely et al. 2002) and *S. repens* has associations with arbuscular mycorrhizae (Fisher and Jayachandran 1999). Ectomycorrhizae may be better able to increase N to *Q. inopina* leading to greater P limitation, while arbuscular mycorrhizae may be better able to increase P to *S. repens* leading to greater N limitation. Heterogeneous nutrient limitation suggests that competition among scrubby flatwoods shrubs may depend on the relative availability of N and P.

There were several limitations of our study. First, the buffer between plots might not have been large enough to ensure that shrubs and palmettos were not connected belowground. Clones of *Quercus geminata*, a common scrubby flatwoods species, often span areas of at least 9 m^2 aboveground and can spread across distances of $\sim$ 35 m aboveground (Ainsworth et al. 2003), and one *S. repens* genet can contain over 100 ramets (Takahashi et al. 2011). If shrub clones connected belowground extended across plots, individuals could have experienced multiple nutrient addition treatments, diluting the effect of any one treatment on productivity. Second, assessment of nutrient limitation may depend on the length of nutrient addition (Niinemets and Kull 2005), but a second year of nutrient addition in scrubby flatwoods also had no effect on aboveground growth of dominant scrubby flatwoods shrubs (Schafer 2010). Third, because we were able to use only three burn units such that all blocks for each time-since-fire were located within the same fire scar, our study lacked true replication. Thus, we made inferences from experimental plots in only one site for each time after fire.

Nutrient limitation of primary productivity in scrubby flatwoods did not change with time after fire as hypothesized. This may be due, in part, to similar N and P availability at intermediate and longer times after fire; limited accumulation of organic matter in long unburned sites may have limited increases in N availability from 8 to 20 years postfire. At the community level, nutrient addition increased allocation to belowground productivity, which may be beneficial for acquiring water and postfire resprouting. Individual species, however, increased aboveground growth and nutrient concentrations, most often 8 or 20 years after fire. We found that scrubby flatwoods were co-limited by N and P at intermediate and longer times postfire, but nutrients made available by fire could have alleviated nutrient limitation in recently burned sites. Thus, shifting from no nutrient limitation to co-limitation by N and P may influence recovery of plant biomass and productivity over time after fire.

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