

EFFECTS OF FIRE ON NUTRIENT AVAILABILITY AND LIMITATION IN FLORIDA
SCRUB ECOSYSTEMS

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2010

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To my Mom, who has provided constant support, and my grandfather, Dr. George
Schafer, who passed away before I decided to follow in his footsteps

ACKNOWLEDGMENTS

I thank my advisor, Michelle Mack, for her guidance and support. I thank my committee members Emilio Bruna, Nick Comerford, Doria Gordon, and Ted Schuur for their advice and comments. I thank my office mates Silvia Alvarez-Clare, Jennie DeMarco, and Caitlin Hicks Pries for their scientific discussions and emotional support. I thank Julia Reiskind for her help in the lab and Grace Crummer for assistance processing samples on the elemental analyzer. Other members of the Mack and Schuur labs, including Heather Alexander, Fay Belshe, Catherine Cardelús, Martin Lavoie, Hanna Lee, Jordan Mayor, Laura Schreeg, and Eddie Watkins, have provided valuable input on a variety of aspects of my research. Participants in the Plant and Ecosystem Ecology Research Symposium (PEERS), including Kaoru Kitajima and Jack Putz, have also given valuable input. The office staff in the Botany and Biology departments at UF, particularly Tangelyn Mitchell, Karen Patterson, and Kim Williams, were very helpful. In addition, I thank Terrell Bostic, James Lange, Natasha Johnson, Olivia Ellen Martin, Nicole Motzer, Jennifer Petriella, Jennifer Tucker, Mirela Vasconcelos, and Olivia Vasquez for help with lab work at the University of Florida.

I thank the Plant ecology lab at Archbold Biological Station, especially Eric Menges and Carl Weekley, for making me always feel welcome in the lab and for providing logistical and personell support. I thank Gretel Clarke, Sarah Haller, Marcia Rickey, and Stacy Smity, research assistants in the Plant Ecology lab during my time there, who were a great help and have become great friends. I thank Kevin Main and all others who have conducted prescribed fires at Archbold, for without them, my research would not have been possible. I thank Roberta Pickert and Kye Ewing for making maps of the fire history in all burn units. I thank Hilary Swain, the director of Archbol Biological

Station, for allowing me to conduct my research there. I thank Silvia Alvarez-Clare, Jeremy Ash, Craig Beatty, Rachel Burnett, Kaitlynn Earnshaw, Megan Larson, Hanna Lee, Jennifer Navarra, Josh Picotte, Catherine Pociask, Harrison Price, Alan Rivero, Melinda Schafer, Morgan Sherwood, Lauren Sullivan, Oona Takano, and Ashley Williams for help in the field and lab at Archbold Biological Station. I thank Patrick Bohlen and Adam Peterson for help processing samples at the MacArthur Agro-Ecology Research Center. I thank Verna Dunbar, Judy Maynard, and Louise for keeping me well fed during my summer field work.

I thank my sister, Melinda, my brothers, Tim and Brian, and my father, Richard, for their support. Most of all, I thank my mom, Charlotte, who collected soil samples with me in the field, helped me process soil samples in the lab, washed many dishes, weighed plant samples, and did a lot of pipetting to help me complete my field and lab work. In addition, she is the one person who I know will read my entire dissertation. Thanks mom!

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Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

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May 2010

Chair: Michelle C. Mack

Major: Botany

Nitrogen (N) and phosphorus (P) are essential plant nutrients that limit productivity in most, if not all, terrestrial ecosystems. Fire, a common disturbance in many shrublands, may have different effects on the relative availability of N and P because N volatilization occurs at lower temperatures than P volatilization. I investigated the short- and long-term effects of fire on soil and plant nutrients in Florida scrub ecosystems. In addition, I tested the hypothesis that nutrient limitation of plant productivity of scrubby flatwoods changes with time after fire. In flatwoods ecosystems, fire caused a greater increase in phosphate (PO_4^{3-}) than ammonium (NH_4^+), resulting in a decrease in the soil available N:P ratio shortly after fire. Similarly, foliar %P of resprouting species increased more than foliar %N, resulting in a decrease in foliar N:P ratios shortly after fire. In scrubby flatwoods, PO_4^{3-} , but not total inorganic N, varied with time after fire, causing N:P ratios to be greatest at intermediate times after fire and lowest 13 years after fire. In surface soils, soil %C and %N, dissolved organic N, net N mineralization, and microbial N were all highest 13 years after fire, and measures of N availability were often highly correlated. In recently burned scrubby flatwoods, shrubs appear to invest more in aboveground productivity, and *Quercus inopina* responded to

P and N + P addition, but *Serenoa repens* responded to N addition. At intermediate times after fire, shrubs appear to invest more in belowground than aboveground productivity and show co-limitation by N and P with a stronger P-limitation, while in long unburned sites, scrubby flatwoods shrubs appear to invest in both aboveground and belowground productivity and show co-limitation by N and P. Overall, my research suggests that: (1) increased soil nutrient availability and reallocation of nutrients from below- to aboveground can be important for plant nutrient status after fire; (2) species composition and fire frequency, as well as time after fire, are important in affecting soil nutrient availability; and (3) the effects of nutrient addition on biomass and growth depend on time after fire and species identity.

CHAPTER 1 INTRODUCTION

Fire is a natural disturbance that maintains the structure and composition of many shrub dominated ecosystems (Little 1979, Abrahamson et al. 1984, Christensen 1985, Keeley and Keeley 1988, Moreno and Oechel 1994, Bradstock et al. 2001). Fire can have profound impacts on nutrient cycling and availability because fire consumes plant biomass, litter, and soil organic matter, converting organic nutrients to inorganic forms (Certini 2005), which can 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. 2000, Wan et al. 2001, Smithwick et al. 2005a, Turner et al. 2007).

Fire has different effects on the relative availability of N and P due to fundamental differences in their biogeochemistry. Since N is more readily volatilized than P, relatively more N than P is lost from an ecosystem during fire (Raison et al. 1985a). In highly weathered soils, most P is in organic matter. Fire rapidly mineralizes the P in these pools, often resulting in enhanced P availability after fire. Nitrogen, however, may be relatively less available than P after fire due to greater combustion losses, and N inputs in unpolluted ecosystems are largely dependent upon biological N-fixation, which accumulates N over the inter-fire cycle. During fire, nutrients can be lost from an ecosystem to the atmosphere through volatilization (non-particulate forms) or

transport of ash (particulate forms). Numerous studies have measured the effect of fire on nutrient loss to the atmosphere by calculating the difference between the pre-fire nutrient content of fuel (i.e. understory plants and/or litter) and the post-fire nutrient content of ash. For example, in a low-intensity fire in a Mediterranean forest, 77% of N and 35% of P was lost (Gillon and Rapp 1989); during fires in Australian forests and woodlands, 92-94% of N and 41-53% of P was lost (Cook 1994); during slash-and-burn agriculture in Amazonia, 93-98% of N and 27-47% of P was lost (Mackensen et al. 1996); and fires in Brazilian savannas caused 95% of N and 51% of P to be lost (Pivello and Coutinho 1992). Regardless of the type of ecosystem or fire, approximately twice as much N as P is lost to the atmosphere during fire due to differences in volatilization temperatures and forms of nutrient loss. 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). The majority of N in combusted fuel is lost in non-particulate forms, while P is lost in both non-particulate and particulate forms. Thus, ash on the soil surface contains high concentrations of P and low concentrations of N (Debano and Conrad 1978, Raison et al. 1985b).

Nitrogen and phosphorus limit plant growth in most, if not all, terrestrial ecosystems (Vitousek and Howarth 1991). 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. This is important because nutrient limitation of plant productivity is a fundamental control over the structure and function of ecosystems and has consequences for biomass accumulation (Bret-Harte et al. 2004), nutrient retention and

loss (Hedin et al. 1995), biodiversity (Wassen et al. 2005) and composition (Chapin et al. 1987), and the ecosystem values and services provided to humans (Daily et al. 2000).

The different fates of N and P in consumed fuel affect the total nutrient budget of an ecosystem. Inputs of N through symbiotic N-fixation and rainfall are not high enough, over the short-term, to replace the amount of N volatilized in fire (Carter and Foster 2004, Cook 1994). Over time, P in ash becomes relatively less available as it is immobilized by plants and microbes or fixed via geochemical reactions. Nitrogen availability, in contrast, tends to increase as inputs accumulate. Because plant growth is limited by any nutrient present in the soil below an optimum supply (Chapin et al. 2002), fire mediated differences in nutrient supply suggest that nutrient limitation may change with time since fire, with recently burned sites being N-limited and long unburned sites being P-limited, particularly in old, highly weathered soils.

Research on the effects of fire on nutrient limitation, however, is scarce. Pines and oaks in a fire-adapted Mediterranean forest were P-limited in a site 5 years post-fire (Sardans et al. 2004), only one of four species was N-limited in a lodgepole pine forest 3-5 years after fire (Romme et al. 2009), and N limits productivity of trees in secondary Amazonian forests, possibly due to the residual effects of fire on N availability (Davidson et al. 2004). In a study of aquatic systems, phytoplankton biomass was limited by P or co-limited by N and P in lakes within unburned catchments, while phytoplankton biomass was limited by N in lakes within burned catchments, likely due to increased loading of P relative to N post-fire (McEachern et al. 2002). Although the differential effects of fire on the fate of N and P suggest that the nutrient most limiting to

plant production may change with time since fire, research has not directly addressed this question.

Florida scrub provides a novel and interesting ecosystem in which to investigate the effects of fire on nutrient availability and limitation. Fire-dependent Florida scrub ecosystems occur on infertile, sandy, well drained soils. Scrub ecosystems are found along both the Atlantic and Gulf coasts of Florida and along ridges in central Florida (Myers 1990). The broad definition of scrub includes many vegetation types including sand pine scrub, oak scrub, rosemary scrub, coastal scrub, and scrubby flatwoods (Myers 1990). Shrubby oaks, palmettos, and ericaceous shrubs occur in all of these scrub types, but the dominant species varies and can be sand pine (*Pinus clausa*) or Florida rosemary (*Ceratolia ericoides*). Flatwoods occur at slightly lower elevations than scrubby flatwoods (Abrahamson et al. 1984), are fire-adapted, have less well drained soils, and are often dominated by palmettos. Scrubby flatwoods are often an ecotone between flatwoods and other scrub vegetation types (Myers 1990).

Previous research on nutrient availability in scrub ecosystems has focused on differences among plant communities (Abrahamson et al. 1984, Kalisz and Stone 1984) or the effects of elevated CO₂ (e.g. Hungate et al. 1999, Johnson et al. 2001, Johnson et al. 2003, McKinley et al. 2009). Few studies have focused on changes in soil nutrients with time after fire (Schmalzer and Hinkle 1992, Schmalzer and Hinkle 1996). Furthermore, the majority of these studies have been conducted in sites where the dominant oak species is *Quercus myrtifolia* (Schmalzer and Hinkle 1992). In many scrub areas along the central Florida Lake Wales Ridge, however, *Quercus inopina* is the dominant oak species.

The dominant shrubby species in Florida scrub ecosystems resprout after fire. Belowground biomass may comprise up to 88% of total biomass of resprouting shrubs in Florida scrub (Saha et al. in review), and in a coastal scrub-oak ecosystem, root biomass to one meter depth is $8000 \text{ g} \cdot \text{m}^{-2}$ (Brown et al. 2007). Belowground reserves (McPherson and Williams 1998, Paula and Ojeda 2009), pre-fire plant size (Bonfil et al. 2004, Konstantinidis et al. 2006), and fire intensity (Moreno and Oechel 1991, Lloret and López-Soria, 1993) affect resprouting ability (Moreno and Oechel 1991) and biomass of resprouts (Lloret and López-Soria, 1993, Cruz et al. 2002). The growth and biomass allocation of resprouts may depend on pre-fire plant status and fire characteristics and may vary among species because the differential growth of and resource allocation to aboveground plant parts depends on species specific constraints (Niklas 1995a). These differences may influence how nutrient availability affects growth of dominant shrubs.

Understanding the role of fire in nutrient cycling may provide insight into the factors that contribute to the maintenance of ecosystem structure and function of Florida scrub. While many studies have investigated the demography of endangered plants (e.g. Quintana-Ascencio et al. 2003, Menges and Quintana-Ascencio 2004) or the effects of fire on plant community composition (e.g. Schmalzer 2003, Weekley and Menges 2003), little is known about nutrient availability, plant productivity, or nutrient limitation in central Florida scrub despite evidence for low fertility. Large areas of land along the central Florida Lake Wales Ridge have been converted to agriculture, pastureland, and urban areas, leading to increased nutrient inputs and reduced fire frequency. Because Florida scrub ecosystems have been shaped over time by fire and

low nutrient availability, human-induced changes complicate restoration efforts. The goal of my dissertation research is to understand the effects of fire on nutrient availability and limitation in central Florida scrub ecosystems.

CHAPTER 2 SHORT-TERM EFFECTS OF FIRE ON SOIL AND PLANT NUTRIENTS IN PALMETTO FLATWOODS

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. 2000; Wan et al. 2001; Smithwick et al. 2005b; 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-since-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 $\delta^{15}\text{N}$ values have been used as indicators of ecosystem nitrogen cycling (Martinelli et al. 1999). Fire consumes surface soils layers and volatilizes N, which can leave post-fire soils enriched in ^{15}N (Högberg 1997) because soil $\delta^{15}\text{N}$ tends to increase with depth (Nadelhoffer et al. 1996; Frank and Evans 1997). Foliar $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ values may provide insight into integrated fire effects on plant and soil N dynamics and the causes of increased foliar N concentrations after fire.

I 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. I assessed the short-term effects of fire on soil and plant nutrients and ^{15}N isotopic signatures. I 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, I hypothesized that N and P concentrations of resprouting plants would increase after fire. I investigated ^{15}N isotopic signatures to differentiate among mechanisms that can cause increased foliar N concentrations.

Methods

Field Sampling and Lab Analyses

This study was conducted at Archbold Biological Station (ABS) in Highlands County, Florida, USA (27°10'50"N, 81°21'0" 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). ABS includes a 5,193 acre preserve, which is divided into burn units that have been managed with prescribed fires for over 35 years. ABS comprises a mosaic of plant communities including seasonal ponds, flatwoods, scrubby flatwoods, oak-hickory scrub, and sand pine scrub.

My 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 elliotii* 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, I 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, I marked a soil sampling site and the nearest individual of five common

flatwoods species (when present within 1 m of the soil sampling location). My 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 Hansen 2003). On 4 August 2006, several hours before ignition of a prescribed fire, I 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 three hours 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. I collected post-fire foliar samples (n=13) on 6 October 2006, 12 December 2006, and 10 December 2007. At all sampling times, I collected the newest leaves from the upper portion of shrub stems. To collect foliar samples of the palmetto *S. repens*, I 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, I collected a portion of only the new leaves that had been produced after the previous sampling event.

Within 24 hours of collection, I 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 $\delta^{15}\text{N}$. Gravimetric moisture content was determined on samples dried at 105°C for 48 hrs. For soil pH, 10 g of air dried soil was added to 10 mL of deionized water, shaken for 30 sec, 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 hrs, 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, Bremen, 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. I stored filtered samples in a refrigerator for up to three weeks before analysis for phosphate (PO_4^{3-}) concentrations on a spectrophotometer microplate reader (μ Quant 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 seconds, and allowed to stand overnight. I 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 ($\sim 24^\circ\text{C}$). After one week, 50 mL of 0.5 M K_2SO_4 was added to the soil, shaken for 30 sec, and allowed to stand overnight. I filtered, stored, and analyzed solutions as described above. Net rates of N mineralization were calculated from the difference in $\mu\text{g N}-(\text{NH}_4^+ + \text{NO}_3^-)$ g soil^{-1} of initial and one week extractions.

Leaf samples were dried at 60°C for 48 hours 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, Bremen, Germany). Abundances of ^{15}N were measured using delta (δ) notation with atmospheric N_2 as the standard. I determined foliar phosphorus for all samples of *Serenoa repens*. Subsamples of 0.05 to 0.5 grams were weighed into crucibles, ashed in a muffle furnace at 500°C for 5 hours, 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, I used a one-way mixed analysis of variance model with repeated measures with time as the within-subjects factor (SAS 9.1; 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 $\delta^{15}\text{N}$, 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.

To examine changes in foliar nutrients (%N, %P, and N:P ratios) and foliar $\delta^{15}\text{N}$ over time after fire, I used one-way repeated measures analysis of variance with time as the within-subjects factor (SPSS 11.5; Field 2009). Differences in foliar nutrients and foliar $\delta^{15}\text{N}$ among times were determined with post-hoc pairwise comparisons with Bonferroni confidence interval adjustments. In addition, I calculated the absolute difference between foliar $\delta^{15}\text{N}$ and soil $\delta^{15}\text{N}$ (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*)).

I used linear regression to assess the relationship between soil and foliar nutrients (Sigma Plot 11.0). I 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. I correlated foliar %P of *S. repens* with the natural log of soil

extractable PO_4^{3-} . 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, soil NH_4^+ concentrations were 5.5 times higher than pre-fire values, and NH_4^+ remained higher through at least 20 days after fire ($F_{5,20} = 6.16$, $p = 0.001$; Figure 2-1). 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 ($F_{5,20} = 15.45$, $p < 0.001$; Figure 2-1). Soil extractable N:P ratios decreased by 40% immediately after fire, from 8.4 to 5.1, due to the larger increase in PO_4^{3-} relative to NH_4^+ , but extractable N:P ratios were only significantly different between 62 days and 129 and 494 days after fire ($F_{5,20} = 5.85$, $p = 0.001$, Figure 2-1). Soil pH increased over time after fire, and by 494 days, was significantly higher than pre-fire values (Table 2-1). There were no differences in soil %N, %C, C:N ratios, NO_3^- concentrations, or soil $\delta^{15}\text{N}$ over time after fire (Table 2-1).

Foliar %N and %P of *Serenoa repens* increased after fire (Figure 2-2). 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 %N, %P, and N:P ratios of *S. repens* were similar to pre-fire values by 494 days post-fire (Figure 2-2). Foliar %N of *Quercus geminata* and ericaceous species increased shortly after fire then decreased to pre-fire values by 494 days post-fire (Figure 2-3).

Foliar $\delta^{15}\text{N}$ of *S. repens* decreased significantly over time after fire, while foliar $\delta^{15}\text{N}$ of *Q. geminata* increased then decreased after fire (Figure 2-3), although this change was only marginally significant (Table 2-2). Foliar $\delta^{15}\text{N}$ of ericaceous species

did not change with time since fire (Table 2-2). The absolute difference between foliar $\delta^{15}\text{N}$ and soil $\delta^{15}\text{N}$ did not vary over time after fire for any plant species/family (Table 2-2). Over the entire study period, the mean (+ se) difference between foliar and soil $\delta^{15}\text{N}$ 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 ($F_{1,14} = 5.49$, $p = 0.034$, $R^2 = 0.28$). Total extractable inorganic N was not correlated with foliar %N of *S. repens* ($F_{1,18} = 0.85$, $p = 0.368$, $R^2 = 0.04$; Figure 2-4). Foliar %P of *S. repens* was positively correlated with soil extractable PO_4^{3-} ($F_{1,18} = 10.57$, $p = 0.004$, $R^2 = 0.37$; Figure 2-5).

Discussion

Fire caused a short-term increase in soil extractable nutrients in the palmetto flatwoods ecosystem investigated in my study. While soil N concentrations remained elevated above pre-fire levels for at least one month after fire, soil P, in contrast, remained elevated above pre-fire levels for at least two months after fire (Figure 2-1). 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 soil P increase was greater than that of soil N, leading to a decrease in the soil extractable N:P ratio shortly after fire (Figure 2-1). 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 (Figure 2-2). Soil $\delta^{15}\text{N}$ did not

vary with time since fire (Table 2-1), and only *S. repens* showed significant variation in foliar $\delta^{15}\text{N}$ with time after fire (Table 2-2).

Soil ammonium (NH_4^+) concentrations increased immediately after fire and decreased to pre-fire levels within two months after fire (Figure 2-1). 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 my study (Table 2-1), 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 four months after fire (Figure 2-1). 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 my study, the first rain event occurred two 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 (Figure 2-1). This result is consistent 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 my flatwoods site, but the pre-fire soil extractable N:P ratio was greater than in my 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^+ (Figure 2-1). 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 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 2-1). 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 my 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 my study (Table 2-1). 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 the flatwoods 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 (Skylberg 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 my 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 (Figure 2-2). 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 (Figure 2-3). 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 my 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 (Figure 2-4), 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 *V. myrsinites* increase and decrease, respectively, with time-since-fire (Olano et al. 2006), suggesting that these species vary in their capacity to resprout after fire and that time-since-fire may affect the ability of shrubs to reallocate nutrients to aboveground tissues. In my 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 I have not investigated the effects of age

on foliar %N of flatwoods species, I 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 grown 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 my 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 my 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 (Figure 2-2). 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 $\delta^{15}\text{N}$ (Table 2-1). Saito et al. (2007) found that soils had to be burned at 400°C for at least 5 minutes to cause a significant enrichment of soil $\delta^{15}\text{N}$, 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 one or two minutes (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 $\delta^{15}\text{N}$. 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 $\delta^{15}\text{N}$ and soil $\delta^{15}\text{N}$ over time after fire (Table 2-2). Fire did, however, affect the foliar $\delta^{15}\text{N}$ signatures of flatwoods species; *Quercus geminata* tended to be more enriched in ^{15}N 62 and 130 days post-fire compared to pre-fire and 494 days post-fire, while *Serenoa repens* became more depleted in ^{15}N over time (Figure 2-3). 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 $\delta^{15}\text{N}$ after fire (Grogan et al. 2000). Considering that I found no change in soil $\delta^{15}\text{N}$ after fire, changes in foliar $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ signatures (Evans 2001); however, extractable NO_3^- was low throughout my 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 $\delta^{15}\text{N}$ over time suggests that neither a change in N sources nor greater discrimination occurred in my study.

Soil $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ of *Q. geminata* immediately after fire, while a shift in uptake from deeper to surface roots could cause the foliar $\delta^{15}\text{N}$ 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 \leq 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 $\delta^{15}\text{N}$ of *Q. geminata* could be more enriched shortly after fire if species reduced nutrient uptake through mycorrhizae, while foliar $\delta^{15}\text{N}$ of *S. repens* could become more depleted over time if nutrient uptake through AM increased. Soil $\delta^{15}\text{N}$ and the difference between foliar and soil $\delta^{15}\text{N}$ 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 species $\delta^{15}\text{N}$ signatures were more similar among plants with the same mycorrhizal status than among plants 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 $\delta^{15}\text{N}$ after fire.

Foliar $\delta^{15}\text{N}$ signatures decrease over time after leaf initiation (Bergersen et al. 1988), suggesting that reallocation of N within a plant can affect foliar $\delta^{15}\text{N}$ signatures (Evans 2001). Although I sampled the newest leaves, as leaf number increased, I was more likely to sample leaves of varying ages, which could cause a decline in foliar $\delta^{15}\text{N}$ over time after fire. In addition, leaves may be enriched in ^{15}N compared to roots (Evans et al. 1996), and the foliar $\delta^{15}\text{N}$ of *S. repens* could have decreased over time due to reallocation of N depleted in ^{15}N from belowground to aboveground tissues. I 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 $\delta^{15}\text{N}$.

One limitation of my experimental design is that I did not measure soil or plant nutrients in an unburned control site over the same time period that I measured soil and plant nutrients after fire in my flatwoods site; however, fire effects are the most likely explanation for my 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 my flatwoods site, extractable NH_4^+ and PO_4^{3-} were 5.5 and 30 times higher, respectively, three hours 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 palmettos 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. I did not measure foliar nutrient concentrations of clipped plants over the same time scale that I 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 my study, fire caused a short-term increase in soil extractable NH_4^+ and PO_4^{3-} in a palmetto flatwoods ecosystem (Figure 2-1); 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 2-2). 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 (Figure 2-1) and the foliar N:P ratio of the palmetto *Serenoa repens* (Figure 2-2) shortly after fire. The relationships between soil and foliar nutrients coupled with measurements of soil and foliar $\delta^{15}\text{N}$ 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). I found that a pulse of nutrients is detectable if soils are sampled soon enough after fire. Furthermore, my 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.

Table 2-1. 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 $\alpha = 0.05$ 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 ($\mu\text{g} \cdot \text{g soil}^{-1}$)	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 ($\mu\text{g} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$)	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 $\delta^{15}\text{N}^b$	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

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

Species/Family	%N			$\delta^{15}\text{N}$			Foliar $\delta^{15}\text{N}$ - Soil $\delta^{15}\text{N}$			%P			N:P		
	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
<i>S. repens</i>	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
<i>Q. geminata</i>	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						

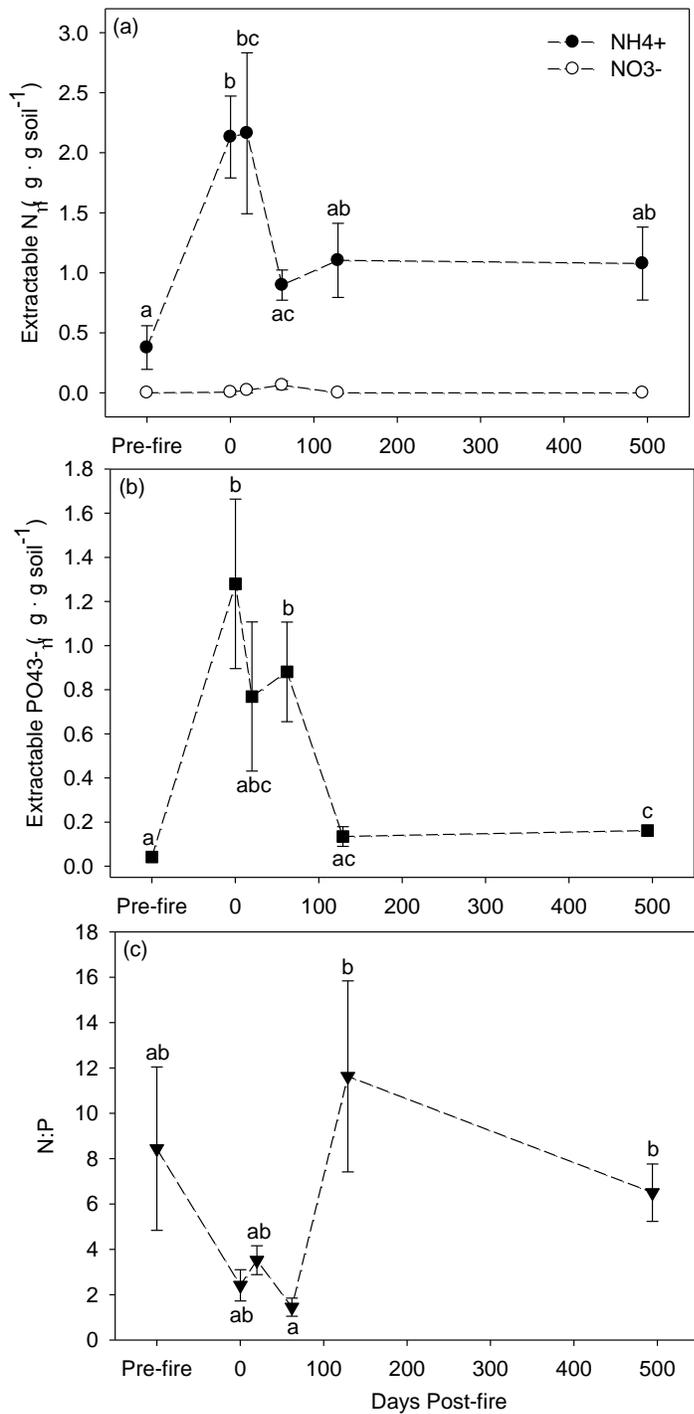


Figure 2-1. Mean (\pm SE) soil extractable NH_4^+ and NO_3^- (A), soil extractable PO_4^{3-} (B), and soil inorganic N:P ratios (C) in palmetto flatwoods pre-fire and 0.125, 20, 62, 129, and 494 days post-fire. Different letters represent significantly different means at $\alpha = 0.05$ determined by repeated measures analysis of variance with post-hoc pairwise comparisons with Bonferroni confidence interval adjustments.

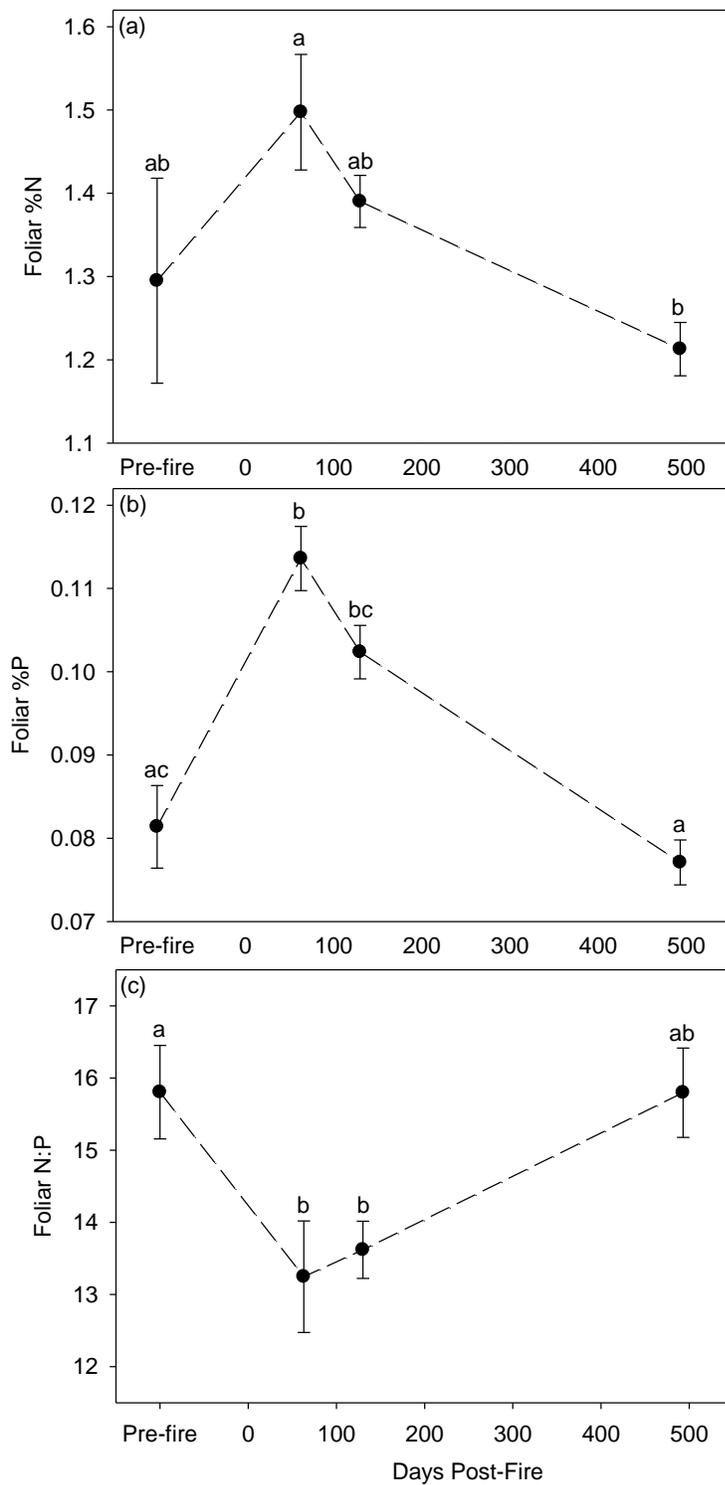


Figure 2-2. Mean (\pm SE) foliar %N (A), foliar %P (B), and foliar N:P ratios (C) for *Serenoa repens* (n = 5) in palmetto flatwoods pre-fire and 63, 130, and 493 days post-fire. Different letters represent significantly different means at $\alpha = 0.05$ determined by repeated measures analysis of variance with post-hoc pairwise comparisons with Bonferroni confidence interval adjustments.

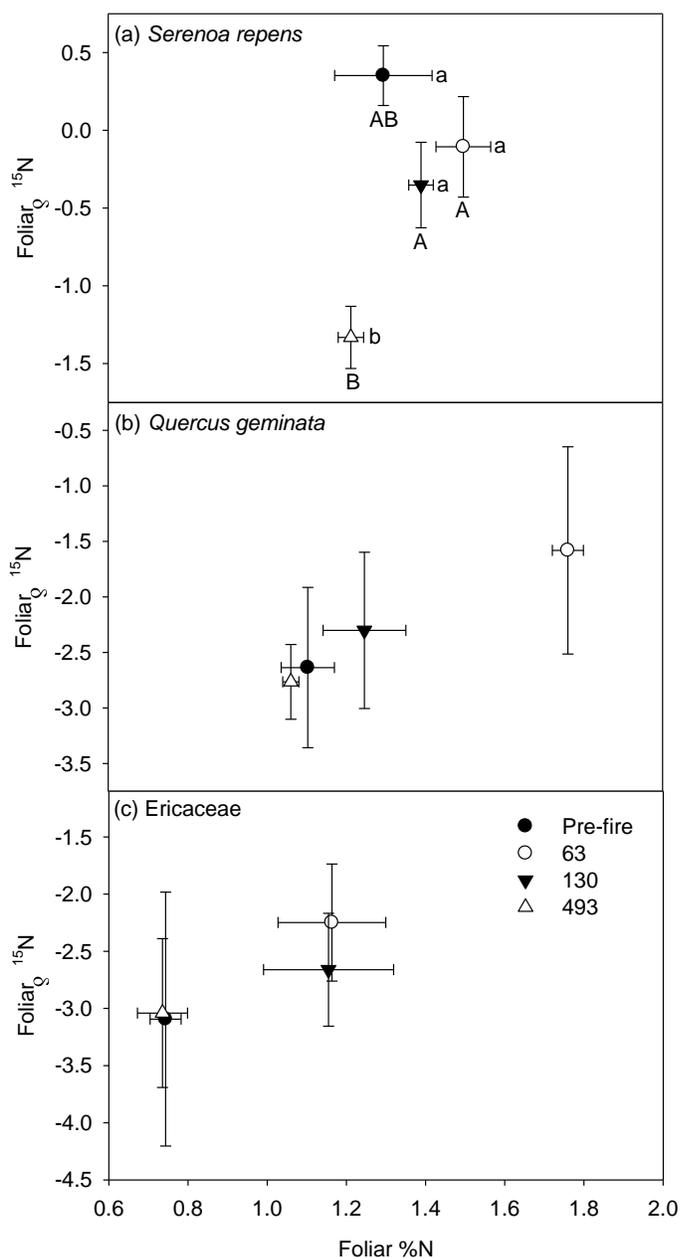


Figure 2-3. Mean (\pm SE) foliar %N and $\delta^{15}\text{N}$ for *Serenoa repens* (n = 5) (A), *Quercus geminata* (n = 4) (B), and three ericaceous species (*Lyonia fruticosa*, *Lyonia lucida*, and *Vaccinium myrsinites*; n = 4) (C) pre-fire and 63, 130, and 493 days post-fire in palmetto flatwoods. Uppercase letters represent significant differences in foliar %N and lowercase letters represent significant differences in foliar $\delta^{15}\text{N}$ at $\alpha = 0.05$ 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 $\delta^{15}\text{N}$ among times after fire for *Q. geminata* or ericaceous species.

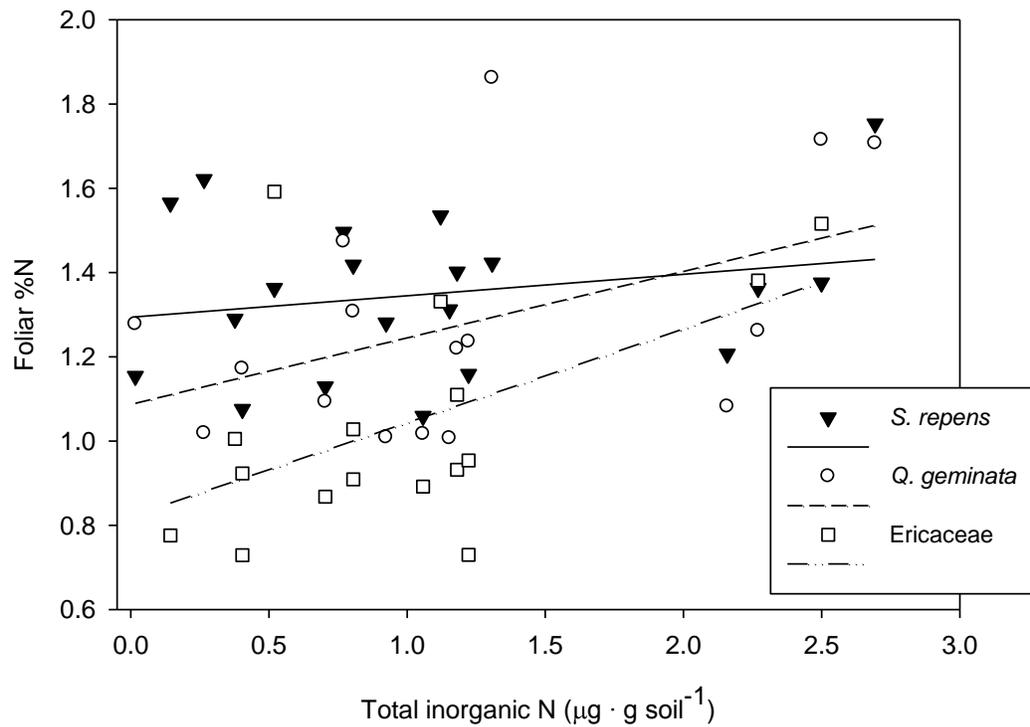


Figure 2-4. Relationship between total extractable inorganic N and foliar %N of *Serenoa repens* ($p = 0.368$, $R^2 = 0.04$; foliar %N = $1.29 + (0.05 * \text{inorganic N})$), *Quercus geminata* ($p = 0.073$, $R^2 = 0.21$; foliar %N = $1.09 + (0.16 * \text{inorganic N})$), and ericaceous shrubs ($p =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

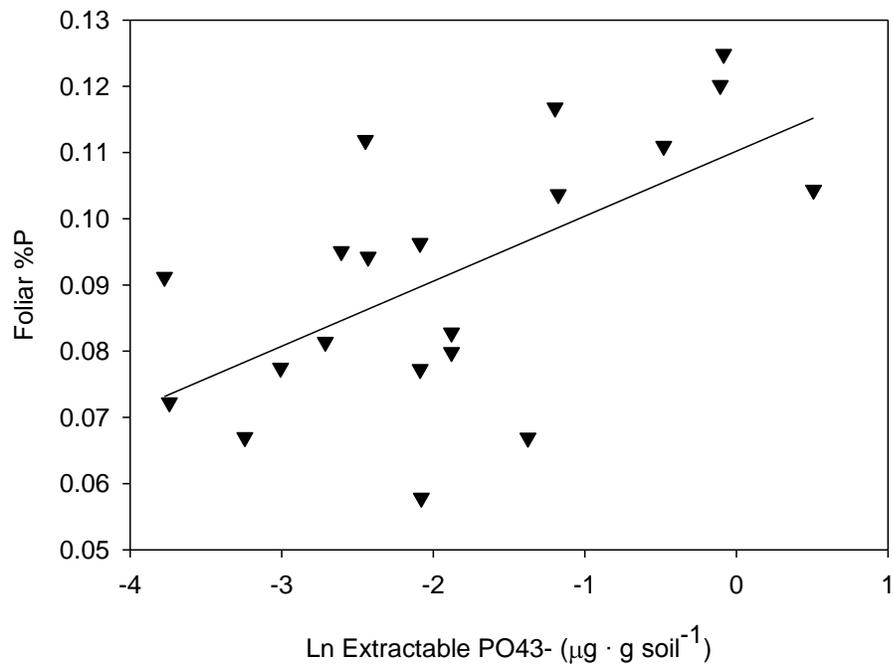


Figure 2-5. Relationship between soil extractable PO43- (natural log transformed) and foliar %P of *Serenoa repens* ($p = 0.004$, $R^2 = 0.37$; foliar %P = $0.11 + (0.01 * \ln \text{ PO43-})$).

CHAPTER 3
VARIATION IN GROWTH RATIOS, ABOVEGROUND BIOMASS ALLOCATION, AND
ALLOMETRIC RELATIONSHIPS OF RESPROUTING SHRUBS WITH TIME AFTER
FIRE

Introduction

Plant allometry theory predicts that leaf and stem biomass scale in relation to each other and in relation to stem height and diameter (Niklas 1994; West et al. 1999; Enquist and Niklas 2001; Niklas and Enquist 2001; Enquist and Niklas 2002; Niklas and Enquist 2002a). While allometric relationships hold across many species, the relationships have been developed from species that grow from seed. Stems of resprouting shrubs, particularly those in fire-adapted habitats, may differ from the predicted allometric relationships. While trees build one stem during their lifetime, shrub stems consumed by fire are rebuilt from belowground resources. Root biomass comprises approximately 25% of total plant biomass in angiosperm species (Niklas and Enquist 2002b); whereas, belowground biomass may comprise up to 88% of total biomass of resprouting shrubs (Saha et al. in review). Thus, the constraints on the allometry of resprouted shrub stems may differ from the constraints on stems of other plant growth forms.

Belowground reserves (McPherson and Williams 1998; Paula and Ojeda 2009), pre-fire plant size (Bonfil et al. 2004; Konstantinidis et al. 2006), and fire intensity (Moreno and Oechel 1991; Lloret and López-Soria, 1993) affect resprouting ability (Moreno and Oechel 1991) and biomass of resprouts (Lloret and López-Soria, 1993; Cruz et al. 2002). Thus, the allometric relationships of resprouts may depend on pre-fire plant status and fire characteristics in addition to the effects of metabolic rate on size-dependent changes in plant architecture (West et al. 1999; Enquist and Niklas 2002),

and may vary among species because the differential growth of and resource allocation to aboveground plant parts depends on species specific constraints (Niklas 1995a). As stems grow taller, they must increase their mechanical strength through diameter growth (King 1986), but there is a tradeoff between height and diameter growth (Tilman 1988). Diameter should increase faster than height as a stem grows (Niklas 1994); however, height growth per unit diameter is expected to differ between crowded and uncrowded individuals, and the magnitude and direction of change depends on cohort age and light environment (Henry and Aarssen 1999). In resprouting species, new stems occur in clumps (Silva et al. 2009), often around dead charred stems. The number of stems per clump is higher in more recently burned sites (Davies and Myerscough 1991), suggesting that intra-specific crowding of resprouts is high after fire. The effects of a clumped distribution may cause resprouted stems to deviate from allometric growth models. In addition, the differential growth of and resource allocation to aboveground plant parts is affected by light environment (Coomes and Grubb 1998) and competition (Weiner and Thomas 1992; Kozovits et al. 2005), which vary with time since fire.

Patterns of post-fire recovery of aboveground biomass differ among ecosystems. In forests, aboveground biomass may increase logarithmically (Vargas et al. 2008) or linearly (White et al. 2004) with time since fire. In shrublands dominated by species that recruit from seed after fire, aboveground biomass may increase linearly (Johnson et al. 1986) or exponentially (Cleary et al. 2008) for at least 40 years after fire. In shrublands dominated by resprouting species, however, aboveground biomass fluctuates, but does not increase, after four years since fire (Johnson et al. 1986; Sah et al. 2004),

suggesting that acquired resources are allocated to belowground biomass. Growth rates of leaves, stems, and roots are expected to scale isometrically (Niklas and Enquist 2002a; Niklas and Enquist 2002b); however, if this does not hold for resprouting species, then scaling relationships between leaf and stem biomass, and between stem height, diameter, and biomass, may not adhere to allometric model predictions.

Measurements of aboveground biomass may require harvesting of all plant material. This method, however, does not allow for repeated measurements of the same individuals over time, and is often not feasible in ecosystems with woody species. Thus, it is necessary to use non-destructive measurements and allometric relationships to estimate recovery of biomass after fire (e.g. Toma et al. 2005); however, the variability of sites from which species are sampled to develop allometric equations can affect estimates of biomass. For example, regression models predicting biomass of aspen trees were significantly different among sites varying in resource availability (Koerper and Richardson 1980), and allometric equations developed from black spruce trees from sites varying in soil moisture and geographic region produced different estimates of black spruce biomass (Mack et al. 2008). Despite the potential site-specific error in biomass estimates, different allometric equations to estimate biomass of plants at different stages post-fire are seldom used. In addition, research on allometric relationships of species in fire-adapted habitats has focused on dominant trees (e.g. Turner et al. 2004; Mack et al. 2008) or understory shrubs (Sah et al. 2004), rather than dominant resprouting shrubs, and many allometric equations for estimating aboveground biomass of shrubs use measurements of crown area or crown volume

(e.g. Murray and Jacobson 1982; Vora 1988; Huenneke et al. 2001; Sah et al. 2004) instead of measurements of stem diameter and height.

I examined the effects of time since fire on allometric relationships of shrub species in scrubby flatwoods ecosystems of the Lake Wales Ridge in central peninsular Florida. Scrubby flatwoods are fire-adapted ecosystems, and the dominant species are shrubs that resprout after fire (Abrahamson et al. 1984; Menges and Kohfeldt 1995). I tested the hypotheses that: (1) plant size and biomass increase logarithmically with time since fire; (2) height growth per unit diameter decreases with time since fire; (3) leaf:shoot and new:old shoot biomass ratios decrease with time since fire; and (4) plant size and biomass allocation ratios vary among dominant scrubby flatwood species. Furthermore, I developed allometric relationships to estimate aboveground biomass of the dominant shrubs at different times since fire.

Methods

Study Site and Species

This study was conducted at Archbold Biological Station (ABS) in Highlands County, Florida, USA (27°10'50"N, 81°21'0" W). Archbold Biological Station typically has warm wet summers and cool dry winters (Abrahamson et al. 1984). Mean annual precipitation is 136.5 cm (ABS weather records, 1932-2004), and mean annual temperature is 22.3°C (ABS weather records, 1952-2004). Archbold Biological Station includes a 5,193 acre scrub preserve, which is divided into burn units that have been managed with prescribed fires for over 35 years.

My research focused on the scrub oak (*Quercus inopina* Ashe) phase of scrubby flatwood communities (Abrahamson et al. 1984), which occur on sandy soils that have no horizon development, little organic matter, and low ion exchange capacity (Brown et

al. 1990). Scrubby flatwoods experience fire return intervals of 8-16 years (Menges 2007), and the dominant shrubs resprout after fire. Shrub height averages 1-2 m, but varies with resource availability and time since fire, and herbaceous species are sparse (Abrahamson et al. 1984).

I focused on the most abundant species in scrubby flatwoods: the shrubby oaks *Quercus chapmanii* Sarg., *Quercus geminata* Small, and *Q. inopina*, the ericaceous shrubs *Lyonia fruticosa* (Michx.) G. S. Torr. and *Lyonia lucida* (Lam.) K. Koch, and the palmettos *Sabal etonia* Swingle ex Nash (Arecaceae), and *Serenoa repens* (W. Bartram) Small (Arecaceae) (nomenclature follows Wunderlin and Hanson 2003). The oak species vary in abundance and phylogeny; *Q. inopina* has the highest percent cover (37%) and is a red oak, *Q. chapmanii* is intermediate in percent cover (22%) and is a white oak, and *Q. geminata* has the lowest percent cover (4%) and is also a white oak (Abrahamson et al. 1984). Percent cover of *L. lucida* and *L. fruticosa* is 3% and 2%, respectively (Abrahamson et al. 1984). The oaks and ericaceous shrubs are clonal, multi-stemmed species. *Sabal etonia* and *S. repens* are low growing palms with large fan-shaped leaves, and percent cover of *S. repens* (22%) is greater than percent cover of *S. etonia* (8%) (Abrahamson et al. 1984). *Sabal etonia* leaves are longer in length and width, and thus, are larger in area than *S. repens* leaves, while *S. repens* has more leaves than *S. etonia* (Abrahamson 2007).

During summer 2007, I measured and harvested aboveground stems of *L. fruticosa*, *L. lyonia*, *Q. chapmanii*, *Q. geminata*, and *Q. inopina* from sites 6 weeks and 8 and 20 years since fire. During summer 2008, I measured and harvested aboveground stems of the same species from the same sites, which were then 1, 9, and 21 years

since fire. I measured the basal diameter (to the nearest 0.01 mm using digital calipers) and height (to the nearest cm) of each stem, harvested each stem, and separated stems into leaves and shoots. In 2008, I separated all oak stems into new and old growth, and for *Q. geminata* and *Q. inopina*, I counted the number of new apical shoot growth increments, measured the length of each new apical shoot growth increment, and counted leaves on the new shoots. All samples were dried at 60°C for 48 hrs then weighed.

During spring and summer 2009, I measured and harvested leaves of *S. etonia* and *S. repens* from sites 6 weeks and 1, 2, 8, 10, and 22 years since fire. I measured the maximum crown diameter (length), minimum crown diameter (width), and height and counted the number of leaves of each individual. Leaves were harvested and separated into leaf lamina and petiole and dried at 60-70°C for 48 hrs then weighed.

Statistical Analyses

Allometry of growth and biomass allocation

Total aboveground biomass per stem, stem diameter, and stem height were natural log transformed then analyzed using a two-way ANOVA with time since fire, species, and their interaction as main effects. Differences among species and times since fire were determined with post-hoc Tukey HSD tests (JMP 8.0). Kruskal-Wallis tests were used to analyze differences in leaf:shoot biomass ratios and height:diameter ratios of shrub species because these variables could not be transformed to fit normality (SPSS 11.5). Significant differences among species and times since fire were determined using Bonferroni adjusted significance values (Sokal and Rohlf 1995). I used an ANCOVA model, with diameter as the dependent variable, time since fire as a fixed factor, and height as the covariate, to test for homogeneity of regression slopes to

determine if the relationship between stem height and stem diameter changes with time since fire (SPSS 11.5).

Kruskall-Wallis tests were used to analyze new:old shoot biomass ratios of oak species, and the number of new apical shoot growth increments, the mean length of new apical shoot growth increments per stem, the number of leaves per cm of new shoot growth, and the ratio of height to the number of new shoot growth increments (a measure of height vs. branching) of *Q. geminata* and *Q. inopina* because these variables could not be transformed to fit normality (SPSS 11.5). Significant differences among times since fire and among species were determined using Bonferroni adjusted significance values (Sokal and Rohlf 1995). Total length of new apical shoot growth and total number of leaves were natural log transformed before analysis using one-way ANOVAs and post-hoc Tukey tests to assess differences among times since fire. Differences between species for each time since fire were analyzed with t-tests (SPSS 11.5).

Total aboveground biomass of palmetto species was analyzed using one-way ANOVAs; *S. etonia* data was natural log transformed and *S. repens* data was square root transformed before analyses. A Kruskal-Wallis test was used to analyze differences between palmetto species in aboveground biomass at each time since fire. Kruskal-Wallis tests were also used to analyze differences in petiole:leaf lamina biomass ratios and biomass per leaf of palmetto species because these variables could not be transformed to fit normality (SPSS 11.5); significant differences among times since fire and among species were determined using Bonferroni adjusted significance values (Sokal and Rohlf 1995). Height, area, height:area ratios, and leaf number of

palmettos were analyzed using two-way ANOVAs with time since fire, species, and their interaction as main effects. Area was square root transformed and height:area ratios were natural log transformed before analyses. One extreme outlier (*S. etonia*, 8-10 years since fire) was removed from the analysis of height:area ratios because its removal made the data normally distributed. This *S. etonia* individual had only one leaf that was tall but narrow, so the height:area ratio was 0.69, which was 9.7 times greater than the next highest height:area ratio and over five standard deviations away from the mean. Differences among species and times since fire were determined with post-hoc Tukey HSD tests (JMP 8.0).

Allometric equations to estimate biomass

I used separate ANCOVA models for each shrub species, with total stem biomass as the dependent variable, time since fire as a fixed factor, and either height or diameter as the covariate to determine if the relationship between total stem biomass and the covariates changed with time since fire. Stem diameter, stem height, and aboveground biomass were natural log transformed before analyses. I used separate ANCOVA models for each palmetto species, with total biomass as the dependent variable, time since fire as a fixed factor, and either length, width, height, or number of leaves as the covariate to determine if the relationship between total biomass and the covariates changes with time since fire (SPSS 11.5). Aboveground biomass of *S. etonia* was natural log transformed before analyses, and aboveground biomass of *S. repens* was square root transformed before analyses.

To develop allometric equations to estimate aboveground biomass, I used multiple linear regressions with biomass as the dependent variable and all field measures (i.e. stem diameter and stem height for shrubs; length, width, height, and number of leaves

for palmettos) as independent variables (Sigma Plot 11.0), because in simple linear regressions, all independent variables were significant predictors of biomass. In some multiple regressions, only a subset of field measures significantly predicted biomass, so I conducted further multiple linear regressions or simple linear regressions to predict biomass. This procedure was carried out to estimate both total aboveground biomass (i.e. leaves + shoot for shrubs and leaf lamina + petiole for palmettos) and total leaf biomass (leaf lamina for palmettos). Allometric equations were developed for shrub stems and palmetto individuals separately for each time since fire and together across all times since fire. For *S. etonia* in sites 22 years since fire, all field measures could not be included in the multiple linear regressions because only five individuals were sampled; thus, I used height and number of leaves with either length or width in multiple regressions.

Results

Allometry of Growth and Biomass Allocation

Height and basal diameter of all shrub species increased from six weeks to one year after fire and from one year to eight-nine years since fire (Table 3-1); however, from eight-nine to 20-21 years after fire, height and diameter remained similar or decreased (Figure 3-1). Basal diameter did not vary among species one year or eight-nine years after fire, but 20-21 years after fire, *L. lucida* had the smallest basal diameters, which were, on average, at least 2 mm smaller than all other species (Figure 3-1). Six weeks after fire, *Q. chapmanii* and *Q. inopina* had the tallest resprouts, which were 1.3 to 2.4 times taller than resprouts of other species (Figure 3-1). *L. fruticosa* stems reached greater maximum heights than other species in longer unburned sites; eight to nine years after fire, *L. fruticosa* stems were, on average, 16-26 cm taller than

stems of other species. Twenty to twenty-one years after fire, *L. lucida* stems were, on average, 10 cm shorter than all other species (Figure 3-1).

Height:diameter ratios of all species were lowest six weeks after fire (Table 3-2). Height:diameter ratios of *Lyonia* species were 2-3 times greater eight-nine years since fire than six weeks after fire (Figure 3-2). Height:diameter ratios of *Q. chapmanii* and *Q. geminata* increased with time since fire and were 1.3 times higher 20-21 years since fire than six weeks after fire, while height:diameter ratios of *Q. inopina* were highest one year after fire (Figure 3-2). *Quercus* species had higher height:diameter ratios than *Lyonia* species six weeks after fire; whereas, eight-nine years after fire *Lyonia* species had higher height:diameter ratios than *Quercus* species (Table 3-2).

The slope of the relationship between stem height and stem diameter changed with time since fire for *L. fruticosa* ($F = 10.62$, $df = 3$, $p < 0.001$), *L. lucida* ($F = 6.59$, $df = 3$, $p < 0.001$), *Q. chapmanii* ($F = 11.62$, $df = 3$, $p < 0.001$), *Q. geminata* ($F = 10.49$, $df = 3$, $p < 0.001$), and *Q. inopina* ($F = 39.71$, $df = 3$, $p < 0.001$). For all species, the slope of the height vs. diameter relationship was lowest six weeks after fire, and slopes were twice as steep eight-nine years after fire compared to six weeks after fire (Figure 3-3). Twenty to twenty-one years after fire, slopes were similar to or less than slopes eight-nine years after fire (Table 3-3).

Total aboveground biomass per stem was 6 times higher one year after fire than six weeks after fire and 4.6 times higher eight-nine years after fire than one year after fire, but decreased slightly from eight-nine to 20-21 years since fire (Figure 3-1). Biomass per stem of *Quercus* species tended to be higher than biomass per stem of *Lyonia* species, with *L. lucida* having the lowest biomass per stem at all times since fire,

but eight-nine years since fire, *L. fruticosa* had the highest mean biomass per stem. *Q. chapmanii* and *Q. inopina* had greater biomass per stem than *Q. geminata* (Figure 3-1).

Leaf:shoot biomass ratios of *Quercus* species decreased with time since fire (Table 3-4) and were 4-5 times higher six weeks after fire than 20-21 years after fire (Figure 3-4). Leaf:shoot biomass ratios of *Lyonia* species were highest one year after fire (Figure 3-4). At all times since fire, leaf:shoot biomass ratios varied among species (Table 3-5); *Q. inopina* had the highest leaf:shoot biomass ratios six weeks after fire, whereas *L. lucida* had the highest leaf:shoot biomass ratios 20-21 years after fire (Figure 3-4).

New:old shoot biomass ratios of *Quercus* species were 1.7 to 4.3 times higher one year after fire than nine and 21 years after fire (Figure 3-5). One year after fire, *Q. geminata* new:old shoot biomass ratios were 1.2 and 1.7 times lower than *Q. chapmanii* and *Q. inopina* new:old shoot biomass ratios, respectively (Table 3-5).

The number of new apical shoot growth increments and the ratio of height to the number of new growth increment ratios of *Q. geminata* did not vary with time since fire (Table 3-6). *Q. geminata* new apical shoot growth increments generally were longer one year after fire than nine and 21 years after fire (Figure 3-6). Total length of new apical shoot growth of *Q. geminata* did not vary with time since fire (Table 3-6). *Q. inopina* had three to six times more new apical shoot growth increments nine and 21 years since fire than one year after fire, and *Q. inopina* new apical shoot growth increments were twice as long one year after fire compared to nine and 21 years since fire (Figure 3-6). The total length of new apical shoot growth of *Q. inopina* did not vary with time since fire

(Figure 3-7). The ratios of height to the number of new growth increments of *Q. inopina* were twice as high one year after fire than nine and 21 years after fire (Figure 3-6).

One year after fire, *Q. geminata* had more new apical shoot growth increments than *Q. inopina*, while *Q. inopina* had longer new apical shoot growth increments than *Q. geminata* (Table 3-7), so the total length of new apical shoot growth did not differ between *Q. geminata* and *Q. inopina* (Figure 3-7). *Q. inopina* also had a higher ratio of height to the number of new growth increments than *Q. geminata* one year after fire (Table 3-7). The number of new growth increments, the total length of new apical shoot growth, and the ratio of height to the number of new growth increments did not differ between *Q. inopina* and *Q. geminata* nine or 21 years after fire (Table 3-7).

The number of new leaves produced by *Q. geminata* did not vary with time since fire (Table 3-6), but *Q. inopina* produced fewer new leaves one year after fire than nine and 21 years since fire (Figure 3-7). *Q. geminata* had more new leaves than *Q. inopina* one year after fire, but not nine or 21 years after fire (Table 3-7). The number of leaves per centimeter of new shoot growth of *Q. inopina* increased with time since fire (Figure 3-6), while the number of leaves per centimeter of new shoot growth of *Q. geminata* did not change with time since fire (Table 3-6). *Q. geminata* produced more leaves per centimeter of new shoot growth than *Q. inopina* at all times since fire (Table 3-7).

Height of palmettos did not vary with time since fire, and height and area of palmettos did not differ between species (Table 3-1). Palmettos covered twice as much area 22 years since fire than six weeks since fire (Figure 3-8). The height:area ratio of palmettos was at least 2.4 times higher six weeks after fire than other times since fire. Overall, the height:area ratio of *S. repens* was 1.3 times greater than the height:area

ratio of *S. etonia* (Figure 3-8). Palmettos had more leaves in longer unburned sites than in sites six weeks since fire, and *S. repens* had twice as many leaves as *S. etonia* at all times except six weeks after fire (Figure 3-8).

Aboveground biomass of *S. etonia* tended to increase, but not significantly, with time since fire ($F = 1.68$, $df = 3$, $p = 0.192$), while aboveground biomass of *S. repens* was higher one-two and 22 years since fire than six weeks after fire ($F = 4.29$, $df = 3$, $p = 0.008$) (Figure 3-9). Aboveground biomass of *S. repens* was greater than biomass of *S. etonia* one-two years after fire (Table 3-5). Petiole:lamina biomass ratios of palmetto species increased with time-since-fire (Table 3-4) and were approximately three times greater 22 years since fire than six weeks since fire (Figure 3-10). Biomass per leaf of palmetto species did not change with time since fire (Table 3-4).

Allometric Relationships to Estimate Biomass

The slope of the relationship between height and total stem biomass varied with time since fire for *L. lucida* ($F = 10.47$, $df = 3$, $p < 0.001$), *Q. chapmanii* ($F = 7.08$, $df = 3$, $p < 0.001$), *Q. geminata* ($F = 6.82$, $df = 3$, $p < 0.001$), and *Q. inopina* ($F = 25.35$, $df = 3$, $p < 0.001$), but not for *L. fruticosa* ($F = 0.93$, $df = 3$, $p = 0.427$) (Figure 3-11). Slopes tended to be steeper for longer unburned (8-21 years) than more recently burned (6 wks – 1 year) sites (Table 3-8). On the contrary, the slope of the relationship between diameter and total aboveground biomass varied with time since fire for *L. lucida* ($F = 3.55$, $df = 3$, $p = 0.016$), but not for *L. fruticosa* ($F = 1.93$, $df = 3$, $p = 0.128$), *Q. chapmanii* ($F = 0.15$, $df = 3$, $p = 0.928$), *Q. geminata* ($F = 0.79$, $df = 3$, $p = 0.502$), or *Q. inopina* ($F = 0.69$, $df = 3$, $p = 0.560$) (Figure 3-11).

For *S. etonia*, the slope of the relationships between total biomass and length ($F = 1.21$, $df = 3$, $p = 0.326$), total biomass and width ($F = 0.97$, $df = 3$, $p = 0.421$), total

biomass and height ($F = 0.31$, $df = 3$, $p = 0.816$), and total biomass and number of leaves ($F = 0.34$, $df = 3$, $p = 0.795$) did not change with time since fire (Figure 3-12). For *S. repens*, the slope of the relationships between total biomass and length ($F = 1.64$, $df = 3$, $p = 0.191$), total biomass and width ($F = 1.78$, $df = 3$, $p = 0.161$), and total biomass and number of leaves ($F = 0.59$, $df = 3$, $p = 0.624$) did not change with time since fire. The slope of the relationship between total biomass and height changed slightly with time since fire ($F = 2.65$, $df = 3$, $p = 0.058$); the slope for six week old individuals was lower than for other times since fire (Table 3-9).

In all but one case, both stem diameter and stem height were significant predictors of total biomass of shrub stems (Table 3-10); however, in several cases, either stem diameter or stem height was not a significant predictor of leaf biomass of shrub stems (Table 3-11). Overall, total stem biomass was better predicted by stem diameter and height than leaf biomass of shrub stems. The R^2 of allometric equations for all stems combined across times since fire was similar to or higher than the R^2 of equations for stems from specific times since fire for both total biomass and leaf biomass of shrub stems (Tables 3-10 and 3-11). For *Quercus* species, the R^2 of equations predicting total biomass tended to increase with time since fire (Table 3-10).

Palmetto total leaf biomass was predicted slightly better than leaf lamina biomass. Only maximum crown diameter and height were significant predictors of total leaf biomass and leaf lamina biomass of *S. etonia*; whereas, maximum and minimum crown diameter, height, and number of leaves were all significant predictors of total leaf biomass and leaf lamina biomass of *S. repens* (Tables 3-12 and 3-13). In several cases,

none of the variables in the multiple regressions significantly predicted biomass, but the predictive equations had a high R^2 .

Discussion

Allometry of Growth and Biomass Allocation

Growth ratios and aboveground biomass allocation changed with time since fire for all dominant scrubby flatwood species, with the greatest changes occurring from six weeks to eight-ten years after fire. The patterns of change in growth ratios and aboveground biomass allocation with time since fire, however, were not consistent species.

Belowground starch and non-structural carbohydrate reserves (McPherson and Williams 1998; Paula and Ojeda 2009) and pre-fire plant size (Bonfil et al. 2004; Konstantinidis et al. 2006) are important in determining post-fire resprouting ability, and thus size and biomass of resprouts. Six weeks after fire, oak (*Quercus* species) resprouts tended to be taller, larger in diameter, and have greater biomass than ericaceous shrub (*Lyonia* species) resprouts. Total nonstructural carbohydrate concentrations of Florida scrub species may increase or decrease with time since fire (Olano et al. 2006); however, all resprouts were collected from sites with the same fire history. Rhizome resprouting potential is similar for *Q. chapmanii* and *Q. geminata* (Cavender-Bares et al. 2004), but oak species have greater belowground biomass than other scrub species, including *Lyonia* species (Saha et al. in review). Based on heights of shrub stems in longer unburned sites (Figure 3-3) and measurements of dead charred stems in the sites where resprouts were collected (J. Schafer, unpublished data), *L. lucida* was shorter than other species pre-fire. Differences in both belowground

storage and pre-fire size likely enable oaks to produce larger resprouts than *Lyonia* species.

All species were larger in diameter, taller, and had greater biomass per stem one year after fire compared to six weeks after fire, but oaks and ericaceous shrubs did not differ from each other. Eight to nine years after fire, there was no difference in diameter, height, or aboveground biomass per stem among shrub species. Stems of all species had larger diameters, and all species except *Q. chapmanii* were taller, eight-nine years compared to one year after fire; however, only *L. fruticosa* and *Q. inopina* had significantly more aboveground biomass eight-nine than one year after fire.

Overall, stem diameter, height, and biomass per stem decreased from eight-nine years to 20-21 years since fire. This trend was driven more by *Lyonia* species than by *Quercus* species (Figure 3-1). Several mechanisms could explain the lack of change or decrease in stem diameter, height, and biomass per stem from eight to 21 years since fire. First, there is a negative relationship between abundance and total plant mass (Allen et al. 2008); however, percent cover of shrubs overall and the number of stems within clumps does not vary between eight and 20 years since fire (J. Schafer, unpublished data). Second, as stem diameter increases, resources are allocated to the root system to increase stability (Drexhage et al. 1999). Stem diameter did not increase from eight-nine to 20-21 years since fire, and root productivity does not differ between sites 8 and 20 years since fire (Chapter 5). I hypothesize that shrub stems experience die-back due to water (Saha et al. 2008) or nutrient limitation. Although the longer unburned sites have received similar amounts of precipitation over the last eight-nine years, the 20-21 years since fire sites were located at the southern end of Archbold

Biological Station, where scrubby flatwoods occur 2m higher in elevation than further North, where the eight-nine years since fire sites were located (Abrahamson et al. 1984). Thus, the 20-21 years since fire sites are located further above the water table, suggesting that during times of drought, species such as *Q. chapmanii* and *Q. geminata*, which take up water from 40-200 cm (Saha et al. 2008), may experience greater water stress. Percent dieback (Au and Tardif 2007) and the ratio of biomass loss to the gross production of aboveground biomass (Kawamura and Takeda 2008) increase with stem age; however, the mean and maximum life span of *Q. inopina* stems is 4 years and 9 years, respectively, and the rate of stem die-off is lower in recently burned than long unburned sites (Johnson and Abrahamson 2002), so it is unlikely that stem age alone causes the observed patterns in stem size.

Previous research found that the height of *Q. inopina* stems did not vary over a nine year period in a long-unburned site (Johnson and Abrahamson 2002). Aboveground biomass of *Q. inopina* did not vary from 2-34 years after fire in Florida rosemary scrub (Johnson et al. 1986); whereas, aboveground biomass of oak shoots increased, while aboveground biomass of other shrub species, including *Lyonia* species, did not vary, from 3-25 years since fire in scrubby flatwoods (Saha et al. in review). Biomass of shrubs in Florida Keys pine forests did not increase from 12 to 30 years after fire (Sah et al. 2004).

The height:diameter ratio of all species increased from six weeks to one year after fire, and the relative increase was greater for ericaceous shrubs than for oaks; but overall, height:diameter ratios were similar one, eight-nine, and 20-21 years since fire. Crowded individuals have larger height:diameter ratios than trees growing in the open

(Holbrook and Putz 1989), suggesting that shrub stems experience crowding within the first year after fire. In addition, the slopes of the relationship between stem height and diameter tended to become steeper with time since fire (Figure 3-3). The relationship between stem diameter and height may be dependent on light conditions (Coomes and Grubb 1998), with height growth per unit diameter being greater in crowded trees, causing a shallower slope in the relationship between height and diameter (Henry and Aarssen 1999). This suggests that resprouts are more crowded than shrub stems in sites with longer times since fire, and since resprouts tend to occur in clumps, the increase in crowding is likely caused by intra-specific rather than inter-specific competition. Henry and Aarssen (1999) predict that height increases faster than diameter in young stems and diameter increases faster than height in older stems. This may have contributed to the observed height diameter relationships, as stems in the recently burned sites were less than one year old and stems in the other sites could have been one to many years old. Furthermore, stems of taller species can be disproportionately more slender than stems of shorter species (Niklas 1995b), so species specific differences may also affect height diameter relationships.

Six weeks after fire, oaks allocated a greater proportion of resprout biomass to leaves than did ericaceous shrubs. The leaf:shoot biomass ratio decreased in oak species from six weeks to one year since fire; whereas, the leaf:shoot biomass ratio increased in ericaceous shrubs and tended to be higher than in oaks (Figure 3-4). For all species, the leaf:shoot biomass ratio was lower eight-nine and 20-21 years after fire than one year after fire, which may be related to a decrease in the proportion of shoot mass in leaf laminae with increasing plant height (Anten and Hirose 1998). Species

from other habitats have shown similar allocation patterns, with younger stems having a greater proportion of biomass in leaf tissue than older stems (Cleary et al. 2008; Zewdie et al. 2009). This pattern of allocation to photosynthetic versus structural tissue may be related to the effect of removal of aboveground stems by disturbance on shoot biomass (Scogings and Mopipi 2008) or to changes in allocation with an increase in stem biomass (Johnson et al. 1986; Aikawa and Hori 2006). In addition, both shading (Vilà 1997) and aboveground competition (Kozovits et al. 2005) have been shown to cause a decrease in leaf:shoot biomass ratios. Resprouts of the shrub species I studied often occur in clumps, and shortly after fire, oaks tend to have a greater number of resprouts within a clump than ericaceous shrubs (J. Schafer, unpublished data). This suggests that oaks experience greater self-shading and intra-specific competition than ericaceous shrubs within the first year after fire, which could explain the difference in patterns of change in leaf:shoot biomass ratios between oaks and ericaceous shrubs shortly after fire. Although plants from dense understories allocate more biomass to supporting tissue than leaf tissue (den Dubbelden and Knops 1993), my data suggest that greater shading and aboveground competition may lead to an increase in leaf:shoot biomass ratios; in sites 20-21 years since fire, *L. lucida* had the shortest stems and the highest leaf:shoot biomass ratios. This strategy may be beneficial in shrub-dominated ecosystems where shrubs do not create a closed canopy.

New:old shoot biomass ratios of oak species were higher one year post-fire compared to longer unburned sites, which is due to greater shoot elongation in resprouts than in mature stems (DeSouza et al. 1986; Clemente et al. 2005) and a decrease in new:total shoot length with age (Aikawa and Hori 2006). Species

differences in new:old shoot biomass only occurred one year after fire, with *Q. geminata* having lower new:old shoot biomass ratios than *Q. chapmanii* and *Q. inopina* (Table 3-5). These differences may be related to genetic constraints in the ability of live oaks and red and white oaks to produce new apical shoot growth.

Q. geminata had slight or no differences in several measures of new growth with time since fire (Table 3-6), suggesting that allometry of growth of *Q. geminata* is constrained. On the contrary, only total length of new apical shoot growth of *Q. inopina* did not differ with time since fire (Table 3-6), suggesting that the allometry of growth of *Q. inopina* is more plastic. Within the constraints of plant architecture, the response of plants to environmental differences varies with ontogeny (Farnsworth and Ellison 1996). Plasticity in allometry tends to be strongest in early development (Bosner and Aarssen 2001), as was the case for *Q. inopina*, with young resprouts differing from older stems. One year after fire, compared to nine and 21 years since fire, *Q. inopina* produced fewer, but longer, new apical shoot growth increments, fewer leaves, and fewer leaves per unit of new shoot growth. In other species, non-crowded plants produce more, longer branches than crowded plants (Weiner et al. 1990), and old plants produce more leaves than young plants (Oñate and Munné-Bosch 2008). The number of new apical shoot growth increments are indicative of the number of shoot endings; thus, the variation in the ratio of height to the number of new shoot growth increments (Figure 3-6) suggests that *Q. inopina* invests more in increasing crown area one year after fire and invests more in height growth nine and 21 years after fire. Similarly, the ratio of height to number of shoot endings of *Acer saccharum* tended to decrease with seedling and sapling age, especially in open habitats (Bosner and Aarssen 1994). Plasticity in

branching may also be related resource availability (Salemaa and Sievanen 2002), which changes with time since fire in scrubby flatwoods (Chapter 4).

Variation in aboveground allocation patterns may be important in determining patterns of species abundances, as the use of resources to sequester space aboveground may be a quantitative parameter of competitiveness (Kozovits et al. 2005). For example, six weeks after fire, *Q. inopina*, the most abundant species in the scrubby flatwoods communities studied (Abrahamson et al. 1984), had the highest leaf:shoot biomass ratio. One year after fire, *Q. inopina* invests in branching rather than height. By 20-21 years after fire, *Q. inopina* had the highest biomass per stem. The ability of *Q. inopina* to sequester space aboveground after fire, may contribute to the ability of *Q. inopina* to maintain dominance in scrubby flatwood communities over many fire cycles.

Aboveground biomass of *S. etonia* increased, though not significantly, with time since fire, while biomass of *S. repens* was higher one-two and 22 years since fire than six weeks since fire (Figure 3-9). Abrahamson (2007) found that *S. etonia* had fewer leaves and lower biomass than *S. repens* in scrubby flatwoods. Similarly, I found that *S. etonia* had fewer leaves than *S. repens*; however, I found that biomass of *S. repens* was greater than biomass of *S. etonia* only in sites one to two years since fire. The petiole:lamina biomass ratio of *S. etonia* and *S. repens* was highest twenty-two years since fire, suggesting that palmettos increase allocation to leaf support relative to leaf photosynthetic tissue. The height:area ratio of palmettos tends to be lower in longer unburned sites, suggesting that the increase in allocation to petiole biomass occurs to increase width rather than height of leaves, which is important in preventing self-shading. Previous research has found that palm species increase investment to petiole

biomass (Takenaka et al. 2001) and length to reduce self-shading (Kimura and Simbolon 2002). Furthermore, *S. repens* may experience greater self-shading since having more leaves increases self-shading (Takenaka et al. 2001). The height of shrubs in scrubby flatwoods increases with time since fire (Figure 3-1) and shrubs can reach greater maximum heights than palmettos, but on average, palmettos are taller than shrubs. Thus, palmettos may experience more within plant competition for light than competition from other species. Abrahamson (2007) found that total leaf canopy area of *S. etonia* and *S. repens* increased with percent overstory. In my study, leaf canopy area was similar from one to 22 years since fire, suggesting that percent overstory does not vary significantly with time since fire.

Allometric Relationships to Estimate Biomass

The relationship between stem diameter and stem biomass changed with time since fire for only one shrub species; whereas, the relationship between stem height and stem biomass changed with time since fire for all but one species (Figure 3-11). This suggests that biomass scales with diameter more consistently than biomass scales with height. Previous research has found that allometric relationships of wetland species were size dependent (Maio et al. 2008), and allometric equations of shrubs differ between study years (Lufafa et al. 2009), suggesting that variation in precipitation or nutrient availability may affect allometric relationships. Cleary et al. (2008) found that allometric equations estimating aboveground biomass of sagebrush did not differ across a fire chronosequence. Sagebrush, however, recruits from seed after fire, whereas all of the shrubs in my study resprout after fire. Furthermore, the sagebrush chronosequence ranged from 3-60 years since fire, and I found the biggest changes in allometric relationships from six weeks to eight-nine years since fire. Contrary to the oak and

ericaceous shrubs studied, the relationships between biomass and length, width, height, and number of leaves of palmettos did not change with time since fire, suggesting that variation in allometry is dependent on or constrained by growth form. My results suggest that changes in allometric relationships with time since fire should be considered when estimating variation in stand biomass with time since fire, particularly for resprouting species.

Competition affects allometric relationships (Weiner and Thomas 1992); the relationship between height and mass differed for plants growing with competition and in isolation (Anten and Hirose 1998). Variation in the height diameter relationships of the shrubs studied suggest that crowding, and thus competition, varies with time since fire. This likely contributes to the variation in height biomass relationships with time since fire.

For oaks and ericaceous shrubs, both height and diameter were significant predictors of total stem biomass. Miao et al. (2008) found that plant height had a relatively greater influence on plant biomass than basal area. Seiler et al. (2009) developed allometric relationships for *Q. chapmanii* and *Q. geminata* using only stem diameter; however, I found that multiple regressions with stem height and stem diameter resulted in better predictive power than simple regression with only height or diameter (Table 3-8 vs. Table 3-10). In addition, stem basal diameter and height were better predictors of total stem biomass than total leaf biomass (Table 3-8 vs. Table 3-9), which is similar to results of other studies (Robertson and Ostertag 2009). Measures such as maximum and minimum crown area are likely more indicative of leaf biomass than stem diameter. Although the oaks and ericaceous shrubs studied are clonal, and

each genetic individual may have one or many stems, I measured allometric relationships of individual stems because it is difficult to distinguish individuals without excavation. Considering that local position on the lignotuber can affect stem growth (Riba 1998), not distinguishing genets from ramets may have affected allometric relationships.

Abrahamson (1995) developed allometric relationships to determine total (aboveground and belowground stem) biomass of *S. etonia* and *S. repens* based on minimum crown width and the number of number of leaves. Using a larger sample size overall, I found that length (maximum crown diameter), width (minimum crown diameter), height, and number of green leaves were all significant predictors of aboveground leaf biomass depending on time since fire and the species of palmetto. Aboveground measures of palmettos were equally good at predicting total leaf biomass and leaf lamina biomass, likely because petioles make up a small proportion of total leaf biomass.

Overall, growth, allocation of resources to aboveground tissues, and allometric equations tended to differ with time since fire, but the majority of differences occurred between recently burned and intermediate and longer unburned sites. Resprouting ability of scrubby flatwood species appears to be important in determining growth and allometry immediately after fire. The fire return interval for scrubby flatwoods is 8-16 years (Menges 2007), and there was little or no difference in plant size, biomass, or allometric relationships from 8-22 years since fire within a species; however, there were differences among species within these times since fire. Thus, as time since fire increases, species specific constraints in growth and allometry appear to become more

important. My results also suggest that caution should be taken in using allometric equations developed for plants from longer unburned sites to estimate biomass of plants in recently burned sites.

Table 3-1. Results of two-way ANOVA analyses with time since fire, species, and their interaction as main effects with dependent variables for both shrubs and palmettos.

Oaks and Ericaceous Shrubs			
	F	df	P
Diameter (mm)*			
TSF	8.91	3	<0.001
Species	213.87	4	<0.001
TSF * Species	2.20	12	0.010
Height (cm)*			
TSF	10.48	3	<0.001
Species	246.27	4	<0.001
TSF * Species	3.39	12	<0.001
Stem Biomass (g)*			
TSF	226.88	3	<0.001
Species	34.37	4	<0.001
TSF * Species	4.29	12	<0.001
Palmettos			
	F	df	P
Height (cm)			
TSF	1.83	3	0.147
Species	0.01	1	0.923
TSF * Species	0.82	3	0.484
Area (cm ²)*			
TSF	5.73	3	0.001
Species	1.97	1	0.164
TSF * Species	0.77	3	0.511
Height:Area [^]			
TSF	12.54	3	<0.001
Species	5.24	1	0.024
TSF*Species	1.56	3	0.217
# of Leaves			
TSF	8.81	3	<0.001
Species	29.23	1	<0.001
TSF * Species	2.24	3	0.089

* natural log transformed before analyses

[^] square root transformed before analyses

Table 3-2. Results of Kruskal-Wallis tests analyzing differences in height:diameter ratios among times since fire for each shrub species (left) and among species for each time since fire (right).

Species	Height:Diameter			TSF	Height:Diameter		
	χ^2	df	p		χ^2	df	p
<i>L. fruticosa</i>	39.09	3	<0.001	6 wks	96.42	4	<0.001
<i>L. lucida</i>	97.53	3	<0.001	1 yr	33.21	4	<0.001
<i>Q. chapmanii</i>	11.74	3	0.008	8-9 yrs	26.01	4	<0.001
<i>Q. geminata</i>	15.13	3	0.002	20-21 yrs	11.48	4	0.022
<i>Q. inopina</i>	43.65	3	<0.001				

Table 3-3. Results of regressions analyses comparing stem height to stem diameter for shrub species at different times since fire. In diameter = $\alpha + \beta * \ln$ height.

	A	β	R ²	Adj R ²	p
<i>L. fruticosa</i>					
6 wks	0.256	0.202	0.305	0.290	<0.001
1 yr	-0.395	0.485	0.742	0.733	<0.001
8-9 yrs	-1.125	0.739	0.827	0.818	<0.001
20-21 yrs	-0.535	0.602	0.564	0.541	<0.001
<i>L. lucida</i>					
6 wks	0.194	0.263	0.193	0.181	<0.001
1 yr	-0.580	0.525	0.640	0.631	<0.001
8-9 yrs	-2.047	0.932	0.796	0.785	<0.001
20-21 yrs	-1.469	0.792	0.452	0.433	<0.001
<i>Q. chapmanii</i>					
6 wks	-0.174	0.374	0.408	0.399	<0.001
1 yr	-0.991	0.674	0.672	0.662	<0.001
8-9 yrs	-1.883	0.958	0.703	0.687	<0.001
20-21 yrs	-1.789	0.912	0.767	0.756	<0.001
<i>Q. geminata</i>					
6 wks	-0.086	0.325	0.548	0.540	<0.001
1 yr	-1.015	0.734	0.761	0.753	<0.001
8-9 yrs	-0.454	0.609	0.436	0.413	<0.001
20-21 yrs	-1.144	0.776	0.758	0.748	<0.001
<i>Q. inopina</i>					
6 wks	0.068	0.252	0.298	0.293	<0.001
1 yr	-0.811	0.587	0.720	0.717	<0.001
8-9 yrs	-1.205	0.799	0.843	0.839	<0.001
20-21 yrs	-1.090	0.758	0.857	0.854	<0.001

Table 3-4. Results of Kruskal-Wallis tests analyzing differences in biomass ratios among times since fire for each species.

Species	Leaf:Shoot			New:Old Shoot		
	χ^2	df	P	χ^2	df	P
<i>L. fruticosa</i>	39.84	3	<0.001			
<i>L. lucida</i>	14.28	3	0.003			
<i>Q. chapmanii</i>	93.63	3	<0.001	18.27	2	<0.001
<i>Q. geminata</i>	77.54	3	<0.001	16.88	2	<0.001
<i>Q. inopina</i>	209.41	3	<0.001	21.39	2	<0.001

Species	Petiole:Lamina			Biomass/Leaf		
	χ^2	df	P	χ^2	df	p
<i>S. etonia</i>	16.83	3	0.001	3.29	3	0.349
<i>S. repens</i>	20.15	3	<0.001	3.81	3	0.282

Table 3-5. Results of Kruskal-Wallis tests analyzing differences in biomass and biomass ratios among species within each time since fire (TSF). Numbers in parentheses indicate degrees of freedom for each test.

TSF	Oaks and Ericaceous Shrubs				Palmettos				
	Leaf:Shoot Biomass (4)		New:Old Shoot Biomass* (2)		Aboveground Biomass (1)		Petiole:Leaf Biomass (1)		
	χ^2	p	χ^2	p	χ^2	p	χ^2	P	
6 wks	178.12	<0.001	na	na	6 wks	0.15	0.699	2.40	0.121
1 yr	43.04	<0.001	8.01	0.018	1-2 yrs	4.46	0.035	10.77	0.001
8-9 yrs	10.56	0.032	1.59	0.451	8-10 yrs	0.01	0.933	1.61	0.204
20-21 yrs	32.22	<0.001	3.41	0.182	22 yrs	0.20	0.655	0.94	0.333

* oaks only; time since fire is 1, 9, and 21 years

Table 3-6. Results of Kruskal-Wallis tests and one-way ANOVAs (indicated by *) analyzing differences in growth measures for *Q. geminata* and *Q. inopina* among times since fire. Degrees of freedom = 2 for all statistical tests.

Variable	<i>Q. geminata</i>		<i>Q. inopina</i>	
	χ^2 , F	p	χ^2 , F	p
# of new growth increments	2.93	0.231	23.21	<0.001
Mean length (cm) of new growth increments per stem	6.72	0.035	29.39	<0.001
Total length of new growth (cm)*	0.02	0.977	1.02	0.365
# of new leaves*	0.76	0.762	5.89	0.004
# of leaves per cm of new shoot growth	5.04	0.081	23.25	<0.001
Height (cm) / # of new shoot growth increments	1.59	0.451	27.66	<0.001

Table 3-7. Results of Kruskal-Wallis and t-tests (indicated by *) analyzing difference in growth measures between *Q. geminata* and *Q. inopina* at each time since fire.

Variable	Time since fire								
	1 year			9 years			21 years		
	χ^2 , t	df	P	χ^2 , t	df	p	χ^2 , t	df	p
# of new growth increments	11.74	1	0.001	0.24	1	0.623	0.00	1	0.985
Mean length (cm) of new growth increments per stem	33.10	1	<0.001	2.39	1	0.122	4.32	1	0.038
Total length of new growth (cm)*	-0.83	107	0.405	-0.77	30	0.466	-1.03	32	0.311
# of new leaves*	2.41	107	0.018	0.39	30	0.700	0.29	32	0.775
# of leaves per cm of new shoot growth	42.89	1	<0.001	4.78	1	0.029	9.14	1	0.002
Height (cm) / # of new shoot growth increments	30.91	1	<0.001	2.39	1	0.122	0.06	1	0.806

Table 3-8. Results of regressions analyses for shrub species at each time since fire. In total biomass = $\alpha + \beta_1 * \ln$ height (left side) and \ln total biomass = $\alpha + \beta_1 * \ln$ diameter (right side).

	Height					Diameter				
	α	β_1	R ²	Adj R ²	p	α	β_1	R ²	Adj R ²	p
<i>L. fruticosa</i>					0.427					0.128
6 wks	-5.152	1.712	0.888	0.885	<0.001	-3.982	3.398	0.469	0.458	<0.001
1 yr	-4.241	1.701	0.870	0.866	<0.001	-2.301	3.000	0.858	0.853	<0.001
8-9 yrs	-5.260	1.999	0.897	0.892	<0.001	-1.878	2.520	0.939	0.936	<0.001
20-21 yrs	-3.559	1.540	0.584	0.562	<0.001	-2.005	2.442	0.945	0.942	<0.001
<i>L. lucida</i>					<0.001					0.016
6 wks	-4.812	1.571	0.862	0.859	<0.001	-3.147	1.692	0.332	0.322	<0.001
1 yr	-4.506	1.678	0.736	0.729	<0.001	-2.122	2.680	0.809	0.804	<0.001
8-9 yrs	-7.475	2.444	0.873	0.866	<0.001	-1.741	2.374	0.898	0.892	<0.001
20-21 yrs	-5.571	1.971	0.602	0.589	<0.001	-1.186	1.863	0.746	0.738	<0.001
<i>Q. chapmanii</i>					<0.001					0.928
6 wks	-5.329	1.946	0.848	0.846	<0.001	-2.397	2.757	0.581	0.575	<0.001
1 yr	-6.369	2.272	0.889	0.885	<0.001	-2.190	2.705	0.851	0.846	<0.001
8-9 yrs	-7.495	2.640	0.785	0.773	<0.001	-1.920	2.536	0.945	0.942	<0.001
20-21 yrs	-8.250	2.774	0.923	0.920	<0.001	-2.186	2.654	0.916	0.912	<0.001
<i>Q. geminata</i>					<0.001					0.502
6 wks	-4.076	1.501	0.723	0.718	<0.001	-2.773	3.157	0.618	0.611	<0.001
1 yr	-5.566	2.261	0.898	0.895	<0.001	-1.892	2.628	0.859	0.855	<0.001
8-9 yrs	-5.715	2.224	0.697	0.685	<0.001	-2.412	2.701	0.874	0.869	<0.001
20-21 yrs	-6.575	2.421	0.785	0.777	<0.001	-2.624	2.879	0.883	0.878	<0.001
<i>Q. inopina</i>					<0.001					0.560
6 wks	-3.867	1.465	0.738	0.736	<0.001	-2.071	2.723	0.542	0.539	<0.001
1 yr	-5.017	1.826	0.864	0.862	<0.001	-1.910	2.599	0.836	0.834	<0.001
8-9 yrs	-6.694	2.457	0.923	0.921	<0.001	-2.521	2.817	0.918	0.916	<0.001
20-21 yrs	-6.116	2.321	0.922	0.920	<0.001	-2.435	2.862	0.940	0.938	<0.001

Table 3-9. Results of regressions analyses for palmettos *S. etonia* (left side; \ln total biomass = $\alpha + \beta_1$ * independent variable) and *S. repens* (right side; $\sqrt{\text{total biomass}} = \alpha + \beta_1$ * independent variable) at each time since fire.

	<i>S. etonia</i>					<i>S. repens</i>				
	α	β_1	R^2	Adj R^2	p	α	β_1	R^2	Adj R^2	p
Length										
6 wks	1.414	0.0308	0.792	0.740	0.018	-2.410	0.154	0.711	0.663	0.009
1-2 yrs	1.931	0.0261	0.853	0.837	<0.001	-0.603	0.167	0.834	0.823	<0.001
8-10 yrs	1.386	0.0307	0.945	0.940	<0.001	-2.391	0.168	0.846	0.836	<0.001
22 yrs	-0.552	0.0458	0.953	0.937	0.004	-6.099	0.220	0.832	0.822	<0.001
Width										
6 wks	1.392	0.0476	0.839	0.798	0.010	-0.195	0.211	0.913	0.898	<0.001
1-2 yrs	2.333	0.0290	0.836	0.818	<0.001	-2.715	0.224	0.861	0.852	<0.001
8-10 yrs	1.773	0.0325	0.905	0.895	<0.001	-0.201	0.170	0.856	0.847	<0.001
22 yrs	1.189	0.0444	0.808	0.744	0.038	-4.139	0.227	0.852	0.842	<0.001
Height										
6 wks	0.798	0.0457	0.871	0.838	0.007	-1.275	0.141	0.875	0.854	<0.001
1-2 yrs	0.547	0.0606	0.870	0.855	<0.001	-8.632	0.323	0.881	0.873	<0.001
8-10 yrs	0.506	0.0625	0.694	0.663	<0.001	-3.637	0.254	0.850	0.841	<0.001
22 yrs	1.468	0.0521	0.787	0.716	0.045	-5.221	0.280	0.806	0.794	<0.001
# of leaves										
6 wks	2.007	1.143	0.409	0.261	0.171	0.263	3.227	0.636	0.575	0.018
1-2 yrs	1.525	0.958	0.702	0.669	0.001	-0.680	2.130	0.743	0.727	<0.001
8-10 yrs	1.536	0.846	0.764	0.740	<0.001	-0.624	1.874	0.852	0.842	<0.001
22 yrs	2.850	0.652	0.983	0.977	<0.001	-2.667	2.128	0.933	0.929	<0.001

Table 3-10. Allometric equations predicting total stem biomass for shrub species overall and at each time since fire; In total biomass = $\alpha + \beta_1 * \ln \text{diameter} + \beta_2 * \ln \text{height}$; n.s. indicates that the corresponding independent variable was not significant in the multiple regression model.

Species	N	α	β_1	β_2	MSE	R ²	Adj R ²	p
<i>L. fruticosa</i>	119	-4.904	1.424	1.260	0.372	0.938	0.937	<0.001
6 wks	48	-5.454	1.176	1.474	0.168	0.927	0.923	<0.001
1 yr	29	-3.632	1.541	0.954	0.185	0.929	0.923	<0.001
8-9 yrs	21	-3.436	1.622	0.802	0.097	0.964	0.960	<0.001
20-21 yrs	21	-2.055	2.442	n.s.	0.241	0.945	0.942	<0.001
<i>L. lucida</i>	164	-5.176	0.868	1.531	0.205	0.944	0.943	<0.001
6 wks	69	-4.926	0.590	1.416	0.125	0.897	0.894	<0.001
1 yr	43	-3.483	1.764	0.752	0.209	0.862	0.855	<0.001
8-9 yrs	20	-4.607	1.402	1.138	0.098	0.936	0.929	<0.001
20-21 yrs	32	-3.593	1.347	0.985	0.157	0.816	0.803	<0.001
<i>Q. chapmanii</i>	144	-4.873	1.351	1.327	0.125	0.959	0.959	<0.001
6 wks	66	-5.144	1.063	1.549	0.138	0.899	0.896	<0.001
1 yr	33	-5.045	1.337	1.371	0.068	0.957	0.954	<0.001
8-9 yrs	21	-3.699	2.015	0.710	0.100	0.962	0.958	<0.001
20-21 yrs	24	-5.792	1.374	1.522	0.093	0.980	0.978	<0.001
<i>Q. geminata</i>	146	-3.947	1.629	0.985	0.266	0.925	0.923	<0.001
6 wks	60	-3.956	1.392	1.048	0.395	0.777	0.769	<0.001
1 yr	33	-4.360	1.189	1.388	0.091	0.940	0.936	<0.001
8-9 yrs	27	-4.822	1.966	1.027	0.087	0.958	0.955	<0.001
20-21 yrs	26	-4.144	2.126	0.771	0.223	0.902	0.893	<0.001
<i>Q. inopina</i>	327	-3.891	1.443	1.037	0.168	0.945	0.945	<0.001
6 wks	149	-3.964	1.409	1.111	0.173	0.840	0.838	<0.001
1 yr	87	-3.982	1.277	1.077	0.160	0.920	0.918	<0.001
8-9 yrs	43	-4.984	1.419	1.323	0.122	0.960	0.958	<0.001
20-21 yrs	48	-4.304	1.663	1.060	0.104	0.967	0.966	<0.001

Table 3-11. Allometric equations predicting leaf biomass for shrub species overall and at each time since fire; \ln leaf biomass = $\alpha + \beta_1 * \ln$ diameter + $\beta_2 * \ln$ height; n.s. indicates that the corresponding independent variable was not significant in the multiple regression model.

Species	α	β_1	β_2	MSE	R ²	Adj R ²	p
<i>L. fruticosa</i>	-5.421	0.745	1.485	0.669	0.877	0.875	<0.001
6 wks	-6.465	1.103	1.722	0.369	0.880	0.874	<0.001
1 yr	-3.741	1.408	0.931	0.261	0.892	0.884	<0.001
8-9 yrs	-1.279	1.635	n.s.	0.187	0.844	0.836	<0.001
20-21 yrs	-2.345	2.099	n.s.	0.432	0.877	0.870	<0.001
<i>L. lucida</i>	-5.590	0.521	1.643	0.406	0.981	0.889	<0.001
6 wks	-5.427	n.s.	1.668	0.229	0.834	0.832	<0.001
1 yr	-3.631	1.692	0.718	0.345	0.776	0.765	<0.001
8-9 yrs	-2.441	2.370	n.s.	0.689	0.654	0.635	<0.001
20-21 yrs	-4.390	0.835	1.186	0.313	0.625	0.599	<0.001
<i>Q. chapmanii</i>	-4.784	0.934	1.280	0.311	0.871	0.869	<0.001
6 wks	-5.456	0.906	1.609	0.206	0.855	0.850	<0.001
1 yr	-5.816	1.100	1.518	0.152	0.907	0.900	<0.001
8-9 yrs	-1.920	2.031	n.s.	0.251	0.858	0.851	<0.001
20-21 yrs	-6.320	0.997	1.557	0.465	0.885	0.874	<0.001
<i>Q. geminata</i>	-4.176	1.019	1.097	0.583	0.802	0.800	<0.001
6 wks	-4.475	1.070	1.235	0.581	0.718	0.708	<0.001
1 yr	-4.714	0.791	1.514	0.177	0.872	0.863	<0.001
8-9 yrs	-5.134	1.498	1.045	0.299	0.828	0.814	<0.001
20-21 yrs	-3.250	2.659	n.s.	0.852	0.658	0.644	<0.001
<i>Q. inopina</i>	-3.816	0.805	1.077	0.381	0.828	0.827	<0.001
6 wks	-4.154	1.385	1.124	0.207	0.815	0.812	<0.001
1 yr	-4.235	1.041	1.064	0.401	0.793	0.788	<0.001
8-9 yrs	-6.427	n.s.	2.080	0.630	0.756	0.750	<0.001
20-21 yrs	-4.398	0.903	1.194	0.262	0.881	0.876	<0.001

Table 3-12. Allometric equations predicting total leaf biomass for palmetto species overall and at each time since fire; for *S. etonia* \ln total biomass = $\alpha + \beta_1 * \text{length} + \beta_2 * \text{width} + \beta_3 * \text{height} + \beta_4 * \text{number of leaves}$; for *S. repens* $\sqrt{\text{total biomass}} = \alpha + \beta_1 * \text{length} + \beta_2 * \text{width} + \beta_3 * \text{height} + \beta_4 * \text{number of leaves}$; n.s. indicates that the corresponding independent variable was not significant in the multiple regression model; n.a. indicates that the corresponding independent variable was not included in the multiple regression model; equations with all predictors and only significant predictors are both shown if the difference in R^2 is greater than 0.01.

	N	α	β_1	β_2	β_3	β_4	MSE	R^2	Adj R^2	P
<i>S. etonia</i>	34	1.083	0.0154	0.00639	0.0157	0.155	0.147	0.936	0.928	<0.001
		1.110	0.0248	n.s.	0.0137	n.s.	0.168	0.922	0.917	<0.001
6 wks**	6	0.618	0.0202	0.0138	0.00459	0.414	0.010	0.998	0.989	0.070
1-2 yrs**	11	0.812	-0.00486	0.0116	0.0435	0.149	0.214	0.910	0.849	0.003
8-10 yrs	12	1.386	0.0307	n.s.	n.s.	n.s.	0.188	0.945	0.940	<0.001
22 yrs^	5	-0.302	0.0320	n.a.	0.0181	0.0397	0.0013	1	0.999	0.024
		-0.552	0.0458	n.s.	n.s.	n.s.	0.059	0.953	0.937	0.004
<i>S. repens</i>	62	-5.088	0.058	n.s.	0.103	0.901	2.378	0.960	0.958	<0.001
6 wks	8	-2.823	0.0153	-0.00781	0.0989	1.654	0.576	0.974	0.939	0.011
		-1.275	n.s.	n.s.	0.141	n.s.	1.369	0.875	0.854	<0.001
1-2 yrs	18	-7.541	0.075	n.s.	0.167	0.428	1.147	0.978	0.973	<0.001
8-10 yrs	18	-3.311	n.s.	0.0652	0.0874	0.773	1.412	0.972	0.966	<0.001
22 yrs	18	-5.404	n.s.	n.s.	0.106	1.524	2.410	0.974	0.970	<0.001

** no field measures were significant predictors of biomass in multiple regression with all predictors

^ only three of four predictive factor included

Table 3-13. Allometric equations predicting leaf lamina biomass for palmetto species overall and at each time since fire; for *S. etonia* \ln lamina biomass = $\alpha + \beta_1 * \text{length} + \beta_2 * \text{width} + \beta_3 * \text{height} + \beta_4 * \text{number of leaves}$; for *S. repens* $\sqrt{\text{lamina biomass}} = \alpha + \beta_1 * \text{length} + \beta_2 * \text{width} + \beta_3 * \text{height} + \beta_4 * \text{number of leaves}$; n.s. indicates that the corresponding independent variable was not significant in the multiple regression model; n.a. indicates that the corresponding independent variable was not included in the multiple regression model; equations with all predictors and only significant predictors are both shown if the difference in R^2 is greater than 0.01.

	α	β_1	β_2	β_3	β_4	MSE	R^2	Adj R^2	p
<i>S. etonia</i>	1.114	0.0239	n.s.	0.0131	n.s.	0.164	0.918	0.913	<0.001
6 wks	0.657	0.0186	0.0147	0.00539	0.360	0.0044	0.999	0.995	0.047
	1.420	0.0298	n.s.	n.s.	n.s.	0.239	0.789	0.736	0.018
1-2 yrs**	0.854	-0.00322	0.0107	0.0404	0.135	0.213	0.905	0.841	0.003
8-10 yrs	1.330	0.0298	n.s.	n.s.	n.s.	0.195	0.940	0.934	<0.001
22 yrs^	-0.436	0.032	n.a.	0.0191	n.s.	0.0003	1	1	<0.001
<i>S. repens</i>	-3.819	0.0527	n.s.	0.0861	0.746	2.049	0.953	0.951	<0.001
6 wks	-2.443	0.0127	0.00121	0.0887	1.513	0.513	0.973	0.937	0.011
	-1.064	n.s.	n.s.	0.132	n.s.	1.253	0.869	0.847	<0.001
1-2 yrs	-5.922	0.060	n.s.	0.151	0.367	1.090	0.971	0.965	<0.001
8-10 yrs	-2.322	n.s.	0.0574	0.0662	0.720	1.017	0.973	0.967	<0.001
22 yrs	-4.067	n.s.	n.s.	0.0819	1.341	2.137	0.968	0.963	<0.001

** no field measures were significant predictors of biomass in multiple regression with all predictors

^ only three of four predictive factor included

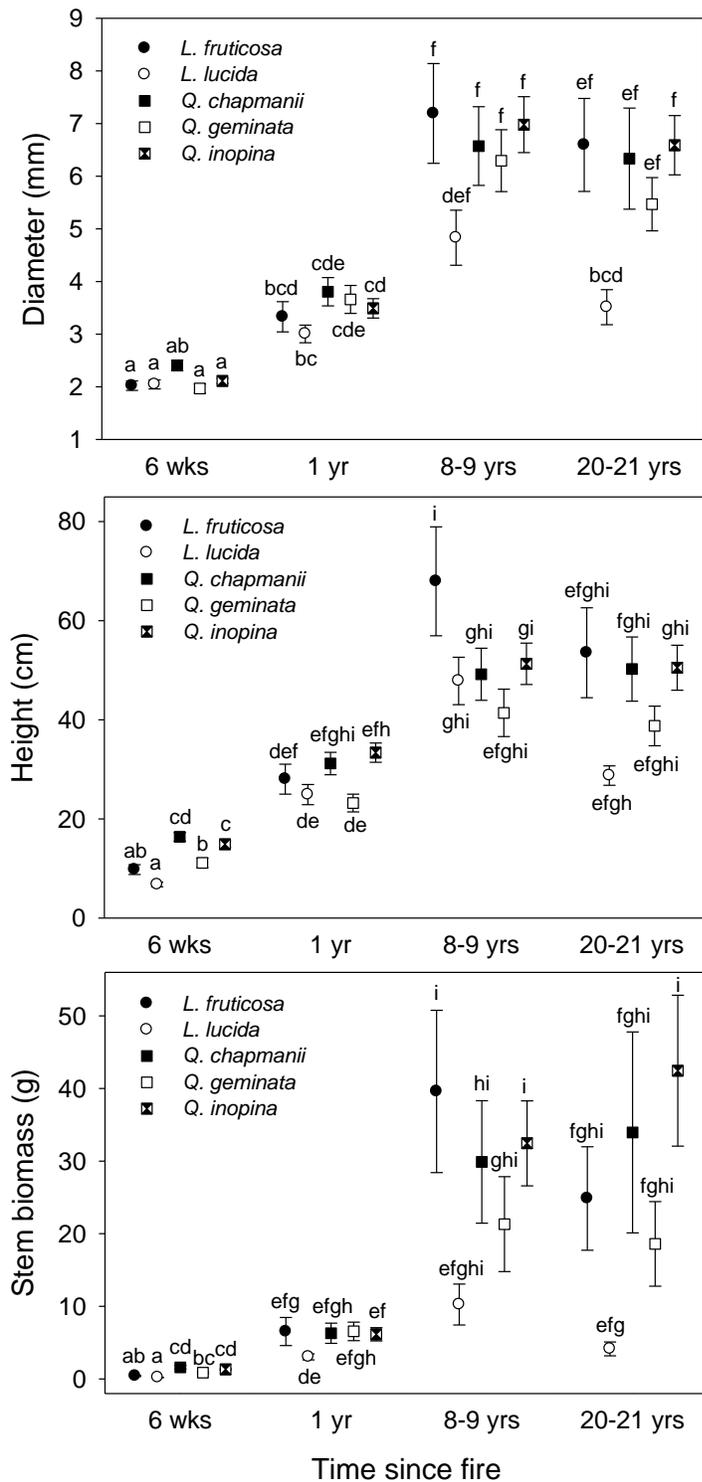


Figure 3-1. Mean (\pm se) diameter (top panel), height (middle panel), and total stem biomass (bottom panel) of shrub species at each time since fire. Different letters represent significantly different means.

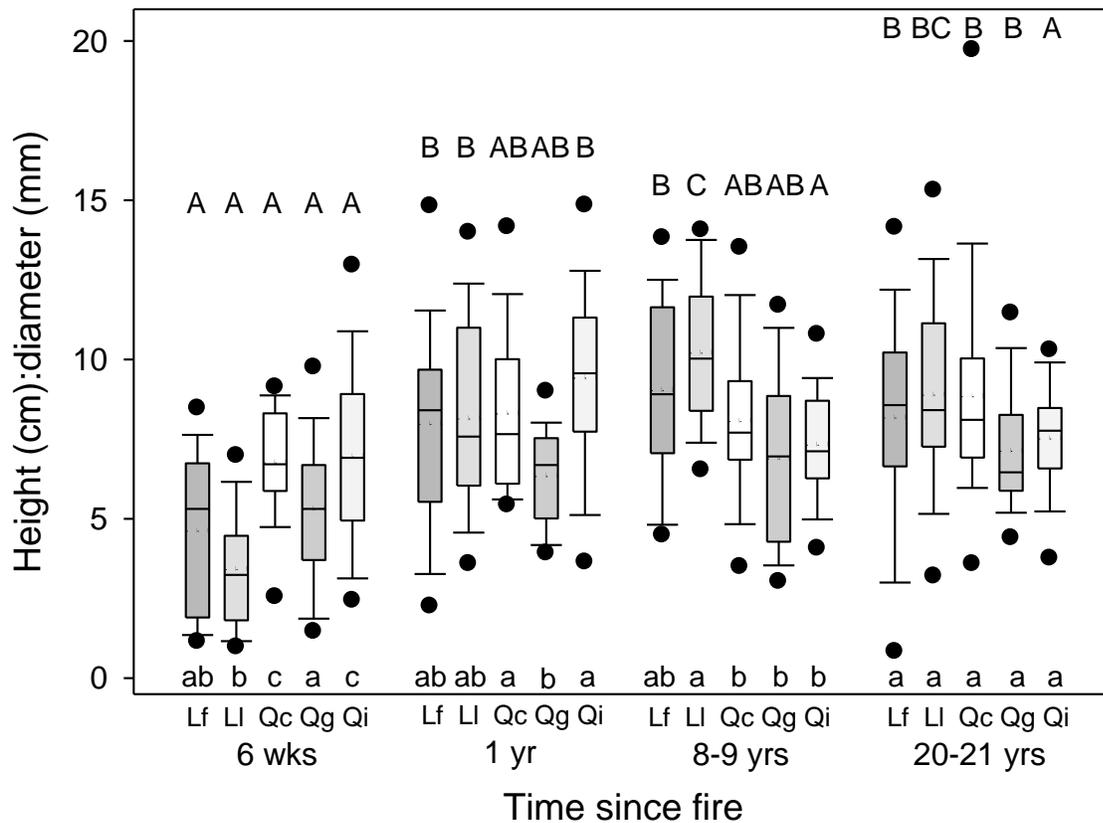


Figure 3-2. Grouped boxplots of height (cm):diameter (mm) ratios of shrub species at each time since fire. The lower and upper bars of the boxplot represent the 25th and 75th percentiles, respectively; the solid middle bar represents the median and the dotted bar represents the mean. The lower and upper “whiskers” show the largest and smallest values that are not outliers. The circles show the 5th and 95th percentiles; outliers are not shown. Different lowercase letters below the boxplots indicate significant differences among species within each time since fire. Different uppercase letters above the boxplots indicate significant differences among times since fire within a species.

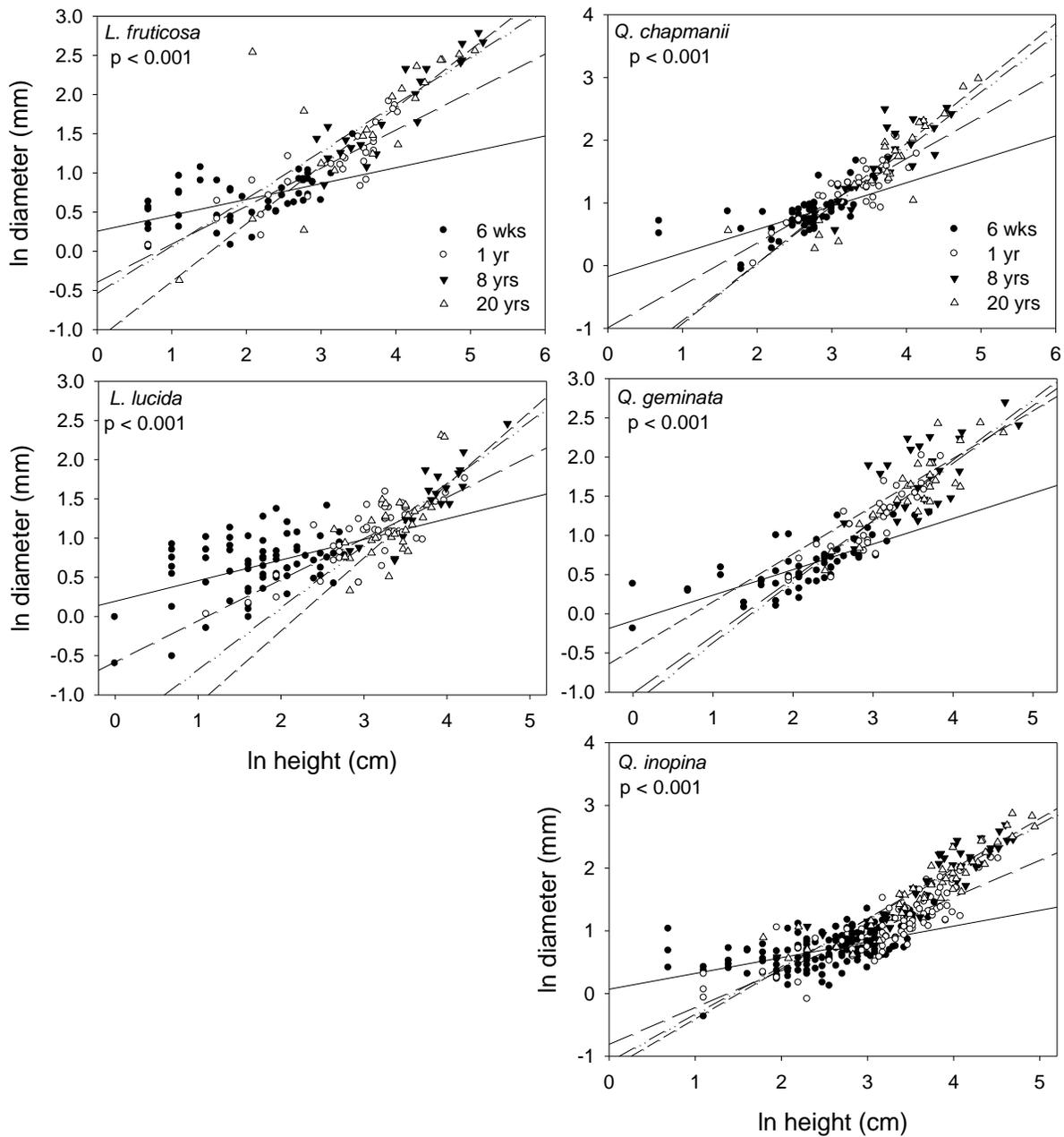


Figure 3-3. Relationship between height and diameter (both natural log transformed) for all shrub species at each time since fire. p values < 0.05 indicate that regression slopes are not homogeneous.

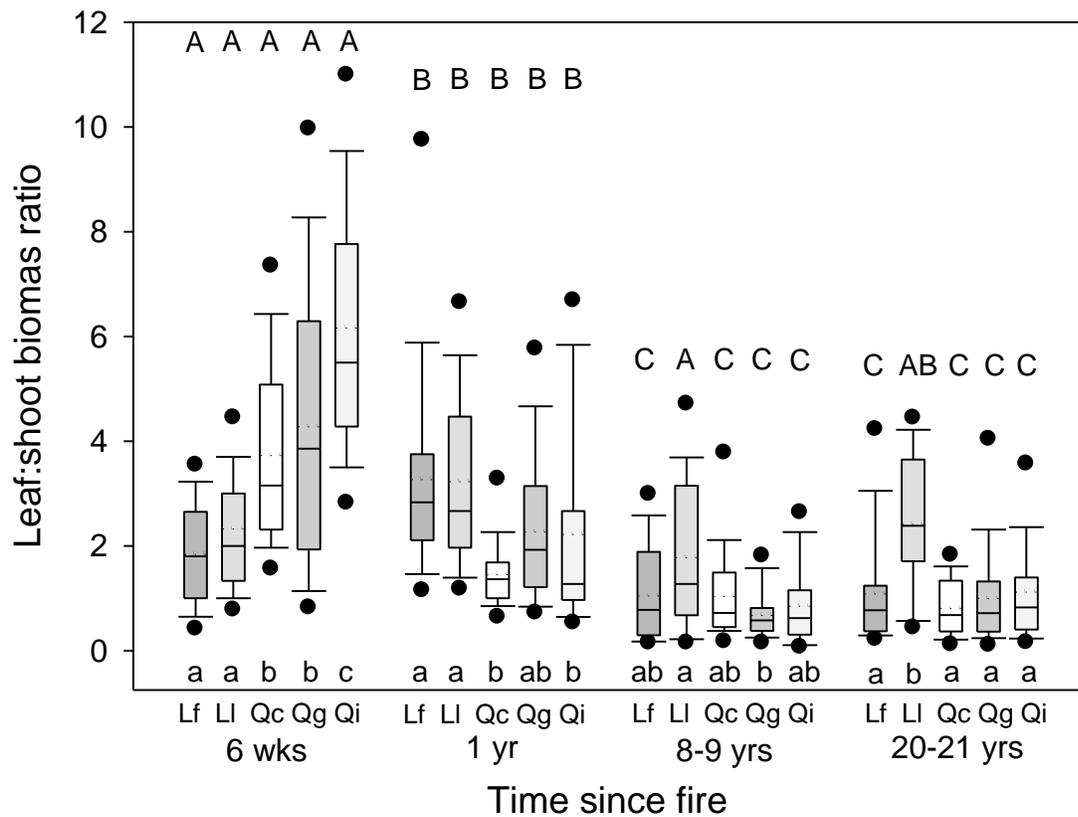


Figure 3-4. Grouped boxplots of leaf:shoot biomass ratios of shrub species at each time since fire. Specifics of the boxplots are the same as in Figure 3-2. Different letters represent significant differences. Different lowercase letters below the boxplots indicate significant differences among species within each time since fire. Different uppercase letters above the boxplots indicate significant differences among times since fire within a species.

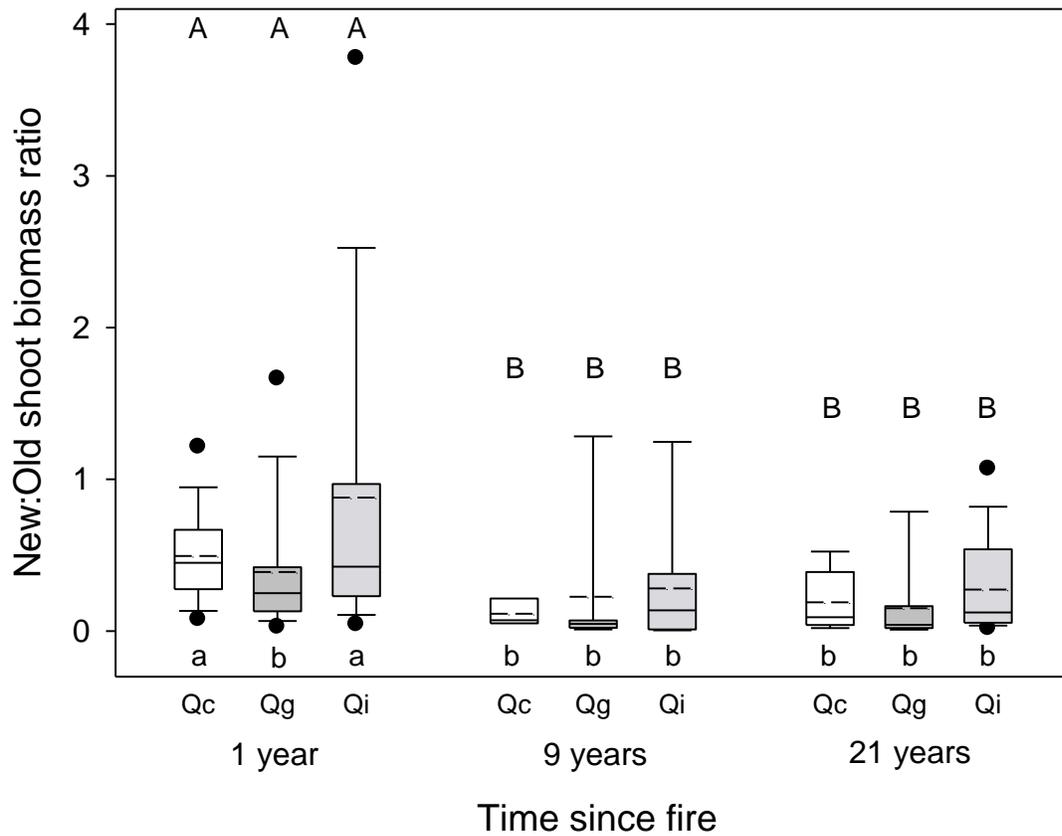


Figure 3-5. Grouped boxplots of new:old shoot biomass ratios of oak species at each time since fire. Specifics of the boxplots are the same as in Figure 3-2. Different letters represent significant differences. Different lowercase letters below the boxplots indicate significant differences among species within each time since fire. Different uppercase letters above the boxplots indicate significant differences among times since fire within a species.

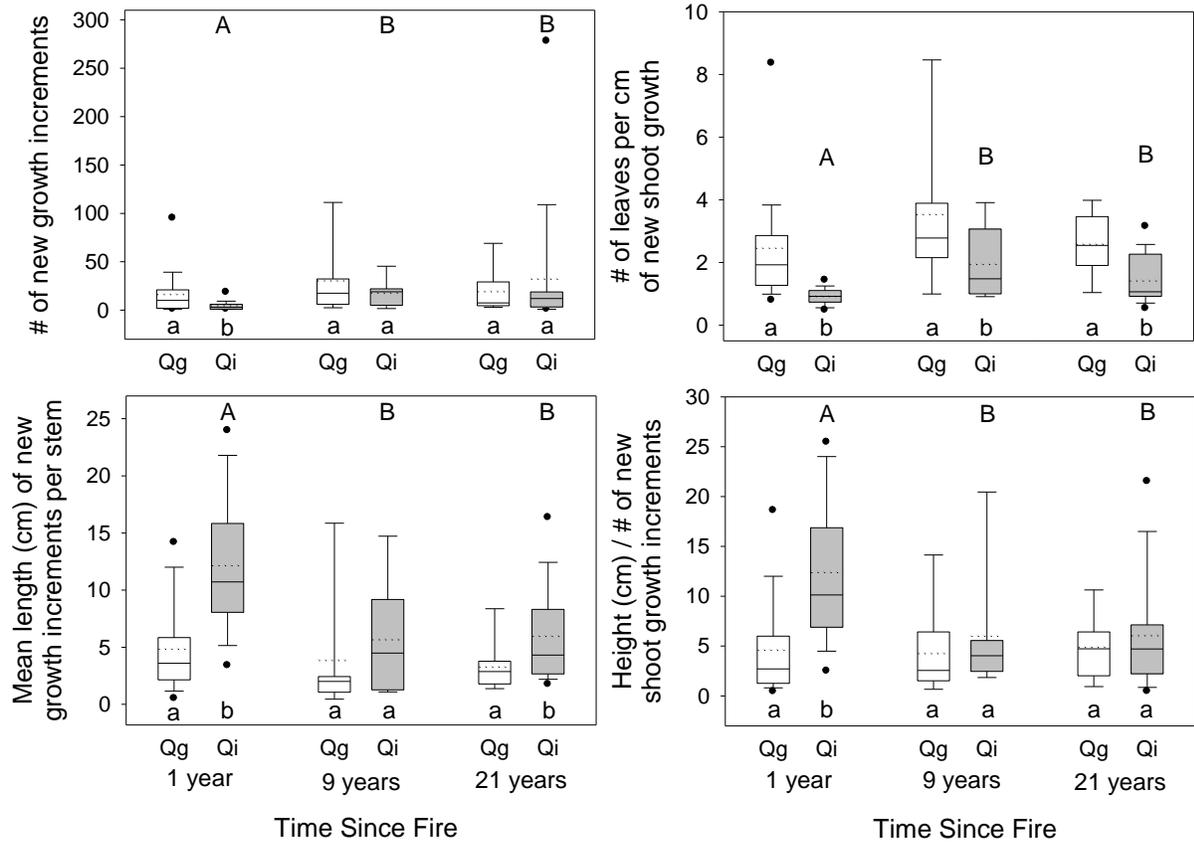


Figure 3-6. Grouped boxplots of the number of new apical shoot growth increments, mean length of new apical shoot growth increments per stem, number of leaves per cm of new shoot growth, and the ratio of height to the number of new apical shoot growth increments of *Q. geminata* and *Q. inopina* at each time since fire. Specifics of the boxplots are the same as in Figure 3-2. Different lowercase letters below the boxplots indicate significant differences between *Q. geminata* and *Q. inopina* within each time since fire. Different uppercase letters above the boxplots indicate significant differences among times since fire for *Q. inopina*.

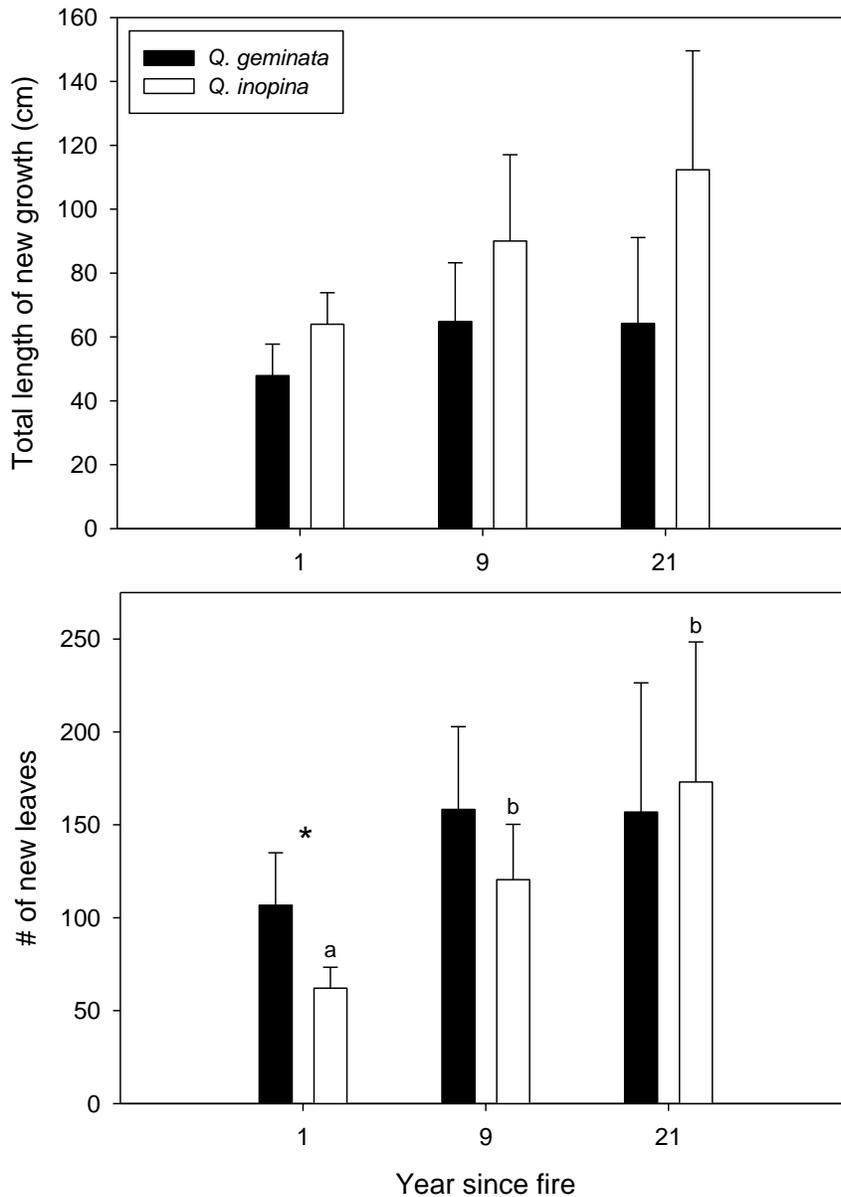


Figure 3-7. Mean (+ se) total length of new apical shoot growth (top panel) and total number of new leaves (bottom panel) for *Q. geminata* and *Q. inopina* at each time since fire. Different letters represent significantly different means within a species. * indicates a significant difference between species.

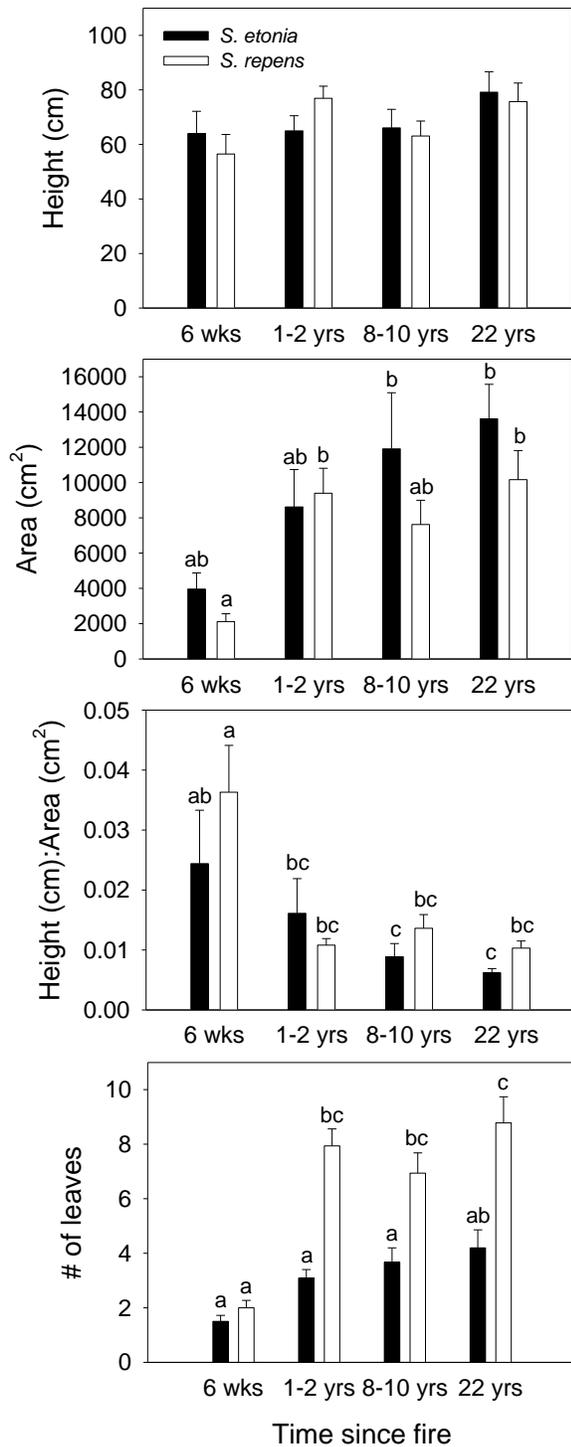


Figure 3-8. Mean (+ se) height, area, height(cm):area(cm²) ratio, and number of leaves of palmettos at each time since fire. Different letters represent significantly different means.

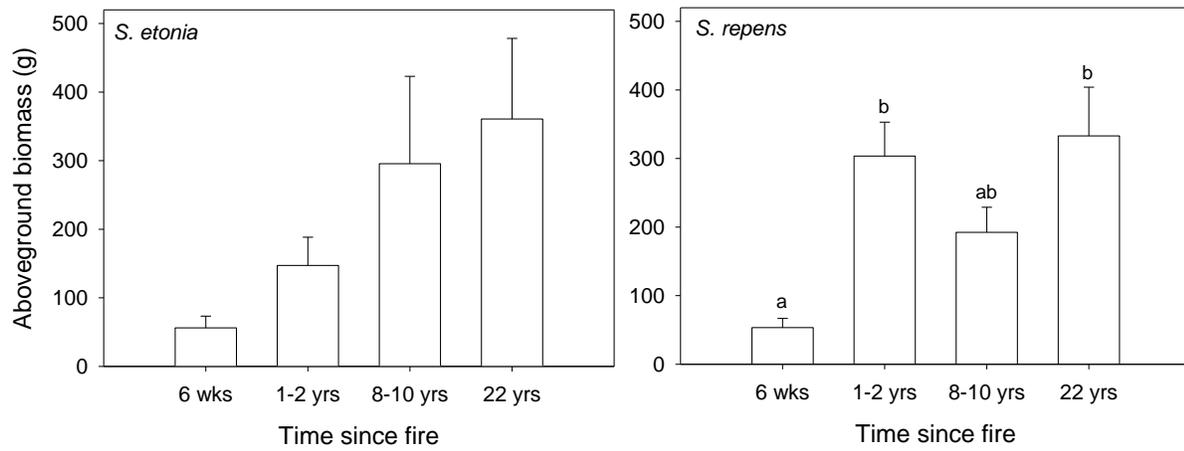


Figure 3-9. Mean (+ se) total aboveground biomass of *S. etonia* (left panel) and *S. repens* (right panel) at each time since fire. Different letters represent significantly different means.

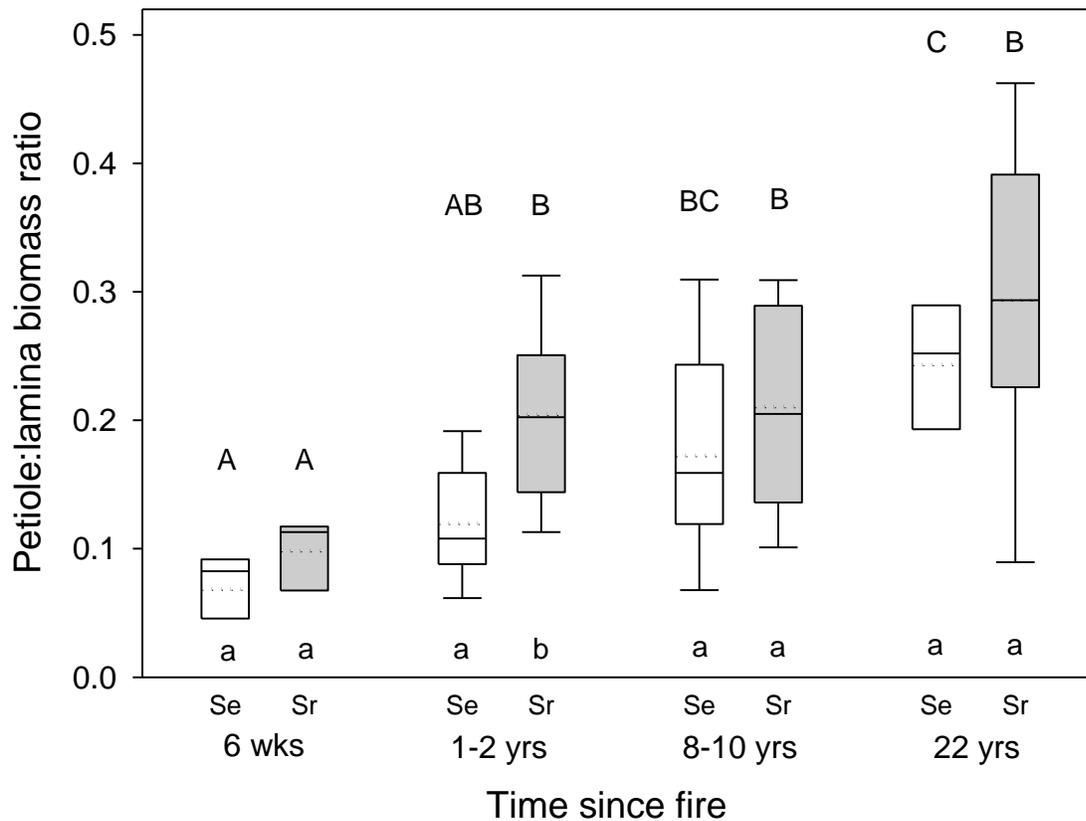


Figure 3-10. Grouped boxplots of petiole:lamina biomass ratios of palmettos at each time since fire. The lower and upper bars of the boxplot represent the 25th and 75th percentiles, respectively; the solid middle bar represents the median and the dotted bar represents the mean. The lower and upper “whiskers” show the largest and smallest values that are not outliers; outliers are not shown. Different lowercase letters below the boxplots indicate significant differences between *S. etonia* and *S. repens* within each time since fire. Different uppercase letters above the boxplots indicate significant differences among times since fire within a species.

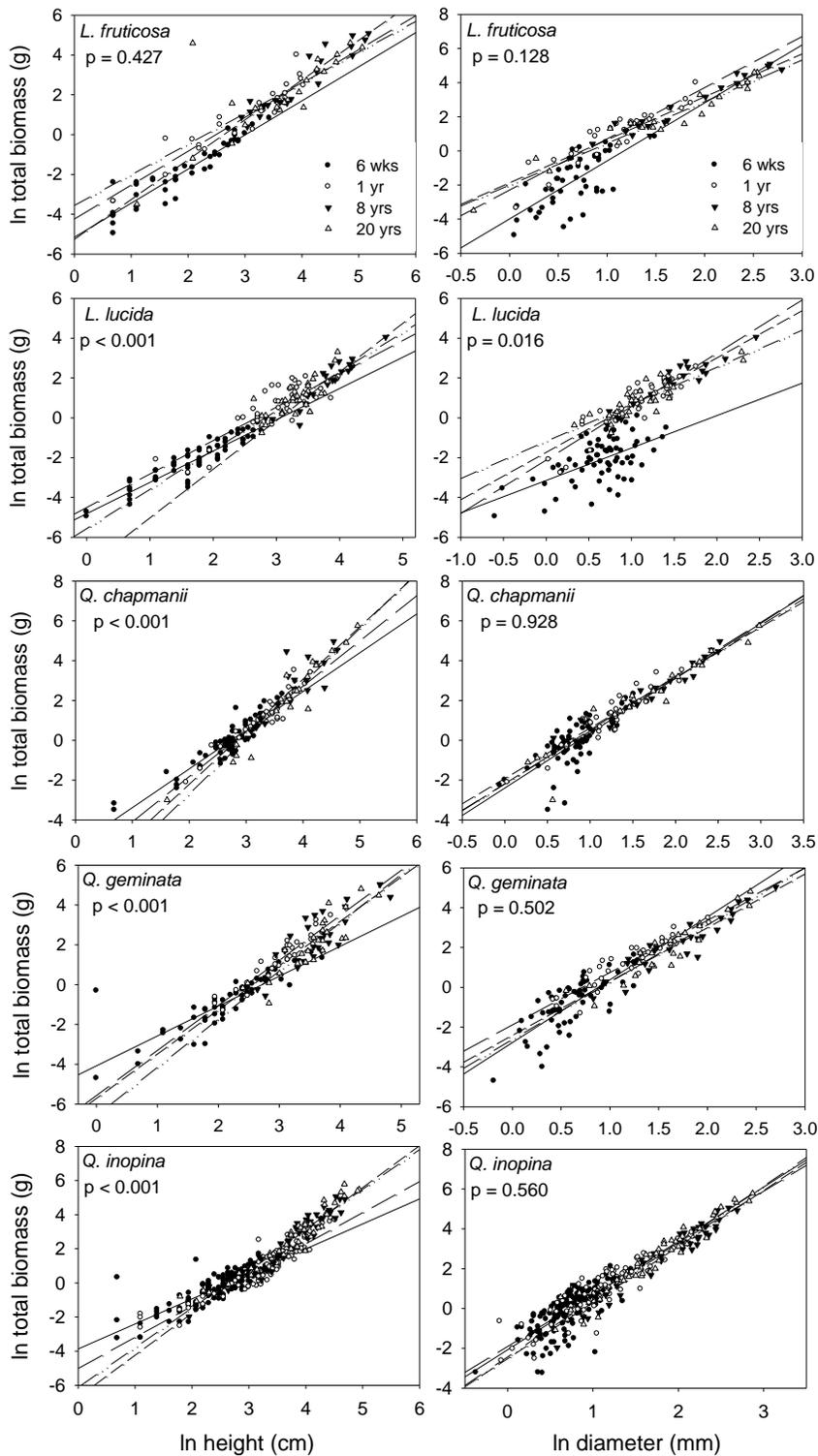


Figure 3-11. Relationships between height and total stem biomass (left panels; both natural log transformed) and between diameter and total stem biomass (right panels; both natural log transformed) for all shrub species at each time since fire; p values < 0.05 indicate that regression slopes are not homogeneous.

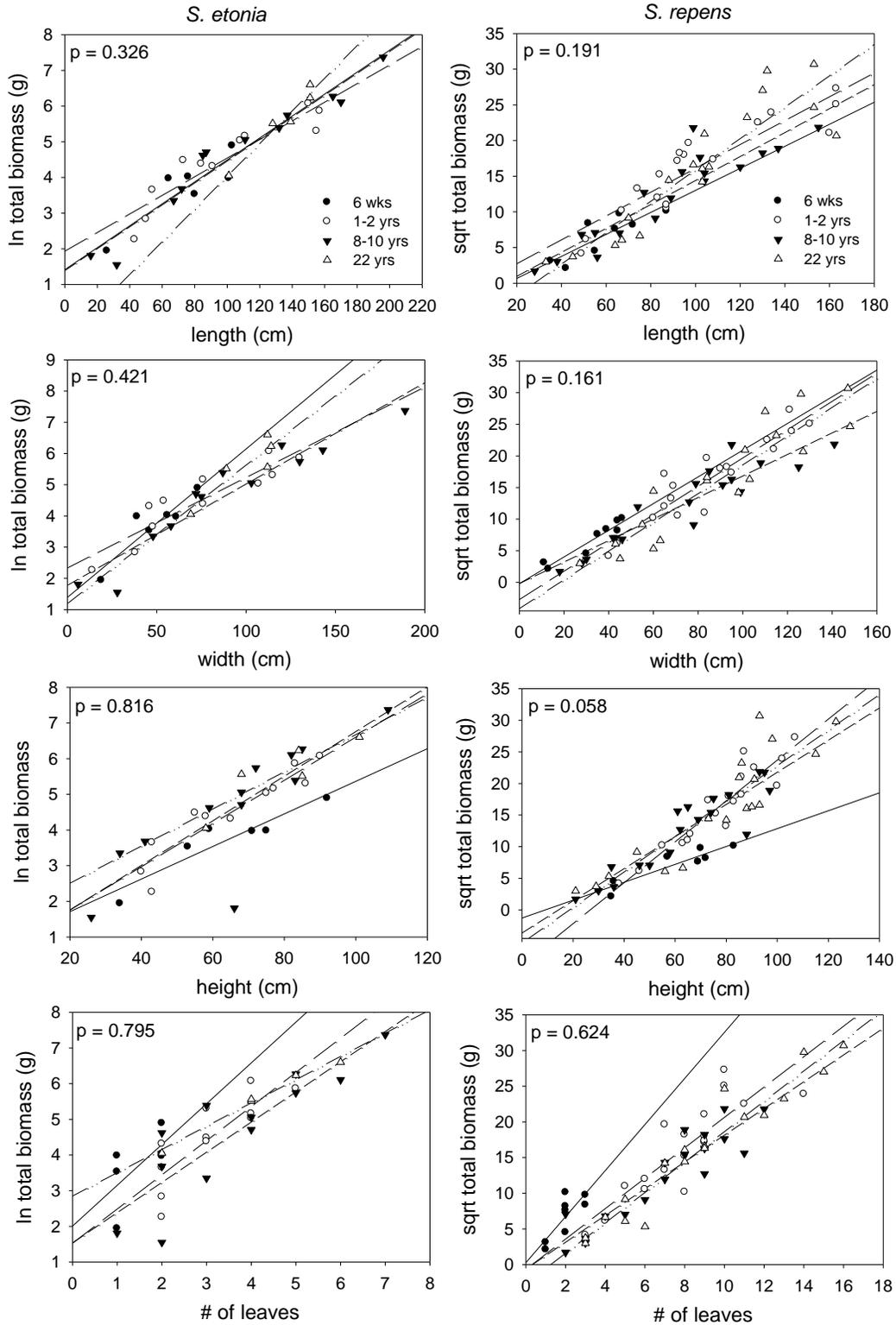


Figure 3-12. Relationships between length, width, height, and number of leaves versus total biomass for *S. etonia* (left panels) and *S. repens* (right panels); p values > 0.05 indicate that regression slopes are homogeneous.

CHAPTER 4 SOIL NUTRIENT DYNAMICS ALONG A TIME SINCE FIRE CHRONOSEQUENCE IN SCRUBBY FLATWOODS

Introduction

Nitrogen (N) and phosphorus (P) are essential plant nutrients that limit plant growth in most, if not all, terrestrial ecosystems (Vitousek and Howarth 1991). Fire, a natural disturbance in many ecosystems, consumes plant biomass, litter, and soil organic matter, converting organically bound N and P into inorganic forms (Certini 2005) that may be lost to the atmosphere or returned to the ecosystem in ash. 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). Fire rapidly mineralizes P in soil organic matter, often resulting in enhanced P availability after fire (e.g. Lewis 1974; Wilbur and Christensen 1983; Adams et al. 1994; Giardina et al. 2000). Although N availability often increases after fire (e.g. Wilbur and Christensen 1983; Covington and Sackett 1992; Schmidt and Stewart 1997; Wan et al. 2001; Smithwick et al. 2005a; Turner et al. 2007), N may be relatively less available than P after fire (Chapter 1) because 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). Over the long-term, P in ash may become relatively less available as it is immobilized by plants and microbes or fixed via geochemical reactions, while N may increase as N inputs accumulate (Carter and Foster 2004).

Previous studies, however, have not found consistent patterns in N and P availability across time after fire chronosequences. Ammonium (NH_4^+), nitrate (NO_3^-), and/or available P may increase (MacKenzie et al. 2004; Durán et al. 2008) or decrease

with time after fire (Marion and Black 1998; Wan et al. 2001; DeLuca et al. 2002; Bloom and Mallik 2006; MacKenzie and DeLuca 2006; Durán et al. 2008), and total soil N increases (MacKenzie et al. 2004; Pérez et al. 2004; Yermakov and Rothstein 2006) or does not change (Wan et al. 2001; Bond-Lamberty et al. 2006) with time after fire, causing soil N:P ratios to increase (Bloom and Mallik 2006; Lagerström et al. 2009) or decrease with time after fire (Durán et al. 2008; Durán et al. 2009). Variation in patterns of N and P availability with time after fire may be due to differences in the fundamental ecosystem components that control nutrient availability or differences in fire intensity. Nitrogen availability is controlled by mineralization and nitrification rates, which are positively correlated with soil %N (Marion and Black 1988; Evans et al. 1998; Frank 2008) and may increase or decrease with time after fire (Pérez et al. 2004; White et al. 2004; MacKenzie et al. 2006; Yermakov and Rothstein 2006). Microbial biomass, soil temperature, and soil moisture also affect N availability (Smithwick et al. 2005a) and are influenced by fire (Peet et al. 1975; Singh et al. 1991; Weekley et al. 2007; Marcos et al. 2009). Phosphorus availability is affected by soil pH (Jaggi et al. 2005), and ash on the soil surface after fire may increase soil pH (Grogan et al. 2000; Badía and Martí 2003; Molina et al. 2007). An increase in soil pH concomitant with high concentrations of calcium (Ca^{2+}) in ash (Ewel et al. 1981; Kauffman et al. 1993) may lead to an increase in calcium phosphate (Hsu and Jackson 1960), thus occluding P made available by fire. High fire intensity causes greater availability of N and P than moderate or low intensity fires (Gimeno-García et al. 2000; Kennard and Gholz 2001; Romanyà et al. 2001). Consideration of the mechanisms causing changes in N and P availability over time after fire is necessary for understanding more general patterns.

Because fire has the potential to alter the relative availability of N versus P both immediately following fire and over inter-fire cycles, fire may cause shifts in N versus P limitation, with recently burned sites being N-limited and long unburned sites being P-limited, particularly in old, highly weathered soils. Fire frequency and intensity varies across ecosystems (Sousa 1984), causing differences in the time frame for changes in N and P availability after fire and in the impacts of fire on the plant community. In many ecosystems, fire frequency and intensity has changed, or is predicted to change, due to the spread of non-native invasive species (e.g. D'Antonio et al. 2000; Stevens and Beckage 2009), human activities (DeWilde and Chapin 2006), and climate change (e.g. Beckage et al. 2003; Flannigan et al. 2005). Understanding how nutrient availability changes over time after fire is particularly important considering that an increase in fire frequency may prohibit accumulation of N over inter-fire cycles and contribute to increased N limitation, whereas a decrease in fire frequency may exacerbate P limitation if P remains stored in plant tissue.

Much of the research investigating changes in nutrient availability with time after fire has been conducted in conifer dominated (e.g. DeLuca et al. 2002; Bloom and Mallik 2006; MacKenzie and DeLuca 2006; Durán et al. 2008) or chaparral (e.g. Christensen and Muller 1975; Marion and Black 1988; Fenn et al. 1993) ecosystems. Scrubby flatwoods are a novel and intriguing ecosystem in which to investigate the effects of fire on nutrient availability for several reasons. First, scrubby flatwoods occur on well-drained, nutrient-poor quartz sand soils (Abrahamson and Hartnett 1990). Because the soil has low clay content and few weatherable minerals, the amount and type of dead organic matter is a primary control on nutrient availability and storage

(Abrahamson and Hartnett 1990). High leaching, due to low clay content, contributes to low amounts of soil organic matter (Gholz and Fisher 1982), except in long unburned sites where litter accumulates. Because nutrient availability is low in scrubby flatwoods, fire related changes in nutrient availability are likely to be detectable from background fluxes in nutrient availability. Second, the dominant species resprout within weeks after fire and may utilize nutrients made available by fire or reallocate nutrients from below- to aboveground tissues (El Omari et al. 2003). Regardless, low background nutrient availability suggests that a post-fire flux in nutrient availability is likely to be an important source of plant nutrition. Third, scrubby flatwoods have been shaped over time by fire and low nutrient availability, yet little is known about nutrient availability, plant productivity, or nutrient limitation. Furthermore, large areas of land that previously supported scrubby flatwoods ecosystems have been converted to agriculture, pastureland, and urban areas, leading to increased nutrient inputs and reduced fire frequency.

My main objective was to determine how soil nutrient availability varies over time after fire. Specifically, I tested the hypotheses that: (1) N availability increases with time after fire, while P availability decreases with time after fire; (2) N pools increase with time after fire; and (3) N-mineralization rates increase with time after fire. Because soil microbes can be killed by fire, I hypothesized that microbial N would increase with time after fire. In addition, I tested the hypotheses that N availability is positively correlated with soil moisture and substrate availability and P availability is positively correlated with soil pH. Furthermore, I investigated differences in soil nutrient availability with depth.

Methods

Study Site

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

My research focused on scrubby flatwoods, a distinctive plant community of Florida scrub. Scrubby flatwoods are dominated by shrubby oaks (Fagaceae), palmettos (Arecaceae), and ericaceous shrubs (Ericaceae). The shrubs are primarily evergreen with an average height of 1-2 m and herbaceous species are sparse (Abrahamson et al. 1984). Scrubby flatwoods experience fire return intervals of 8-16 years (Menges 2007), and the dominant vegetation resprouts after fire (Menges and Kohfeldt 1995). Soils are entisols derived from paleo dunes (Abrahamson et al. 1984) that have no horizon development, little organic matter, and low exchange capacity and base saturation (Brown et al. 1990).

Field and Lab Sampling

In May 2005, I established eighteen 30 x 30 m plots in scrubby flatwoods communities (Abrahamson et al. 1984), three each in sites 1, 4, 6, 8, 10, and 13 years after fire (hereafter called the 1 yr, 4 yr, 6 yr, 8 yr, 10 yr, and 13 yr plots or sites). Within a time after fire, plots were located in different burn units when possible. Plots in the same burn unit were separated by at least 150 m and may have experienced

differences in fire intensity (Table 4-1). Therefore, each plot represents an independent replicate of the time after fire treatment. Overall, plots covered a distance of approximately four miles, and although summer thunderstorms can be patchy, all plots experienced the same climate. All plots were established in scrubby flatwoods dominated by scrub oak (*Quercus inopina* Ashe) on flat or gently sloped sites. Thus, the climate, organisms, relief, and parent material were the same in all sites (Jenny 1941); the only state factor that varied among sites was time after fire. In each plot, I established 30m transects across each plot that were initiated at 5m, 10m, 15m, 20m, and 25m along the NW to SW side of the plot.

In all plots, I used ion exchange resins to measure soil nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}). At a random location on each transect, separate anion and cation exchange resin bags (5 x 5 cm) were placed in the top 5 cm of the soil and left in the field for 3 month intervals. Resin bags were in the field for one year continuously (Mid June – Mid Sept. 2005, Mid Sept. – Mid Dec. 2005, Mid Dec. 2005 – Mid March 2006, and Mid March – Mid June 2006). Before being buried in the field, anion and cation resin bags were charged with 2M HCl and 2M NaCl, respectively. After resin bags were removed from the field, they were rinsed with DI H_2O to remove dirt and any attached roots. Anion and cation resin bags were extracted with 50 mL of 0.5 M HCl and 0.5 M NaCl, respectively and shaken for six hours. Resin extracts were frozen and taken to the University of Florida where NO_3^- , NH_4^+ , and PO_4^{3-} concentrations were determined colorimetrically on a continuous flow autoanalyzer (Astoria-Pacific, Inc., Clackamas, Oregon, USA).

In the two plots within each time after fire with the greatest spatial separation (12 plots total), I collected soil from a random location on each transect and one year later, recorded all species present in the plot (Table 4-2). During June and July 2005, one soil core was taken at each location and divided into 0-5, 5-10, 10-15, and 15-20 cm depths. Within 24 hours of collection, soil samples were passed through a 2 mm sieve; roots remaining in the sieve were separated into < 2 mm and > 2 mm, dried at 60°C and weighed. Soils were sub-sampled for determination of gravimetric soil moisture, pH, total percentages of N and C, soil $\delta^{15}\text{N}$, inorganic and organic N concentration, N mineralization rates, and microbial N. Gravimetric moisture content was determined on samples dried at 105°C for 48 hrs. For soil pH, 10 g of air dried soil was added to 10 mL of deionized water, shaken for 30 sec, 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 hrs, hand ground with a mortar and pestle, and analyzed for percentages of N, C, and $\delta^{15}\text{N}$ 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, Bremen, Germany). Soil bulk density increases with depth in acidic sandy soils (Skylberg et al. 2001); thus, I used the mean bulk density for each depth for each time since fire to calculate N and C pools.

To measure dissolved inorganic and organic N concentrations, 50 mL of 0.5 M K_2SO_4 was added to 10 g of field moist soil, shaken for 30 seconds, and allowed to stand overnight. Solutions were filtered through Whatman #1 filter paper that was pre-leached with 0.5 M K_2SO_4 . Filtered extracts were sub-sampled, frozen, then taken to the

University of Florida. Dissolved inorganic N ($\text{NH}_4^+ + \text{NO}_3^-$) concentrations of one sub-sample were determined colorimetrically on a segmented flow autoanalyzer (Astoria-Pacific, Inc., Clackamas, Oregon, USA). I measured dissolved organic N (DON) on a separate sub-sample of the soil extract using the persulfate oxidation digestion method (Sollins et al. 1999), which converts all N into NO_3^- . I added 5 ml of the oxidizing reagent to 5 ml of the soil extract, then autoclaved the solution at 121°C for 55 minutes. To determine the efficiency of the digestion procedure, an organic and inorganic standard were processed with each batch of samples. The NO_3^- concentration of the digested sample was determined colorimetrically on a continuous flow autoanalyzer. To determine the concentration of DON, I divided the NO_3^- concentration of the digested samples by the digestion efficiency, and then subtracted the DIN measured in the undigested samples.

Field capacity of scrubby flatwood soils was determined by measuring gravimetric moisture content of saturated soils (from sites four and 13 years after fire), and I measured N mineralization rates of soils at field capacity because soils were collected over a one month period with variation in daily precipitation (0 – 50 mm per day). A sub-sample of 10 g of field moist soil was contained in a specimen cup and stored in a refrigerator (~ 4°C) for two days until gravimetric moisture content was determined. An average gravimetric moisture content was determined from all soils within each plot, and the same amount of de-ionized (DI) H_2O was added (169 – 226 μL) to bring the soils to field capacity; for a few samples, when soil moisture was much different than the mean, a lower amount of DI H_2O was added. Specimen cups were then stored in the dark at room temperature (~ 23°C) for one week. After one week, 50

mL of 0.5 M K_2SO_4 was added to the soil, shaken for 30 sec, and allowed to stand overnight. Solutions were filtered, stored, and analyzed for NO_3^- and NH_4^+ as described above. Because cool temperatures ($\sim 4^\circ C$) limit microbial activity, I considered these as seven day incubations. For half of the soil samples (from one plot for each time since fire) a second sub-sample of 10 g of field moist soil was contained in a specimen cup and stored in the dark at room temperature ($\sim 23^\circ C$) for one week. After one week, 50 mL of 0.5 M K_2SO_4 was added to the soil, shaken for 30 sec, and allowed to stand overnight. Solutions were filtered, stored, and analyzed for NO_3^- and NH_4^+ as described above. Net rates of N mineralization, for both samples at field capacity and samples at ambient field moisture conditions, were calculated from the difference in $\mu g N-(NH_4^+ + NO_3^-)$ $g\ soil^{-1}$ of initial and one week extractions.

The fumigation extraction method was used to measure microbial N (Horwath and Paul 1994). A 10 g sample of field moist soil was contained in a glass beaker and fumigated with chloroform in a desiccator for 24 hours. Soil samples were then transferred to a specimen cup, extracted with 50 ml of 0.5M K_2SO_4 , and processed the same as for DIN. Fumigated soil extracts were digested to convert all N to NO_3^- using the same persulfate oxidation digestion used to measure DON. The NO_3^- concentration of the fumigated, digested sample was determined colorimetrically on a continuous flow autoanalyzer. To determine the concentration of chloroform labile microbial N, I divided the NO_3^- concentration of the fumigated samples by the digestion efficiency, then subtracted the DIN and DON measured in unfumigated samples.

Statistical Analyses

I calculated total resin exchangeable nutrients over one year by summing NH_4^+ , NO_3^- , total inorganic N, and PO_4^{3-} over each sample period. Resin exchangeable N:P

ratios were determined from the total inorganic N and total PO_4^{3-} for each site within a plot. Missing values (when a resin bag was found on the soil surface) were replaced with the plot mean for that time period. I averaged values for each plot so that plot was the statistical unit. Data were analyzed with one-way ANOVAs with post-hoc comparisons with Bonferroni confidence interval adjustments. Resin exchangeable NO_3^- and PO_4^{3-} were natural log transformed before analyses. I analyzed the correlation between the total resin extractable N and P over one year using Pearson's partial correlation coefficients, to control for the effects of time since fire, with one-tailed significance tests.

I analyzed differences in soil properties (root biomass (≤ 2 mm diameter), soil pH, soil %C, soil %N, soil C:N, soil C pools, soil N pools, total dissolved inorganic N (DIN), dissolved organic N (DON), DIN:DON, N mineralization with H_2O addition (both $\mu\text{g N} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$ and $\mu\text{g N} \cdot \text{g N}^{-1} \cdot \text{day}^{-1}$), nitrification rates with H_2O addition ($\mu\text{g N} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$), and soil $\delta^{15}\text{N}$) among times since fire separately for each soil depth (0-5, 5-10, 10-15, and 15-20 cm) using a nested ANOVA model with time since fire and plot nested within time since fire as main effects. I used a nested model because variability in soil nutrients can be spatially dependent at a scale of 30 m or less (Blair 2005). Differences among times since fire were determined with pairwise comparisons with Bonferroni confidence interval adjustments. The effects of water addition on N mineralization and nitrification rates were analyzed separately for each time since fire and depth with paired, one-tailed t-tests. Differences in soil properties with depth were determined separately for each time since fire using repeated measures analysis with depth as the within-subjects factor and plot as the between-subjects factor. When the assumptions of

sphericity were not met, the degrees of freedom were adjusted using the Greenhouse-Geisser estimated epsilon values, which is a conservative correction (Field 2009), and differences among dates and times since fire were determined with post-hoc pairwise comparisons with Bonferroni confidence interval adjustments. Data were transformed before analyses to meet the assumption of normality when necessary.

I used separate linear regressions for each depth within each time since fire to analyze the relationship between soil %N and N mineralization rates ($\mu\text{g N} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$). I calculated mean pH per plot of surface soils (0-5 cm), and used linear regression to investigate the relationship between pH of surface soils and resin extractable PO_4^{3-} (resin bags were located in surface soils) for the plots in which both soil pH and resin extractable PO_4^{3-} were measured. I conducted partial correlations between soil variables (%C, %N, C:N, DIN, DON, DIN:DON, chloroform labile microbial N, $\delta^{15}\text{N}$, and pH) for each depth while controlling for the effect of time since fire. I conducted a multiple regression with root biomass at the dependent variable and DIN, DON, and soil %N as independent variables. Root biomass data were square root transformed before analyses. All other data were natural log transformed.

I calculated microbial biomass N using the equation $B_N = F_N / K_{EN}$, where B_N = microbial biomass N, F_N = chloroform labile N, and $K_{EN} = 0.54$, the efficiency of the fumigation (Brookes et al. 1985). I used 0.54 for K_{EN} because this value was determined from K_2SO_4 extractions of a variety of soils (Brookes et al. 1985), and because this value is in the middle of the range of previous estimates of K_{EN} (Shen et al. 1984, Jonasson et al. 1996). I used linear regression to analyze the relationship between microbial biomass N and DON. I conducted a multiple regression with N mineralization

rates with H₂O addition ($\mu\text{g N} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$) as the dependent variable and microbial biomass N, DON, C:N, and %N as independent variables. I conducted a multiple regression with DIN ($\mu\text{g N} \cdot \text{g soil}^{-1}$) as the dependent variable and microbial biomass N, DON, N mineralization, and C:N as independent variables. All variables were natural log transformed before analysis. Data were analyzed using SPSS 11.5.

Results

Species Composition

Composition of resprouting shrubs was similar among plots (Table 4-2). *Lyonia fruticosa*, *Quercus chapmanii*, *Quercus geminata*, *Quercus inopina*, and *Serenoa repens* occurred in all twelve plots, while *Lyonia lucida*, *Palafoxia feayi*, and *Sabal etonia*, were present in eleven plots. The two most common graminoid species, *Aristida beyrichiana* and *Rhynchospora megalocarpa*, were present in 92% and 83% of the plots, respectively. A nitrogen-fixing species was present in all 1 yr, 4 yr, and 6 yr plots; whereas, a nitrogen-fixing species was present in only one 8 yr, 10 yr, and 13 yr plot. Herbaceous species that recruit from seed after fire were sparse in general, but a greater number of the most common species occurred at intermediate times after fire. Lichens did not colonize plots until at least eight years after fire. Pines were found only in plots that had burned once (Table 4-2). Sand pine, *Pinus clausa*, was present in both 13 yr plots and in one 8 yr plot. Species composition of the plots where soil samples were not collected was similar to the other plots of the same time after fire except for the 13 yr plot in burn unit 24A (Table 4-1) where a few *Pinus elliotii* var. *densa* individuals were found.

Root Biomass

Root (≤ 2 mm diameter) biomass ($\text{g} \cdot \text{m}^{-2}$) tended to increase with time after fire in surface soils (0-5 cm) (Table 4-3) and varied with depth in 4 yr, 6 yr, and 8 yr sites (Table 4-4; Table 4-5). In surface soils, root biomass was 3.0 and 2.4 times greater in 13 yr sites than in 4 yr and 6 yr sites, respectively (Figure 4-1). Total root biomass per 20 cm depth ranged from $1938 \text{ g} \cdot \text{m}^{-2}$ in 4 yr sites to $2874 \text{ g} \cdot \text{m}^{-2}$ in 10 yr sites. At all soil depths, soil %N was positively correlated with root biomass (Figure 4-2). Dissolved inorganic and organic N, however, were not significant predictors of root biomass (Table 4-6).

Resin Exchangeable Nutrients

Over one year, resin exchangeable NH_4^+ ($F_{5,12} = 2.28$, $p = 0.112$) and total inorganic N ($F_{5,12} = 2.37$, $p = 0.102$) were highest in 8 yr sites, but did not differ significantly across the time after fire chronosequence. By contrast, resin exchangeable NO_3^- ($F_{5,12} = 6.17$, $p = 0.005$) and PO_4^{3-} ($F_{5,12} = 3.46$, $p = 0.036$) decreased then increased with time after fire (Figure 4-3). Resin exchangeable NO_3^- and PO_4^{3-} were both five times greater in 13 yr than in 6 yr sites. Resin exchangeable N:P ratios increased then decreased with time after fire ($F_{5,12} = 7.82$, $p = 0.002$), and were approximately four times lower in 13 yr sites compared to 6 yr and 8 yr sites (Figure 4-3C). Variation in N:P ratios with time after fire was primarily driven by changes in P. Resin exchangeable N was positively correlated with resin exchangeable P ($r = 0.199$, $p = 0.031$). Mean resin exchangeable PO_4^{3-} over one year was negatively correlated with mean pH of surface soils (Figure 4-4; $r = 0.569$, $p = 0.053$).

Nitrogen Pools and Fluxes

Time after fire had a significant effect on dissolved inorganic N (DIN) only in deep soils (15-20 cm); whereas, dissolved organic N (DON) varied with time after fire in all soils except deep soils (Table 4-3). In deep soils, DIN tended to be higher in recently burned and longer unburned sites than in sites at intermediate times after fire (Figure 4-5D). In surface soils (0-5 cm), DON was 2.2 times greater in 13 yr than in 6 yr sites, and in 5-10 cm soils, DON was 1.5 times greater in 4 yr than 1 yr sites (Figure 4-5E). Across all times since fire, DIN was 2.0 to 2.9 times greater in surface soils (0-5 cm) than in deep soils (Figure 4-5D). Significant differences in DON among depths were not consistent among times after fire, but DON tended to be lowest in the deepest soils (Figure 4-5E). The ratio of DIN:DON did not vary with time after fire (Table 4-4). Across all times after fire and depths, mean DIN ranged from 0.49 to 1.79 $\mu\text{g N} \cdot \text{g soil}^{-1}$, mean DON ranged from 1.22 to 5.21 $\mu\text{g N} \cdot \text{g soil}^{-1}$, and mean DIN:DON was always less than one.

Potential N mineralization rates ($\mu\text{g N g soil}^{-1} \text{ day}^{-1}$) measured in the lab did not vary with time after fire in deeper soils (>5 cm) at field capacity (Table 4-3). In surface soils (0-5 cm), N immobilization occurred in 1 yr sites, while N mineralization occurred at all other times after fire; N mineralization was 2.5 to 55 times greater in 13 yr sites than in other sites (Figure 4-6A). Potential N mineralization tended to be highest in surface soils (Table 4-4; Table 5-5). Soil %N and N mineralization rates per g soil ($\mu\text{g N} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$) were positively correlated in surface soils (0-5 cm) in 4 yr sites ($r = 0.678$, $p = 0.045$) and 13 yr sites ($r = 0.784$, $p = 0.007$), which caused there to be no differences in N mineralization per g N ($\mu\text{g N} \cdot \text{g N}^{-1} \cdot \text{day}^{-1}$) with time after fire in surface soils (Table 4-3) or with depth (Table 4-4; Table 4-5). Similar to N mineralization, nitrification rates

($\mu\text{g NO}_3^- \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$) tended to be highest in surface soils (0-5 cm) (Figure 4-6B). Differences with time after fire, however, were significant at intermediate soil depths (5-10 cm and 10-15 cm) (Table 4-3) and not in surface soils.

The effect of water addition on N mineralization ($\mu\text{g N g soil}^{-1} \text{ day}^{-1}$) and nitrification ($\mu\text{g NO}_3^- \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$) depended on time after fire and soil depth (Figure 4-7). In surface soils (0-5 cm), water addition increased N mineralization in 4 yr and 6 yr sites, and in 5-10 cm soils, water addition increased N mineralization in 6 yr, 8 yr, and 10 yr sites. In deep soils (15-20 cm), water addition caused N immobilization in 1 yr and 4 yr sites (Figure 4-7).

Chloroform labile microbial N (CLMN) was highest in long unburned sites (Table 4-3). In surface soils (0-5 cm), CLMN was 2.3 to 3.0 times greater in 13 yr sites than all other times after fire (Figure 4-5G). CLMN decreased with depth at all times after fire (Table 4-4; Table 4-5), and on average, was 2.5 to 5.6 times greater in surface soils than in deep soils (Figure 4-5G). Across all times after fire and depths, mean CLMN ranged from 0.94 to 16.26 $\mu\text{g N} \cdot \text{g soil}^{-1}$.

Bulk Soil Properties

In surface soils (0-5 cm), soil %C was 2.0 to 3.4 times greater in 13 yr sites than other times after fire (Figure 4-5A), soil %N was 2.5 to 4.5 times greater in 13 yr sites than other times after fire (Figure 4-5B), and soil C:N ratios were 1.29 and 1.36 times greater in 13 yr sites than in 1 yr and 6 yr sites, respectively (Figure 4-5C). Soil %C and %N were significantly higher in surface soils than in deep soils (15-20 cm) at all times after fire, yet soil C:N varied with depth only in 6 yr sites (Table 4-4; Table 4-5). Similar to soil %C and %N, surface soil C pools ($\text{g C} \cdot \text{m}^{-2}$) and N pools ($\text{g N} \cdot \text{m}^{-2}$) were highest in long unburned sites (Table 4-3). Carbon pools were 2.5 and 3.4 times greater in 13 yr

sites than in 8 yr and 6 yr sites, respectively (Figure 4-8A), and N pools were 2.5 times greater in 13 yr sites than in 6 yr sites (Figure 4-8B). Carbon and N pools varied with depth, but these differences were not as strong as or as consistent as differences in soil %C and soil %N because of variation in bulk density (Table 4-4; Table 4-5). Total C pools per 20 cm depth ranged from $1285 \text{ g} \cdot \text{m}^{-2}$ in 6 yr sites to $3729 \text{ g} \cdot \text{m}^{-2}$ in 13 yr sites. Total N pools per 20 cm depth ranged from $45.6 \text{ g} \cdot \text{m}^{-2}$ in 6 yr sites to $93.2 \text{ g} \cdot \text{m}^{-2}$ in 13 yr sites.

Differences in soil pH with time since fire depended on soil depth (Table 4-3) and were most pronounced in the 0-5 cm soil layer where soil pH was approximately 15% greater in 1 yr, 4 yr, 6 yr, and 10 yr sites compared to 13 yr sites (Figure 4-5I). In 1 yr, 4 yr, and 6 yr sites, soil pH was highest in surface (0-5 cm) soils. Differences in soil pH with depth were most pronounced one year after fire, when mean pH was at least 0.44 units greater in surface soils (0-5 cm) than in any other soil depths.

Soil $\delta^{15}\text{N}$ tended to increase then decrease with time after fire for surface (0-5 cm) and 10-15 cm soils (Table 4-3). In surface soils, soil $\delta^{15}\text{N}$ was negative in 1 yr sites and positive at all other times after fire (Figure 4-5H), but was only significantly different between 1 yr and 8 yr sites. At all times after fire, soil $\delta^{15}\text{N}$ was lowest in surface soils (Table 4-4; Table 4-5). Soil $\delta^{15}\text{N}$ was more enriched in 5-10 cm soils than in surface soils, increasing 1.21 to 1.86 ‰ (Figure 4-5H).

Relationships Among Soil Variables

Dissolved organic N (DON) and dissolved inorganic N (DIN) were positively correlated with soil %C and %N (Table 4-7). DON was positively correlated with CLMN (Table 4-7) and microbial biomass N (Figure 4-9) for all soil depths except 5-10 cm. Across soil depths, microbial biomass N was the only consistent predictor of DIN (Table

4-8). In surface soils (0-5 cm), DON was the only significant predictor of N mineralization rates; whereas, in sub-surface soils (5-10 cm), microbial biomass N was the only significant predictor of N mineralization rates (Table 4-9). Soil %N was positively correlated with soil %C, while CLMN was positively correlated with both soil %C and %N. Both soil %N and CLMN were negatively correlated with soil pH (Table 4-7).

Discussion

Over one year, PO_4^{3-} was highest in recently burned and long unburned sites. Total inorganic N was highest at intermediate times after fire, but did not vary significantly. This caused N:P ratios to be greatest at intermediate times after fire and lowest in long unburned sites. In surface soils, soil %C and %N, C and N pools, dissolved organic N (DON), net N mineralization, and chloroform labile microbial N were all highest in long unburned sites.

Effects of Time After Fire on Soil Characteristics and Nutrient Availability

Inorganic N availability, measured as resin exchangeable N or K_2SO_4 extractable N, did not vary significantly with time after fire in scrubby flatwoods. In many ecosystems, post-fire increases in NH_4^+ and NO_3^- persist for only five months or less (Schmidt and Stewart 1997; Jensen et al. 2001; Bennett et al. 2002). In palmetto flatwoods, which contains some of the same species as scrubby flatwoods but has more mesic soils, the post-fire pulse of NH_4^+ persisted for less than three months (Chapter 2). Recovery of aboveground biomass, which occurs within months in scrubby flatwoods, may contribute to short-lived increases in nutrient availability (Hobbs and Schimel 1984). Thus, fire-induced changes in inorganic N availability may not persist for a year after fire. While fire-induced changes in inorganic N availability occur over short time

scales (Chapter 2), fire appears to have little direct effect on differences in N availability over longer time scales in scrubby flatwoods.

Net N immobilization occurred in surface soils (0-5 cm) of recently burned sites. Turner et al. (2007) also measured net N immobilization after fire, which, in their case, may be due to the N deficiency of the site and high quantities of low N wood remaining on the soil surface after fire. An increase in net N mineralization shortly after fire (Hobbs and Schimel 1984; Adams and Attiwill 1991; Kaye and Hart 1998) due to the positive correlation between N mineralization and soil temperature (Wilson et al. 2002) would not have been detected in my lab incubations. Nitrogen mineralization rates ($\mu\text{g N} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$) in surface soils (0-5 cm) were highest in long unburned sites, likely because dissolved organic N (DON) was highest in long unburned sites and mineralization rates were positively correlated with DON (Table 4-9). Higher N mineralization rates in longer unburned sites may also be related to the positive correlation between N mineralization and soil %N (Marion and Black 1988; Carreira et al. 1994). In addition, N mineralization decreases with an increase in fire frequency (Reich et al. 2001), and all of my 13 yr sites have burned only once over the past 35 years.

Similarly to N mineralization, dissolved organic N (DON) and chloroform labile microbial N (CLMN) in surface soils were highest in long unburned sites. DON and CLMN were positively correlated with soil %N and %C, which were also highest in long unburned sites. Furthermore, CLMN was a significant predictor of DON. Fire can kill soil microbes, and the effects of fire on soil temperature decrease with depth (Ewel et al. 1981; Giardina et al. 2000; Jensen et al. 2001), so the effects of fire should be greatest

in surface soils. The lack of a difference in CLMN from one to ten years after fire suggests that fire had limited direct effects on CLMN. In contrast to my results, MacKenzie et al. (2006) found that microbial activity declined with time after fire.

Soil %N and total N pools ($\text{g} \cdot \text{m}^{-2}$) in surface soils (0-5 cm) tended to be greater in recently burned and long unburned sites than in sites at intermediate times after fire. This pattern is likely related to changes in litter quality feedbacks, N inputs, and accumulation of organic matter with time after fire. The first leaves flushed after fire have higher N concentrations than leaves pre-fire (Chapter 2), and incorporation of these leaves to soil organic matter may contribute to high soil %N and N pools in recently burned sites. Both an increase in the recalcitrance of litter and a decrease in photodegradation of litter (Austin and Vivanco 2006), caused by decreased light availability over time, could lead to N accumulation in long unburned sites. Over the short-term, inputs of N through symbiotic N-fixation and rainfall are not high enough to replace the amount of N volatilized in fire (Carter and Foster 2004; Cook 1994), but over longer time intervals, N-fixation can lead to an accumulation of N in the soil (Bormann and Sidle 1990). Soil crusts in Florida scrub have a high N-fixing capacity, which decreases immediately after fire (Hawkes 2003). The abundance of photosynthetic microbes present in soil crusts peaks at intermediate times since fire (10-15 years) in rosemary scrub (Hawkes and Flechtner 2002) and declines in long unburned sites likely because of increased litter cover and light limitation. Non-symbiotic N_2 -fixation increases with time since fire (Pérez et al. 2004), so high N-fixing capacity of soil crusts may contribute to high soil %N and large soil N pools in long unburned sites. In addition, N-

fixing plants, which contribute N inputs to scrubby flatwood soils, occurred across the scrubby flatwoods time after fire chronosequence (Table 4-1).

Soil %N was correlated with soil %C (Table 4-7), suggesting that accumulation of organic matter may regulate N availability and soil N concentrations. Yermakov and Rothstein (2006) found that total soil N increased with time after fire due to an increase in organic soil N with time after fire. In my study, 13 yr scrubby flatwoods sites had more organic matter than any other time after fire (J. Schafer, personal observation). In addition, total soil N may decrease with an increase in fire frequency (DeLuca and Sala 2006; Cech et al. 2008), and all of my 13 yr sites have burned only once over the past 35 years (Table 4-1).

Soil $\delta^{15}\text{N}$ was more enriched at intermediate times since fire compared to recently burned and long unburned sites (Figure 4-5H). This suggests that N losses are greater at intermediate times after fire (Martinelli et al. 1999). Resin exchangeable N was highest at intermediate times after fire, but N availability was not significantly different among times after fire. Fire consumes surface soil layers and volatilizes N, which can leave post-fire soils enriched in ^{15}N (Högberg 1997); however, soils were not enriched in ^{15}N after fire likely because scrubby flatwoods soils generally have little soil organic matter. Fractionation during the transfer of N from mycorrhizal fungi to a host plants results in plant tissue depleted in ^{15}N relative to the N source (Evans 2001; Hobbie and Colpaert 2003).

Soil %C and soil C pools ($\text{g} \cdot \text{m}^{-2}$) followed the same pattern as soil %N and soil N pools; soil %C and C pools were highest in long unburned sites, and tended to be higher in recently burned sites than in sites at intermediate times since fire. Soil %C and

C content are high in recently burned sites likely due to the presence of charcoal, because soil C is positively correlated with charcoal C (MacKenzie et al. 2008). Soil charcoal has a lower C concentration than recently produced charcoal, suggesting that the C content of charcoal decreases over time (Ohlson et al. 2009), and that the contribution of charcoal C to soil %C decreases with time after fire. Carbon accumulation over time after fire (MacKenzie et al. 2004; Vargas et al. 2008) is likely related to litter accumulation, which is positively correlated with canopy cover (Hall et al. 2006), and the transformation of plant material into soil organic matter, which increases over time after fire (Treseder et al. 2004). In fact, total soil C can increase due to an increase in organic soil C with time after fire (Yermakov and Rothstein 2006). Thus, as organic material accumulates in long unburned scrubby flatwoods, soil %C and C content also increase.

In surface soils, soil pH tended to be higher in more recently burned sites than in longer unburned sites. Ash on the soil surface after fire 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). Persistence of high soil pH with time since fire is likely related to persistence of ash in the soil.

Resin exchangeable PO_4^{3-} tended to be higher in recently burned and long unburned sites than intermediate times after fire (Figure 4-3). High PO_4^{3-} availability in recently burned sites is likely due to high concentrations of P in ash post-fire (Wilbur and Christensen 1983; Raison et al. 1985b), since mineral soil PO_4^{3-} is correlated with

ash depth (Rice 1993). Microbial immobilization or plant uptake may contribute to the decrease in resin exchangeable PO_4^{3-} at intermediate times since fire. Furthermore, PO_4^{3-} may become bound in calcium phosphate (Hsu and Jackson 1960; Stephens et al. 2004) due to high concentrations of calcium (Ca^{2+}) in ash (Ewel et al. 1981; Kauffman et al. 1993). There are several explanations for the increase in resin exchangeable PO_4^{3-} in long unburned sites. First, phosphatase activity is highest when plants are fertilized with organic P (DeLucia et al. 1997), and increased phosphatase activity in long unburned sites, which had high amounts of soil organic matter, could increase PO_4^{3-} availability. Second, soil phosphatase activity (Chen et al. 2004) and the quantity and quality of root exudates (Grayston et al. 1996) varies among plant species, and the biggest difference in plant species composition across my time after fire chronosequence was the presence of pines (*Pinus clausa* and *Pinus elliotii*) in long unburned sites. Several *Pinus* species, including *Pinus elliotii*, produce root exudates (Agnihotri and Vaartaja 1969; Fox and Comerford 1990; van Schöll et al. 2006) such as low molecular weight organic acids, which can bind cations covalently linked to P, liberating inorganic P (Jurinak et al. 1986; DeLucia et al. 1997). Third, an increase in the abundance of lichens with time after fire (Menges and Kohfeldt 1995) may affect P availability if lichens differ from other scrubby flatwood species in their effect on soil pH or their production of organic acids. Fourth, fire frequency may have an impact on P availability. Availability of PO_4^{3-} is lower in sites with more frequent fires (Hernández and Hobbie 2008), and 13 yr sites had burned only once in the last 35 years.

Resin exchangeable N was highest in 8 yr sites, while resin exchangeable PO_4^{3-} was higher in recently burned and long unburned sites. Thus, resin exchangeable N:P

ratios increased from one to eight years after fire, then decreased from eight to 13 years after fire. My results suggest that N-limitation may be greater in recently burned and longer unburned sites and that P-limitation may be greater at intermediate times after fire; however, soil N:P ratios have not been used to indicate N limitation, P limitation, or co-limitation by N and P as have foliar N:P ratios (Koerselman and Meuleman 1996; Güsewell 2004). The relationship between soil N:P ratios and nutrient limitation is unclear because foliar N and P concentrations are not always correlated with soil N and P availability (Frank 2008; Litaor et al. 2008).

In many cases, there were differences in soil characteristics and nutrient availability between plots within a time after fire (Table 4-3), suggesting that differences in fire intensity and fire frequency affect nutrient availability. High fire intensity causes greater availability of soil N and P than moderate or low intensity fires (Gimeno-García et al. 2000; Kennard and Gholz 2001; Romanyà et al. 2001), and there may be little difference in soil properties between unburned sites and sites burned by low severity fires (Hatten et al. 2005). Fire intensity is positively correlated with ash depth (Rice 1993) and high intensity fires cause a greater increase in soil pH (Kennard and Gholz 2001), which affects P availability (Jaggi et al. 2005). Furthermore, losses of P may be greater in high intensity fires (Gimeno-García et al. 2000). Fire intensity can be highly variable over distances of only 10 m (Rice 1993), so variation in fire intensity among my plots (Table 4-1) likely contributed to variation in soil nutrients. Nitrogen availability (Hernández and Hobbie 2008) and N mineralization (Reich et al. 2001) decrease with an increase in fire frequency, while nutrient losses increase with an increase in fire frequency (Wanthongchai et al. 2008). Differences in species composition can affect the

nutrient content of ash (Qian et al. 2009), and greater plant biomass can lead to an increase in fire severity (Romanyà et al. 2001). Thus, differences in fire history among scrubby flatwoods sites may cause variation in nutrient availability with time after fire.

Variation in Soil Characteristics and Nutrient Availability with Soil Depth

Differences in nutrient availability and bulk soil characteristics with depth were relatively consistent among times after fire. Soil %N, soil %C, dissolved inorganic N (DIN), chloroform labile microbial N (CLMN), N mineralization, and nitrification tended to be highest in surface soils, while soil $\delta^{15}\text{N}$ was more negative in surface soils (Figure 4-5; Figure 4-6). Concentrations of NH_4^+ and NO_3^- (Fenn et al. 1993) and net ammonification rates (Bloom and Mallik 2006) are affected by the identity and cover of plant species, respectively, and soil %N is higher under rather than outside the plant canopy (Aguilera et al. 1999). It is likely that the influence of plant leaf litter is greatest in surface soils, which may contribute to higher DIN, soil %N, and CLMN in surface soils. Soil N and soil C are positively correlated with charcoal content (MacKenzie et al. 2008), so persistence of charcoal in surface soils may contribute to high soil %N and %C. Because plants are more depleted in ^{15}N than their N source (Chapter 2; Michelsen et al. 1998, Schmidt and Stewart 2003), surface soils depleted in ^{15}N reflect inputs of plant litter to soil organic matter.

Patterns in soil pH with depth depended on time after fire. Soil pH was higher in surface soils (0-5 cm) than in deeper soils only in recently burned sites (one to six years after fire). Ash on the soil surface may increase soil pH (Grogan et al. 2000; Badía and Martí 2003; Molina et al. 2007). Leaching of ash covered soils increases soil pH (Molina et al. 2007), so it is likely that as ash becomes integrated through the soil profile over time after fire, soil pH becomes more similar across depths.

Effects of Abiotic Factors on Soil Nutrient Availability

In scrubby flatwood surface soils, N mineralization and nitrification rates tended to be higher in soils at field capacity than in soils at ambient field moisture conditions (Figure 4-7), likely due to the positive effects of soil moisture on microbial biomass and activity. Abundance of soil bacteria and fungi is higher after the wet season than after the dry season (Aguilera et al. 1999); in litter subjected to wetting and drying, microbial biomass is higher after rewetting (Schimel et al. 1999); and microbial biomass C is positively correlated with soil moisture (Tate and Terry 1980). Furthermore, dehydrogenase activity, a measure of microbial activity, is positively correlated with soil moisture (Tate and Terry 1980; Paradelo and Barral 2009). In deeper scrubby flatwoods soils, however, the effect of water addition on N mineralization and nitrification rates depended on time since fire (Figure 4-7). Increased soil moisture can inhibit growth of bacteria deeper in the soil profile (Tate and Terry 1980), and specific respiration increment can be negatively correlated with soil moisture (Merilä and Ohtonen 1997), suggesting that too much moisture may limit oxygen, and thus microbial activity. Across a variety of ecosystems, net mineralization is positively correlated with precipitation (Pérez et al. 2004) and soil moisture (Cassman and Munns 1980; Powers 1990; Evans et al. 1998; Frank 2008), but soil may have a maximum mineralization capacity above which more water does not increase mineralization (Cassman and Munns 1980).

Resin exchangeable PO_4^{3-} was negatively correlated with pH of surface soils (Figure 4-4). Over one year, resin exchangeable PO_4^{3-} was highest in sites with the most acidic soil. Phosphatase activity is negatively correlated with soil pH (Sinsabaugh et al. 2008), and low phosphatase activity leads to low PO_4^{3-} availability. Frank (2008) found that soil pH (ranging from 6.3 to 7.9) was negatively correlated with net P

mineralization in grasslands, so it is not surprising that the change in mean pH from 3.95 to 4.98 across my scrubby flatwoods sites had significant effects on P availability. Furthermore, PO_4^{3-} can form minerals with Ca^{2+} , and high concentrations of Ca^{2+} in ash may limit mobility and availability of PO_4^{3-} in more basic soils (Hsu and Jackson 1960).

Conclusion

In scrubby flatwoods soils, inorganic N availability is not affected by time after fire, but is related to soil moisture, while variation in PO_4^{3-} availability is related to soil pH. Soil %N, soil %C, N mineralization rates, dissolved organic N, chloroform labile microbial N, and PO_4^{3-} availability were highest in long unburned sites. Variation in measures of nutrient availability may be due to the differences in species composition and fire history of 13 yr sites compared to scrubby flatwoods sites of other times after fire rather than the effects of fire. In this study, 13 yr sites had numerous pine trees, high soil organic matter, and had only been burned once in the past 35 years, which may have contributed to high PO_4^{3-} , soil %N, and soil %C in surface soils; however, in scrubby flatwoods sites 20 years after fire with low soil organic matter, and where pines are less abundant or absent, soil %N and %C are lower (J. Schafer, unpublished data). My 1 yr to 10 yr sites are characteristic of scrubby flatwoods sites in general; whereas, my 13 yr sites differ from the characteristic scrubby flatwood sites. Thus, my results indicating high nutrient availability in long unburned scrubby flatwoods may not apply to all scrubby flatwoods. Species composition and fire frequency, as well as time after fire, appear to be important in affecting nutrient availability in Florida scrub soils.

Table 4-1. Description of study sites. Fire intensity 1 = low intensity, 2 = intermediate intensity, 3 = high intensity. The total number of burns is based on the record of fire history at Archbold Biological Station (1970 – present) and includes the most recent burn after which measurements were made. Multiple numbers in a column indicate that there may have been differences in fire intensity or fire history within the plot area. Intensive sampling indicates plots where soil samples were collected and species composition was assessed.

Time after fire (years)	Date of Burn	Burn Unit	Area (acres)	Fire Intensity	Total # of Burns	Intensive Sampling
1	22 June 2004	54B	49	3	3	X
1	22 June 2004	54C	53	3	1,2	
1	24 May 2004	61A	40	3	3	X
4	12 Feb 2001	44	163	1,3	2	X
4	12 Feb 2001	45C	81	3	3,4	
4	12 Feb 2001	47A	67	3	3	X
6	7 July 1999	48B	100	1-3	2	X
6	7 July 1999	48B	100	3	1	
6	26 July 1999	56B	27	2-3	3	X
8	7 May 1997	55	117	2-3	1	X
8	7 May 1997	55	117	3	1,2	
8	7 May 1997	55	117	3	1	X
10	15 June 1995	49B	76	3	3,4	X
10	15 June 1995	49B	76	2-3	3,4	
10	24 May 1995	56C	24	3	2	X
13	19 May 1992	25B	5	2-3	1	X
13	20 May 1992	24A	12	2-3	1	
13	9 Dec 1992	31B	15	1-3	1	X

Table 4-2. Species composition (in 2006) of the twelve plots where soil samples were collected (in 2005). Values are the number of plots in which species occurred except for the total number of species found in plots of each time since fire. Only shrubs and sub-shrubs present in at least two plots are included. Only herbs present in at least three plots are included. Species identifiable to genus only are included if present in at least three plots.

Species	Family	Years since fire in 2005 (in 2006)						Total
		1 (2)	4 (5)	6 (7)	8 (9)	10 (11)	13 (14)	
Trees								
<i>Pinus clausa</i>	Pinaceae				1		2	3
Shrubs								
<i>Asimina obovata</i> *	Annonaceae			1	1			2
<i>Bejaria racemosa</i>	Ericaceae	1				2	2	5
<i>Ilex opaca</i> var. <i>arenicola</i> *	Aquifoliaceae		1			1	1	3
<i>Lyonia ferruginea</i>	Ericaceae			1	1			2
<i>Lyonia fruticosa</i>	Ericaceae	2	2	2	2	2	2	12
<i>Lyonia lucida</i>	Ericaceae	2	2	1	2	2	2	11
<i>Palafoxia feayi</i> *	Asteraceae	1	2	2	2	2	2	11
<i>Persea borbonia</i> var. <i>humilis</i> *	Lauraceae				1		1	2
<i>Quercus champanii</i>	Fagaceae	2	2	2	2	2	2	12
<i>Quercus geminate</i>	Fagaceae	2	2	2	2	2	2	12
<i>Quercus inopina</i> *	Fagaceae	2	2	2	2	2	2	12
<i>Sabal etonia</i> *	Arecaceae	2	2	2	1	2	2	11
<i>Serenoa repens</i>	Arecaceae	2	2	2	2	2	2	12
<i>Sideroxylon tenax</i>	Sapotaceae			1	1			2
<i>Ximenia americana</i> ^	Olacaceae	2	2	2	1	1		8
Suffrutescent/Sub-shrubs								
<i>Gaylussacia dumosa</i>	Ericaceae	1	2	2		2	1	8
<i>Helianthemum nashii</i> *	Cistaceae		1	1	1			3
<i>Lechea deckertii</i>	Cistaceae	1	2	2	2	1	1	9
<i>Licania michauxii</i>	Chrysobalanaceae	1	2	2	1	1	1	8
<i>Opuntia humifusa</i>	Cactaceae	1	1	2	2	1	1	8
<i>Polygala polygama</i>	Polygalaceae	2	1	2	1		1	7
<i>Smilax auriculata</i>	Smilacaceae	2	1	2	2	2	2	11
<i>Vaccinium darrowii</i>	Ericaceae	1		1		1	2	5
<i>Vaccinium myrsinites</i>	Ericaceae	2	2	2	2	2	2	12
N-fixers								
<i>Chapmanii floridana</i> *	Fabaceae	1	1	2	1			5
<i>Galactia regularis/elliottii</i>	Fabaceae	1	2	1	1		1	6
<i>Mimosa quadrivalvis</i> *	Fabaceae		1			1	1	3
Graminoids								
<i>Andropogon floridanus</i> *	Poaceae	2				1	1	4
<i>Aristida beyrichiana</i>	Poaceae	2	2	2	2	2	1	11
<i>Dicanthelium</i> sp.	Poaceae	2		1				3
<i>Rhynchospora megalocarpa</i>	Cyperaceae	2	2	2	1	2	1	10

Table 4-2 continued.

Species	Family	Years since fire in 2005 (in 2006)						Total
		1 (2)	4 (5)	6 (7)	8 (9)	10 (11)	13 (14)	
Herbs								
<i>Ambrosia artemisiifolia</i>	Asteraceae	1		1	1			3
<i>Balduina angustifolia</i>	Asteraceae			1	1	1		3
<i>Cnidoscolus stimulosus</i>	Euphorbiaceae		1	1	1	1		4
<i>Commelina</i> sp.	Commelinaceae	1	1	1	1	1	1	6
<i>Liatris ohlingerae</i> *	Asteraceae		1	1	1			3
<i>Paronychia chartacea</i> *	Caryophyllaceae	1	1		1			3
Other								
<i>Selaginella arenicola</i>	Selaginellaceae	1	2	2	2	2	1	10
Lichens (<i>Cladina</i> sp., <i>Cladonia</i> sp.)					1	2	2	5
Total # of species		28	28	32	33	27	28	40

* endemic to Florida

^ hemi-parasitic

Table 4-3. Results of nested analyses of variance of soil variables at each depth.
Degrees of freedom = 5 for YSF and 6 for Plot(YSF).

	Soil Depth (cm)							
	0-5		5-10		10-15		15-20	
	F	p	F	p	F	P	F	p
Root Biomass (g/m ²) [^]								
YSF	3.09	0.017	0.87	0.510	0.98	0.440	0.79	0.558
Plot(YSF)	1.89	0.101	3.49	0.006	1.68	0.146	0.83	0.555
pH								
YSF	8.29	<0.001	1.85	0.121	2.55	0.040	2.33	0.057
Plot(YSF)	2.64	0.027	2.61	0.028	3.72	0.004	4.10	0.002
%N*								
YSF	6.58	<0.001	1.38	0.248	0.39	0.855	1.60	0.178
Plot(YSF)	1.28	0.282	1.66	0.152	2.61	0.029	0.97	0.453
%C*								
YSF	6.50	<0.001	0.99	0.435	0.24	0.944	1.82	0.127
Plot(YSF)	0.92	0.486	1.21	0.319	2.91	0.017	1.38	0.243
CN*								
YSF	3.07	0.017	0.70	0.627	0.29	0.917	1.53	0.197
Plot(YSF)	1.40	0.235	1.11	0.372	2.88	0.017	1.75	0.129
N (g · m ⁻²)*								
YSF	3.75	0.006	1.37	0.250	1.20	0.324	1.54	0.194
Plot(YSF)	1.28	0.282	1.66	0.152	2.61	0.029	0.97	0.453
C (g · m ⁻²)*								
YSF	6.14	<0.001	4.06	0.004	2.30	0.060	3.91	0.005
Plot(YSF)	0.71	0.646	5.18	<0.001	4.13	0.002	0.81	0.565
δ ¹⁵ N								
YSF	2.52	0.042	1.05	0.402	2.74	0.030	0.23	0.947
Plot(YSF)	1.41	0.231	2.01	0.083	2.25	0.054	1.61	0.165
Inorganic N (NH ₄ ⁺ + NO ₃ ⁻) *								
(μg · g soil ⁻¹)								
YSF	0.66	0.657	0.41	0.837	1.51	0.205	2.51	0.043
Plot(YSF)	1.12	0.362	0.74	0.618	2.16	0.063	2.38	0.043
Dissolved Organic N*								
(μg N · g soil ⁻¹)								
YSF	2.46	0.046	3.48	0.009	4.33	0.003	1.57	0.187
Plot(YSF)	1.63	0.159	0.57	0.753	1.17	0.338	1.10	0.373
DIN:DON*								
(μg N · g soil ⁻¹)								
YSF	1.50	0.208	1.48	0.213	0.92	0.478	1.19	0.328
Plot(YSF)	1.57	0.176	0.98	0.450	1.40	0.234	2.14	0.066
Chloroform labile microbial N*								
(μg N · g soil ⁻¹)								
YSF	6.14	<0.001	4.06	0.004	2.30	0.060	3.91	0.005
Plot(YSF)	0.71	0.646	5.18	<0.001	4.13	0.002	0.81	0.565
N mineralization (+ H ₂ O)*								
(μg N · g soil ⁻¹ · day ⁻¹)								
YSF	3.42	0.010	1.20	0.322	2.02	0.093	1.82	0.127
Plot(YSF)	0.64	0.698	2.86	0.019	1.67	0.150	1.02	0.425
N mineralization (+ H ₂ O)								
(μg N · g N ⁻¹ · day ⁻¹)								
YSF	0.85	0.524	0.97	0.443	2.53	0.042	2.42	0.049
Plot(YSF)	1.19	0.330	3.42	0.007	2.97	0.015	1.90	0.100

Table 4-3 continued.

	Soil Depth (cm)								
	0-5		5-10		10-15		15-20		
	F	p	F	p	F	P	F	p	
Nitrification (+ H ₂ O)* (µg N g soil ⁻¹ day ⁻¹)									
YSF	1.70	0.154	3.47	0.009	2.73	0.030	0.84	0.526	
Plot(YSF)	1.53	0.189	2.73	0.023	0.96	0.460	1.07	0.395	

* data were natural log transformed before analyses

^ data were square root transformed before analyses

Table 4-4. Results of repeated measures analyses of differences with depth for sites one, four, and six years after fire.

	1 year after fire			4 years after fire			6 years after fire		
	F	df	p	F	df	p	F	df	p
Root Biomass [^] (g · m ⁻²)									
Depth	1.27	3	0.306	6.34	3	0.003	3.32	3	0.037
Plot	7.34	1	0.027	0.22	1	0.651	14.61	1	0.005
Depth * Plot	1.67	3	0.201	0.89	3	0.457	0.21	3	0.887
pH									
Depth	8.87	1.56	0.006	3.33	3	0.036	5.22	3	0.006
Plot	0.001	1	0.981	3.05	1	0.698	13.22	1	0.007
Depth * Plot	0.46	1.56	0.594	0.48	3	0.119	5.38	3	0.006
%C*									
Depth	10.90	3	<0.001	10.34	3	<0.001	11.98	1.69	<0.001
Plot	0.42	1	0.532	1.02	1	0.342	1.38	1	0.273
Depth * Plot	5.77	3	0.004	0.69	3	0.564	4.69	1.69	0.033
%N*									
Depth	17.20	3	<0.001	16.57	3	<0.001	13.04	3	<0.001
Plot	0.65	1	0.443	2.71	1	0.138	0.46	1	0.514
Depth * Plot	3.32	3	0.037	1.22	3	0.324	3.20	3	0.041
C:N*									
Depth	0.73	3	0.544	1.16	3	0.344	5.38	1.75	0.021
Plot	0.10	1	0.759	0.20	1	0.665	2.99	1	0.122
Depth * Plot	7.34	3	0.001	0.89	3	0.460	3.55	1.75	0.061
N (g · m ⁻²)*									
Depth	6.11	3	0.003	9.50	3	<0.001	2.68	3	0.069
Plot	0.65	1	0.443	2.71	1	0.138	0.46	1	0.514
Depth * Plot	3.32	3	0.037	1.22	3	0.324	3.20	3	0.041
C (g · m ⁻²)*									
Depth	3.95	3	0.020	6.03	3	0.003	4.49	1.69	0.037
Plot	0.42	1	0.532	1.02	1	0.342	1.38	1	0.273
Depth * Plot	5.77	3	0.004	0.69	3	0.564	4.69	1.69	0.033
δ ¹⁵ N									
Depth	6.60	3	0.002	4.40	3	0.013	23.69	3	<0.001
Plot	0.02	1	0.881	0.003	1	0.959	22.66	1	0.001
Depth * Plot	1.16	3	0.346	0.09	3	0.965	3.89	3	0.021
DIN*									
Depth	17.76	3	<0.001	6.94	3	0.002	22.93	3	<0.001
Plot	0.16	1	0.696	3.90	1	0.089	0.28	1	0.609
Depth * Plot	1.63	3	0.208	2.70	3	0.071	2.55	3	0.079
DON*									
Depth	1.41	3	0.265	6.12	3	0.004	3.32	3	0.037
Plot	0.24	1	0.639	1.32	1	0.287	0.63	1	0.449
Depth * Plot	4.93	3	0.008	2.80	3	0.065	2.45	3	0.088
DIN:DON*									
Depth	4.02	3	0.019	2.72	3	0.070	7.97	3	0.001
Plot	0.02	1	0.875	1.58	1	0.249	0.07	1	0.801
Depth * Plot	1.26	3	0.311	4.10	3	0.019	3.13	3	0.044
Microbial N*									
Depth	18.16	3	<0.001	23.43	3	<0.001	38.48	3	<0.001
Plot	1.95	1	0.200	10.62	1	0.014	8.23	1	0.021
Depth * Plot	3.38	3	0.035	0.87	3	0.471	4.53	3	0.012

Table 4-4 continued.

	1 year after fire			4 years after fire			6 years after fire		
	F	df	p	F	df	p	F	df	p
N mineralization ($\mu\text{g N} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$)									
Depth	0.40	3	0.750	2.48	3	0.089	0.26	1.69	0.740
Plot	1.41	1	0.269	0.01	1	0.932	2.87	1	0.129
Depth * Plot	0.10	3	0.958	1.34	3	0.287	1.19	1.69	0.325
N mineralization ($\mu\text{g N} \cdot \text{g N}^{-1} \cdot \text{day}^{-1}$)									
Depth	1.96	3	0.146	2.30	1.22	0.165	0.38	3	0.764
Plot	2.13	1	0.183	0.01	1	0.926	3.48	1	0.099
Depth * Plot	0.98	3	0.418	1.52	1.22	0.258	0.72	3	0.549
Nitrification*									
Depth	1.73	3	0.188	4.80	1.46	0.039	1.19	1.09	0.310
Plot	2.44	1	0.156	0.11	1	0.752	1.78	1	0.219
Depth * Plot	0.68	3	0.616	0.49	1.46	0.569	0.89	1.09	0.381

* data were natural log transformed

^ data were square root transformed

Table 4-5. Results of repeated measures analyses of differences with depth for sites eight, ten, and thirteen years after fire.

	8 year after fire			10 years after fire			13 years after fire		
	F	df	p	F	df	p	F	df	p
Root Biomass [^] (g · m ⁻²)									
Depth	5.57	3	0.005	2.54	1.39	0.133	1.40	3	0.267
Plot	3.62	1	0.093	0.01	1	0.927	0.38	1	0.556
Depth * Plot	0.17	3	0.916	0.85	1.39	0.412	0.98	3	0.420
pH									
Depth	2.62	3	0.074	0.68	2.04	0.524	1.03	1.85	0.376
Plot	0.83	1	0.388	0.02	1	0.892	1.09	1	0.327
Depth * Plot	26.89	3	<0.01	9.58	2.04	0.002	1.63	1.85	0.228
%C*									
Depth	11.01	1.87	0.001	10.83	3	0.001	13.12	3	<0.001
Plot	12.37	1	0.008	0.31	1	0.594	0.18	1	0.988
Depth * Plot	4.41	1.87	0.033	0.39	3	0.761	0.04	3	0.679
%N*									
Depth	21.00	3	<0.001	15.87	3	<0.001	28.82	2.02	<0.001
Plot	11.08	1	0.010	0.08	1	0.781	0.08	1	0.783
Depth * Plot	3.84	3	0.022	0.51	3	0.677	0.21	2.02	0.814
C:N*									
Depth	1.22	3	0.323	1.10	3	0.367	0.14	3	0.934
Plot	7.09	1	0.029	3.24	1	0.110	0.40	1	0.546
Depth * Plot	4.99	3	0.008	0.06	3	0.977	0.16	3	0.921
N (g · m ⁻²)*									
Depth	5.22	3	0.006	7.47	3	0.001	10.10	2.02	0.001
Plot	11.08	1	0.010	0.08	1	0.781	0.08	1	0.783
Depth * Plot	3.84	3	0.022	0.51	3	0.677	0.21	2.02	0.814
C (g · m ⁻²)*									
Depth	3.28	1.87	0.069	5.43	3	0.005	4.91	3	0.008
Plot	12.37	1	0.008	0.31	1	0.594	0.18	1	0.679
Depth * Plot	4.41	1.87	0.033	0.39	3	0.761	0.04	3	0.988
δ ¹⁵ N									
Depth	10.99	3	<0.001	17.02	3	<0.001	8.48	3	0.001
Plot	2.69	1	0.139	0.13	1	0.729	0.10	1	0.763
Depth * Plot	0.21	3	0.888	2.25	3	0.108	1.11	3	0.364
DIN*									
Depth	10.03	3	<0.001	9.36	3	<0.001	8.78	3	<0.001
Plot	1.58	1	0.244	0.08	1	0.785	0.65	1	0.443
Depth * Plot	0.68	3	0.571	1.24	3	0.315	2.60	3	0.075
DON*									
Depth	5.13	1.43	0.034	24.09	3	<0.001	13.19	3	<0.001
Plot	2.13	1	0.183	0.14	1	0.713	0.01	1	0.922
Depth * Plot	0.37	1.43	0.632	0.44	3	0.719	3.31	3	0.037
DIN:DON*									
Depth	3.56	1.77	0.060	0.80	3	0.503	0.25	3	0.857
Plot	0.20	1	0.662	<0.01	1	0.998	0.31	1	0.591
Depth * Plot	0.30	1.77	0.721	1.67	3	0.199	4.99	3	0.008
Microbial N*									
Depth	33.80	1.90	<0.001	28.18	3	<0.001	25.22	3	<0.001
Plot	22.64	1	0.001	0.03	1	0.876	0.05	1	0.836
Depth * Plot	5.72	1.90	0.015	0.71	3	0.554	0.15	3	0.927

Table 4-5 continued.

	8 year after fire			10 years after fire			13 years after fire		
	F	df	p	F	df	p	F	df	p
N mineralization ($\mu\text{g N} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$)									
Depth	0.67	3	0.578	0.55	3	0.650	4.85	3	0.009
Plot	10.29	1	0.012	4.07	1	0.078	0.06	1	0.811
Depth * Plot	1.97	3	0.145	0.44	3	0.728	1.18	3	0.336
N mineralization ($\mu\text{g N} \cdot \text{g N}^{-1} \cdot \text{day}^{-1}$)									
Depth	0.75	3	0.532	0.61	3	0.617	0.03	3	0.992
Plot	9.26	1	0.016	8.87	1	0.018	0.001	1	0.975
Depth * Plot	2.40	3	0.093	1.48	3	0.244	1.96	3	0.147
Nitrification*									
Depth	4.71	3	0.010	2.36	3	0.096	1.12	3	0.362
Plot	4.65	1	0.063	0.01	1	0.925	3.74	1	0.029
Depth * Plot	0.47	3	0.702	4.35	3	0.014	7.02	3	0.025

* data were natural log transformed

^ data were square root transformed

Table 4-6. Results of multiple regressions, with root biomass ($\text{g} \cdot \text{m}^{-2}$) as the dependent variable and dissolved inorganic N (DIN), dissolved organic N (DON), and percent N, for each soil depth. Root biomass was square root transformed and all other variables were natural log transformed before analyses.

		B	SE B	β	p	R ²	F	df	p
0-5 cm	Constant	34.16	10.44			0.286	7.36	3,55	<0.001
	DIN	0.77	2.81	0.035	0.783				
	DON	4.40	2.73	0.241	0.112				
	%N	5.17	2.45	0.330	0.039				
5-10 cm	Constant	49.78	7.54			0.226	5.36	3,55	0.003
	DIN	0.68	2.23	0.037	0.762				
	DON	1.14	2.83	0.050	0.688				
	%N	6.10	1.68	0.450	0.001				
10-15 cm	Constant	52.04	6.85			0.328	8.93	3,55	<0.001
	DIN	-3.39	1.70	-0.237	0.051				
	DON	0.19	2.22	0.011	0.933				
	%N	6.71	1.44	0.606	<0.001				
15-20 cm	Constant	50.34	8.99			0.256	6.31	3,55	0.001
	DIN	-0.95	1.78	-0.069	0.593				
	DON	0.19	2.26	0.012	0.933				
	%N	6.36	1.88	0.523	0.001				

Table 4-7. Partial correlations between soil variables at each depth (controlling for time since fire). Pearson's r values are above the diagonal and p values are below the diagonal.

0-5 cm									
	%C*	%N*	C:N*	DIN*	DON*	DIN:DON*	CLMN*	$\delta^{15}\text{N}$	pH
%C*		.969	.730	.355	.617	-.292	.774	.085	-.496
%N*	<0.001		.539	.460	.605	-.196	.794	.024	-.443
C:N*	<0.001	<0.001		-.062	.432	-.456	.443	.222	-.469
DIN*	0.003	<0.001	0.322		.352	.478	.431	-.007	-.222
DON*	<0.001	<0.001	<0.001	0.003		-.653	.522	-.075	-.351
DIN:DON*	0.013	0.071	<0.001	<0.001	<0.001		-.141	.065	.149
CLMN*	<0.001	<0.001	<0.001	<0.001	<0.001	0.146		.132	-.510
$\delta^{15}\text{N}$	0.263	0.427	0.047	0.480	0.287	0.313	0.162		-.117
pH	<0.001	<0.001	<0.001	0.047	0.003	0.131	<0.001	0.191	
5-10 cm									
	%C*	%N*	C:N*	DIN*	DON*	DIN:DON*	CLMN*	$\delta^{15}\text{N}$	pH
%C*		.947	.792	.105	.269	-.098	.674	.357	-.671
%N*	<0.001		.553	.229	.242	.031	.704	.352	-.597
C:N*	<0.001	<0.001		-.162	.238	-.312	.409	.258	-.603
DIN*	0.216	0.042	0.112		.226	.724	.272	-.047	.134
DON*	0.020	0.034	0.036	0.044		-.508	.192	.141	-.168
DIN:DON*	0.233	0.407	0.009	<0.001	<0.001		.105	-.141	.238
CLMN*	<0.001	<0.001	0.001	0.019	0.074	0.217		.354	-.568
$\delta^{15}\text{N}$	0.003	0.003	0.025	0.364	0.146	0.145	0.003		-.320
pH	<0.001	<0.001	<0.001	0.157	0.104	0.036	<0.001	0.007	
10-15 cm									
	%C*	%N*	C:N*	DIN*	DON*	DIN:DON*	CLMN*	$\delta^{15}\text{N}$	pH
%C*		.957	.903	.228	.493	-.156	.734	.518	-.668
%N*	<0.001		.739	.351	.469	-.028	.733	.518	-.630
C:N*	<0.001	<0.001		.009	.445	-.321	.617	.434	-.616
DIN*	0.043	0.003	0.472		.261	.708	.366	.020	-.077
DON*	<0.001	<0.001	<0.001	0.024		-.496	.441	.301	-.470
DIN:DON*	0.121	0.418	0.007	<0.001	<0.001		.006	-.202	.275
CLMN*	<0.001	<0.001	<0.001	0.002	<0.001	0.481		.409	-.542
$\delta^{15}\text{N}$	<0.001	<0.001	<0.001	0.442	0.011	0.064	0.001		-.364
pH	<0.001	<0.001	<0.001	0.283	<0.001	0.018	<0.001	0.002	
15-20 cm									
	%C*	%N*	C:N*	DIN*	DON*	DIN:DON*	CLMN*	$\delta^{15}\text{N}$	pH
%C*		.939	.910	.402	.607	-.118	.767	.482	-.625
%N*	<0.001		.713	.437	.617	-.096	.799	.459	-.522
C:N*	<0.001	<0.001		.294	.497	-.126	.604	.430	-.647
DIN*	0.001	<0.001	0.013		.208	.681	.459	.324	-.294
DON*	<0.001	<0.001	<0.001	0.058		-.574	.541	.313	-.417
DIN:DON*	0.188	0.237	0.173	<0.001	<0.001		-.020	.036	.067
CLMN*	<0.001	<0.001	<0.001	<0.001	<0.001	0.440		.383	-.518
$\delta^{15}\text{N}$	<0.001	<0.001	<0.001	0.007	0.008	0.393	0.002		-.429
pH	<0.001	<0.001	<0.001	0.012	0.001	0.312	<0.001	<0.001	

Table 4-8. Results of multiple regressions, with dissolved inorganic N ($\mu\text{g N g soil}^{-1}$) as the dependent variable and microbial biomass N (MBN), dissolved organic N (DON), N mineralization ($\mu\text{g N} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$) (N min), and soil C:N as independent variables, for each soil depth. All variables were natural log transformed before analyses.

		B	SE B	β	P	R^2	F	df	p
0-5 cm	Constant	1.864	0.776			0.296	5.66	4	0.001
	MBN	0.329	0.118	0.423	0.007				
	DON	0.216	0.131	0.263	0.104				
	N min	0.266	0.630	0.060	0.674				
	C:N	-0.827	0.276	-0.420	0.004				
5-10 cm	Constant	0.825	0.521			0.303	5.86	4	0.001
	MBN	0.353	0.100	0.460	0.001				
	DON	0.370	0.150	0.298	0.017				
	N min	-2.213	0.815	-0.331	0.009				
	C:N	-0.661	0.184	-0.474	0.001				
10-15 cm	Constant	0.230	0.444			0.294	5.61	4	0.001
	MBN	0.334	0.105	0.468	0.002				
	DON	0.376	0.165	0.305	0.027				
	N min	-1.776	0.849	-0.247	0.041				
	C:N	-0.448	0.170	-0.392	0.011				
15-20 cm	Constant	-1.057	0.409			0.272	5.05	4	0.002
	MBN	0.339	0.126	0.415	0.009				
	DON	0.093	0.158	0.082	0.560				
	N min	-2.770	1.042	-0.315	0.010				
	C:N	-0.015	0.160	-0.014	0.925				

Table 4-9. Results of multiple regressions, with N mineralization ($\mu\text{g N} \cdot \text{g soil}^{-1} \cdot \text{day}^{-1}$) as the dependent variable and microbial biomass N (MBN), dissolved organic N (DON), soil C:N, and soil %N as independent variables, for each soil depth. All variables were natural log transformed before analyses.

		B	SE B	β	p	R ²	F	df	p
0-5 cm	Constant	0.397	0.283			0.375	8.08	4	<0.001
	MBN	0.015	0.033	0.085	0.652				
	DON	0.074	0.026	0.402	0.007				
	C:N	-0.094	0.060	-0.213	0.121				
	%N	0.049	0.033	0.311	0.143				
5-10 cm	Constant	-0.012	0.179			0.138	2.16	4	0.086
	MBN	0.042	0.020	0.365	0.045				
	DON	0.038	0.025	0.202	0.131				
	C:N	-0.051	0.032	-0.245	0.117				
	%N	-0.015	0.022	-0.134	0.497				
10-15 cm	Constant	-0.070	0.189			0.065	0.94	4	0.445
	MBN	-0.008	0.019	-0.083	0.664				
	DON	0.047	0.026	0.274	0.076				
	C:N	0.009	0.032	0.057	0.778				
	%N	-0.006	0.024	-0.053	0.814				
15-20 cm	Constant	0.114	0.174			0.051	0.72	4	0.580
	MBN	-0.004	0.020	-0.048	0.824				
	DON	0.025	0.021	0.195	0.245				
	C:N	-0.017	0.023	-0.143	0.462				
	%N	0.016	0.025	0.153	0.536				

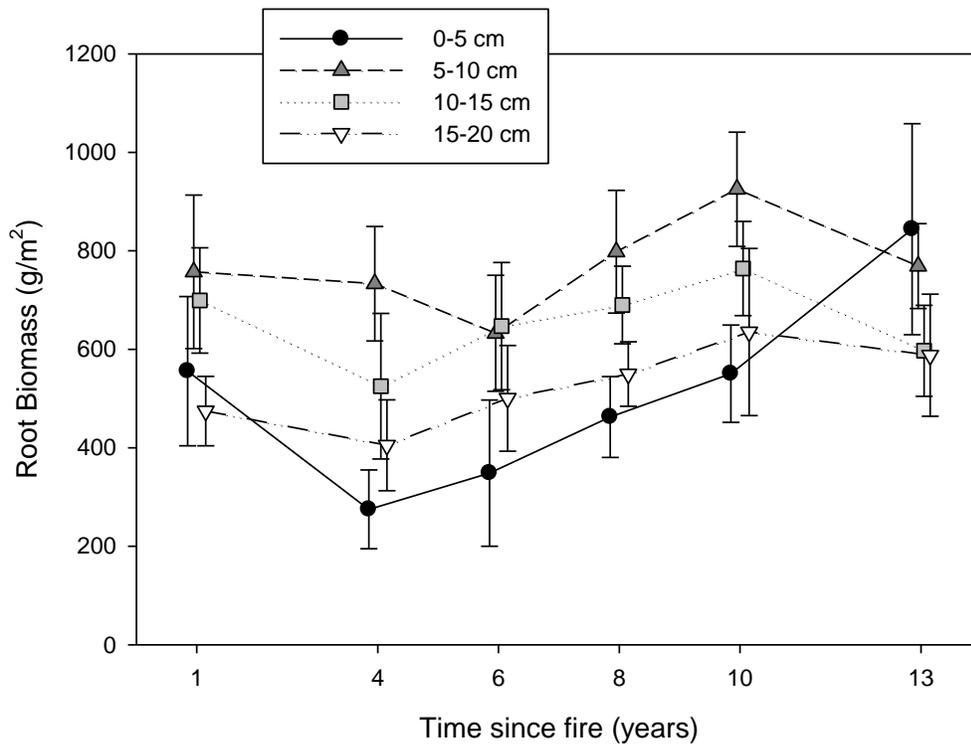


Figure 4-1. Mean (\pm se) root biomass ($\text{g} \cdot \text{m}^{-2}$) at each sampling depth for each time since fire.

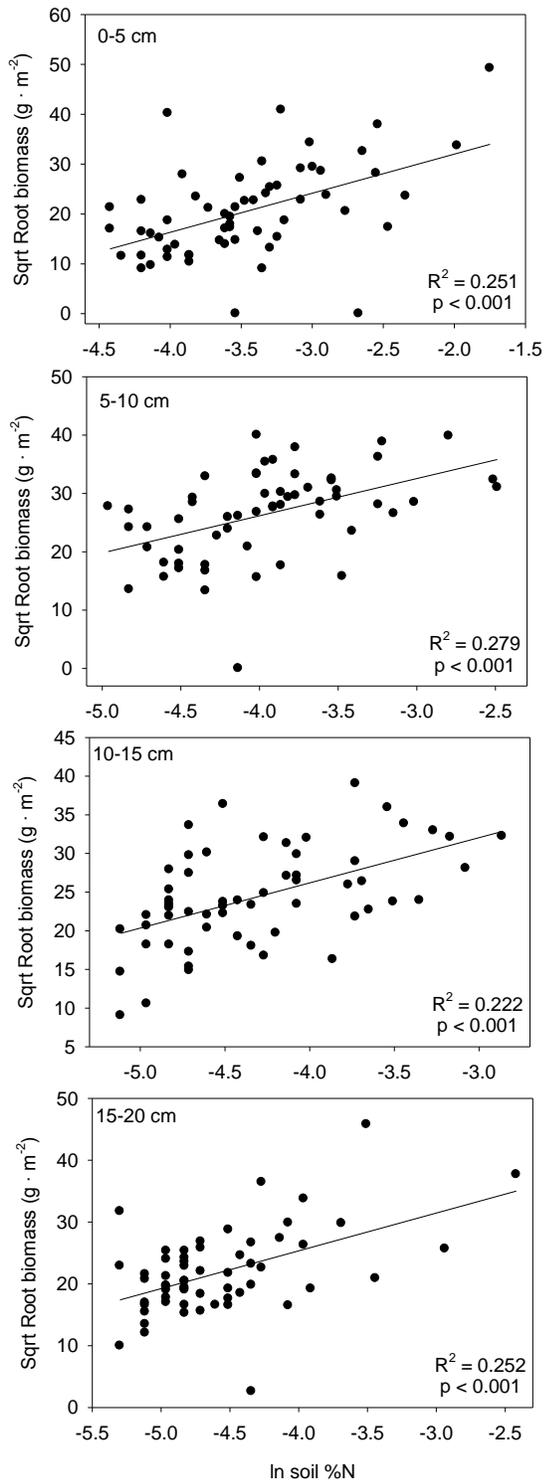


Figure 4-2. Relationship between root biomass and soil percent N for each sampling depth.

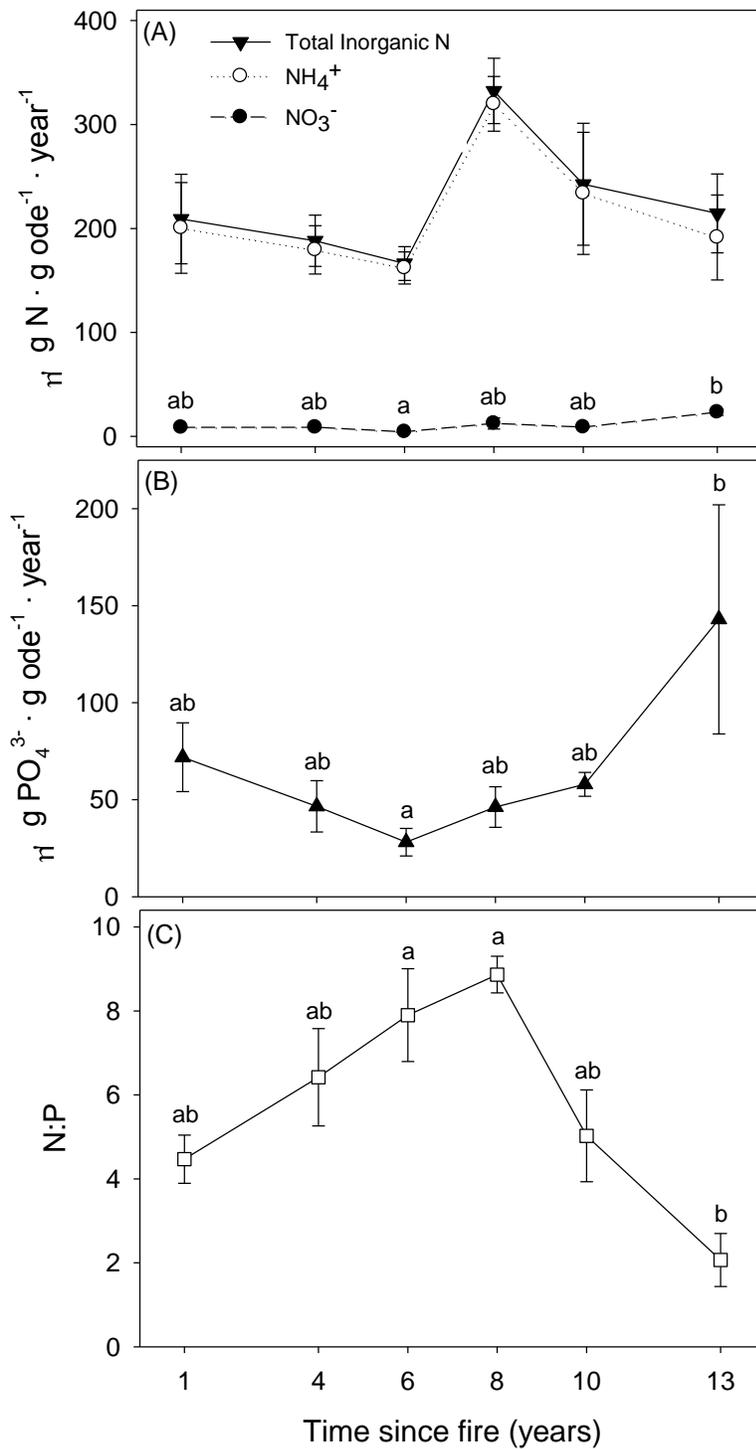


Figure 4-3. Mean (\pm se) resin extractable NH₄⁺, NO₃⁻, total inorganic N (A), PO₄³⁻ (B), and N:P ratios (C) over one year. Different letters represent significant differences among times since fire at $\alpha = 0.05$.

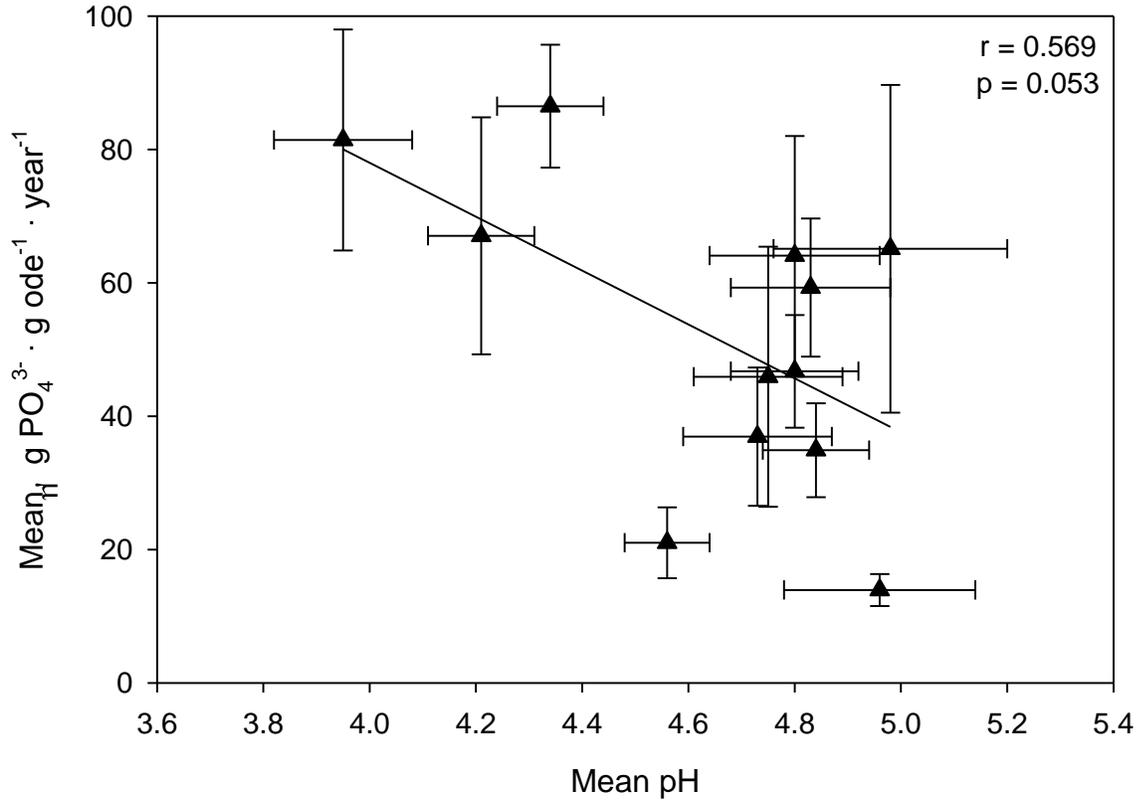


Figure 4-4. Relationship between pH of surface soils (0-5 cm) and resin exchangeable PO₄³⁻. Data is included from the 12 plots in which both variables were measured.

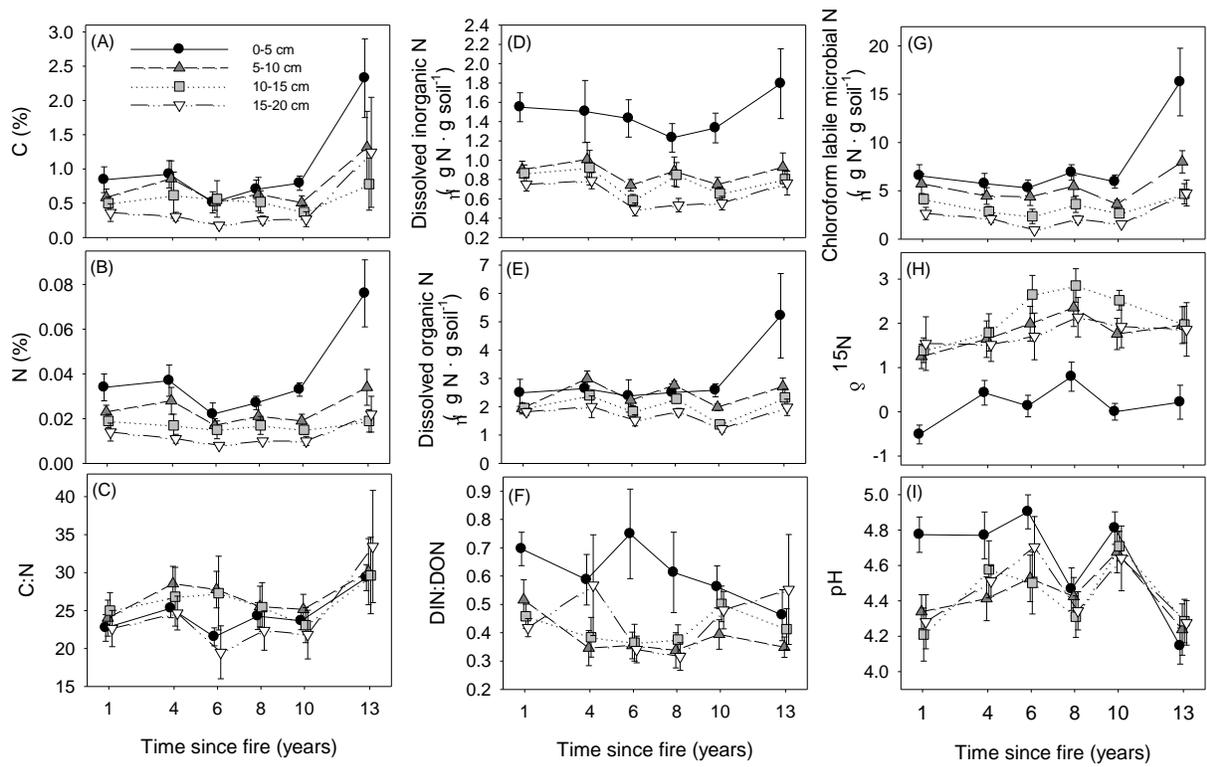


Figure 4-5. Mean (\pm se) soil %C (A), soil %N (B), soil C:N (C), K₂SO₄ extractable dissolved inorganic N (DIN) (D), dissolved organic N (DON) (E), ratio of DIN to DON (F), chloroform labile microbial N (G), soil $\delta^{15}\text{N}$ (H), and soil pH (I) at each sampling depth for each time since fire.

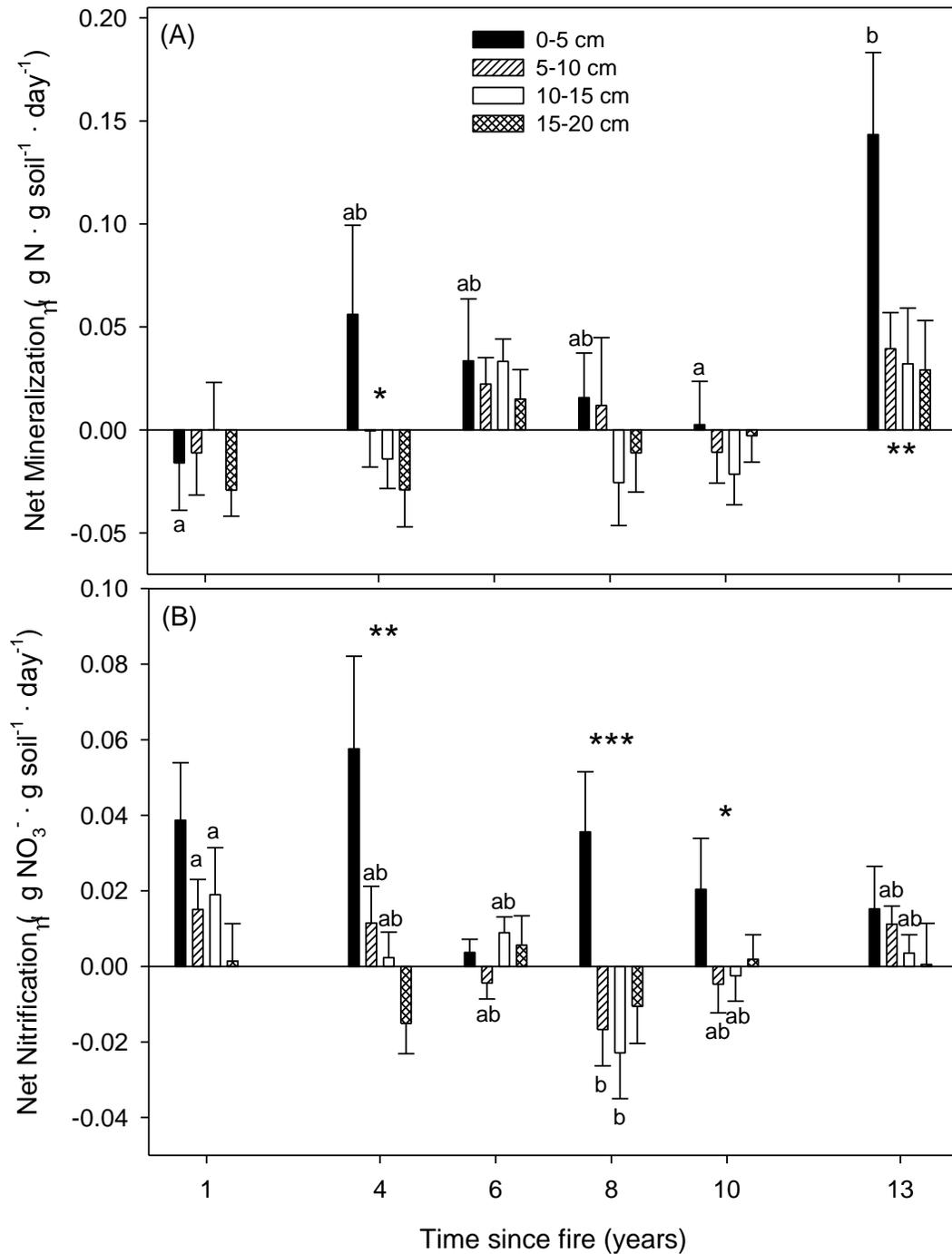


Figure 4-6. Mean (+ se) net N mineralization rates (A) and nitrification rates (B) with H₂O addition at each sampling depth for each time since fire. Different letters represent significant differences among times since fire within a depth at $\alpha = 0.05$. Differences among depths within a time since fire are indicated by * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$.

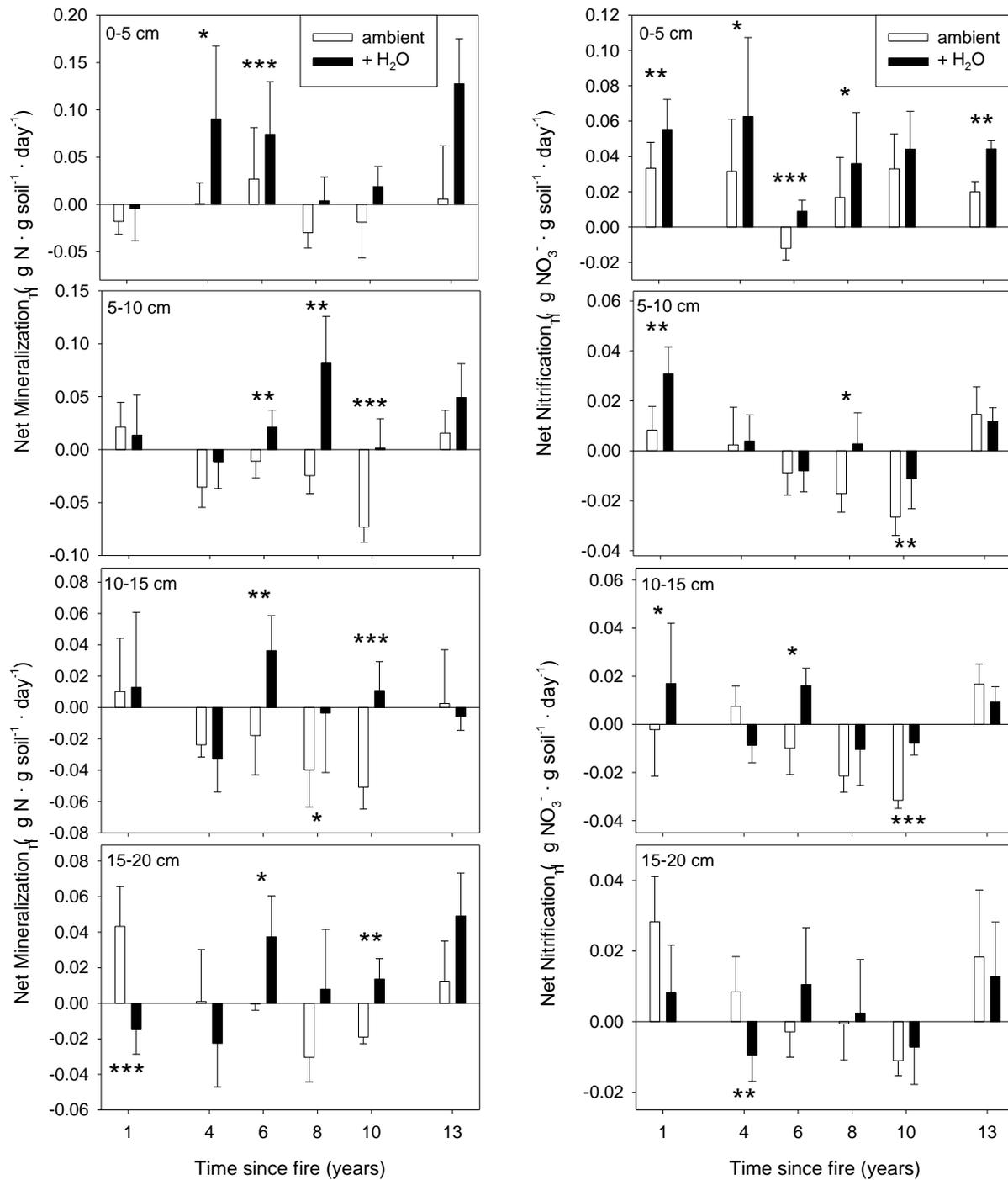


Figure 4-7. Mean (+ or - se) net N mineralization rates (left panels) and nitrification rates (right panels) at ambient field conditions and with H₂O addition at each time since fire for each sampling depth. Differences between ambient and H₂O addition for each time since fire at each depth are indicated by * p < 0.1, ** p < 0.05, *** p < 0.01.

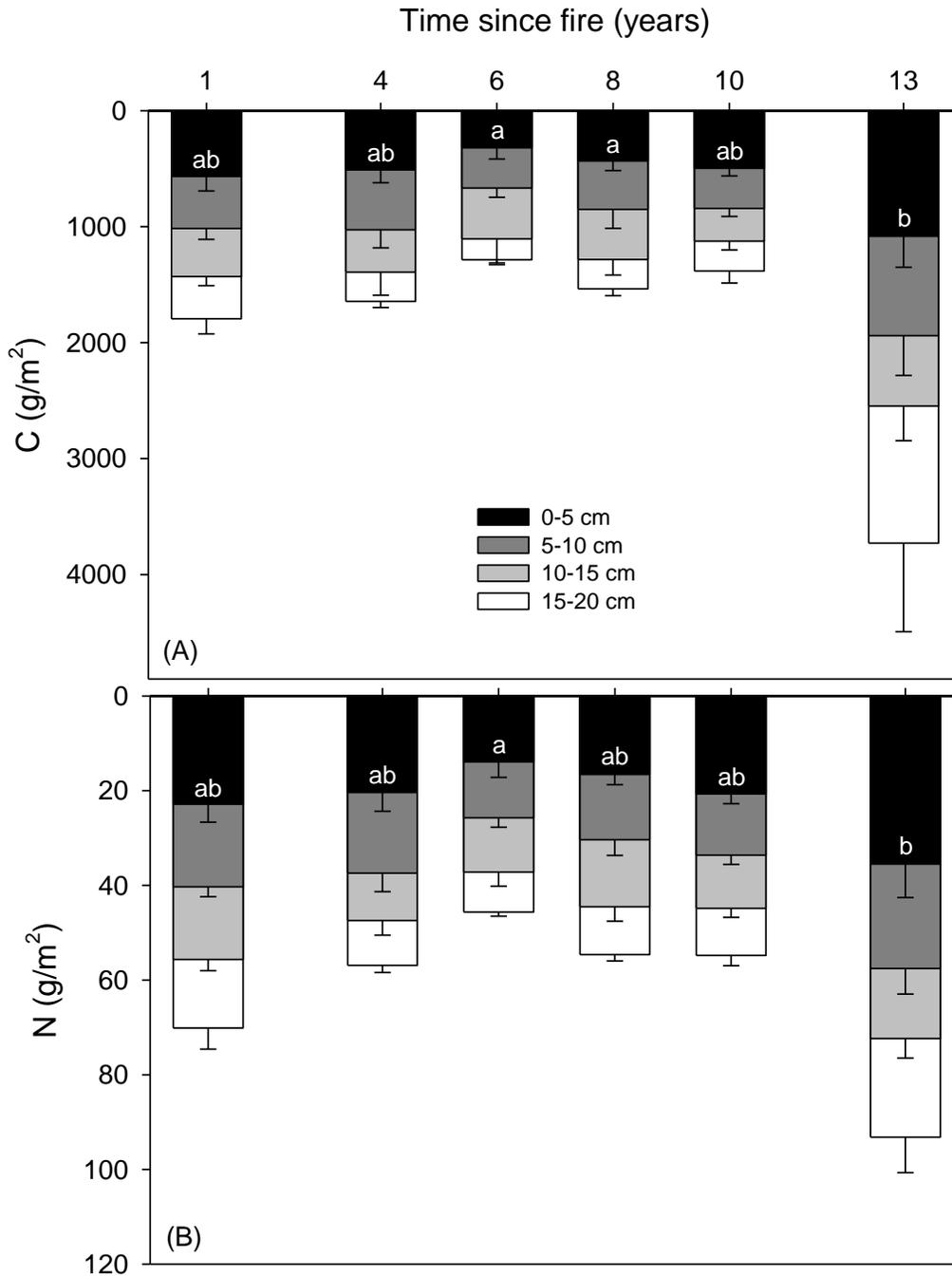


Figure 4-8. Mean (- se) C pools (A) and N pools (B) with depth for each time since fire. Different letters indicate significant differences among times since fire in surface soils at $\alpha = 0.05$.

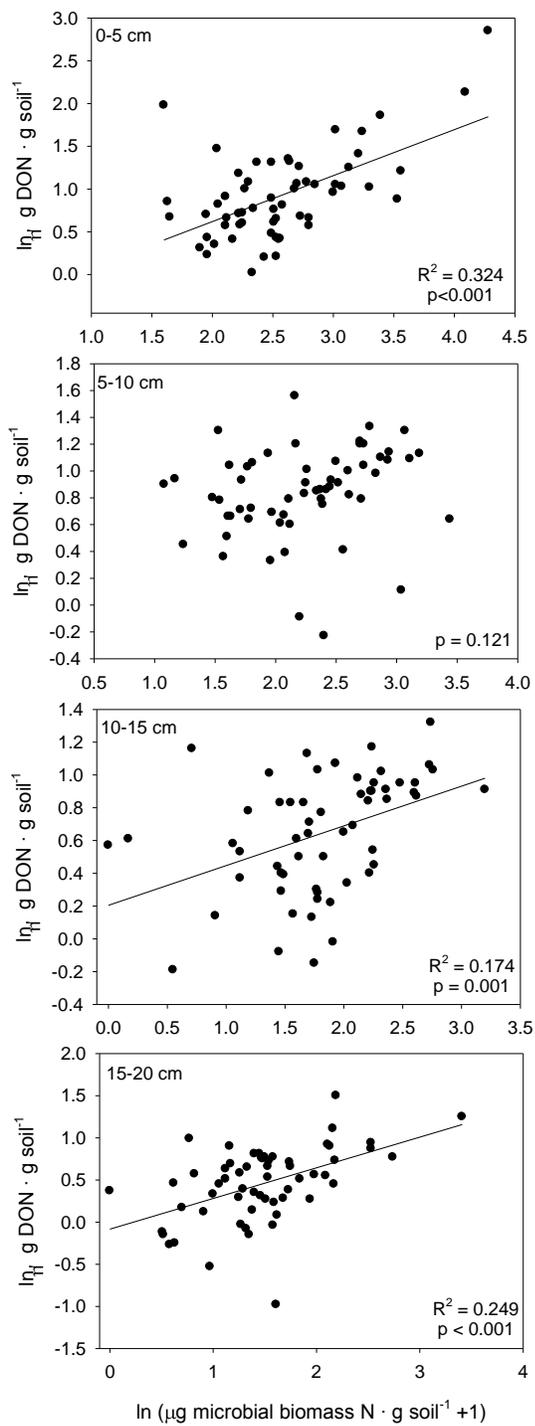


Figure 4-9. Relationship between microbial biomass N and dissolved inorganic N (DON) for each sampling depth.

CHAPTER 5
DISTURBANCE EFFECTS ON NUTRIENT LIMITATION OF PLANT PRODUCTIVITY
IN SCRUBBY FLATWOODS: DOES FIRE SHIFT NITROGEN VERSUS
PHOSPHORUS LIMITATION?

Introduction

Fire is a common disturbance in many ecosystems and can have profound impacts on nutrient cycling and availability. Fire consumes plant biomass, litter, and soil organic matter, converting organic nutrients to inorganic forms (Certini 2005), which can be lost to the atmosphere or returned to the ecosystem in ash. Nitrogen (N) and phosphorus (P) are essential plant nutrients that limit plant growth in most, if not all, terrestrial ecosystems (Vitousek and Howarth 1991). Yet fire has different effects on N and P due to fundamental differences in their biogeochemistry. Since N is more readily volatilized than P, relatively more N than P is lost from an ecosystem during fire (Raison et al. 1985a). In highly weathered soils, most P is in organic matter. Fire rapidly mineralizes the P in these pools, often resulting in enhanced P availability after fire. Nitrogen, however, may be relatively less available than P after fire due to greater combustion losses, and N inputs in unpolluted ecosystems are largely dependent upon biological N-fixation, which accumulates N over the inter-fire cycle.

During fire, nutrients can be lost from an ecosystem to the atmosphere through volatilization (non-particulate forms) or transport of ash (particulate forms). Numerous studies have measured the effect of fire on nutrient loss to the atmosphere by calculating the difference between the pre-fire nutrient content of fuel (i.e. understory plants and/or litter) and the post-fire nutrient content of ash. For example, in a low-intensity fire in a Mediterranean forest, 77% of N and 35% of P was lost (Gillon and Rapp 1989); during fires in Australian forests and woodlands, 92-94% of N and 41-53%

of P was lost (Cook 1994); during slash-and-burn agriculture in Amazonia, 93-98% of N and 27-47% of P was lost (Mackensen et al. 1996); and fires in Brazilian savannas caused 95% of N and 51% of P to be lost (Pivello and Coutinho 1992). Regardless of the type of ecosystem or fire, approximately twice as much N as P is lost to the atmosphere during fire due to differences in volatilization temperatures and forms of nutrient loss. 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). The majority of N in combusted fuel is lost in non-particulate forms, while P is lost in both non-particulate and particulate forms. Thus, ash on the soil surface contains high concentrations of P and low concentrations of N (Debano and Conrad 1978; Raison et al. 1985b).

The different fates of N and P in consumed fuel affect the total nutrient budget of an ecosystem. Inputs of N through symbiotic N-fixation and rainfall are not high enough, over the short-term, to replace the amount of N volatilized in fire (Carter and Foster 2004; Cook 1994). Over time, P in ash becomes relatively less available as it is immobilized by plants and microbes or fixed via geochemical reactions. Nitrogen availability, in contrast, tends to increase as inputs accumulate. 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. This is important because nutrient limitation of plant productivity is a fundamental control over the structure and function of ecosystems and has consequences for biomass accumulation (Bret-Harte et al. 2004), nutrient retention and loss (Hedin et al. 1995), biodiversity (Wassen et al. 2005), composition

(Chapin et al. 1987), and the ecosystem values and services provided to humans (Daily et al. 2000).

Plant growth is limited by any nutrient present in the soil below an optimum supply (Chapin et al. 2002). Thus, fire mediated differences in nutrient supply suggest that nutrient limitation may change with time since fire, with recently burned sites being N-limited and long unburned sites being P-limited, particularly in old, highly weathered soils. Research on the effects of fire on nutrient limitation, however, is scarce. Pines and oaks in a fire-adapted Mediterranean forest were P-limited in a site 5 years post-fire (Sardans et al. 2004). One of four species was N-limited in a lodgepole pine forest 3-5 years after fire (Romme et al. 2009). Nitrogen limits productivity of trees in secondary Amazonian forests, possibly due to the residual effects of fire on N availability (Davidson et al. 2004). In lakes within unburned catchments, phytoplankton biomass was limited by P or co-limited by N and P, while in lakes within burned catchments, phytoplankton biomass was limited by N, likely due to increased loading of P relative to N post-fire (McEachern et al. 2002).

Fire-dependent Florida scrub ecosystems occur on old, highly weathered, oligotrophic soils (Myers 1990). Previous research in this system suggests that the nutrient most limiting to plant production may change with time since fire. In palmetto flatwoods, soil and foliar N:P ratios decreased shortly after fire (Chapter 1). In scrubby flatwoods, phosphate, but not total inorganic N, varied with time since fire, causing soil N:P ratios to be highest at intermediate times since fire (6-8 years). Although inorganic N:P ratios were low in longer unburned sites (13 years), bulk soil %N was high, suggesting that N accumulates in soil over time (Chapter 3). Thus, I tested the

hypotheses that: (1) plant productivity in recently burned scrubby flatwoods is N-limited; (2) plant productivity in intermediately burned scrubby flatwoods is P-limited; and (3) plant productivity in long unburned scrubby flatwoods is co-limited by N and P.

Methods

Study Site

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

My research focused on scrubby flatwoods, a distinctive plant community of Florida scrub. Scrubby flatwoods are dominated by shrubby oaks (Fagaceae), palmettos (Arecaceae), and ericaceous shrubs (Ericaceae). Scrubby flatwoods experience fire return intervals of 8-16 years (Menges 2007), and the dominant vegetation resprouts after fire (Menges and Kohfeldt 1995). Soils are entisols (Abrahamson et al. 1984) that have no horizon development, little organic matter, and low exchange capacity and base saturation (Brown et al. 1990).

Experimental Design

In July 2007, I located burn units 6 weeks after fire (recently burned), 8 years after fire (intermediate), and 20 years after fire (long unburned). For each time since fire, I established three blocks in scrubby flatwoods communities. Within each block, I established ten 3 x 3 m plots, with a buffer of 2 to 4.5 m between each plot, for a total of

30 plots for each time since fire. Plots were established where there were at least three individuals of scrub oak (*Quercus inopina* Ashe) and saw palmetto (*Serenoa repens* (W. Bartram) Small (Arecaceae)) because these are two of the most dominant scrubby flatwoods species, with 37 and 22 percent cover, respectively (Abrahamson et al. 1984).

Each plot was randomly assigned one of the following treatments (3 replicates of each per time since fire): control, low N addition ($2 \text{ g N} \cdot \text{m}^{-2}$), intermediate N addition ($5 \text{ g N} \cdot \text{m}^{-2}$), high N addition ($10 \text{ g N} \cdot \text{m}^{-2}$), low P addition ($1 \text{ g P} \cdot \text{m}^{-2}$), intermediate P addition ($2.5 \text{ g P} \cdot \text{m}^{-2}$), high P addition ($5 \text{ g P} \cdot \text{m}^{-2}$), low N + P addition ($2 \text{ g N} + 1 \text{ g P} \cdot \text{m}^{-2}$), intermediate N + P addition ($5 \text{ g N} + 2.5 \text{ g P} \cdot \text{m}^{-2}$), or high N + P addition ($10 \text{ g N} + 5 \text{ g P} \cdot \text{m}^{-2}$). According to the National Atmospheric Deposition Program, deposition of N in the area of ABS is $5\text{-}10 \text{ kg} \cdot \text{ha}^{-1}$. Thus, my low N treatment doubled background N deposition. I added P fertilizer at half the rate of N, as is commonly done in nutrient fertilization experiments (Vitousek et al. 1993; Davidson et al. 2004), because plant demand for N is greater than plant demand for P. While most fertilization studies apply one level of fertilizer (Davidson et al. 2004; Vitousek and Farrington 1997), I applied different levels of fertilizer as this is likely more realistic in relation to different degrees of habitat alteration. Nitrogen was added as ammonium urea and ammonium nitrate (half of each) and P was added as Triple Superphosphate.

The annual dose of fertilizer was divided into quarters and added several times over one year because sandy soils in Florida scrub have low sorption capacity (N. Comerford, personal communication), and because a large rain event could cause high leaching of added nutrients. During the first year of the experiment, fertilizer was added in 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) (Figure 1). In September 2008, the 20 year since fire sites were burned in a prescribed fire. Thus, during the second year of the experiment, only the recently burned sites (now 1 year after fire) and the sites at intermediate times since fire (now 9 year after fire), were used. Fertilizer was added in October 2008 (half of the yearly amount), January 2009 (one quarter of the yearly amount), and April 2009 (one quarter of the yearly amount). Hereafter, sites will be referred to by their time after fire at the beginning of the experiment in July 2007 (e.g. 8 years after fire or 8 yr sites).

Soil Nutrients

To monitor background nutrient availability in each site, I buried four anion and four cation exchange resin bags in the soil near each control plot before the first nutrient addition in July 2007. These resin bags were removed before the nutrient addition in October 2007 and new bags were buried. I continued this for subsequent fertilization events (i.e. bags removed and buried in January 2008; bags removed and buried in April 2008; bags removed in July 2008), thus measuring background nutrient availability in 3-month intervals over the first year of the experiment.

In August 2008, I collected soil from three random locations in all plots. Each soil core (2.5 cm diameter) was separated by depths (0-10 cm and 10-20 cm), and the three cores from each depth were bulked. Within 24 hours of collection, soil samples were passed through a 2 mm sieve and sub-sampled for determination of gravimetric soil moisture, pH, total percentages of N and C, inorganic N concentrations, N mineralization rates, and inorganic P concentrations. Gravimetric moisture content was determined on samples dried at 105°C for 48 hrs. For soil pH, 10 g of air dried soil was added to 10 mL of deionized water, shaken for 30 sec, allowed to stand for 10 min

(Thomas 1996), and 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 hrs and ground on a spex mill (8000D dual mixer/mill, Spex Certiprep Inc., Metuchen, New Jersey). One sub-sample of ground surface (0-10 cm) soils was analyzed for percentages of N and C at the University of Florida on an elemental analyzer (ECS 4010, Costech Analytical, Valencia, California, USA). A subsample of ground soils from each control plot for each time since fire (both 0-10 cm and 10-20 cm depths) was sent to the ALS Laboratory Group (www.alsglobal.com) for analysis of macro- and micronutrients using the four acid “near-total” digestion method.

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 seconds, and allowed to stand overnight. Solutions were filtered through Whatman #42 filter paper that was pre-leached with 0.5 M K_2SO_4 . Filtered extracts were frozen and taken to the University of Florida. Dissolved inorganic N ($NH_4^+ + NO_3^-$) concentrations were determined colorimetrically on a segmented flow autoanalyzer (Astoria-Pacific, Inc., Clackamas, Oregon, USA).

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. I stored filtered samples in a refrigerator for up to three weeks before analysis for phosphate (PO_4^{3-}) concentrations on a spectrophotometer microplate reader (μ Quant 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).

I calculated the mean resin exchangeable nutrients per plot and used a one-way ANOVA to analyze differences with time since fire. I analyzed differences in macronutrients and micronutrients (determined with the “four-acid” digestion) with time since fire separately for surface (0-10 cm) soils and deep (10-20 cm) soils. One-way ANOVAs were used when data were normally distributed and Kruskal-Wallis tests were used when data were not normally distributed. In addition, I used Kruskal-Wallis tests to analyze differences in total P and calcium (Ca) with depth for each time since fire. The effects of nutrient addition on soil extractable N and P, N:P ratios, soil %N, %C, C:N ratios, and soil pH were determined separately for each time after fire and depth. All data were analyzed using a general linear model with treatment as a fixed effect and block as a random effect. I used post-hoc Dunnett’s tests to determine if treatment differences were greater than the control. Data were natural log transformed when necessary to meet the assumptions of normality (SPSS 11.5).

Aboveground Biomass and Growth

In each plot, before the first fertilization event, I marked three individuals of *Q. inopina* and *S. repens*, and up to three individuals 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 2003). These species account for over 97% of the shrub cover in my experimental plots (Table 5-1). The oaks (*Quercus* species) and ericaceous shrubs (*Lyonia* species) are clonal, multi-stemmed species, and the number of stems per individual (defined by a circle of 10 cm in diameter centered on the tallest stem), at the beginning of the experiment, ranged from 1 to 22 in recently burned sites, from 1 to 11 in sites at intermediate times since fire, and from 1 to 9 in long unburned sites. For the shrubs *L.*

lucida, *L. fruticosa*, *Q. chapmanii*, *Q. geminata*, and *Q. inopina*, I measured crown length and width, and measured the diameter and height of each stem. In addition, I measured apical shoot growth on a randomly selected subset of stems for *Q. inopina* each individual. If a stem had many new apical shoot growth increments, I measured a subset of them and scaled up to the entire stem. For the palmettos *S. etonia* and *S. repens*, I measured maximum crown length, minimum crown length, and height, and counted leaves. In July 2008, after one year of fertilization, I made the same measurements listed above and estimated percent cover of all shrub species. In July 2009, after two years of fertilization, I measured only the most dominant species, *Q. inopina* and *S. repens*. In addition, I estimated percent cover of all shrub species pre-fertilization and one year after fertilization. Differences in percent cover of shrubs and contribution to total shrub cover with time since fire were determined with Kruskal-Wallis tests.

I used age specific allometric equations (Chapter 2) for different times after fire (6 weeks, 1-2 years, 8-10 years, 20-22 years) to estimate total stem biomass and leaf biomass of each stem of each shrub species and total leaf biomass of each palmetto individual. For several shrub stems in sites 6 weeks after fire, leaf biomass estimates were greater than total stem biomass estimates, so leaf biomass was used for total stem biomass. I used several methods to investigate the effects of nutrient addition on aboveground shrub biomass. I assessed differences in total shrub biomass among treatments at each time after fire. I used measurements of shrub length (maximum crown length) and width (minimum crown length) to calculate the area of each marked individual. For oaks and lyonias, I summed stem biomasses to determine the biomass

of each individual. I then calculated the total measured biomass and total area for each species in each plot. If the area covered by a species was greater than what I measured, I used estimates of percent cover of each species to scale up biomass of each species to the entire plot. Total plot biomass was analyzed using a general linear model with treatment as a fixed effect and block as a random effect.

I assessed differences in total plant biomass among treatments for *Quercus inopina* and *Serenoa repens* because these species occurred in all plots. For *Q. inopina*, I summed stem biomass to determine the biomass of each individual. For both species, I calculated the percent change in total biomass for each species separately for the first and second years of fertilization. Because stem turnover occurred during the course of the experiment, I assessed differences in basal diameter and height for *Q. inopina* stems that were alive for multiple years. I calculated the mean percent change in basal diameter and height of stems per individual. For sites six weeks and eight years since fire, I analyzed differences in stems that were alive over the first year of fertilization, over the second year of fertilization, and over both years of fertilization. For apical shoot growth, I calculated mean growth per individual (based on a subset of stems if individuals had more than 3 stems). To analyze the effects of treatment on percent change in total plant biomass, basal diameter, height, and apical shoot growth, I used general linear univariate models with treatment as a fixed effect and block as a random effect. I used post-hoc Dunnett's tests to determine if the percent change in treatment plots was greater than in the control plots. Extreme outliers (> 3 standard deviations from the mean) were removed if the percent change for a measure was negative. I analyzed differences in percent change in biomass because the number of

new leaves produced per year by *S. repens* and *S. etonia* is positively correlated with palmetto biomass (Abrahamson 2007), suggesting that pre-treatment biomass may affect the biomass response to added nutrients. For sites six weeks and eight years after fire (the sites that were fertilized for two years), I used paired t-tests to compare differences in percent change in total biomass, basal diameter, and height between years. In addition, I assessed differences in stem percent survival, number of new stems, and percent change in stem number, which accounts for both stem death and stem recruitment, over the first year of fertilization for each *Q. inopina* individual. I analyzed the effects of treatment separately for each time since fire using Kruskal-Wallis tests after confirming with Kruskal-Wallis tests that there were no block effects (SPSS 11.5).

Litterfall

In each plot pre-fertilization (July 2007), I measured litter depth at 12 locations. I measured litterfall over one year by placing 4 litter traps in a cross formation on the ground of each 3 x 3 m plot. Litter traps were 0.09 m², 10 cm deep, and made of 2 mm hardware cloth. Litter was collected in December 2007 (the first time at which there was litter to collect), March 2008, May 2008, and July 2008. Litter was pooled at the plot level, sorted to fractions (leaf, twig, and reproductive litter), dried at 60°C for 48 hours, and weighed. Leaf and reproductive litter collected in May and July was sorted to species before being dried and weighed. *Quercus inopina* litter samples from May 2008 were ground on a wiley mill and analyzed for percentages of N at the University of Florida on an elemental analyzer (ECS 4010, Costech Analytical, Valencia, California, USA).

I calculated total leaf litterfall ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) for each plot and used a separate general linear model for each time after fire with treatment as a fixed effect, block as a random effect, and mean (of pre- and one year post-fertilization) total percent shrub cover as the covariate to analyze the effects of nutrient addition on leaf litterfall. Because oak leaf turnover occurs in the spring (Abrams and Menges 1992), and *Quercus inopina* was the dominant oak in my plots, I analyzed treatment effects on *Q. inopina* litterfall from March-May 2008. I used a separate general linear model for each time after fire with treatment as a fixed effect, block as a random effect, and post-fertilization *Q. inopina* percent cover (measured in July 2008) as a covariate to analyze the effects of nutrient addition on *Q. inopina* leaf litterfall and *Q. inopina* leaf litterfall N ($\text{g N} \cdot \text{m}^{-2} \cdot 2 \text{ months}^{-1}$). I analyzed differences in %N of *Q. inopina* litter collected in May 2008 using a general linear model with treatment as a fixed effect and block as a random effect. I used post-hoc Dunnett's tests to determine if litterfall biomass and N in treatment plots was greater than in the control plot. Data was natural log transformed when necessary to meet the assumptions of normality (SPSS 11.5).

Foliar Nutrients

I collected foliar samples of all marked *Quercus inopina* and *Serenoa repens* individuals pre-fertilization. In July 2008, after one year of fertilization, and July 2009, after two years of fertilization, I collected foliar samples of all *Q. inopina* and *S. repens* individuals that were still alive. All samples from pre-fertilization and one year after fertilization, but only samples from control and high nutrient addition plots from two years after fertilization, were dried, ground, and analyzed for percentages of N following the same methods as for litter samples. I measured foliar phosphorus of pre-fertilization and one year after fertilization samples of *Q. inopina* and *S. repens* from the control,

high N, high P, and high N + P plots. Subsamples of 0.05 to 0.5 grams were weighed into crucibles, ashed in a muffle furnace at 500°C for 5 hours, extracted with 6 M HCl, then brought to volume so that the solution was 0.6 M HCl. 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.

To analyze differences in all measures of pre-fertilization foliar nutrients (%N, %P, and N:P ratios) I fit a model with species and time since fire and their interaction as main effects. Differences among species and times since fire were determined with post-hoc Tukey HSD tests (JMP 8.0). I analyzed the effect of treatment on the percent change in foliar %N, %P, and N:P ratios one year after fertilization using general linear models with treatment as a fixed effect and block as a random effect. I used post-hoc Dunnett's tests to determine if the percent change in treatment plots was greater (%N and %P) or less (N:P) than in the control plot (SPSS 11.5).

Root Productivity

I used root ingrowth cores (Cuevas and Medina 1988) to measure root productivity during the first year of fertilization. In each plot pre-fertilization (July 2007), I randomly established three cylindrical, closed-bottom root ingrowth cores (2 mm mesh, 20 cm deep, 8 cm diameter). I collected soil cores, sieved the soil through 2mm and 1mm sieves to remove roots (< 2 mm diameter) and underground stems (> 2 mm diameter), placed the ingrowth cores in the ground, and then filled the cores with the root free soil. I weighed the sieved roots after drying at 65°C for 48 hours. Root ingrowth

cores were removed from the ground in August 2008, and each core was immediately put into a plastic bag. I hand picked roots from the inside of each core and sieved all sand from inside each core through 2mm and 1mm sieves. Long thin roots that passed through the sieve were picked out by hand. Roots were dried at 60°C for 48 hours then weighed. I used a general linear univariate model with treatment as a fixed effect, block as a random effect, and pre-fertilization root biomass (>2mm + 2mm fraction; $\text{g} \cdot \text{m}^{-2}$) as the covariate to analyze the effects of nutrient addition on root productivity (> 2 mm + 2 mm fraction; $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$). I used post-hoc Dunnett's tests to determine if the root productivity in treatment plots was greater than in the control plot (SPSS 11.5).

Results

Soil Nutrients

Over one year, resin exchangeable NH_4^+ ($F_{2,6} = 4.62$, $p = 0.061$) and NO_3^- ($F_{2,6} = 4.22$, $p = 0.072$) tended to be highest during the first year after fire (Figure 5-2). Total resin exchangeable N was 3.2 and 2.6 times greater during the first year after fire than in 8 yr and 20 yr sites, respectively ($F_{2,6} = 9.60$, $p = 0.013$). Resin exchangeable PO_4^{3-} was 5.1 and 3.8 times greater during the first year after fire than in 8 yr and 20 yr sites, respectively ($F_{2,6} = 11.86$, $p = 0.008$). There was no difference, however, in resin exchangeable N:P ratios with time after fire ($F_{2,6} = 0.34$, $p = 0.726$).

In surface soils (0-10 cm) of control plots, P was highest in recently burned sites, while zinc (Zn) was lowest in 8 yr sites. Soil P and Zn did not differ with time after fire in deep soils (Table 5-3). In recently burned sites, soil P ($\chi^2 = 5.00$, $df = 1$, $p = 0.025$) and Ca ($\chi^2 = 3.33$, $df = 1$, $p = 0.068$) were higher in surface soils than in deep soils. In 8 yr and 20 yr sites, P ($\chi^2 = 0$, $p = 1$ and $\chi^2 = 0.41$, $p = 0.317$, respectively) and Ca ($\chi^2 = 2.50$, $p = 0.114$ and $\chi^2 = 0.67$, $p = 0.414$, respectively) did not vary with soil depth. Other

elements were below detection limits (Table 5-2) or did not vary with time after fire (Table 5-3) in control plots.

After one year of fertilization, N addition had a minimal impact on soil N (Table 5-4), only increasing inorganic N availability in deep soils (10-20 cm) in 20 yr sites (Figure 5-3). Eight years after fire, the significant effect of treatment occurred because high P addition caused a decrease in inorganic N availability (Figure 5-3). After one year of fertilization, P addition had a minimal effect on soil extractable P in recently burned sites (Table 5-4). Eight years after fire, all levels of P addition increased soil extractable P, while 21 years after fire, only high and intermediate P addition increased soil extractable P above levels in control plots (Figure 5-4). In 8 yr and 20 yr sites, high P addition increased extractable P 10-fold in surface and deep soils. Soil extractable P in high P and high N+P plots was similar in recently burned and long unburned sites. Due to the effects of P addition on soil extractable P, soil N:P ratios were higher in control and N addition plots than in P and N+P addition plots eight and twenty years after fire. There was no effect of nutrient addition on soil %N, soil %C, C:N ratios, or soil pH at any time after fire (Table 5-4).

Aboveground Cover, Biomass, and Growth

Pre-fertilization, percent cover of *Quercus inopina* and *Serenoa repens*, as well as total percent cover of dominant shrubs, was lowest in 6 wk sites (Table 5-1). In recently burned sites, aboveground biomass of dominant shrubs was $71 \text{ g} \cdot \text{m}^{-2} \pm 5 \text{ g} \cdot \text{m}^{-2}$ (mean \pm se), and dominant shrubs covered, on average, 23% (2.1 m^2) of the plot area (9 m^2) (Table 5-1). Eight years after fire, aboveground biomass of dominant shrubs was $334 \text{ g} \cdot \text{m}^{-2} \pm 20 \text{ g} \cdot \text{m}^{-2}$ (mean \pm se), and dominant shrubs covered, on average, 58% (5.2 m^2) of the plot area. Twenty years after fire, aboveground biomass of

dominant shrubs was $377 \text{ g} \cdot \text{m}^{-2} \pm 25 \text{ g} \cdot \text{m}^{-2}$ (mean \pm se), and dominant shrubs covered, on average, 59% (5.3 m^2) of the plot area.

At all times after fire, nutrient addition did not have a significant effect on the percent change in total shrub biomass (Table 5-5). In recently burned sites, mean percent change in total shrub biomass was highest in high N plots (542%) and lowest in high P plots (273%). Mean percent change in total shrub biomass across treatments was negative in two of the three blocks at intermediate times after fire and was negative in one block in long unburned sites.

Over the first year of fertilization in recently burned sites, mean percent change in *S. repens* biomass was 662% in high N plots, which was significantly higher than the control (Figure 5-5A). Percent change in biomass of *Serenoa repens* was not affected by nutrient addition over the first year of fertilization at intermediate times after fire (Table 5-5); however, in long unburned sites, the mean increase in percent change in biomass was approximately 12 times greater in high N addition plots than in control plots (Figure 5-5E). Percent change in *S. repens* biomass was greater in the first than in the second year of fertilization in both 6 wk ($t = 21.09$, $df = 29$, $p < 0.001$) and 8 yr ($t = 3.67$, $df = 29$, $p = 0.001$) sites, and was not affected by nutrient addition over the second year of fertilization.

Over the first year of fertilization in recently burned sites, mean percent change in biomass of *Quercus inopina* was 645% in high P addition plots, which was significantly greater than the control (Figure 5-6A). In 8 yr and 20 yr sites, however, nutrient addition had no effect on percent change in *Q. inopina* biomass; in 8 yr sites, mean percent change in biomass was higher in control plots than in treatment plots (Figure 5-6C).

Percent change in *Q. inopina* biomass was greater in the first than in the second year of fertilization in 6 wk sites ($t = 9.84$, $df = 29$, $p < 0.001$), but not 8 yr sites ($t = 0.35$, $df = 29$, $p = 0.726$), and was not affected by nutrient addition over the second year of fertilization.

Over the first year of fertilization in recently burned sites, mean percent change in height of *Q. inopina* stems was significantly higher in high P plots (195%) compared to control plots (90%) (Figure 5-7A), while intermediate N + P addition significantly increased mean percent change in basal diameter (Figure 5-8A) and apical shoot growth (Figure 5-9A) of *Q. inopina*. Over the first year of fertilization in 8 yr and 20 yr sites, nutrient addition did not affect mean percent change in height or basal diameter of *Q. inopina* stems (Table 5-5). Apical shoot growth of *Q. inopina*, however, was significantly higher in low N + P addition, intermediate N addition, and high P addition plots than in control plots in 8 yr sites, and significantly higher in high P addition plots than in control plots in 20 yr sites (Figure 5-9). For stems alive all three years of the experiment (in 6 wk and 8 yr sites), percent change in basal diameter (6 wk sites: $t = 14.19$, $df = 29$, $p < 0.001$; 8 yr sites: $t = 14.19$, $df = 29$, $p < 0.001$) and height (6 wk sites: $t = 9.53$, $df = 29$, $p < 0.001$; 8 yr sites: $t = 2.45$, $df = 29$, $p = 0.020$) were greater in the first year than in the second year of fertilization.

In recently burned and long unburned sites, nutrient addition had no effect on percent survival of stems, the number of new stems, or percent change in stem number of *Quercus inopina* after one year of fertilization (Table 5-6). At intermediate times after fire, percent survival of stems was lower in control plots than in low N plots, but nutrient addition had no effect on percent change in stem number (Table 5-6).

Litterfall

Mean \pm se total leaf litterfall ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) was 75.4 ± 5.3 , 164.3 ± 10.4 , and 147.9 ± 10.9 in 6 wk, 8 yr, and 20 yr sites, respectively. At all times after fire, total leaf litterfall was not affected by nutrient addition, but in 20 yr sites, percent cover of shrubs was a significant predictor of total litterfall (Table 5-7). Similarly, *Q. inopina* spring leaf litterfall was not affected by nutrient addition (Figure 5-10), but post-fertilization percent cover of *Q. inopina* was a significant predictor of *Q. inopina* litterfall in 6 wk and 20 yr sites (Table 5-7). In 8 yr sites, *Q. inopina* litterfall %N was higher in high N + P treatments than in control plots (Table 5-8); however, *Q. inopina* litterfall N was not affected by nutrient addition at any time after fire (Table 5-7). Mean *Q. inopina* litterfall N ($\text{g N} \cdot \text{m}^{-2} \cdot 2 \text{ mos}^{-1}$) was 0.12, 0.23, and 0.23 in 6 wk, 8 yr, and 20 yr sites, respectively.

Foliar Nutrients

Pre-fertilization, foliar %N and %P were consistently higher in *Q. inopina* than in *S. repens* (Table 5-9). The largest difference occurred in 6 wk sites, where foliar %N and %P were 1.27 and 1.53 times higher in *Q. inopina* than in *S. repens*, respectively (Figure 5-11). Proportionally, the decrease in foliar %P of *Q. inopina* and *S. repens* from 6 wk to 8 yr sites was greater than the decrease in foliar %N. Foliar N:P ratios increased 8 and 6 units for *Q. inopina* and *S. repens*, respectively from 6 weeks to 20 years after fire (Figure 5-11). Foliar %N, %P, and N:P ratios were similar in 8 yr and 20 yr sites.

In recently burned sites, foliar %N and %P decreased over the first year of fertilization. Nutrient addition had a significant effect on percent change in foliar %N of *Q. inopina* (Figure 5-12), and high P and N + P addition caused less of a decrease in foliar %P of *Q. inopina* and *S. repens* (Figure 5-13). Eight years after fire, nutrient addition had no effect on percent change in foliar %N of *Q. inopina* or *S. repens*, but the

increase in foliar %P of *Q. inopina* was seven times greater in high P plots than in control plots (Figure 5-13A). This caused the percent change in foliar N:P ratios of *Q. inopina* to be positive in control plots and negative in high P addition and high N + P addition plots (Figure 5-13C). In long unburned sites, percent change in foliar %N of *S. repens* was approximately three times higher in high N and N + P plots than in control plots (Figure 5-12E), while high P and N + P addition significantly increased percent change in foliar %P of *Q. inopina* (Figure 5-13A).

Root Productivity

In control plots, mean \pm se root productivity ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) was 193.7 ± 50.7 , 128.8 ± 10.7 , and 145.4 ± 41.1 in 6 wk, 8 yr, and 20 yr sites, respectively. In recently burned sites, nutrient addition had a slightly significant effect on root productivity, and pre-fertilization root biomass was a significant predictor of root productivity (Table 5-7). Eight years after fire, root productivity was 3.6 times higher in high N+P addition plots than in control plots, and pre-fertilization root biomass was a significant predictor of root productivity (Figure 5-14B). Twenty years after fire, root productivity was 2.4 times higher in high N + P plots than in control plots (Figure 5-14C).

Discussion

Soil Nutrients

Over the first year of the experiment, background nutrient availability (resin exchangeable N and P) was highest in recently burned sites, likely due to the short-term effects of fire on nutrient availability. High N availability in burned sites is likely 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. High concentrations of NH_4^+ and NO_3^- in burned sites may also be related to high N mineralization and nitrification rates (DeLuca et al. 2002; DeLuca and Sala 2006); however, previous research in Florida scrub ecosystems has found that N immobilization, rather than N mineralization, may occur within the first year after fire (Chapters 1 and 3). In other scrubby flatwoods sites, resin exchangeable N was slightly lower over the second year after compared to eighth year after fire (Chapter 3), which suggests that the short-term effects of fire on N persist for less than one year after fire (Chapter 1).

High PO_4^{3-} availability in recently burned sites is likely due to high concentrations of P in ash post-fire (Wilbur and Christensen 1983; Raison et al. 1985b), since mineral soil PO_4^{3-} is correlated with ash depth (Rice 1993). In other scrubby flatwoods sites, P availability was higher 13 years after fire than one year after fire (Chapter 3); however, this could be related to the presence of pine trees, which did not occur in plots in this study, or a greater amount of organic matter than in the sites used in this study (1.47 versus 0.66 mean soil %C). Soil N:P ratios were only slightly, and not significantly lower, in recently burned sites than other times after fire. Soil macronutrients and micronutrients in deep soils (10-20 cm) of control plots did not vary with time after fire (Table 5-3). Thus, differences in soil nutrients in surface soils are likely related to fire, and variation in plant growth and biomass across times after fire should not be due to differences in parent material.

Nitrogen addition had a greater effect on soil extractable N 20 years after fire compared to other times after fire (Figure 5-4). Litter depth was highest 20 years after fire suggesting that some of the added fertilizer is retained in the system in organic matter. The lack of an effect of N addition on soil N six weeks and eight years after fire could be due to uptake of added N by plants and/or microbes. In coastal Florida scrub-oak ecosystems, soil microbial communities were primarily N-limited with a secondary P limitation (Brown et al. 2009), and in dry tropical ecosystems, N, but not P, addition caused an increase in microbial biomass C, suggesting that N is more limiting than P (Tripathi et al. 2008). At the global scale, microbial N:P ratios average 7:1 (Cleveland and Liptzin 2007), so microbial demand of N is greater than demand of P. Other studies from a variety of ecosystems have found that N addition increases soil NO_3^- and NH_4^+ (Bret-Harte et al. 2004; Caffrey et al. 2007; Hungate et al. 2007; Iversen and Norby 2008). Scrubby flatwoods differ from other sites by having sandy soils with low exchange capacity, suggesting that leaching may be important in these sites if plants and microbes do not use the added N quickly.

Unlike N, P addition led to a significant increase in soil extractable P after one year of fertilization in sites nine and 21 years since fire, but not in recently burned sites (Figure 5-3). Nine years after fire, high P addition ($5 \text{ g P} \cdot \text{m}^{-2}$) did not increase soil extractable P more than low P addition ($1 \text{ g P} \cdot \text{m}^{-2}$); whereas, 21 years after fire, only high P addition significantly increased soil extractable P. These results support three primary conclusions about P addition. First, the effect of added P was greater in sites with lower background P availability. Based on background soil P concentrations measured in surface soils (0-10 cm) of control plots one year after fertilization, low P

addition in sites eight years since fire had the potential to increase soil P content by the same factor as high P addition in recently burned sites (~60 fold). High P addition in sites eight and 20 years since fire could have increased soil P content approximately 160 and 310 fold, respectively. Second, some added P was retained in the soil, either in organic matter or bound to soil particles. In treatments with high P addition, 6-7% of the added P was retained in the top 20 cm of soil. The other 93-94% of added P was either leached or taken up by plants and microbes. Third, plants and microbes did not use all of the available P because it was leached or bound to soil particles. Alternatively, N may have become limiting, which is possible considering that as P addition increased eight years after fire, N availability decreased (Figure 5-3). Litaor et al. (2008) found that N addition caused a decrease in soil pH, and phosphorus availability is negatively correlated with soil pH (Chapter 3; Jaggi et al. 2005); however, N addition did not affect soil pH in my study. Similar to my study, P fertilization increased resin exchangeable PO_4^{3-} in tundra (Bret-Harte et al. 2004) and increased soil P in alder wetlands (Gökkaya et al. 2006).

Fertilization increased nutrient availability in scrubby flatwoods ecosystems. The independence of soil inorganic N availability six weeks and eight years after fire to N addition is more likely related to the offset in times of nutrient addition and soil collection than a lack of an effect of N addition. Soils were collected four months after the last fertilizer addition, which was only one fourth of the total amount of nutrients added, by which time added N was taken up by plants or microbes, or leached. I likely measured an increase in soil P because fertilizer P may become rapidly immobilized or sorbed (Sarmiento et al. 2006).

Aboveground Biomass and Growth

Nutrient addition did affect biomass and growth of the dominant shrubs in several cases. High N addition increased biomass of *Serenoa repens* individuals six weeks and 20 years after fire (Figure 5-6), suggesting that palmettos are N-limited in recently burned sites and long unburned sites. Over the first year of fertilization in sites six weeks after fire, high P addition increased biomass and height growth of *Quercus inopina*, intermediate N + P addition increased basal diameter change and total apical shoot growth, suggesting that *Q. inopina* is co-limited by N and P, with a stronger P-limitation, in recently burned sites. Eight years after fire, low N + P addition, intermediate N addition, and high N addition increased apical shoot growth, while 20 years after fire, high P addition increased apical shoot growth (Figure 5-9).

These results suggest that different scrubby flatwoods species are limited by different nutrients. Similar results have been documented in other systems (Romme et al. 2009). Foliar N:P ratios suggest that species from the same habitat can be limited by different nutrients, possibly because of differences in mycorrhizal status (Diehl et al. 2008), but nutrient addition can have a positive (Nijjer et al. 2010) or negative (Sims et al. 2007) effect on mycorrhizal fungi. Oaks have associations with ectomycorrhizae (Langely et al. 2002) and *S. repens* has associations with arbuscular mycorrhizae (Fisher and Jayachandran 1999). These differences in mycorrhizal status may contribute to limitation by different nutrients.

Nutrient addition had no effect on total aboveground shrub biomass (Table 5-5). Eight years after fire, *S. repens* biomass was not affected by nutrient addition. Eight and 20 years after fire, biomass, basal diameter, and height growth of *Q. inopina* were not influenced by nutrient addition. The limited response of shrubs to nutrient addition on

shrub biomass and growth eight and 20 years after fire was surprising given that scrubby flatwoods have low nutrient availability and that my focal species have responded to nutrient addition in previous studies in Florida scrub. Abrahamson (1999) found that NPK fertilization increased biomass of *Serenoa repens* and *Sabal etonia*, and Berry and Menges (1997) found that P fertilization increased growth of *Quercus inopina* stems, while N fertilization increased *S. repens* leaf production. These studies, however, added fertilizer around an individual rather than over the area of a plot.

Johnson and Abrahamson (2002) found that 80 to 90% of *Q. inopina* stems died over a 10 year period, but new stems were recruited so that the number of stems of *Q. inopina* individuals remained the same or increased over time. The number of stems per individual decreased only in sites one year after fire; however, individuals in recently burned sites did not decrease in biomass, and percent change in stem number of *Quercus inopina* individuals was not affected by nutrient addition at any time after fire. Thus, the limited effect of nutrient addition on biomass and growth is likely not due to a decrease in stem number of shrubs. Rather, numerous other factors could have influenced the nutrient addition on biomass and growth.

First, I measured a random sub-sample of shrubs in each plot, which is less precise than harvesting and weighing all plant biomass. In addition, I did not measure biomass of sub-shrubs or herbaceous species. In other ecosystems, however, graminoids had a larger response to fertilizer addition than deciduous and evergreen shrubs (Bret-Harte et al. 2004); nutrient addition led to an increase in the abundance of graminoids and forbs, while deciduous and evergreen shrubs declined in abundance (Jägerbrand et al. 2009). Nutrient addition may have had a greater impact on the

biomass of sub-shrubs, graminoids, and forbs because these species may have most of their roots in surface soils giving them greater access to added nutrients. I would not have detected an effect of nutrient addition on biomass if one of the less common species showed the greatest response to added nutrients. Furthermore, P addition increased the annual diameter increment of *Acacia koa* trees increased only when trees were thinned and grasses were controlled with herbicide (Scowcroft et al. 2007), suggesting that competition for nutrients may have limited growth of shrubs and the effects of nutrient addition on shrub biomass.

Second, the buffer between plots may not have been large enough to ensure that oaks and ericaceous shrubs were not connected underground. Clones of the Australian shrub *Zieria baeuerlenii* can cover distances of at least 5 m (Sharma 2001), clones of *Rhododendron ferrugineum* range from < 1.5 to 27 m² (Pornon and Escaravage 1999), and clones of *Quercus geminata*, a common species in scrubby flatwoods, are often at least 9 m² and can cover distances of up to 18 m (Ainsworth et al. 2003). If clones of oaks or ericaceous shrubs extended across plots, and stems were connected underground, individuals that were in the control plots could have had access to nutrients in the fertilized plots. Such a growth pattern could have diluted the effect on nutrient addition on biomass and growth.

Third, if nutrient addition led to an increase in new growth or foliar nutrients higher herbivory may have resulted. Gall-wasp occurrence (Abrahamson et al. 2003) and abundance of leaf-miners (Cornelissen and Stiling 2008) are correlated with oak leaf chemistry. Cornelissen and Stiling (2006) found that fertilized *Q. geminata* had higher foliar %N, lower tannins, and higher densities of numerous herbivore guilds. I did

not quantify herbivory, but I did not observe greater herbivory in fertilized plots 8 and 20 years since fire. In sites six weeks after fire, the tops of several resprouts appeared to have been consumed by larger herbivores, but this occurred across treatments and seemed to occur most often in *Quercus chapmanii*, not the more dominant species.

Fourth, shrubs may have allocated resources to reproductive parts that were not included in my aboveground biomass estimates. Acorn production differs between white oaks (*Quercus chapmanii*, *Quercus geminata*) and red oaks (*Quercus inopina*, *Quercus laevis*, *Quercus myrtifolia*). Cycles of acorn production range from 2 to 2.4 years for white oaks and from 3.6 to 5.5 years for red oaks (Abrahamson and Layne 2003). Resprouts of white oaks produce acorns during the first year after fire, whereas red oaks produce acorns three or four years after fire (Abrahamson and Layne 2002a). In addition, the mean number of acorns per bearing individual tends to increase with ramet size (Abrahamson and Layne 2002b). I assessed acorn production by *Q. inopina* and *Q. geminata* in September 2008, one year after fertilization. Overall, I counted 13 acorns on 735 stems, 273 acorns on 378 stems, and 103 acorns on 350 stems in sites one year, nine years, and 21 years after fire, respectively. Most stems, however, produced no acorns. Only nine stems produced more than 10 acorns, and the stems that produced multiple acorns were from a variety of nutrient treatments. Abrahamson and Layne (2003) found that precipitation accounted for 44% to 74% of the variation in crop-size of the oaks, suggesting that nutrient availability may play a secondary role in affecting oak reproduction. Flowering of *Sabal etonia* or *Serenoa repens* increased in the first year or two after fire, but was not stimulated by fertilization (Abrahamson 1999). I counted reproductive stems, but did not quantify flowering or fruiting, of *S.*

repens individuals after the first and second years of fertilization. Similar to Abrahamson (1999), I found no effect of nutrient addition on allocation to reproductive stems. After the first year of the experiment, more reproductive stems were produced by plants in sites one year after fire, while after the second year of the experiment, plants in sites nine years after fire produced more reproductive stems than plants in sites two years after fire.

Fifth, resources other than N and P may have limited plant growth. Scrubby flatwoods sandy soils have low water holding capacity (Abrahamson et al. 1984), and low water availability may limit the ability of plants to respond to increased nutrient availability. In coastal scrub, the biomass increment of oaks was positively correlated with annual rainfall (Seiler et al. 2009). In my study, rainfall was lower than average and similar to average during the first and second years of fertilization, respectively (Figure 5-1). *Quercus inopina* has a shallower depth of water uptake than *Q. chapmanii* and *Q. geminata*, as indicated by analysis of stable oxygen isotopes (Saha et al. 2008). Thus, *Q. inopina* in particular may have experienced water limitation and drought stress during months with low rainfall. Larger plants, which occur in longer unburned areas, may deplete water resources more rapidly than smaller plants; however, gravimetric soil moisture, leaf water potential, and stomatal conductance do not vary with time since fire (K. Adams and S. Saha, unpublished data), suggesting that water limitation may not be a confounding factor with time after fire. Light limitation, particularly in longer unburned sites, may hinder the ability of plants to respond to increased nutrient availability. For seedlings of the tropical tree *Inga vera*, light levels had a greater effect on growth than N and P addition (Myster 2006). In scrubby flatwoods, oaks and ericaceous shrubs are

the dominant overstory species, and leaf blade area and canopy area of the palmettos *Serenoa repens* and *Sabal etonia* are positively correlated with percent overstory (Abrahamson 2007). Biomass of *S. repens* increased with N addition in sites 20 years after fire, which is when light limitation may be highest, suggesting that plants were investing in increasing leaf and canopy area to increase light reception. In addition, other nutrients such as potassium (K) or calcium (Ca) may have limited productivity or fertilization with only one nutrient, such as N, could have induced P deficiency (Teng and Timmer 1995). In a flooded savanna, only addition of N, P, K, and sulfur (S) together increased plant productivity (Sarmiento et al. 2006), and biomass of *Serenoa repens* and *Sabal etonia* increased with addition of fertilizer that contained N, P, K, Ca, and magnesium (Mg) (Abrahamson 1999). The P fertilizer I used, triple superphosphate, contained 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). At my rate of P addition, however, I only added 0.66 to 3.31 g Ca · m⁻², which likely would not have alleviated any Ca limitation. Furthermore, D'Antonio and Mack (2006) found that N limitation exists despite high annual rates of net N mineralization, possibly because of asynchrony in plant nutrient demand and nutrient availability; however, by adding fertilizer numerous times over one year, I hopefully mitigated asynchrony in nutrient availability and plant nutrient demand.

Sixth, plants may have allocated resources to acquiring more resources rather than in growth. For example, nutrient addition increased root productivity eight and 20 years after fire, when nutrient addition had less of an effect on aboveground biomass

and growth of *Q. inopina* and *S. repens*. In addition, increasing foliar nutrient concentrations may occur at a cost to increasing biomass and growth.

I found large variation in the mean percent change in biomass and growth within a treatment, even when there were not significant block effects. This variation could be related to difference in ages of clumps of stems or differences in growth among specific oak clones or palmetto individuals. Aerts (2009) found intraspecific variation in the response of leaf production to N addition and Bown et al. (2009) found that clones of *Pinus radiata* differ in growth allocation, with the slowest growing genotype partitioning a smaller fraction of GPP to ANPP than the fastest growing genotype. Thus, genotypic variation may have increased variability in the effects of fertilization if all of the individuals of any species in one plot were the same clone.

Assessment of nutrient limitation in an ecosystem may depend on the length of fertilization studies (Niinemets and Kull 2005), and other studies have found significant effects of nutrient addition after two years of fertilization (Gökkaya et al. 2006; Lund et al. 2009). In my study, however, nutrient addition had a significant effect on plant biomass and growth in after one year, but not two years, of fertilization. This could be due to the fact that in sites that were fertilized for two years, the percent change in aboveground biomass, across all treatments, was greater during the first year than during the second year of fertilization. Studies from a variety of other ecosystems have found that N addition (D'Antonio and Mack 2006; Darby and Turner 2008; Iversen and Norby 2008) and P addition (Gökkaya et al. 2006) can increase aboveground biomass and growth. This suggests that scrubby flatwoods shrubs have a limit on their ability to

increase growth in response to nutrient addition, and that shrubs may maximize growth in the first year of increased nutrient availability.

Litterfall

Nutrient addition did not affect total leaf litterfall over the first year of fertilization (Table 5-7). Leaf litterfall of *Quercus inopina* had higher %N in high N + P treatments than in control plots eight years after fire; however, nutrient addition did not affect leaf litterfall N ($\text{g N} \cdot \text{m}^{-2} \cdot 2 \text{ mos}^{-1}$) or biomass ($\text{g} \cdot \text{m}^{-2} \cdot 2 \text{ mos}^{-1}$) of *Q. inopina*. In other fertilization experiments, N and P fertilization increased litterfall in an N-limited montane forest (Tanner et al. 1992) and a P-limited Hawaiian forest (Herbert and Fownes 1995). The lack of an effect of nutrient addition on *Q. inopina* litterfall may be related to the fact that percent cover of *Q. inopina* was a predictor of leaf litterfall. There are gaps within the shrub matrix of scrubby flatwoods, and most shrub species, including *Q. inopina*, have somewhat patchy distributions. Although litter traps were spread throughout each plot, *Q. inopina* litter often accumulates under the canopy, which could have contributed to the large variation in litterfall and the lack of an effect of nutrient addition.

Furthermore, *Q. inopina* stems near litter traps that died, which happened in several plots, contributed high amounts of leaf litter. Other shrub and sub-shrub species had low leaf litterfall in general, but they may have responded differently to nutrient addition than *Q. inopina* because the mechanisms that cause an increase in the amount of N and P transferred to the soil with nutrient fertilization differ among species (Aerts 2009).

Leaves of both *Serenoa repens* and *Sabal etonia* have an average life span of 2 to 3 years, and the number of new leaves produced per year by *S. repens* and *S. etonia* is positively correlated with palmetto biomass (Abrahamson 2007). For palmettos, leaf

turnover may be a better indicator than litterfall of nutrient effects of litter production because leaves remained suspended above the ground for a while after they die.

Foliar Nutrients

Pre-fertilization foliar N:P ratios suggested that *Quercus inopina* and *Serenoa repens* in recently burned sites would be N-limited and in sites eight and 20 years since fire would be P-limited or co-limited by N and P (Koerselman and Meuleman 1996; Güsewell 2004). In recently burned sites, high N addition biomass of *S. repens*; whereas, high P and high N + P increased biomass and growth of *Q. inopina*, suggesting that these species are limited by different nutrients. Eight and 20 years after fire, nutrient addition had little effect on growth of *Q. inopina*, but high N addition increased biomass of *S. repens*. Thus, foliar N:P ratios do not appear to be accurate indicators of aboveground nutrient limitation in scrubby flatwoods. Similarly, in South African grasslands, foliar N:P ratios suggested sites were N-limited when all sites were co-limited by N and P (Craine et al. 2008).

In recently burned sites, foliar %N and %P of *Q. inopina* and *S. repens* decreased from pre-fertilization to one year post-fertilization regardless of fertilization treatment because the effects of fire on foliar nutrient concentrations were greater than the effects of nutrient addition. High N and N + P addition, however, caused less of a decrease in foliar %P of both species. Eight years after fire, high P addition caused a significant increase in foliar %P of *Q. inopina*, which led to a significant decrease in foliar N:P ratios. This is consistent with a study in an alpine ecosystem where P fertilization caused a decrease in foliar N:P ratios (Litaor et al. 2008). Twenty years after fire, high P and high N+ P increased foliar %P of *Q. inopina*, but this did not cause significant decline in foliar N:P ratios. Eight and 20 years after fire, foliar %P and N:P

ratios of *S. repens* were not affected by nutrient addition. Pre-fertilization, foliar %N was significantly higher in *Q. inopina* than in *S. repens* 20 years after fire, and high N and N +P addition increased foliar %N of *S. repens*, but not foliar %N of *Q. inopina*. Similarly, Abrahamson (1999) found that N fertilization increased foliar N concentrations of *Serenoa repens*. My results suggest that *Q. inopina* may be a better competitor for N in long unburned sites and *Q. inopina* has come close to maximizing foliar N content. On the other hand, because *S. repens* had a lower initial foliar %N, it likely had a greater capacity to increase foliar %N. Regardless, across all nutrient treatments, foliar %N of *Q. inopina* tended to increase over the first year of fertilization; whereas, foliar %N of *S. repens* decreased in many treatments (Figure 5-12).

Overall, *Q. inopina* had a greater percent change in aboveground biomass, growth, and foliar nutrient concentrations in response to P addition, while *S. repens* had a greater percent change in aboveground biomass and foliar nutrient in response to N addition. This could in part be related to the different mycorrhizal associations of each species. Ectomycorrhizae may be better able to increase N to *Q. inopina* leading to greater P-limitation; whereas arbuscular mycorrhizae may be better able to increase P to *S. repens* leading to greater N-limitation. This suggests that within scrubby flatwoods ecosystems, differences among species may have a larger effect on nutrient limitation than time after fire.

Root Productivity

Nutrient addition did not affect root productivity in recently burned sites; however high N + P addition significantly increased root productivity eight and 20 years after fire (Figure 5-14). It is not clear if higher root biomass was due to an increase in root length or an increase in root width, but Blair and Perfecto (2008) found that root length, and not

root width, was greater in soils with added N and P. Because aboveground biomass showed a stronger response to nutrient addition in recently burned sites than other times after fire, my results suggest that there is a trade-off between allocation to aboveground and belowground resources with nutrient addition. Although an increase in soil nutrient availability can cause a decrease in allocation to belowground biomass (Nadelhoffer 2000; Darby and Turner 2008), allocation to belowground biomass is proportionally greater in low nutrient and dry ecosystems (Chapin et al. 2002). Eighty percent of biomass may be belowground in Florida scrub ecosystems (Saha et al. in review), and within oak domes, two-thirds of the biomass is belowground (Guerin 1993). Furthermore, belowground reserves (McPherson and Williams 1998; Paula and Ojeda 2009) affect resprouting ability (Moreno and Oechel 1991) and biomass of resprouts (Lloret and López-Soria, 1993; Cruz et al. 2002). Because dominant scrubby flatwoods shrubs resprout after fire, in longer unburned sites (e.g. eight and 20 years after fire), increasing belowground biomass is likely important for future survival; aboveground biomass will be consumed in the next fire. I did not sort roots to species, but roots from all the dominant shrub groups (oaks, palmettos, ericaceous shrubs) were present in root ingrowth cores, suggesting that increased root growth is a common response of dominant scrubby flatwoods species.

Conclusions

The effects of nutrient addition on biomass and growth depend both on time after fire and species. Over the first year of fertilization in recently burned sites, aboveground biomass and growth of *Quercus inopina* responded to P and N + P addition, while aboveground biomass of *Serenoa repens* responded to N addition. Nutrient addition had no effect on leaf litterfall or root productivity. Thus, resprouts of scrubby flatwoods

shrubs are able to respond to nutrient addition above nutrients made available by fire, and they do so by increasing aboveground growth. Different species, however, appear to be limited by different nutrients. Eight years after fire, apical shoot growth and foliar %P of *Q. inopina* increased with nutrient addition, and high N + P addition increased root productivity. At intermediate times after fire, scrubby flatwoods shrubs appear to invest more in belowground than aboveground productivity and show co-limitation by N and P with a stronger P-limitation. Twenty years after fire, N addition increased biomass and foliar %N of *S. repens*, P addition increased apical shoot growth of *Q. inopina*, and N + P addition increased root productivity. In long unburned sites, scrubby flatwoods appear to invest in both aboveground and belowground productivity and show co-limitation by N and P. Thus, my results support my hypothesis that plant productivity in long unburned scrubby flatwoods is co-limited by N and P. My hypotheses that plant productivity in recently burned scrubby flatwoods is N-limited and plant productivity in intermediately burned scrubby flatwoods is P-limited, however, are only partially supported.

In sites that were fertilized for two years, any increase in biomass or growth with nutrient addition occurred during the first year of fertilization. Dominant scrubby flatwoods species were only able to respond to one years of increased nutrient availability, which is what would occur naturally after fire (Chapter 1). This suggests that shrubs are adapted to respond to nutrients made available by fire, but may not be capable of increased growth above what is possible with nutrients made available by fire. Alternatively, microbes may be better competitors for nutrients than plants, and if fire caused a decrease in microbial biomass, over the second year of fertilization in

recently burned sites, once microbes had recovered, microbial uptake of nutrients could have limited the response of plants to nutrient addition. In addition, the sandy soils of scrubby flatwoods likely have a limited ability to retain added nutrients, and in the second year of fertilization added nutrients could have leached from the soil such that plants were not able to acquire the added nutrients. I only fertilized scrubby flatwoods for one or two years, which is a short time in the 8-16 year fire return interval of scrubby flatwoods (Menges 2007). Perhaps over a longer time period, shrubs would be able to adapt to elevated nutrient availability rather than just a pulse of nutrients. Large areas of land along the Lake Wales Ridge have been converted to agriculture and pastureland, leading to increased nutrient inputs. Some of these areas are now being restored to Florida scrub, and my results suggest that increased nutrient availability may not benefit native shrub species.

Table 5-1. Mean (median) percent of total shrub cover of focal shrubs in all plots pre-fertilization at different times after fire and results of Kruskal-Wallis tests analyzing differences with time after fire (df = 2 for all tests). Different letters represent significant differences at $\alpha = 0.0167$ (adjusted for multiple comparisons).

		Percent Cover					Percent of Total Shrub Cover				
		χ^2	P	6	8	20	χ^2	p	6	8	20
				weeks	years	years			weeks	years	years
Ericaceous shrubs	<i>Lyonia fruticosa</i>	5.83	0.054	0.7 (0)	4.9 (0.5)	2.7 (0)	4.97	0.083	2.3 (0)	7.8 (0.7)	4.5 (0)
	<i>Lyonia lucida</i>	8.46	0.015	1.5 a (1)	1.4 b (0)	3.1 ab (1)	12.12	0.002	6.8 a (3.6)	2.0 b (0)	5.2 ab (1.54)
Oaks	<i>Quercus chapmanii</i>	0.73	0.692	1.4 (0)	1.9 (0)	3.4 (0)	0.14	0.931	5.6 (0)	3.4 (0)	5.4 (0)
	<i>Quercus geminata</i>	0.26	0.879	1.3 (1)	3.2 (1)	3.3 (1)	7.34	0.026	5.9 a (4.6)	5.2 b (1.5)	5.8 ab (1.4)
	<i>Quercus inopina</i>	44.6	<0.001	11.2 a (10)	28.0 b (25)	31.8 b (30)	3.52	0.172	44.6 (48.2)	47.0 (45.4)	51.9 (54.9)
Palmettos	<i>Sabal etonia</i>	29.31	<0.001	1.3 a (1)	4.7 b (5)	0.8 c (0)	24.59	<0.001	6.0 a (4.3)	7.9 a (8.0)	1.6 b (0)
	<i>Serenoa repens</i>	43.61	<0.001	6.0 a (5)	14.0 b (12.5)	13.7 b (10)	0.68	0.711	25.9 (25.1)	24.2 (22.1)	23.6 (21.8)
Total		58.16	<0.001	23.4 a	58.1 b	58.9 b	0.99	0.608	96.9	97.5	98.0

Table 5-2. Mean (se) concentrations of macronutrients and micronutrients in scrubby flatwoods soils.

Time since fire	Al (%)	Ca (%)	Co (ppm)	Cu (ppm)	Fe (%)	K (%)	Mg (%)	Mn (ppm)	Mo (ppm)	Na (%)	Ni (ppm)	P (ppm)	S (%)	Zn (ppm)
1 year														
0-10 cm	0.023 (0.003)	0.027 (0.007)	0.67 (0.03)	10.47 (0.96)	0.36 (0.022)	<0.01	<0.01	31.67 (2.18)	7.72 (1.23)	<0.01	5.13 (0.73)	20 (0)	<0.01	7.67 (1.45)
10-20 cm	0.017 (0.003)	0.01 (0)	0.77 (0.18)	8.5 (0.49)	0.36 (0)	<0.01	<0.01	25.67 (2.18)	8.87 (1.60)	<0.01	4.60 (0.78)	10 (0)	<0.01	4.0 (1.0)
8 years														
0-10 cm	0.02 (0)	0.017 (0.003)	0.70 (0.11)	8.43 (0.62)	0.38 (0.017)	<0.01	<0.01	30.83 (5.26)	8.88 (1.72)	<0.01	4.52 (0.57)	10 (0)	<0.01	3.0 (0.58)
10-20 cm	0.02 (0)	0.01 (0)	0.73 (0.09)	14.7 (3.12)	0.48 (0.07)	<0.01	<0.01	32.33 (3.76)	8.54 (0.59)	<0.01	5.23 (0.58)	10 (0)	<0.01	4.0 (1.0)
20 years														
0-10 cm	0.023 (0.003)	0.013 (0.003)	0.73 (0.03)	13.6 (3.18)	0.43 (0.036)	<0.01	<0.01	31.0 (0.58)	9.11 (0.88)	<0.01	5.47 (0.42)	13.3 (3.3)	<0.01	11.0 (4.0)
10-20 cm	0.02 (0)	0.01 (0)	0.70 (0.10)	10.86 (3.03)	0.37 (0.015)	<0.01	<0.01	24.0 (1.73)	8.99 (0.91)	<0.01	4.43 (0.45)	10 (0)	<0.01	3.0 (0.58)

Table 5-3. Results of one-way ANOVAs (df = 2,6) and Kruskal-Wallis tests (df = 2) analyzing differences in soil nutrients with time after fire in surface (0-10 cm) and deep (10-20 cm) soils.

	Element	F/ χ^2	p	df
0-10 cm	Al (%)	1.14	0.565	2
	Ca (%)	3.44	0.179	2
	Co (ppm)	0.96	0.619	2
	Cu (ppm)	1.80	0.244	2,6
	Fe (%)	2.03	0.213	2,6
	Mn (ppm)	0.02	0.982	2,6
	Mo (ppm)	0.32	0.739	2,6
	Ni (ppm)	0.67	0.547	2,6
	P (ppm)	5.60	0.061	2
	Zn (ppm)	5.14	0.077	2
10-20 cm	Al (%)	2.00	0.368	2
	Ca (%)	0.00	1.00	2
	Co (ppm)	0.16	0.921	2
	Cu (ppm)	1.53	0.290	2,6
	Fe (%)	2.59	0.154	2,6
	Mn (ppm)	2.66	0.149	2,6
	Mo (ppm)	0.04	0.958	2,6
	Ni (ppm)	0.47	0.647	2,6
	P (ppm)	0.00	1.00	2
	Zn (ppm)	0.92	0.631	2

Table 5-4. Results of general linear univariate models with treatment as a fixed effect and block as a random effect for soil nutrients.

		1 year after fire			9 years after fire			21 years after fire		
		F	df	p	F	df	p	F	df	p
Total Inorganic N ^b ($\mu\text{g} \cdot \text{g soil}^{-1}$)	0-10 cm									
	Treatment	0.98	9,18	0.485	3.44	9,18	0.012	1.40	9,18	0.257
	Block	8.50	2,18	0.003	12.16	2,18	<0.001	4.20	2,18	0.032
	10-20 cm									
	Treatment	0.80	9,18	0.618	0.75	9,18	0.663	3.70	9,18	0.009
	Block	15.80	2,18	<0.001	5.06	2,18	0.018	7.32	2,18	0.005
NH ₄ ⁺ ^b ($\mu\text{g} \cdot \text{g soil}^{-1}$)	0-10 cm									
	Treatment	1.13	9,18	0.391	3.25	9,18	0.016	1.15	9,18	0.381
	Block	6.96	2,18	0.006	11.99	2,18	<0.001	2.93	2,18	0.079
	10-20 cm									
	Treatment	0.97	9,18	0.495	0.79	9,18	0.630	2.95	9,18	0.024
	Block	16.09	2,18	<0.001	5.10	2,18	0.018	6.65	2,18	0.007
Total Inorganic P ^a ($\mu\text{g} \cdot \text{g soil}^{-1}$)	0-10 cm									
	Treatment	2.32	9,18	0.061	20.51	9,18	<0.001	6.48	9,18	<0.001
	Block	5.59	2,18	0.013	0.45	2,18	0.643	0.24	2,18	0.789
	10-20 cm									
	Treatment	3.87	9,18	0.007	27.57	9,18	<0.001	6.96	9,18	<0.001
	Block	5.18	2,18	0.017	0.41	2,18	0.668	0.13	2,18	0.879
N:P ^a	0-10 cm									
	Treatment	3.51	9,18	0.011	27.77	9,18	<0.001	8.26	9,18	<0.001
	Block	3.34	2,18	0.058	5.15	2,18	0.017	1.35	2,18	0.285
	10-20 cm									
	Treatment	4.60	9,18	0.003	11.45	9,18	<0.001	18.80	9,18	<0.001
	Block	0.39	2,18	0.680	4.48	2,18	0.026	6.17	2,18	0.009

Table 5-4 continued

		1 year after fire			9 years after fire			21 years after fire		
		F	df	p	F	df	p	F	df	p
%N ^{bd}	0-10 cm									
	Treatment	0.39	9,18	0.923	1.87	9,18	0.124	0.41	9,18	0.912
	Block	2.99	2,18	0.076	6.99	2,18	0.006	1.13	2,18	0.346
%C ^{bd}	0-10 cm									
	Treatment	0.54	9,18	0.829	1.65	9,18	0.175	0.45	9,18	0.890
	Block	0.85	2,18	0.445	0.96	2,18	0.402	0.52	2,18	0.603
C:N ^c	0-10 cm									
	Treatment	1.44	9,18	0.242	1.27	9,18	0.317	0.50	9,18	0.858
	Block	12.27	2,18	<0.001	3.45	2,18	0.054	11.60	2,18	0.001
pH ^c	0-10 cm									
	Treatment	0.55	9,18	0.822	1.99	9,18	0.102	1.71	9,18	0.158
	Block	0.98	2,18	0.393	0.13	2,18	0.878	1.20	2,18	0.324
	10-20 cm									
	Treatment	1.05	9,18	0.441	0.22	9,18	0.986	0.38	9,18	0.927
	Block	1.42	2,18	0.267	0.63	2,18	0.544	1.47	2,18	0.256

^a all data natural log transformed

^b data for 1 year after fire natural log transformed

^c data for 9 years after fire natural log transformed

^d data for 20 years after fire natural log transformed

Table 5-5. Results of general linear univariate models with treatment as fixed effect and block as random effect testing for treatment effects on percent change in biomass and growth.

	6 weeks after fire						8 years after fire						20 year after fire		
	1 st year of fertilization			2 nd year of fertilization			1 st year of fertilization			2 nd year of fertilization			1 st year of fertilization		
	F	df	p	F	df	p	F	df	p	F	df	p	F	df	p
Total plot biomass															
Treatment	0.53	9,18	0.837				1.84	9,18	0.130				1.04	9,18	0.450
Block	0.56	2,18	0.582				7.13	2,18	0.005				0.53	2,18	0.600
<i>S. repens</i> biomass															
Treatment	3.01	9,78	0.004	1.25	9,78	0.275	0.93	9,78	0.500	1.54	9,78	0.148	1.84	9,78	0.074
Block	11.30	2,78	<0.001	2.92	2,78	0.060	2.07	2,78	0.133	0.24	2,78	0.788	0.13	2,78	0.876
<i>Q. inopina</i> biomass															
Treatment	3.15	9,77	0.003	1.32	9,76	0.239	0.35	9,77	0.953	0.95	9,72	0.485	0.75	9,76	0.661
Block	2.75	2,77	0.070	1.83	2,76	0.167	0.43	2,77	0.650	1.25	2,72	0.293	0.26	2,76	0.773
<i>Q. inopina</i> basal diameter ^{bc}															
Treatment	2.48	9,76	0.015	1.86	9,75	0.071	2.06	9,77	0.043	1.54	9,70	0.151	1.44	9,73	0.189
Block	0.15	2,76	0.862	4.91	2,75	0.010	2.93	2,77	0.059	0.51	2,70	0.601	0.16	2,73	0.854
<i>Q. inopina</i> height ^a															
Treatment	1.91	9,77	0.062	0.86	9,75	0.560	1.32	9,77	0.241	1.57	9,72	0.141	0.65	9,73	0.750
Block	0.98	2,77	0.381	0.77	2,75	0.466	1.20	2,77	0.306	2.20	2,72	0.118	0.68	2,73	0.509
<i>Q. inopina</i> new growth (mm) ^a															
Treatment	3.88	9,77	<0.001	1.10	9,76	0.107	2.14	9,78	0.036	0.98	9,71	0.463	2.78	9,74	0.007
Block	2.07	2,77	0.134	1.33	2,76	0.138	5.30	2,78	0.007	2.64	2,71	0.079	3.81	2,74	0.027

^a all data natural log transformed

^b data for 1 year after fire natural log transformed

^c data for 20 years after fire natural log transformed

Table 5-6. Results of Kruskal-Wallis tests analyzing the effects of treatment on *Quercus inopina* stem survival and turnover over the first year of fertilization. Degrees of freedom = 9 for all tests. There were no block effects.

	6 weeks after fire		8 years after fire		20 years after fire	
	χ^2	p	χ^2	p	χ^2	p
Percent survival of stems	7.90	0.544	19.57	0.021	10.72	0.295
Number of new stems	7.70	0.565	13.06	0.160	12.57	0.183
Percent change in stem number	10.73	0.294	4.90	0.843	10.87	0.285

Table 5-7. Results of general univariate models with treatment as a fixed effect, block as a random effect, and a covariate.

	Time after fire								
	6 weeks			8 years			20 years		
	F		p	F		p	F		p
Litterfall ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) ^a									
Treatment	0.44	9,17	0.896	1.51	9,17	0.221	0.19	9,17	0.992
Block	0.26	2,17	0.776	0.97	2,17	0.398	0.99	2,17	0.391
Mean (Pre- and Post-fertilization)	0.01	1,17	0.947	0.21	1,17	0.651	5.19	1,17	0.036
<i>Q. inopina</i> % cover									
<i>Q. inopina</i> litterfall ($\text{g} \cdot \text{m}^{-2} \cdot 2 \text{ mos}^{-1}$) ^b									
Treatment	0.40	9,17	0.920	1.45	9,17	0.242	0.25	9,17	0.981
Block	1.61	2,17	0.230	0.97	2,17	0.400	0.56	2,17	0.582
Post-fertilization <i>Q. inopina</i> % cover	10.05	1,17	0.006	3.23	1,17	0.091	11.75	1,17	0.003
<i>Q. inopina</i> litterfall N ($\text{g N} \cdot \text{m}^{-2} \cdot 2 \text{ mos}^{-1}$) ^b									
Treatment	0.56	9,17	0.811	1.28	9,17	0.316	0.29	9,17	0.969
Block	1.77	2,17	0.199	1.58	2,17	0.235	0.44	2,17	0.653
Post-fertilization <i>Q. inopina</i> % cover	11.03	1,17	0.004	2.83	1,17	0.111	10.50	1,17	0.005
Root Productivity ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$)									
Treatment	2.08	9,77	0.041	3.15	9,77	0.003	2.55	9,77	0.013
Block	5.28	2,77	0.007	0.74	2,77	0.479	0.05	2,77	0.952
Pre-fertilization root biomass ($\text{g} \cdot \text{m}^{-2}$)	4.99	1,77	0.028	5.52	1,77	0.021	2.81	1,77	0.098

^a natural log transformed

^b data from sites 6 weeks and 20 years after fire natural log transformed

Table 5-8. Effects of treatment on percent change in foliar and litter nutrients. Results of general linear univariate models with treatment as a fixed effect and block as a random effect.

	6 weeks after fire			8 years after fire			20 years after fire		
	F	df	p	F	df	p	F	df	p
<i>Q. inopina</i>									
litterfall %N ^a									
Treatment	0.71	9,18	0.693	3.44	9,18	0.012	1.03	9,18	0.451
Block	0.07	2,18	0.983	1.21	2,18	0.320	0.07	2,18	0.936
<i>Q. inopina</i>									
foliar %N									
Treatment	2.11	9,77	0.038	1.95	9,78	0.056	1.33	9,75	0.236
Block	6.12	2,77	0.003	2.40	2,78	0.097	9.31	2,75	<0.001
<i>Q. inopina</i>									
foliar %P									
Treatment	2.96	3,29	0.048	9.07	3,30	<0.001	4.82	3,28	0.008
Block	0.42	2,29	0.661	1.82	2,30	0.179	0.14	2,28	0.868
<i>Q. inopina</i>									
foliar N:P									
Treatment	2.32	3,29	0.096	6.41	3,30	0.002	2.28	3,28	0.101
Block	2.16	2,29	0.133	0.10	2,30	0.905	2.69	2,28	0.086
<i>S. repens</i>									
foliar %N (g)									
Treatment	0.50	9,78	0.868	0.96	9,78	0.477	2.56	9,78	0.012
Block	2.32	2,78	0.105	0.04	2,78	0.958	6.51	2,78	0.002
<i>S. repens</i>									
foliar %P									
Treatment	2.85	3,30	0.054	0.24	3,30	0.866	0.77	3,30	0.519
Block	0.79	2,30	0.463	0.27	2,30	0.764	2.91	3,30	0.070
<i>S. repens</i>									
foliar N:P (g)									
Treatment	1.76	3,30	0.176	0.13	3,30	0.941	0.73	3,30	0.544
Block	1.20	2,30	0.315	0.07	2,30	0.931	0.46	2,30	0.634

^a all data natural log transformed

Table 5-9. Results of one-way ANOVAs analyzing pre-fertilization foliar nutrients of *Quercus inopina* and *Serenoa repens*.

	F	df	p
%N			
YSF	154.62	2	<0.001
Species	101.15	1	<0.001
YSF*Species	13.50	2	<0.001
%P			
YSF	403.21	2	<0.001
Species	88.14	1	<0.001
YSF*Species	40.46	2	<0.001
N:P			
YSF	169.96	2	<0.001
Species	4.64	1	0.035
YSF*Species	3.10	2	0.052

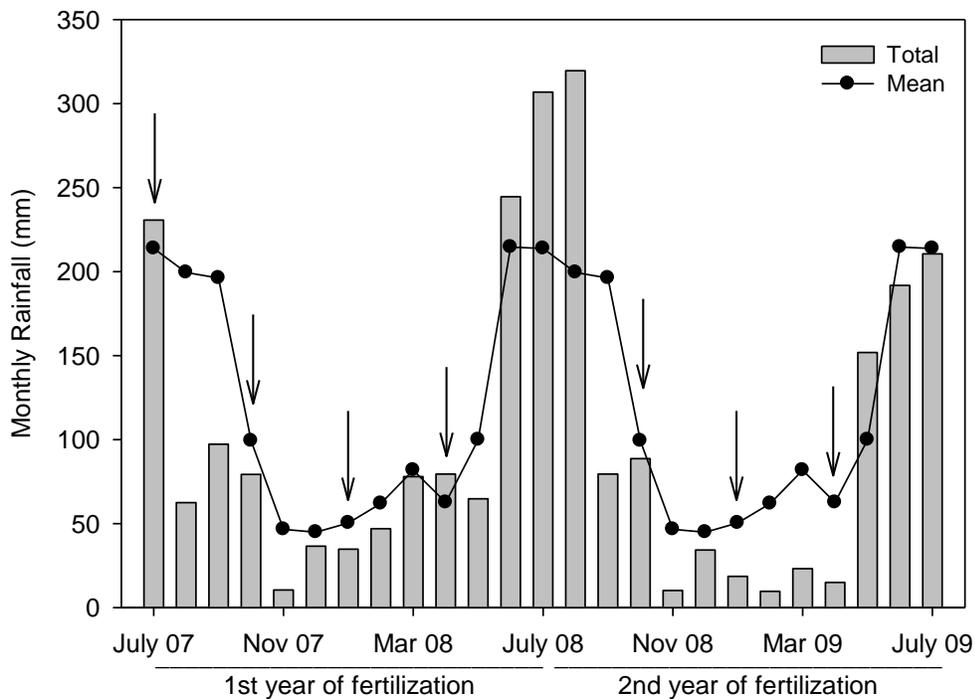


Figure 5-1. Mean monthly precipitation and total monthly precipitation during the study period at Archbold Biological Station. Arrows indicate months in which fertilizer was added.

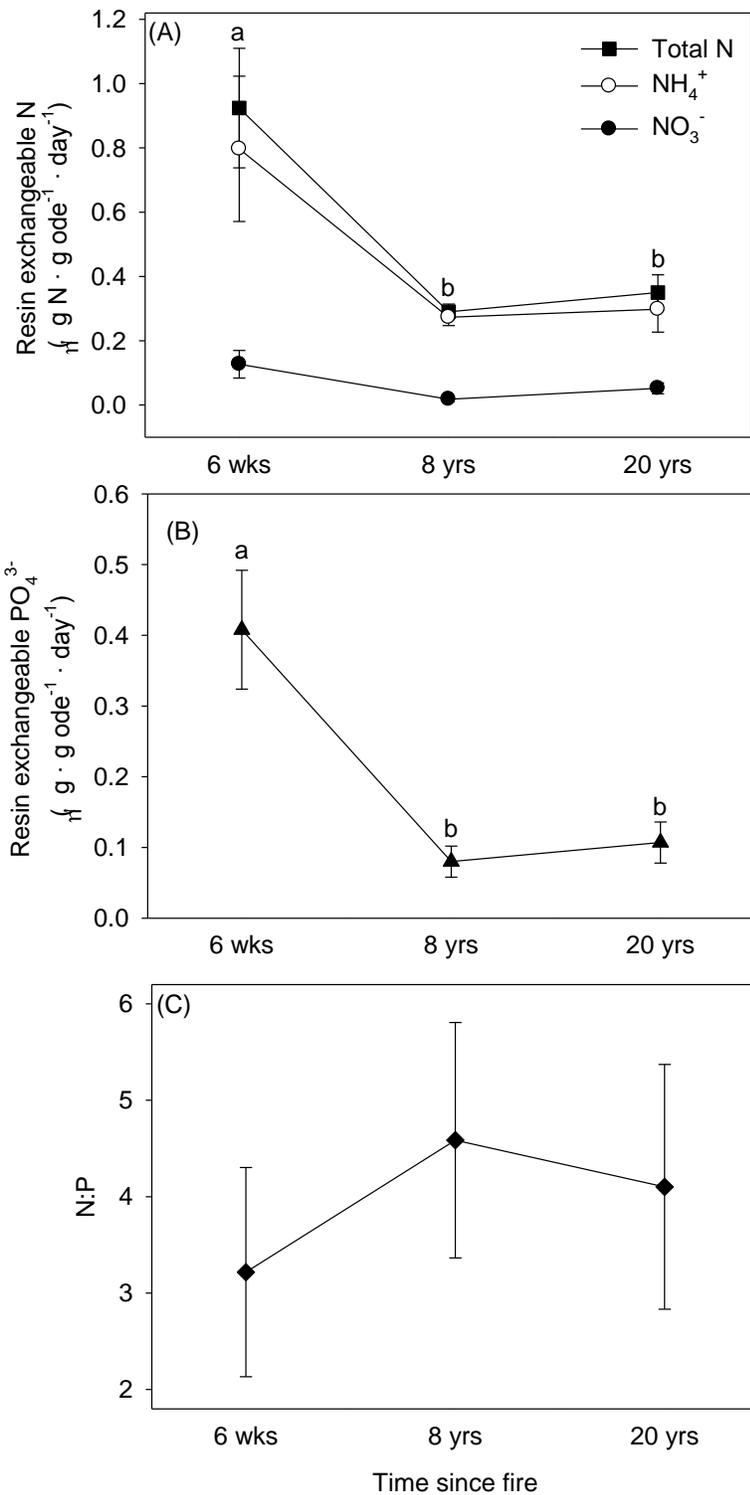


Figure 5-2. Mean (\pm se) resin exchangeable inorganic N (A), phosphorus (B), and N:P ratios (C) in control plots over one year. Different letters represent significant differences at $\alpha = 0.05$.

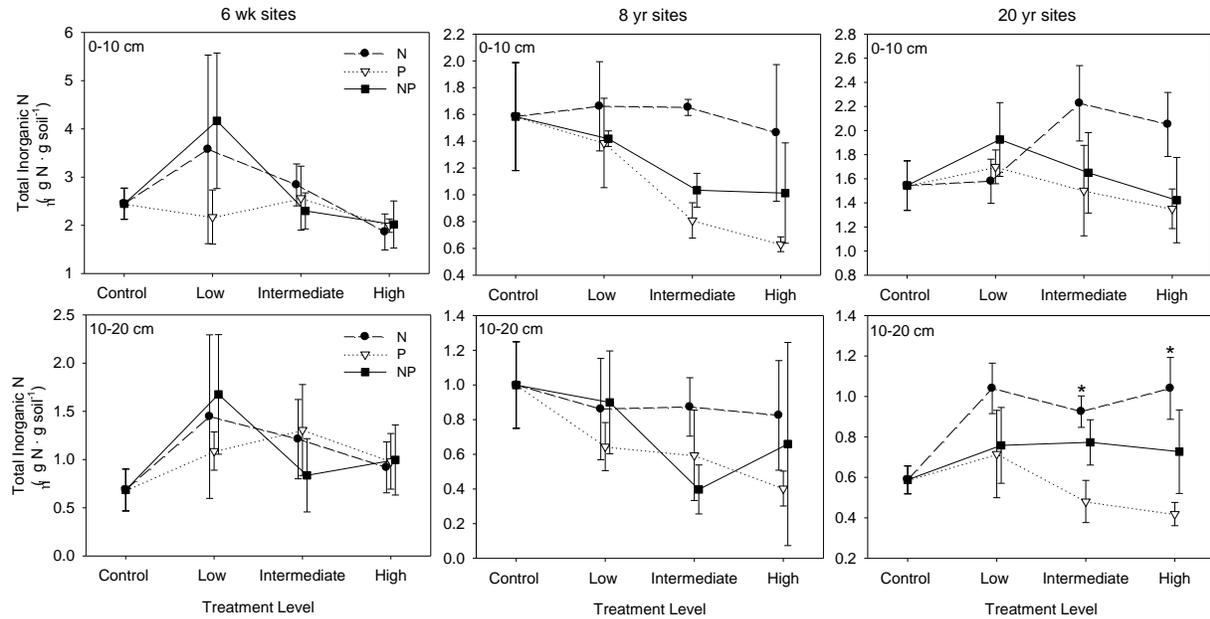


Figure 5-3. Mean (\pm se) soil extractable inorganic N in surface (0-10 cm) and deep (10-20 cm) soils in control and treatment plots in sites 1 year, 9 years, and 21 years after fire. * indicates a treatment is different from the control at $\alpha = 0.05$.

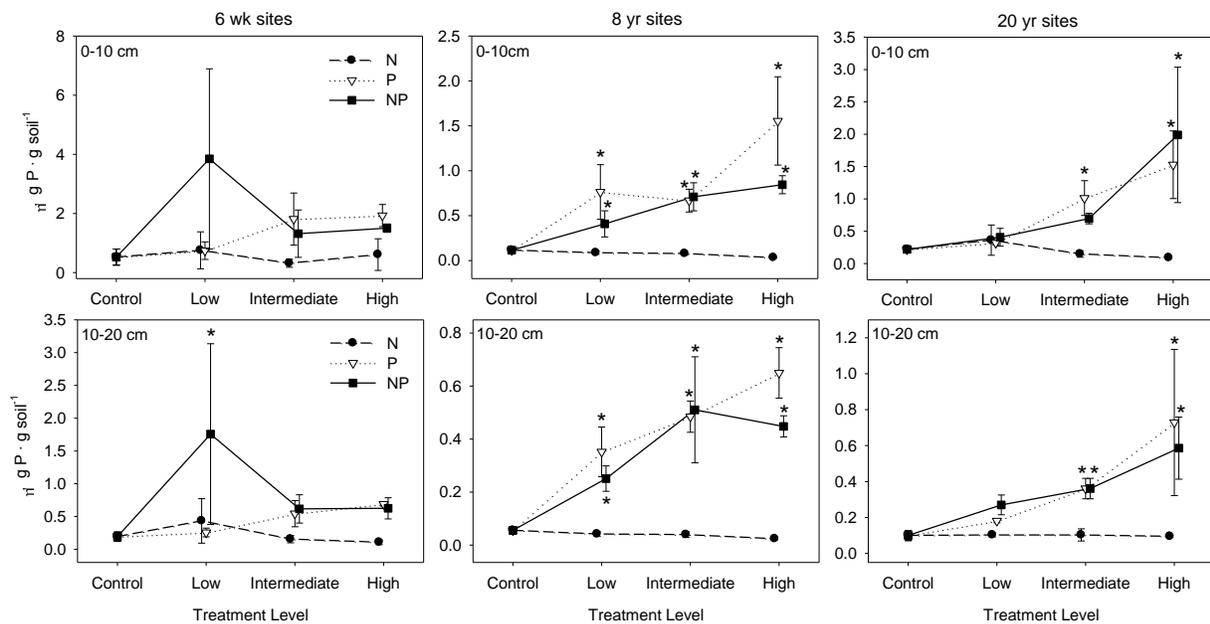


Figure 5-4. Mean (\pm se) soil extractable P in surface (0-10 cm) and deep (10-20 cm) soils in control and treatment plots in sites 1 year, 9 years, and 21 years since fire. * indicates a treatment is different from the control at $\alpha = 0.05$.

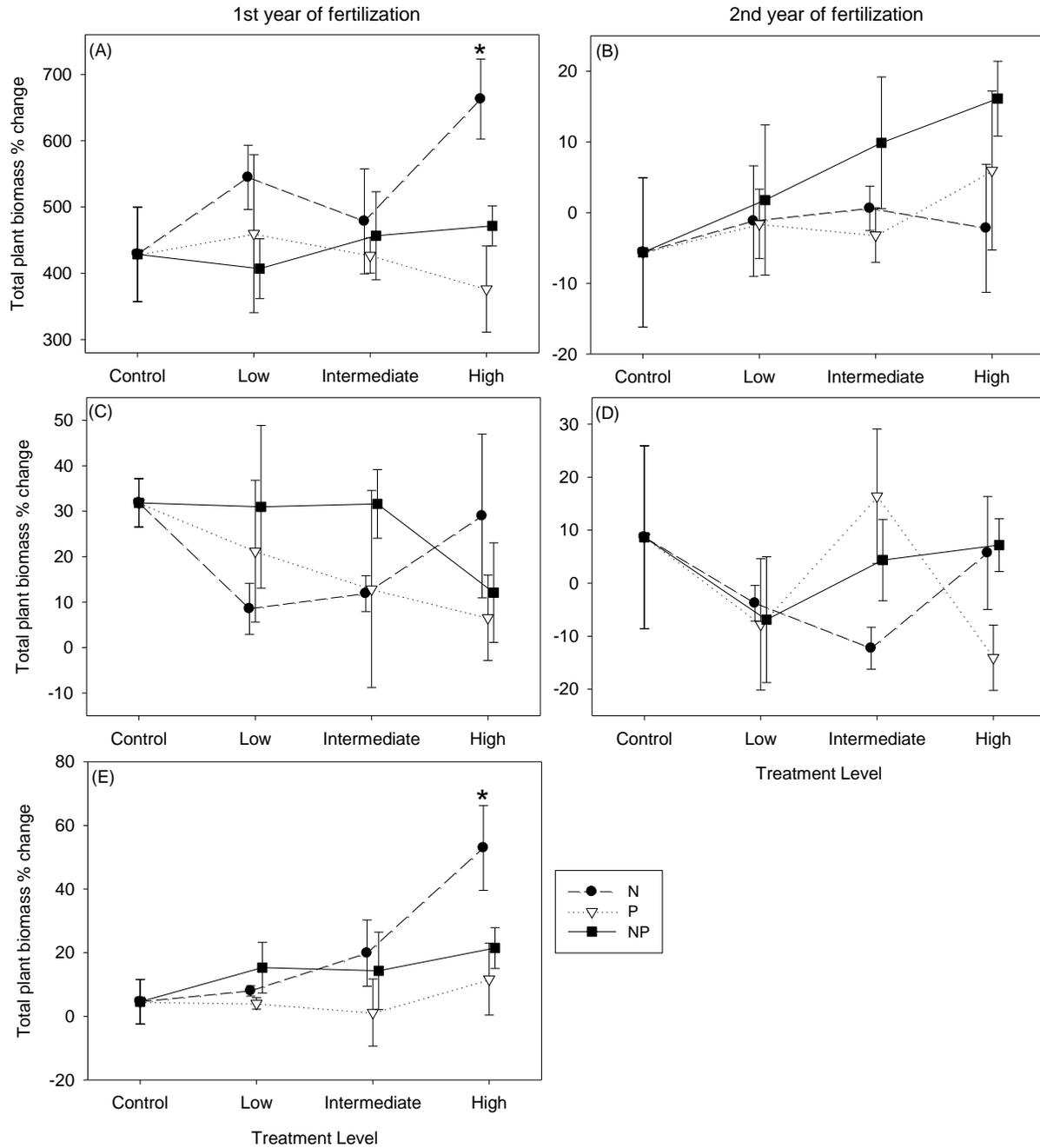


Figure 5-5. Mean (\pm se) percent change in *Serenoa repens* biomass during the first and second years of fertilization in sites 6 weeks (A,B), 8 years (C,D), and 20 years (E) since fire. * indicates a treatment is significantly different from the control at $\alpha = 0.05$.

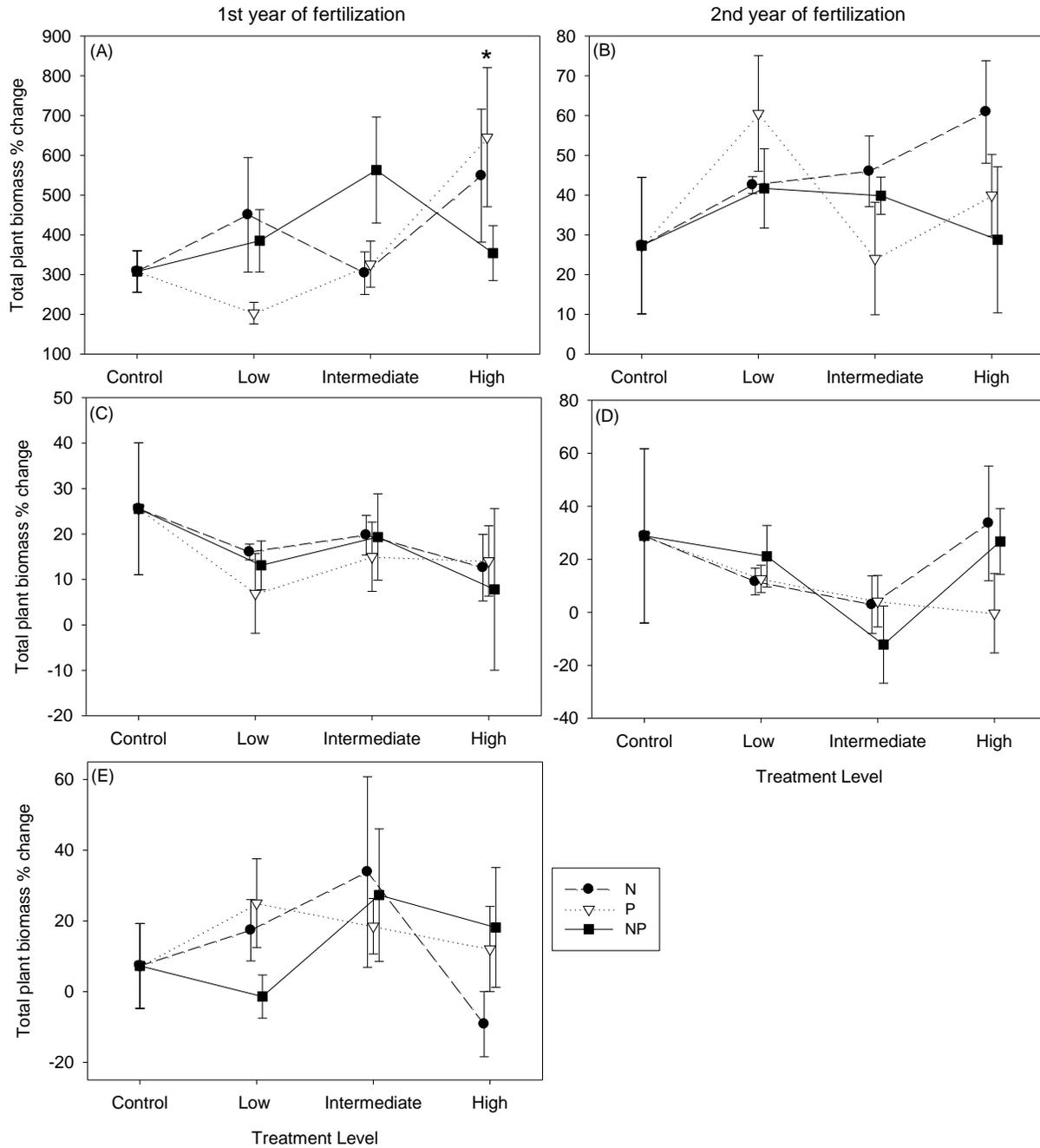


Figure 5-6. Mean (\pm se) percent change in *Quercus inopina* plant biomass during the first and second years of fertilization in sites 6 weeks (A,B), 8 years (C,D), and 20 years (E) since fire. * indicates a treatment is different from the control at $\alpha = 0.05$.

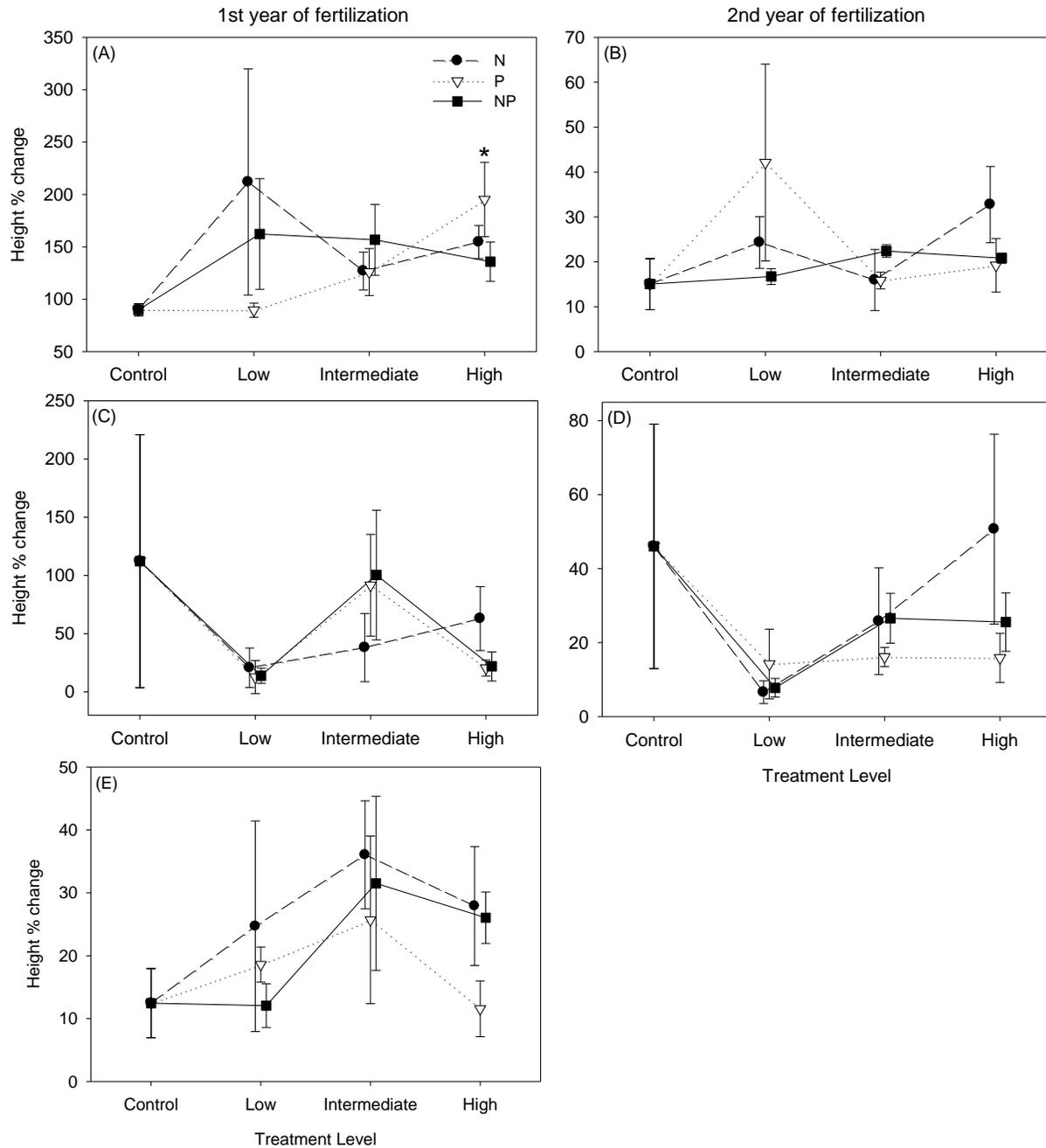


Figure 5-7. Mean (\pm se) percent change in *Quercus inopina* stem height during the first and second years of fertilization in sites 6 weeks (A,B), 8 years (C,D), and 20 years (E) since fire for stems alive during each year of fertilization. * indicates a treatment is different from the control at $\alpha = 0.05$.

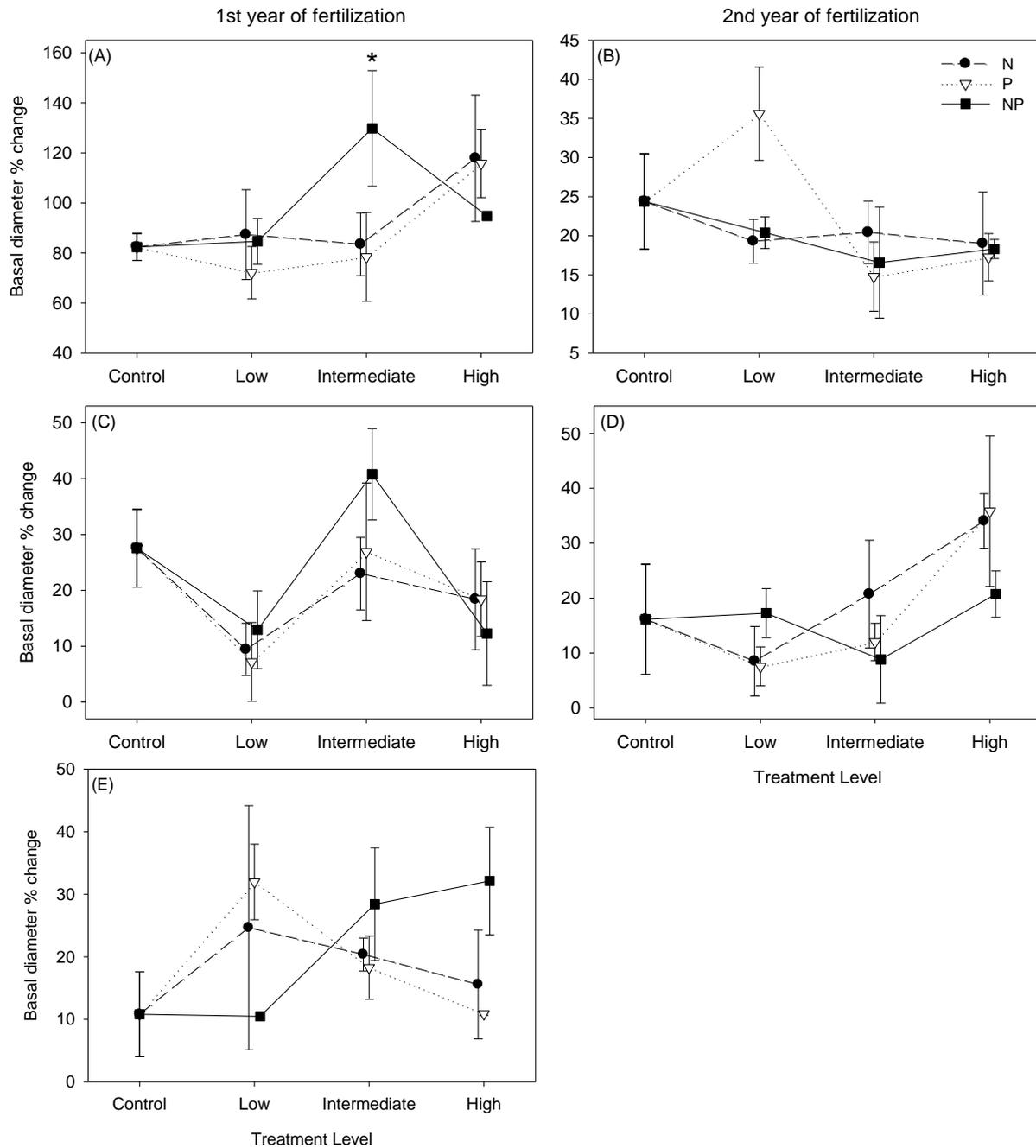


Figure 5-8. Mean (\pm se) percent change in *Quercus inopina* stem basal diameter during the first and second years of fertilization in sites 6 weeks (A,B), 8 years (C,D), and 20 years (E) since fire for stems alive during each year of fertilization. * indicates a treatment is different from the control at $\alpha = 0.05$.

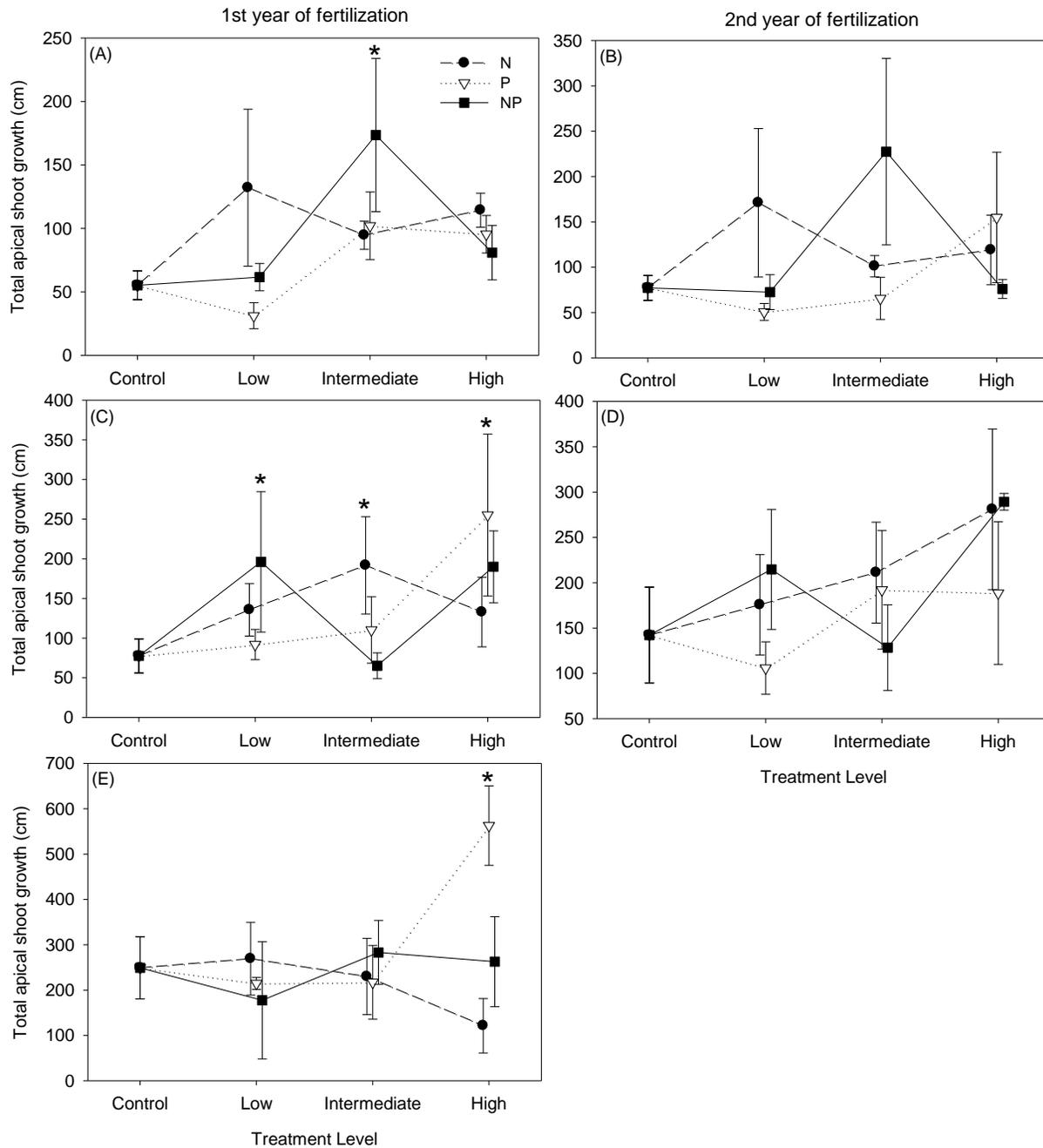


Figure 5-9. Mean (\pm se) length of *Quercus inopina* total apical shoot growth increments during the first and second years of fertilization in sites 6 weeks (A,B), 8 years (C,D), and 20 years (E) since fire. * indicates a treatment that is different from the control at $\alpha = 0.05$.

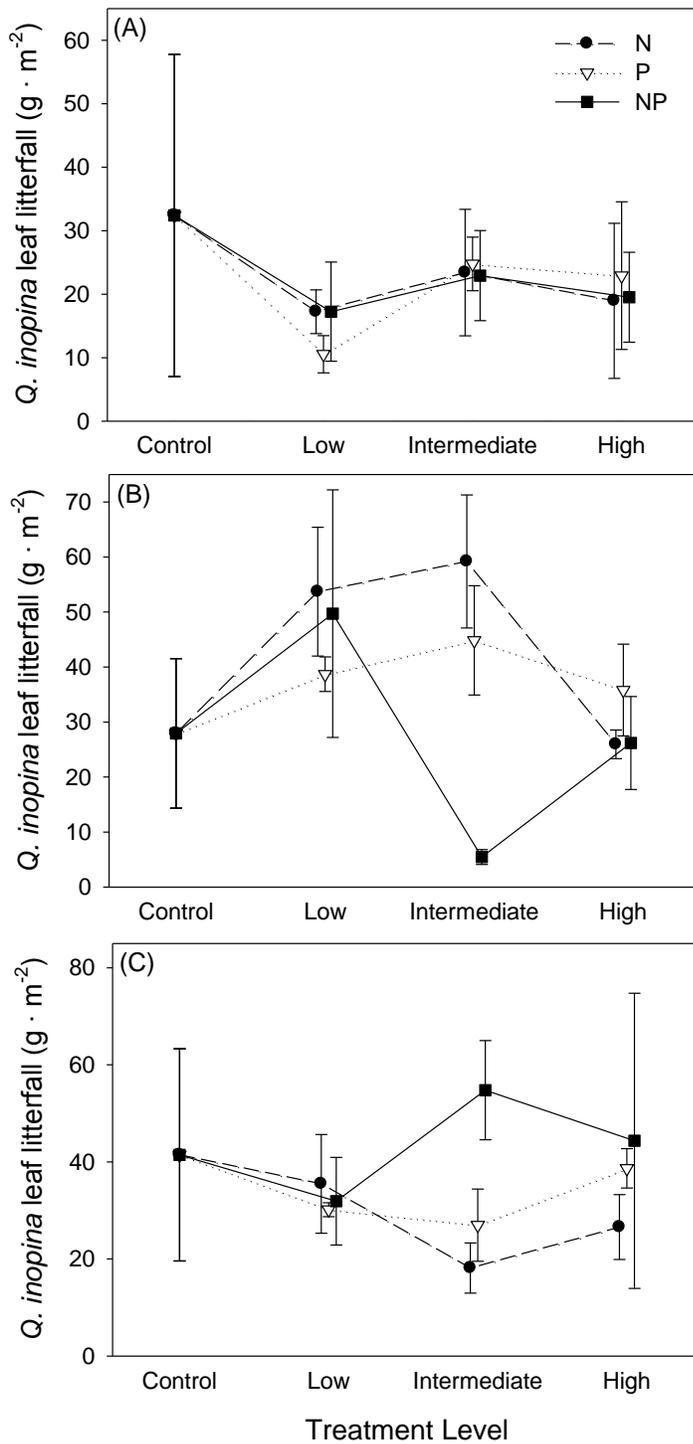


Figure 5-10. Mean (\pm se) *Quercus inopina* leaf litterfall from March to May ($\text{g} \cdot \text{m}^{-2} \cdot 2 \text{ mos}^{-1}$) during the first year of fertilization in sites 6 weeks (A), 8 years (B), and 20 years (C) after fire.

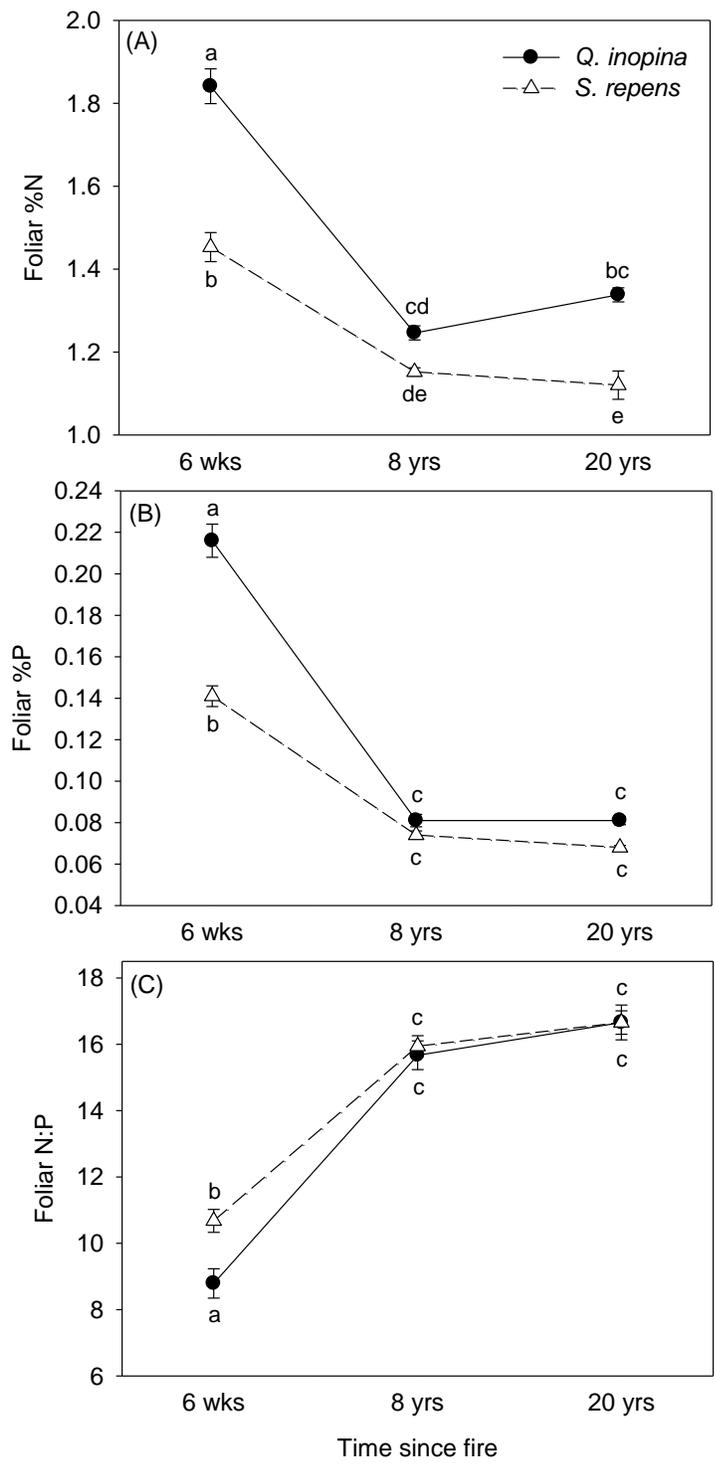


Figure 5-11. Mean (\pm se) foliar %N (A), foliar %P (B), and foliar N:P ratios of *Quercus inopina* and *Serenoa repens* 6 weeks, 8 years, and 20 years since fire in all plots pre-fertilization. Different letters represent significantly different means at $\alpha = 0.05$.

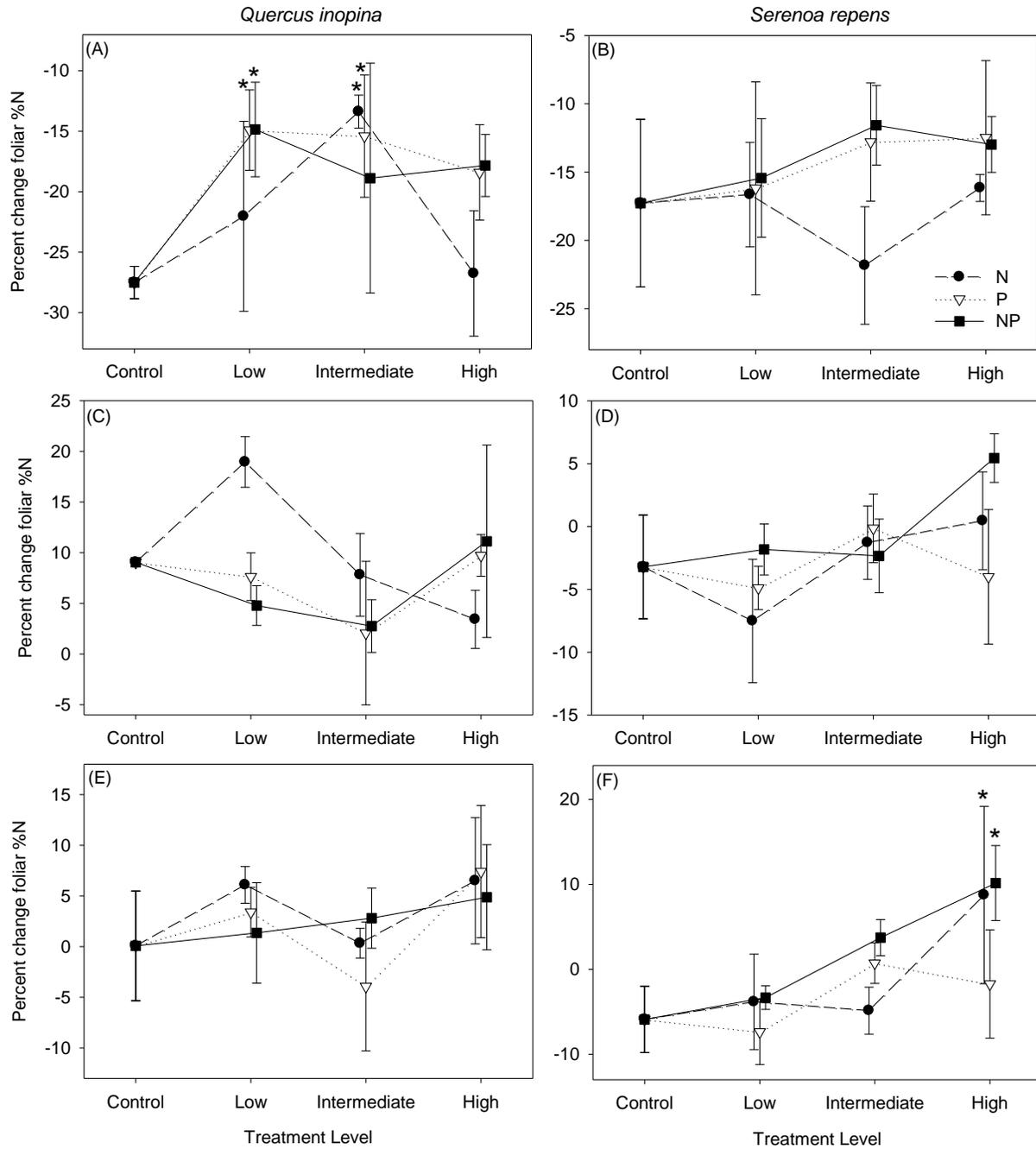


Figure 5-12. Mean (\pm se) percent change in foliar %N of *Q. inopina* and *S. repens* over the first year of fertilization in sites 6 weeks (A,B), 8 years (C,D), and 20 years (E,F) after fire. * indicates a treatment is different from the control at $\alpha = 0.05$.

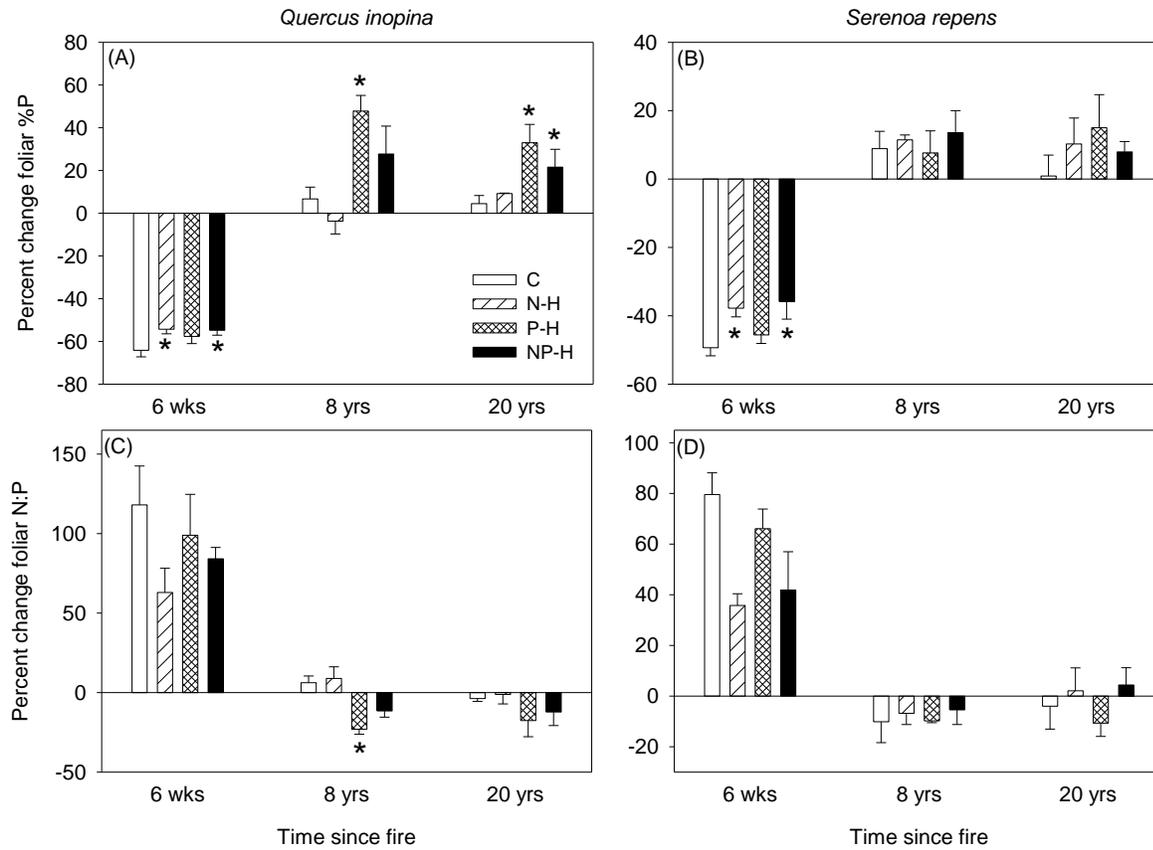


Figure 5-13. Mean (\pm se) percent change in foliar %P (A,B) and N:P ratios (C,D) of *Q. inopina* and *S. repens* over the first year of fertilization. * indicates a treatment is different from the control at $\alpha = 0.05$.

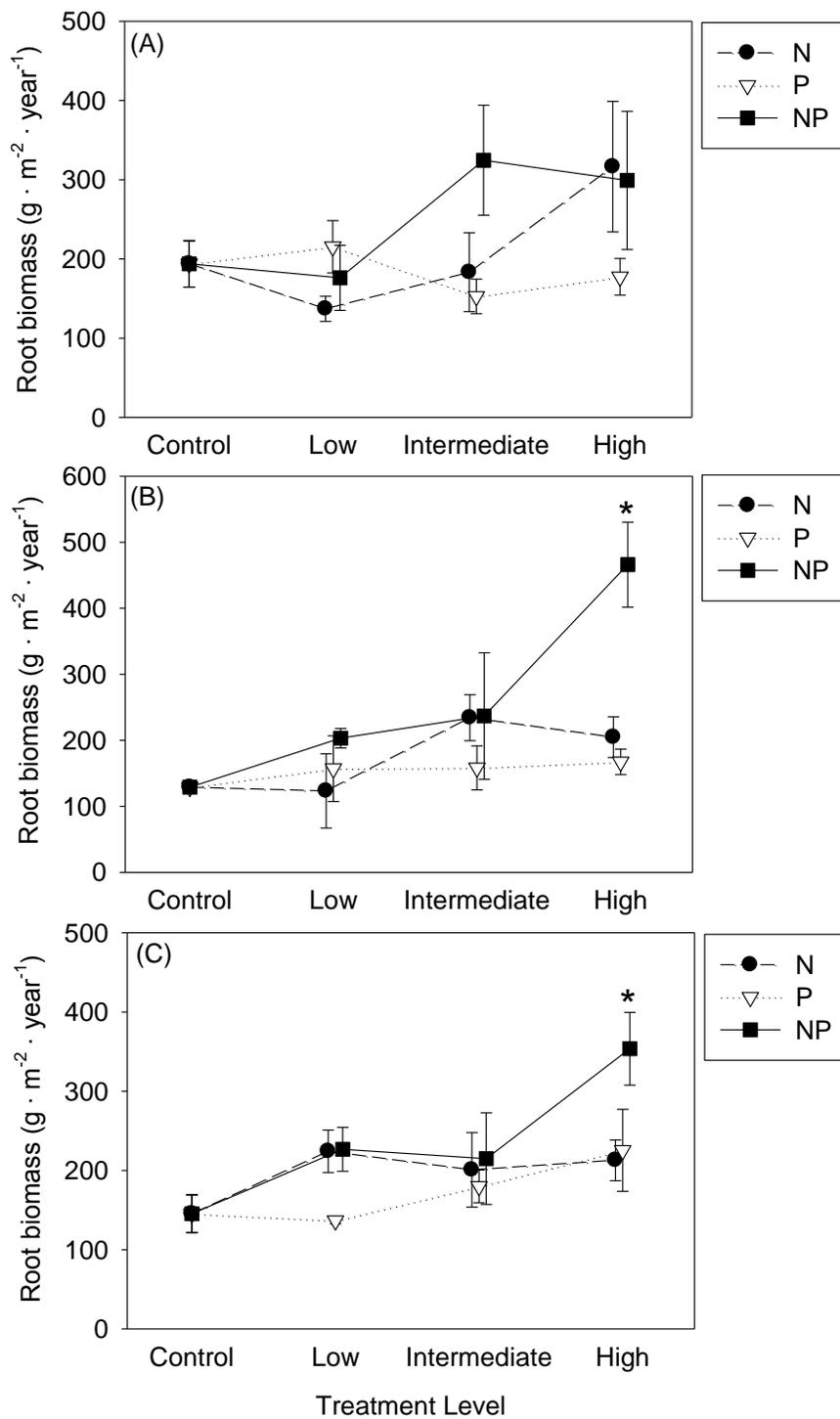


Figure 5-14. Mean (\pm se) root productivity during the first year of fertilization. * indicates a treatment is significantly different from the control at $\alpha = 0.05$.

CHAPTER 6 CONCLUSION

Previous research in Florida scrub ecosystems has found limited effects of fire on soil nutrient availability (Schmalzer and Hinkle 1991). I found that a pulse of nutrients is detectable if soils are sampled soon enough after fire. Fire caused a short-term increase in soil NH_4^+ and PO_4^{3-} in a palmetto flatwoods ecosystem; 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. The relative increase in soil and foliar P was greater than that of soil and foliar N, leading to a decrease in the soil N:P ratio and the foliar N:P ratio of the palmetto *Serenoa repens* shortly after fire. The difference in the magnitude of the decrease in soil and foliar N:P ratios after fire coupled with measurements of soil and foliar $\delta^{15}\text{N}$ suggest that both increased soil nutrient availability and reallocation of nutrients from belowground to aboveground tissue contribute to the increase in foliar %N and %P shortly after fire. My results suggest that even a short-term increase in soil nutrient availability can be important for plant nutrient status, especially in ecosystems with low nutrient availability.

Overall, growth, allocation of resources to aboveground tissues, and allometric equations tended to differ with time after fire, but the majority of differences occurred among species and between recently burned and intermediate and longer unburned sites. Resprouting ability of scrubby flatwood species appears to be important in determining growth and allometry immediately after fire. Six weeks after fire, *Quercus inopina*, the dominant species in my scrubby flatwoods study sites, had the highest height:diameter ratio and the highest leaf:stem biomass ratio. The ability of *Q. inopina* to

resprout and acquire aboveground space after fire may contribute to the maintenance of its dominance in the sites where it occurs.

The fire return interval for scrubby flatwoods is 8-16 years (Menges 2007), and there was little or no difference in plant size, biomass, or allometric relationships from 8-22 years after fire within a species; however, there were differences among species within these times after fire. Thus, as time after fire increases, species specific constraints in growth and allometry appear to become more important. My results also suggest that caution should be taken in using allometric equations developed for plants from longer unburned sites to estimate biomass of plants in recently burned sites.

In scrubby flatwoods soils, inorganic N availability was not affected by time after fire, but is related to soil moisture, while variation in resin exchangeable PO_4^{3-} was related to soil pH. Resin exchangeable N was highest eight years after fire and resin exchangeable PO_4^{3-} was highest 13 years after fire, so N:P ratios increased then decreased with time after fire. Other measures of soil N (mineralization rates, %N, chloroform labile microbial N) were highest in surface soils (0-5 cm) in sites 13 years after fire. In addition, soil %C was highest in sites 13 years after fire.

The increased in soil N and C in long unburned sites may be due to the differences in species composition and fire history of sites 13 years after fire compared to scrubby flatwood sites of other times after fire rather than the direct effects of time after fire. In this study, sites 13 years since fire had numerous pine trees, high soil organic matter, and had only been burned once in the past 35 years, which may have contributed to high PO_4^{3-} , soil %N, and soil %C in surface soils; however, in scrubby flatwoods sites 20 years after fire with low soil organic matter, and where pines are less

abundant or absent, soil %N and %C are lower (J. Schafer, unpublished data). Thus, my results indicating high nutrient availability in long unburned scrubby flatwoods may not apply to all scrubby flatwoods. Species composition and fire frequency, as well as time after fire, appear to be important in affecting nutrient availability in Florida scrub soils. Management of scrubby flatwoods ecosystems should include burning every 8-16 years (Menges 2007). My results suggest that the trajectory of nutrient availability and accumulation may change if fire is suppressed or not prescribed at the suggested return intervals.

The effects of nutrient addition on biomass and growth depend on time after fire. Over the first year of fertilization in recently burned sites, aboveground biomass and growth of *Quercus inopina* responded to P and N + P addition, while aboveground biomass of *Serenoa repens* responded to N addition. Nutrient addition had no effect on leaf litterfall or root productivity. Thus, resprouts of scrubby flatwoods shrubs are able to respond to nutrient addition above nutrients made available by fire, and they do so by increasing aboveground growth. Different species, however, appear to be limited by different nutrients. Eight years after fire, apical shoot growth and foliar %P of *Q. inopina* increased with nutrient addition, and high N + P addition increased root productivity. At intermediate times after fire, scrubby flatwoods shrubs appear to invest more in belowground than aboveground productivity and show co-limitation by N and P with a stronger P-limitation. Twenty years after fire, N addition increased biomass and foliar %N of *S. repens*, P addition increased apical shoot growth of *Q. inopina*, and N + P addition increased root productivity. In long unburned sites, scrubby flatwoods appear to invest in both aboveground and belowground productivity and show co-limitation by N

and P. Thus, my results support my hypothesis that plant productivity in long unburned scrubby flatwoods is co-limited by N and P. My hypotheses that plant productivity in recently burned scrubby flatwoods is N-limited and plant productivity in intermediately burned scrubby flatwoods is P-limited, however, are only partially supported.

In sites that were fertilized for two years, any increase in biomass or growth with nutrient addition occurred during the first year of fertilization. Dominant scrubby flatwoods species were only able to respond to one years of increased nutrient availability, which is what would occur naturally after fire (Chapter 1). This suggests that shrubs are adapted to respond to nutrients made available by fire, but may not be capable of increased growth above what is possible with nutrients made available by fire. Alternatively, microbes may be better competitors for nutrients than plants, and if fire caused a decrease in microbial biomass, over the second year of fertilization in recently burned sites, once microbes had recovered, microbial uptake of nutrients could have limited the response of plants to nutrient addition. In addition, the sandy soils of scrubby flatwoods likely have a limited ability to retain added nutrients, and in the second year of fertilization added nutrients could have leached from the soil such that plants were not able to acquire the added nutrients. I only fertilized scrubby flatwoods for one or two years, which is a short time in the 8-16 year fire return interval of scrubby flatwoods (Menges 2007). Perhaps over a longer time period, shrubs would be able to adapt to elevated nutrient availability rather than just a pulse of nutrients.

Large areas of land along the Lake Wales Ridge have been converted to agriculture and pastureland, leading to increased nutrient inputs. Some of these areas are now being restored to Florida scrub. My results suggest that managing with fire

should cause pulses of nutrient availability that can be used by plants and maintaining the proper fire return intervals could lead to patterns of nutrient availability similar to native scrub soils. Phosphorus increased growth of *Quercus inopina* and N increased growth of *Serenoa repens*, suggesting that these species may occupy different niches in scrubby flatwoods communities. Because scrub species are adapted to low nutrient availability and fire-related increases in nutrient availability, and only increased aboveground growth during the first year of nutrient addition, the increased availability of nutrients in restoration sites may have limited benefits for native shrub species.

APPENDIX A SHORT-TERM EFFECTS OF FIRE ON SOIL AND PLANT NUTRIENTS IN SCRUBBY FLATWOODS

Scrubby flatwoods are dominated by scrub oak (*Quercus inopina*), sand live oak (*Quercus geminata*), palmettos, and ericaceous shrubs. The shrubs are evergreen with an average height of 1-2 m, and herbaceous species are sparse (Abrahamson et al. 1984). Soils are entisols (Abrahamson et al. 1984) with no horizon development, little organic matter, and low exchange capacity and base saturation (Brown et al. 1990). Scrubby flatwoods experience fire return intervals of 8-16 years (Menges 2007), and dominant species resprout after fire. Because scrubby flatwoods have low standing biomass and patches of bare sand, fires often create a mosaic of unburned to intensely burned areas (Abrahamson et al. 1984).

I randomly selected six sampling locations within the scrubby flatwoods vegetation association in a 34 acre burn unit that had previously burned in 1994. At all sampling locations, which were separated by at least 10m, we marked a soil sampling site and the nearest individual of six different species (when present within 1m of the soil sampling location). My focal species, all of which resprout after fire, were the shrubs *Lyonia lucida*, *Quercus geminata*, and *Quercus inopina*, the palmettos *Sabal etonia* and *Serenoa repens*, and the sub-shrub *Vaccinium myrsinities*. On March 14th, 2006, I collected a soil sample (0-15cm depth, 8cm diameter core) at each sampling site and collected a foliar sample from all marked individuals. A prescribed fire was initiated on March 15th, 2006, but had to be extinguished due to high winds (K. Main, pers. comm.), and the fire was re-ignited on March 16th, 2006. The fire was patchy with burned and unburned areas; of my marked plants, 15 were consumed by the fire, 13 were scorched and two were unburned. The maximum one minute average temperature recorded was

680°C, while the absolute maximum temperature recorded was 870°C (E. Menges, unpubl. data). Post-fire soil samples were collected on March 17th, May 8th, July 17th, and October 5th, 2006. The first post-fire foliar samples were collected on May 8th, 2006, but all marked plants had not yet resprouted. Subsequent post-fire foliar collections were made on July 17th, 2006 and October 6th, 2006.

Soil samples were returned to the lab, passed through a 2 mm sieve, and then sub-sampled for determination of pH, total percentages of N and C, and extractable P. Soil pH was measured as described above. Soil subsamples for determination of percent N and C were dried at 60°C for 48 hr then ground to a fine powder with a mortar and a pestle. Leaf samples were dried at 60°C for 48 hours and ground on a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) with a no. 40 screen. Soil and foliage was analyzed for percentages of N and C at the University of Florida on an ECA 4010 elemental analyzer (Costech Analytical, Valencia, California, USA). Foliar P was measured as describe above.

To measure inorganic P concentrations, 30 mL of 0.05 M hydrochloric acid (HCl) and 0.0125 M hydrogen sulfate (H₂SO₄) was added to 15 g of air dried soil, shaken for 5 min, then filtered through Whatman #42 filter paper. Filtered samples were stored in a refrigerator for several days before analysis for phosphate (PO₄³⁻) concentrations on an absorbance microplate reader at the University of Florida using the ascorbic acid molybdenum-blue method (Murphy and Riley 1962).

All data were analyzed using repeated measures analysis of variance to examine changes in variables over time after fire. Variable means were compared with

Bonferroni confidence interval adjustments. Non-normal data were transformed to meet the assumptions of normality. All other data were analyzed using SPSS 11.5.

Soil pH tended to increase over time after fire; however, there were no differences in soil %N, %C, or C:N with time since fire. Although there was not a significant difference in soil P over time after fire, soil P tended to increase then decrease (Table A-1).

For *S. repens* present at the first sampling date, foliar %N and foliar %P increased over time after fire (Figure A-1), and foliar N:P varied over time (Table A-2). Foliar %N of *Q. geminata* and *Q. inopina* increased after fire (Figure A-2). *Sabal etonia* had new leaves by the second sampling date and foliar %N increased over time (Table A-2). Foliar %N of ericaceous species tended to be higher post-fire than pre-fire regardless of the time of first resprouting (Figure A-2).

Foliar %N of the palmettos *S. repens* and *S. etonia* increased over time, while foliar %N of oaks and ericaceous species tended to increase then decreased over time after fire (Figures A-2 and A-3). This suggests that different mechanisms may be causing the observed changes in foliar %N for different species in the same habitat. The ratio of belowground to aboveground biomass of palmettos and oaks in scrubby flatwoods is 7.35 and 2.13, respectively (Saha et al. in review). Higher root to shoot ratios may confer palmettos with a greater capacity to retranslocate nutrients from belowground to aboveground, allowing palmettos in scrubby flatwoods to continue to increase foliar %N after soil N availability has returned to pre-fire levels.

Table A-1. Mean (+ se) of soil variables measured in the scrubby flatwoods site before fire and after fire with results of repeated measures analyses. Degrees of freedom = 4 for all variables.

Variable	F	p	Pre-Fire	Days Post-Fire			
				1	52	122	202
pH*	5.28	0.028	4.44 + 0.17	4.56 + 0.17	4.65 + 0.25	5.11 + 0.26	5.09 + 0.26
P ($\mu\text{g} \cdot \text{g} \cdot \text{soil}^{-1}$)	2.10	0.118	2.25 + 0.39	5.02 + 1.33	4.16 + 0.85	3.87 + 0.85	3.39 + 1.64
%C*	2.06	0.124	1.46 + 0.32	2.09 + 0.61	1.14 + 0.30	1.38 + 0.27	1.11 + 0.35
%N*	2.28	0.096	0.056 + 0.011	0.076 + 0.021	0.041 + 0.009	0.049 + 0.008	0.042 + 0.014
C:N	0.85	0.512	25.68 + 1.68	26.98 + 1.55	26.47 + 2.04	27.73 + 1.43	26.56 + 1.32

* data were natural log transformed

Table A-2. Results of repeated measures analyses of variance for foliar %N, %P, and N:P ratios. Ericaceae includes *L. lucida* and *V. myrsinites*. The number in parentheses indicates the number of post-fire sampling dates based on time of resprouting.

	%N			%P			N:P		
	F	df	p	F	df	p	F	df	p
<i>Quercus geminata</i> (3)	86.41	3	< 0.001						
<i>Quercus geminata</i> (2)	5.66	2	0.068						
<i>Quercus inopina</i> (3)	11.12	3	0.001						
<i>Sabal etonia</i> (2)	31.71	2	< 0.001						
<i>Serenoa repens</i> (3)	14.50	3	< 0.001	16.32	3	< 0.001	5.35	3	0.014
Ericaceae (3)	10.13	3	0.009						
Ericaceae (1)	80.41	1	0.071						

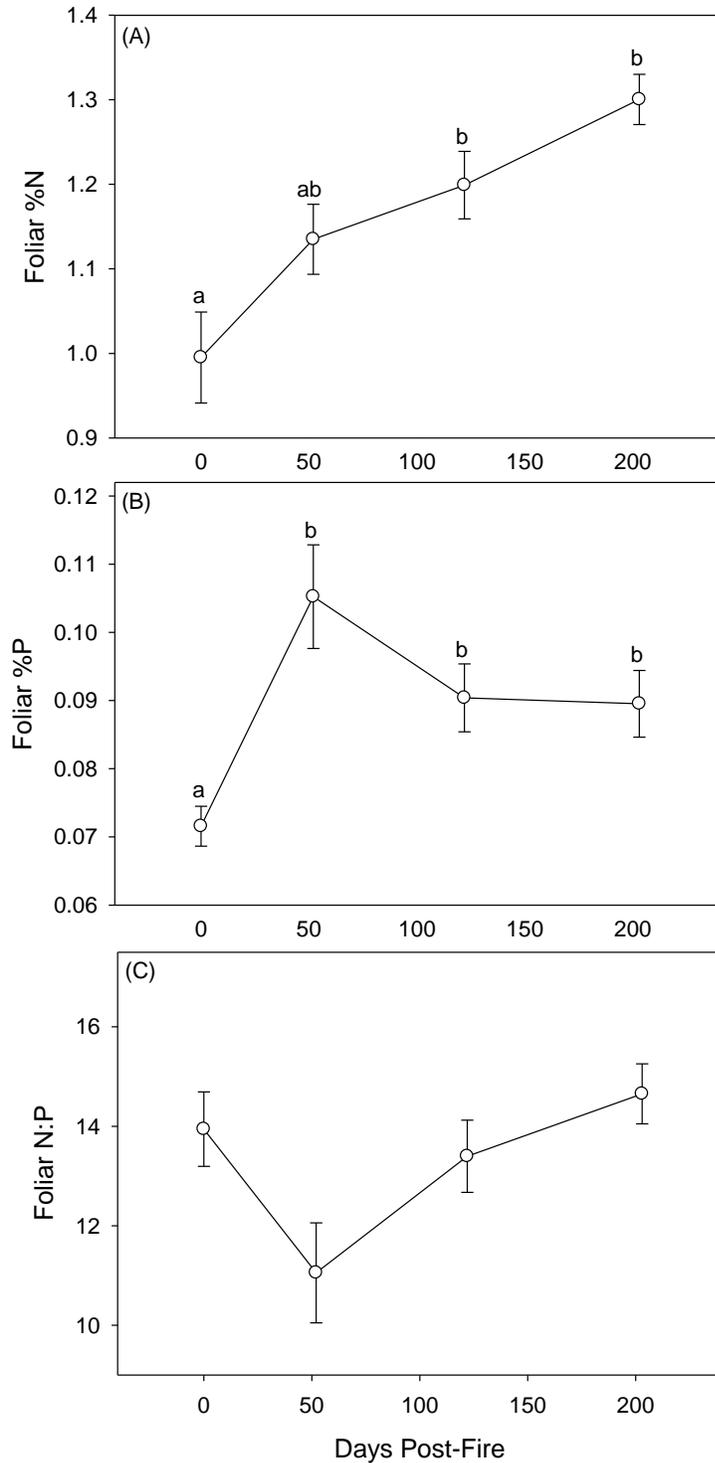


Figure A-1. Mean (\pm se) foliar %N (A), foliar %P (B), and foliar N:P ratios (C) of *S. repens* in scrubby flatwoods ($n = 5$). Different letters represent significant differences in mean values at $\alpha = 0.05$.

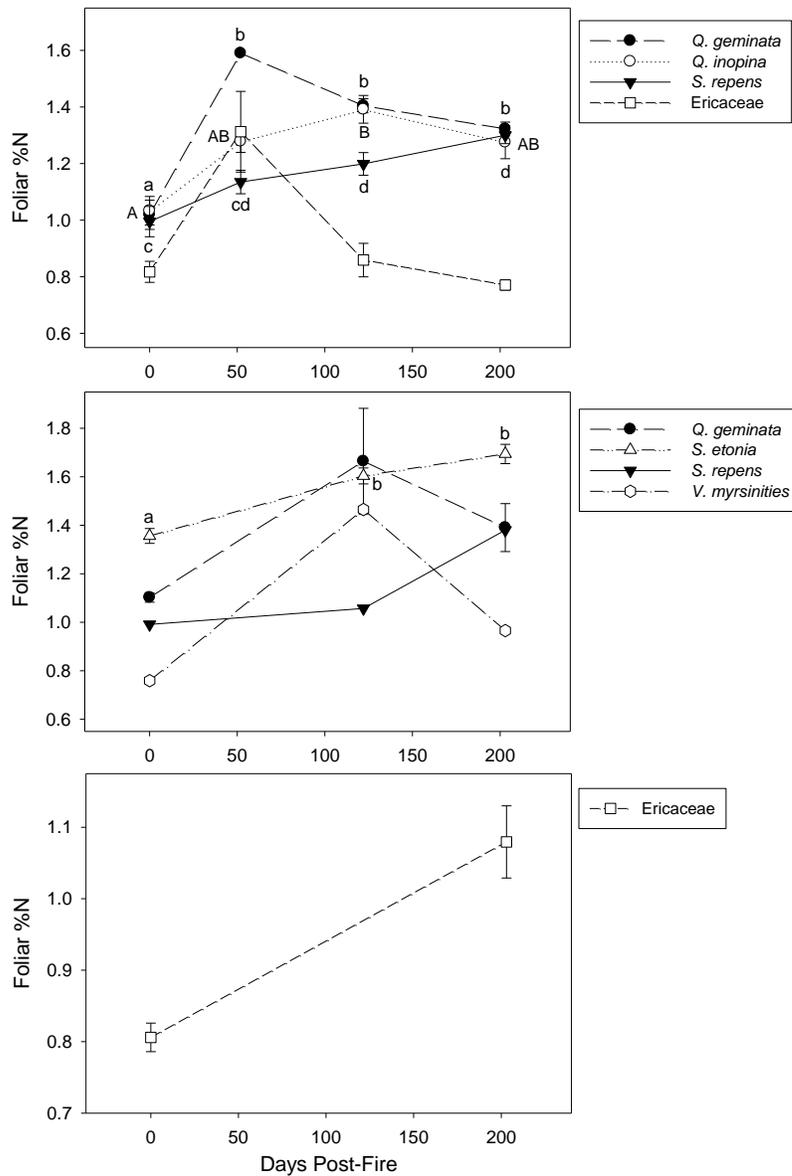


Figure A-2. Mean (\pm se) foliar %N of plants in scrubby flatwoods pre-fire and over time post-fire. Top panel: plants present at three sampling dates post-fire ($n = 3, 5, 5,$ and 3 for *Q. geminata*, *Q. inopina*, *S. repens*, and Ericaceae, respectively). Different letters represent significantly different means at $\alpha = 0.05$ (*Q. geminata*: lowercase a and b; *Q. inopina*: uppercase; *S. repens*: lowercase c and d); Middle panel: plants present at two sampling dates post-fire ($n = 3, 6, 1,$ and 1 for *Q. geminata*, *S. etonia*, *S. repens*, and *V. myrsinites*, respectively). Different letters represent significantly different means at $\alpha = 0.015$; Bottom panel: plants present at one sampling date post-fire ($n = 2$). Ericaceae includes *V. myrsinites* and *L. lucida*.

APPENDIX B
SEASONAL VARIATION IN RESIN EXCHANGEABLE NITROGEN AND
PHOSPHORUS IN SCRUBBY FLATWOODS

Seasonal effects may mediate fire effects on N and P availability. For instance, seasonality of precipitation causes variation in soil moisture, despite fire history (Todd et al. 2000), and net N mineralization is correlated with soil moisture (Evans et al. 1998; Frank 2008). Differences in NH_4^+ and NO_3^- with time since fire may be greater during the winter compared to the spring (Durán et al. 2009), suggesting that seasonality of plant growth and nutrient uptake influences fire effects on nutrient availability. Furthermore, fire severity varies with burn season, and short-term effects of fire on soil abiotic conditions and nutrient availability depend on burn season (Hamman et al. 2008). Thus, I was interested in how availability of N and P varies seasonally.

In May 2005, I established eighteen 30 x 30 m plots in scrubby flatwood communities (Abrahamson et al. 1984), three each in sites 1, 4, 6, 8, 10, and 13 years since fire. Within a time since fire, plots were located in different burn units when possible. Plots in the same burn unit were separated by at least 150 m and may have experienced differences in fire intensity. Overall, plots covered a distance of approximately four miles, and although summer thunderstorms can be patchy, all plots experience the same climate. All plots were established in scrubby flatwoods dominated by scrub oak (*Quercus inopina* Ashe) on flat or gently sloped sites. Thus, the climate, organisms, relief, and parent material were the same in all sites (Jenny 1941); the only state factor that varied among sites was time after fire. In each plot, I established 30m transects across each plot that were initiated at 5m, 10m, 15m, 20m, and 25m along the NW to SW side of the plot.

In all plots, I used ion exchange resins to measure soil nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}). At a random location on each transect, separate anion and cation exchange resin bags (5 x 5 cm) were placed in the top 5 cm of the soil and left in the field for 3 month intervals. Resin bags were in the field for one year continuously (Mid June – Mid Sept. 2005, Mid Sept. – Mid Dec. 2005, Mid Dec. 2005 – Mid March 2006, and Mid March – Mid June 2006). Before being buried in the field, anion and cation resin bags were charged with 2M HCl and 2M NaCl, respectively. After resin bags were removed from the field, they were rinsed with DI H_2O to remove dirt and any attached roots. Anion and cation resin bags were extracted with 50 mL of 0.5 M HCl and 0.5 M NaCl, respectively and shaken for six hours. Resin extracts were frozen and taken to the University of Florida where NO_3^- , NH_4^+ , and PO_4^{3-} concentrations were determined colorimetrically on a continuous flow autoanalyzer (Astoria-Pacific, Inc., Clackamas, Oregon, USA).

To analyze differences in resin exchangeable nutrients, I averaged transect values for each plot so that plot was the statistical unit. Resin bags that were found on the soil surface were not included in plot means; thus, the number of resin bags per plot ranged from one to five. For total inorganic N and N:P ratios, if either the cation or anion bag was found out of the ground, the site was not included in the plot mean. I used repeated measures analysis with date as the within-subjects factor and time since fire as the between-subjects factor to analyze differences in resin exchangeable nutrients. All data were natural log transformed before analyses. One N:P ratio outlier from the June-September sampling period was removed from the analysis because the N:P ratio was 232, which was nine standard deviations above the overall mean for June-

September. For all repeated measures analyses, when the assumptions of sphericity were not met, the degrees of freedom were adjusted using the Greenhouse-Geisser estimated epsilon values, which is a conservative correction (Field 2009), and differences among dates and times since fire were determined with post-hoc pairwise comparisons with Bonferroni confidence interval adjustments.

Monthly rainfall during the year of my study tended to be above average during the wet season and below average during the dry season (Figure B-1). Resin exchangeable NH_4^+ , NO_3^- , total inorganic N, PO_4^{3-} , and N:P ratios tended to increase from the wet to the dry season (Table B-1). Resin exchangeable NH_4^+ increased from the wet season (June-Sept) to the dry-wet transition period (March-June) and was 19 times greater in the dry-wet transition period than in the wet season (Figure B-2). Resin exchangeable NO_3^- was lowest during the late wet/early dry season (Sept-Dec). The ratio of NH_4^+ to NO_3^- was always greater than one and increased 23 fold between the wet season and the dry-wet transition period; thus, total inorganic N increased from the wet season to the dry-wet transition period, mirroring the change in resin exchangeable NH_4^+ over time. Resin exchangeable PO_4^{3-} showed the least amount of seasonal variation; the highest values, which occurred during the dry-wet transition period, were only 1.5 times greater than the lowest values, which occurred during the wet season. Resin extractable N:P ratios were greater during the dry/early wet season (Dec.-June) than the wet/early dry season (June-Dec.) and increased 4 fold from the wet season to the late dry/early wet season (Figure B-2).

Within a season, resin exchangeable N was not significantly correlated with resin exchangeable P (Table B-2). Resin exchangeable NH_4^+ , total inorganic N, and N:P

ratios were negatively correlated with rainfall, but there was not a significant correlation between resin exchangeable NO_3^- or PO_4^{3-} and rainfall (Figure B-3).

Resin exchangeable NH_4^+ , and thus total resin exchangeable N, varied seasonally in scrubby flatwoods, but although N mineralization increased with water addition, resin exchangeable N was negatively correlated with rainfall. Several mechanisms could explain why resin exchangeable NH_4^+ was high during the dry-wet transition period (March-June) when rainfall was low, or why resin exchangeable NH_4^+ was low during the early wet season (June-September) when rainfall was high. First, soil microbial biomass and activity is higher in wet than in dry soils (Tate and Terry 1980; Aguilera et al. 1999; Paradelo and Barral 2009). When rainfall, and thus soil moisture, is low, nitrification rates may be low, causing NH_4^+ to accumulate in soils. This is unlikely, however, because mineralization rates, as well as nitrification rates, are water limited in surface soils, suggesting that resin exchangeable NH_4^+ should be low. Second, plant nutrient uptake affects soil nutrient availability, and NH_4^+ and NO_3^- availability may be higher during the season when plants are not growing (Durán et al. 2009). Rainfall was lowest during the late dry season (March-June), and NH_4^+ could have accumulated on resins if plant N uptake low during this time period. This is unlikely, however, because oaks, the dominant shrubs in scrubby flatwoods, turn over their leaves from March-May (Abrams and Menges 1992), so oaks should be taking up N during this time period. Thus, I hypothesize that resin exchangeable NH_4^+ is negatively correlated with rainfall due to high leaching losses of N. Dissolved organic nitrogen (DON) contributes a large fraction of N lost from terrestrial ecosystems in runoff (Hedin et al. 1995; Schlesinger et al. 1999), particularly in unpolluted ecosystems

(Perakis and Hedin 2002). Atmospheric N deposition is relatively low in central peninsular Florida, and the ratio of DON:DIN in scrubby flatwood soils is greater than one, suggesting that DON makes up a large part of N losses in Florida scrub ecosystems. Losses of DON are positively related to rainfall (Perakis and Hedin 2002), and high rainfall in scrubby flatwoods may lead to high losses of DON. Early wet season rainfall in central peninsular Florida most often occurs as afternoon thunderstorms, and even short, heavy rain events could lead to N losses because DON losses are greatest during the beginning of rainfall events (Schlesinger et al. 1999). DON is a significant predictor of N mineralization rates in surface soils (0-5 cm) of scrubby flatwoods (Chapter 4). Low concentrations of DON contribute to low N mineralization rates, which contributes to low resin exchangeable NH_4^+ . Pérez et al. (2004) found that inorganic N availability is positively correlated with precipitation in forest soils, but the low water holding capacity of sandy scrub soils likely contributes to greater leaching losses. Total rainfall during my one year study period (1130 mm) was slightly lower than, but similar to, mean annual rainfall (1365 mm) at my study site, suggesting that during the average year, resin exchangeable N in scrubby flatwoods is similar to or lower than what I measured. Similar to my results, resin exchangeable N decreased over a rainfall gradient in tropical montane forests (Schuur and Matson 2001); however, the rainfall in all sites was higher than in scrubby flatwoods, and differences in resin exchangeable N were likely related factors such as redox potential.

Although N mineralization rates were positively affected by water availability (Chapter 3), resin exchangeable N was negatively correlated with rainfall. This difference in the effects of water on N availability is likely related to differences in

sampling methods. Resin exchangeable N was measured in an open system, which allowed for leaching losses; whereas, N mineralization and nitrification were measured in a closed system, which did not allow for leaching losses. In the field, N can be leached from the system; whereas, in lab incubations, N is contained. In addition, rainfall was correlated with resin exchangeable N over three months, while N mineralization was determined from one week incubations. In some cases, concentrations of NH_4^+ are positively correlated with soil water content (Todd et al. 2000) and soil moisture tracks rainfall in scrubby flatwoods (Weekley et al. 2007), suggesting that over short time scales, rain events that do not cause high leaching of DON may increase N mineralization, and thus NH_4^+ , in scrubby flatwood soils.

Resin exchangeable PO_4^{3-} varied seasonally in scrubby flatwoods, but was not significantly correlated with rainfall. Similarly, across a larger rainfall gradient in montane forests, resin available P was not correlated with rainfall (Schuur and Matson 2001). The ratio of resin exchangeable N:P was negatively correlated with rainfall. Although resin exchangeable PO_4^{3-} was not correlated with rainfall, there was a negative relationship between rainfall and total inorganic N, which drove the relationship between N:P and rainfall. The N:P acquisition activity ratio of soil enzymes is negatively related to mean annual precipitation (Sinsabaugh et al. 2008). This suggests that precipitation affects the activity of soil microbes in addition to affecting leaching of nutrients.

Table B-1. Results of repeated measures analyses of resin exchangeable nutrients. Date and the date by years since fire (YSF) interaction are within subject factors, and YSF is a between subject factor. All data were natural log transformed before analyses. When the assumption of sphericity was not met, the Greenhouse-Geisser correction for degrees of freedom was used.

	F	Df	P
NH₄⁺			
(μg ode⁻¹ day⁻¹)			
Date	65.26	3	<0.001
YSF	1.93	5	0.162
Date * YSF	1.11	15	0.381
NO₃⁻			
(μg ode⁻¹ day⁻¹)			
Date	11.51	2.006	<0.001
YSF	6.24	5	0.004
Date * YSF	1.98	10.028	0.083
Total Inorganic N			
(μg ode⁻¹ day⁻¹)			
Date	32.20	1.952	<0.001
YSF	1.02	5	0.446
Date * YSF	0.66	9.759	0.742
PO₄³⁻			
(μg ode⁻¹ day⁻¹)			
Date	6.33	3	0.001
YSF	2.96	5	0.058
Date * YSF	1.41	15	0.195
N:P			
Date	19.83	3	<0.001
YSF	3.92	5	0.024
Date * YSF	0.97	15	0.501

Table B-2. Partial correlation coefficients (controlling for the effects of time since fire) for resin exchangeable total inorganic N and PO_4^{3-} for each sampling period and over one year.

Time period	R	df	p
June – September	-.026	82	0.409
September – December	-.154	79	0.085
December – March	.109	65	0.190
March – June	-.049	73	0.336
Total per year	.199	87	0.031

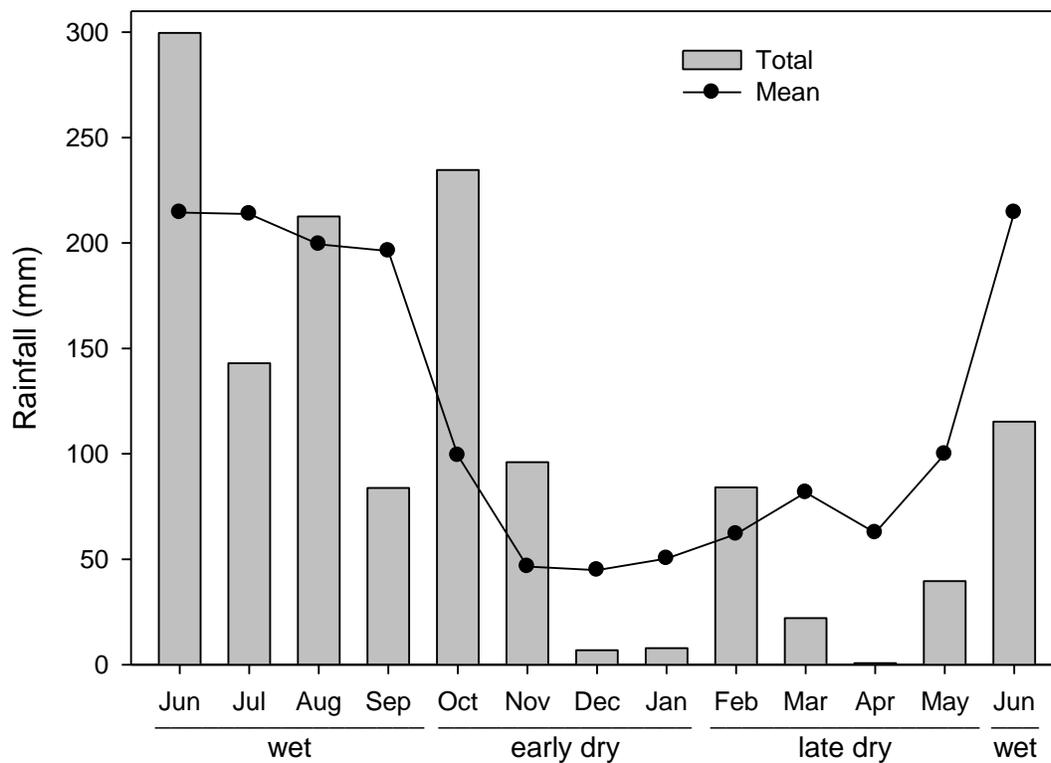


Figure B-1. Mean monthly rainfall (1932-2005) and total monthly rainfall during my study period (June 2005-June 2006) at Archbold Biological Station by soil moisture season. Modified from Weekley et al. 2007.

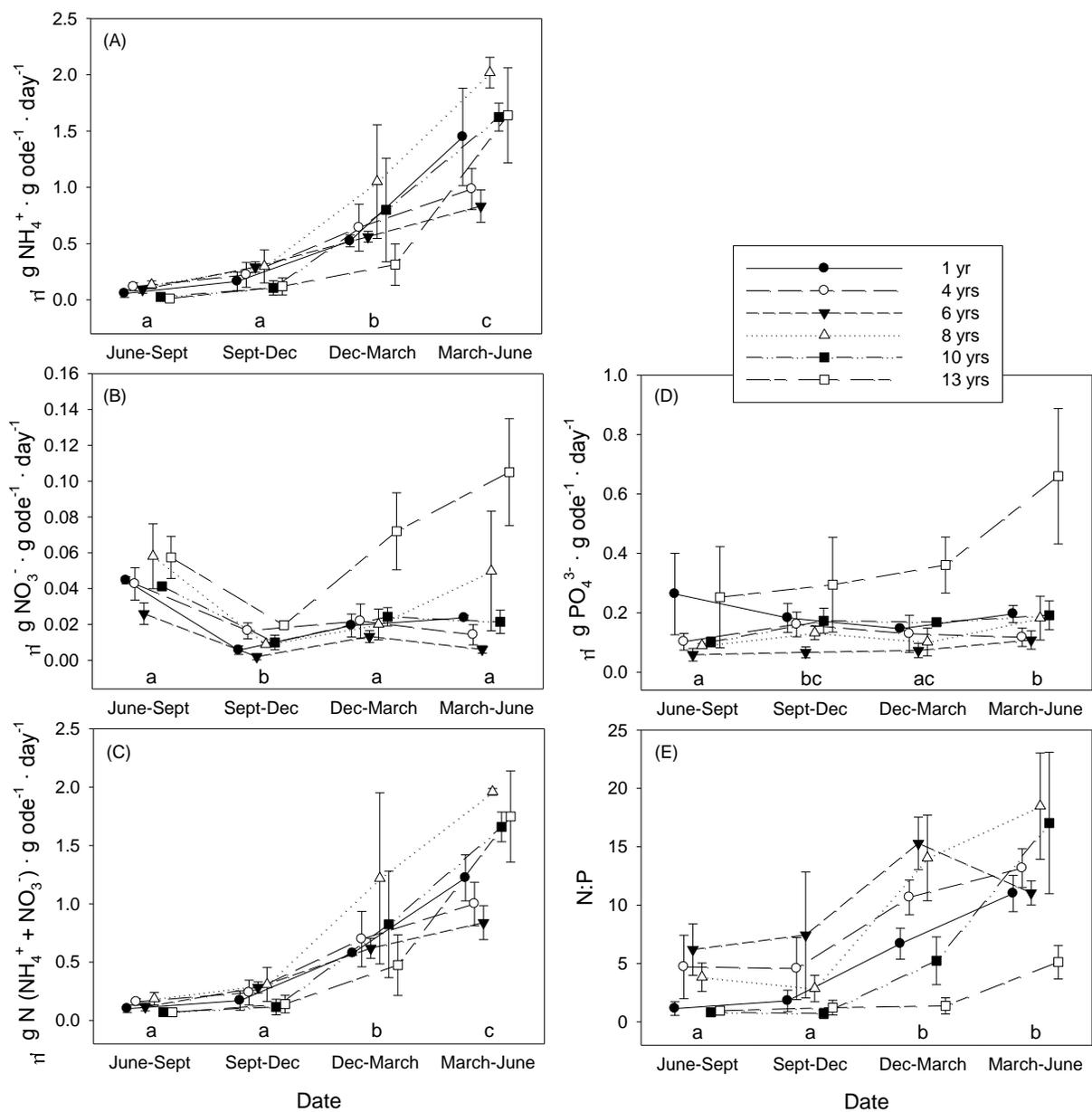


Figure B-2. Mean (\pm se) resin extractable NH_4^+ (A), NO_3^- (B), total inorganic N (C), PO_4^{3-} (D), and N:P (E) during each sampling period. Different letters represent significant differences among sampling periods at $\alpha = 0.05$.

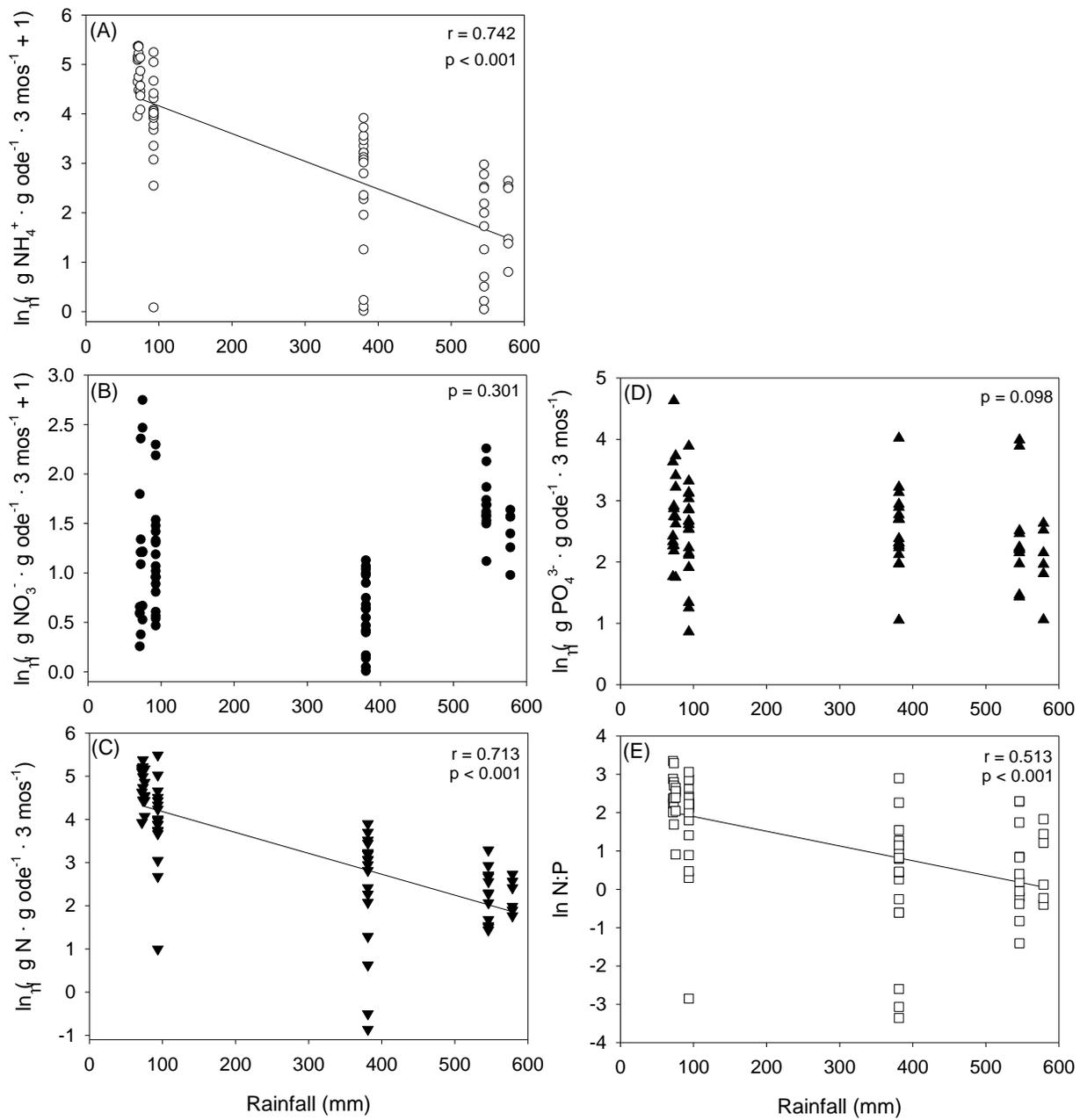


Figure B-3. Relationship between resin extractable NH_4^+ (A), NO_3^- (B), total inorganic N (C), PO_4^{3-} (D), and N:P (E) and rainfall during each 3 month sampling period.

APPENDIX C SCRUBBY FLATWOODS SOIL ANALYSIS

Abrahamson et al. (1984) provides one of the few measurements of multiple soil elements in scrubby flatwood soils. To my knowledge, however, a complete soil analysis has not been conducted on scrubby flatwood soils. A sub-sample of ground soils from each control plot (from the fertilization experiment; Chapter 4) for each time since fire (both 0-10 cm and 10-20 cm depths) was sent to the ALS Laboratory Group (www.alsglobal.com) for analysis using the four acid “near-total” digestion method.

Most elements were similar among times after fire and depths (Table C-1). Several elements were below detectable limits in scrubby flatwoods soils. Arsenic (As) was below detection limits nine and 21 years after fire, but in recently burned sites, arsenic was high in both surface and deep soils. This suggests that fire may increase soil arsenic, which could affect soil microorganisms; however, an increase in phosphate after fire (Chapter 1) may reduce the toxic effects of arsenic compounds (DaCosta 1972). Lead (Pb) and strontium (Sr) were also highest in surface soils of recently burned sites. Further sampling is needed to determine the effects of fire on these soil elements.

Table C-1. Mean (se) concentrations of elements in scrubby flatwoods soils at different times after fire and soil depths. Elements were measured in parts per million (ppm) or percents (%).

Time after fire	Ag (ppm)	As (ppm)	Ba (ppm)	Ce (ppm)	Cr (ppm)	Cs (ppm)	Ga (ppm)	Ge (ppm)	Hf (ppm)	Li (ppm)	Nb (ppm)	Pb (ppm)	Rb (ppm)	Re (ppm)
1 year														
0-10 cm	0.013 (0.003)	1.73 (1.14)	<10	1.18 (0.11)	122 (33.2)	<0.05	0.16 (0)	<0.05	0.17 (0.03)	1.27 (0.07)	0.43 (0.03)	2.80 (1.05)	0.23 (0.03)	<0.002
10-20 cm	0.01 (0)	1.00 (0.56)	<10	0.91 (0.04)	211 (70.8)	<0.05	0.14 (0.01)	<0.05	0.10 (0)	1.20 (0.10)	0.43 (0.03)	1.23 (0.28)	0.10 (0)	0.002
9 years														
0-10 cm	0.01 (0)	<0.2	<10	1.38 (0.29)	142 (51.4)	<0.05	0.17 (0.01)	<0.05	0.15 (0.03)	1.13 (0.03)	0.42 (0.06)	1.60 (0.10)	0.20 (0)	0.0025 (0.001)
10-20 cm	0.02 (0.01)	<0.2	<10	1.25 (0.23)	156 (22.3)	<0.05	0.20 (0.01)	<0.05	0.17 (0.03)	1.23 (0.14)	0.60 (0.06)	1.20 (0.10)	0.17 (0.03)	0.002 (0)
21 years														
0-10 cm	0.01 (0)	<0.2	<10	1.02 (0.04)	162 (31.9)	<0.05	0.21 (0.003)	<0.05	0.13 (0.03)	1.33 (0.07)	0.53 (0.03)	1.77 (0.03)	0.20 (0)	0.002
10-20 cm	0.01 (0)	<0.2	<10	0.97 (0.07)	171 (75.9)	<0.05	0.17 (0.12)	<0.05	0.13 (0.03)	1.33 (0.09)	0.57 (0.03)	0.93 (0.06)	0.17 (0.06)	0.002

Table C-1 continued.

Time after fire	Sb (ppm)	Sc (ppm)	Se (ppm)	Sn (ppm)	Sr (ppm)	Ta (ppm)	Te (ppm)	Th (ppm)	Ti (%)	Tl (ppm)	U (ppm)	V (ppm)	W (ppm)	Y (ppm)	Zr (ppm)
1 year															
0-10 cm	0.16 (0.03)	0.40 (0)	1.67 (0.33)	0.57 (0.12)	2.43 (0.79)	<0.05	0.10	0.27 (0.03)	0.019 (0.001)	<0.02	0.13 (0.03)	3.67 (0.33)	0.53 (0.12)	0.30 (0)	5.10 (0.20)
10-20 cm	0.10 (0.02)	0.27 (0.09)	1.00 (0)	0.40 (0.15)	0.80 (0.21)	<0.05	0.20 (0.12)	0.23 (0.03)	0.020 (0.001)	<0.02	0.10 (0)	4.33 (0.33)	0.57 (0.13)	0.23 (0.03)	4.53 (0.14)
9 years															
0-10 cm	0.11 (0.003)	0.35 (0.08)	1.00 (0)	0.45 (0.03)	1.15 (0.18)	<0.05	0.11	0.27 (0.03)	0.022 (0.003)	<0.02	0.13 (0.03)	4.00 (0.58)	0.37 (0.07)	0.27 (0.03)	5.73 (0.86)
10-20 cm	0.12 (0.03)	0.37 (0.03)	1.67 (0.33)	0.57 (0.13)	0.70 (0)	<0.05	0.11 (0.02)	0.23 (0.03)	0.030 (0.006)	<0.02	0.10 (0)	5.00 (0.58)	0.53 (0.18)	0.33 (0.03)	2.85 (1.59)
21 years															
0-10 cm	0.12 (0.01)	0.40 (0)	1.67 (0.33)	0.50 (0.06)	1.30 (0.21)	<0.05	0.15	0.23 (0.03)	0.022 (0.002)	<0.02	0.10 (0)	4.33 (0.33)	0.60 (0.10)	0.30 (0)	4.57 (0.17)
10-20 cm	0.10 (0.03)	0.30 (0.06)	1.33 (0.33)	0.43 (0.14)	0.70 (0.15)	<0.05	0.36 (0.16)	0.20 (0)	0.025 (0.003)	<0.02	0.10 (0)	4.00 (0.58)	0.50 (0.15)	0.27 (0.03)	4.63 (0.35)

APPENDIX D
DIFFERENCES IN ABOVEGROUND BIOMASS AND STEM TURNOVER WITH TIME
AFTER FIRE IN SCRUBBY FLATWOODS

To measure the effects of nutrient addition on total aboveground biomass (Chapter 5), I used allometric equations to estimate shrub biomass. I used measurements of shrub length (maximum crown length) and width (minimum crown length) to calculate the area of each marked individual. For oaks and *Lyonias*, I summed stem biomasses to determine the biomass of each individual. I then calculated the total measured biomass and total area for each species in each plot. Using my estimates of percent cover of each species, I scaled up biomass of each species to the entire plot. In many cases, the biomass I measured was greater than total plot biomass determined from scaling up, suggesting that I underestimated shrub cover. In these instances, I used the biomass of the plants I measured rather than the biomass scaled to my estimates of shrub percent cover. Differences in pre-fertilization biomass among times after fire were determined with a Kruskal-Wallis test.

Biomass of dominant shrubs was significantly higher eight and 20 years after fire than six weeks after fire ($\chi^2 = 60.01$, $df = 2$, $p < 0.001$). There was no difference in total shrub biomass 8 and 20 years after fire, suggesting that biomass does not increase over this time period. Oak aboveground biomass increased linearly over time after fire (Seiler et al. 2009). Several mechanisms could explain the lack of change in total shrub biomass eight to 20 years after fire. First, there is a negative relationship between abundance and total plant mass (Allen et al. 2008); however, percent cover of shrubs overall and the number of stems within clumps does not vary between eight and 20 years since fire (J. Schafer, unpublished data). Second, as stem diameter increases, resources are allocated to the root system to increase stability (Drexhage et al. 1999).

Stem diameter did not increase from eight to 20 years since fire, and root productivity does not differ between sites 8 and 20 years since fire. I hypothesize that shrub stems experience die-back due to water (Saha et al. 2008) or nutrient limitation. Although the longer unburned sites have received similar amounts of precipitation over the last eight to nine years, the 20 to 21 years since fire sites were located at the southern end of Archbold Biological Station, where scrubby flatwoods occur 2 m higher in elevation than further North, where the eight years since fire sites were located (Abrahamson et al. 1984). Thus, the 20 to 21 years since fire sites are located further above the water table, suggesting that during times of drought, species such as *Q. chapmanii* and *Q. geminata*, which take up water from 40-200 cm (Saha et al. 2008), may experience greater water stress. Percent dieback (Au and Tardif 2007) and the ratio of biomass loss to the gross production of aboveground biomass (Kawamura and Takeda 2008) increase with stem age; however, the mean and maximum life span of *Q. inopina* stems is 4 years and 9 years, respectively (Johnson and Abrahamson 2002), so it is unlikely that stem age alone causes the observed patterns in stem size. Previous research found that the height of *Q. inopina* stems did not vary over a nine year period in a long-unburned site (Johnson and Abrahamson 2002). Aboveground biomass of *Q. inopina* did not vary from 2-34 years after fire in Florida rosemary scrub (Johnson et al. 1986); whereas, aboveground biomass of oak shoots increased, while aboveground biomass of other shrub species, including *Lyonia* species, did not vary, from 3-25 years since fire in scrubby flatwoods (Saha et al. in review). Biomass of shrubs in Florida Keys pine forests did not increase from 12 to 30 years after fire (Sah et al. 2004). Stimulation of

biomass increment of oaks in coastal scrub (increase in biomass per year) decreased over time (Seiler et al. 2009).

For all focal *Quercus inopina* individuals, I followed stem survival and recruitment. I used Kruskal-Wallis tests to analyze differences in mean stem percent survival and percent change in stem number among times since fire. Post-hoc differences among times since fire were determined with Bonferroni adjusted significance values. Both stem percent survival ($\chi^2 = 18.31$, $df = 2$, $p < 0.001$) and percent change in stem number ($\chi^2 = 25.76$, $df = 2$, $p < 0.001$) varied with time since fire (Figure D-1). Mean percent survival was 7% and 13% lower 20 years and 6 weeks after fire, respectively, than 8 years after fire. Mean percent change in stem number was negative six weeks after fire and positive both 8 and 20 years after fire. Johnson and Abrahamson (2002) found that 80 to 90% of *Q. inopina* stems died over a 10 year period, but new stems were recruited so that the number of stems of *Q. inopina* individuals remained the same or increased over time. Survival of *Quercus inopina* stems was lower 1 and 20 years after fire than 8 years since fire, but individuals in sites 20 years since fire recruited new stems so that percent change in stem number was similar 8 and 20 years since fire.

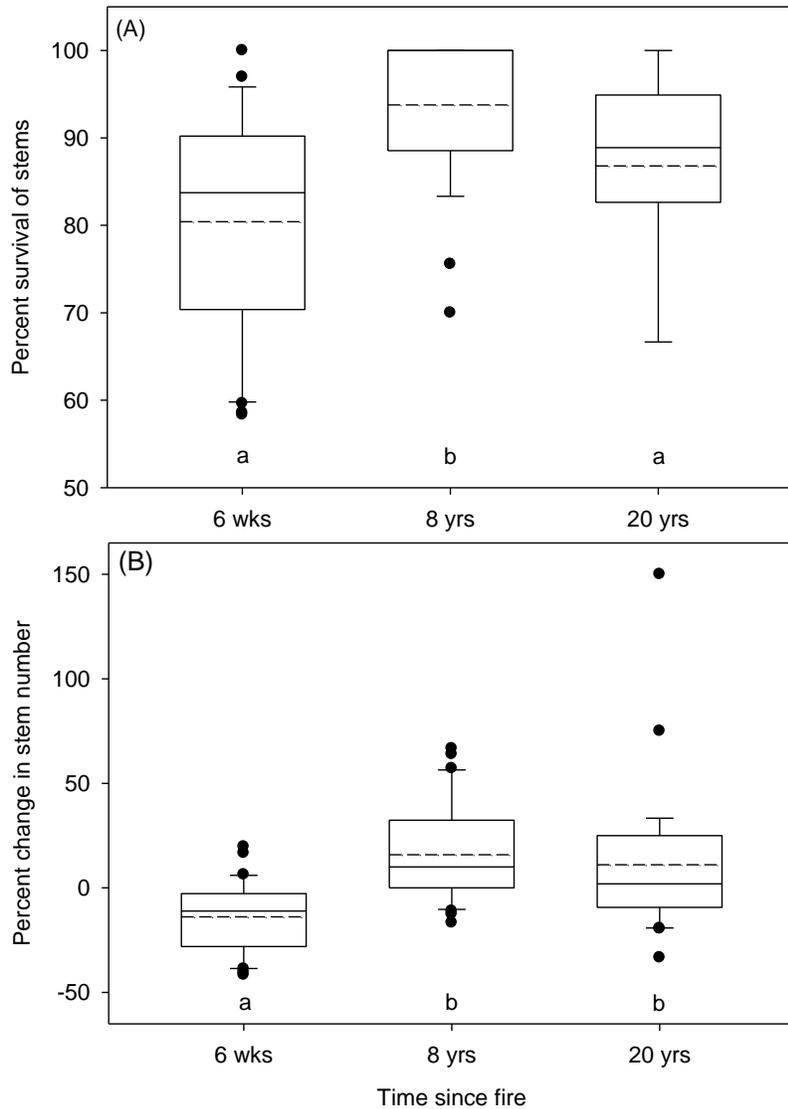


Figure D-1. Boxplots of percent survival (A) and percent change in stem number (B) of *Quercus inopina* plants 6 weeks, 8 years, and 20 years since fire. The lower and upper bars of the boxplot represent the 25th and 75th percentiles, respectively; the solid middle bar represents the median and the dotted bar represents the mean. The lower and upper “whiskers” show the largest and smallest values that are not outliers. The circles indicate outliers. Different lowercase letters below the boxplots indicate significant differences among times since fire.

LIST OF REFERENCES

- Abrahamson WG (1995) Habitat distribution and competitive neighborhoods of two Florida palmettos. *Bull Torrey Bot Club* 122:1-14
- Abrahamson WG (1999) Episodic reproduction in two fire-prone palms, *Serenoa repens* and *Sabal etonia* (Palmae). *Ecology* 80:100-115.
- Abrahamson WG (2007) Leaf traits and leaf life-spans of two xeric-adapted palmettos. *Am J Bot* 94:1297-1308
- Abrahamson WG, Johnson AF, Layne JN, Peroni PA (1984) Vegetation of the Archbold Biological Station, Florida: An example of the southern Lake Wales Ridge. *Florida Sci* 47:209-250
- Abrahamson WG, Hartnett DC (1990) Pine flatwoods and dry prairies. In: Myers RL, Ewel JJ (eds) *Ecosystems of Florida*. University of Central Florida Press, Orlando pp 103-149
- Abrahamson WG, Layne JN (2002a) Post-fire recovery of acorn production by four oak species in southern ridge sandhill associations in South-central Florida. *Am J Bot* 89:119-123
- Abrahamson WG, Layne JN (2002b) Relation of ramet size to acorn production in five oak species of xeric upland habitats in South-central Florida. *Am J Bot* 89:124-131
- Abrahamson WG, Layne JN (2003) Long-term patterns of acorn production for five oak species in xeric Florida uplands. *Ecology* 84:2476-2492
- Abrahamson WG, Hunter MD, Melika G, Price PW (2003) Cynipid gall-wasp communities correlate with oak chemistry. *J Chem Ecol* 29:209-223
- Abrams MD and ES Menges (1992) Leaf ageing and plateau effects on seasonal pressure-volume relationships in three sclerophyllous *Quercus* species in south-eastern USA. *Functional Ecol* 6:353-360.
- Aciego Pietri JC, Brookes PC (2009) Substrate inputs and pH as factors controlling microbial biomass, activity and community structure in an arable soil. *Soil Biol Biochem* 41:1396-1405
- Adams MA, Attiwill PM (1991) Nutrient balance in forests of northern Tasmania. 2. Alteration of nutrient availability and soil-water chemistry as a result of logging, slash-burning and fertilizer application. *Forest Ecol Manag* 44:115-131
- Adams MA, Iser J, Keleher AD, Cheal DC (1994) Nitrogen and phosphorus availability and the role of fire in heathlands. *Aust J Bot* 42:269-281

- Aerts R (2009) Nitrogen supply effects on leaf dynamics and nutrient input into the soil of plant species in a sub-arctic tundra ecosystem. *Polar Biol* 32:207-214
- Agnihotri VP, Vaartaja O (1969) Stimulation of *Waitea circinata* by root exudates of *Pinus cembroides*. *Can J Microbiol* 15:1319-1323
- Aguilera LE, Gutiérrez JR, Meserve PL (1999) Variation in soil micro-organisms and nutrients underneath and outside the canopy of *Adesmia bedwellii* (Papilionaceae) shrubs in arid coastal Chile following drought and above average rainfall. *J Arid Environ* 42:61-70
- Aikawa S, Hori Y (2006) Effect of a multi-stemmed growth form on matter production of an understory shrub, *Stephanandra incisa*. *Plant Spec Biol* 21:31-39
- Ainsworth EA, Tranel PJ, Drake BG, Long SP (2003) The clonal structure of *Quercus geminata* revealed by conserved microsatellite loci. *Molecular Ecol* 12:527-532
- Allen AP, Pockman WT, Restrepo C, Milne BT (2008) Allometry, growth and population regulation of the desert shrub *Larrea tridentata*. *Funct Ecol* 22:197-204
- Anderson RC, Menges ES (1997) Effects of fire on sandhill herbs: Nutrients, mycorrhizae, and biomass allocation. *Am J Bot* 84:938-948
- Anten NPR, Hirose T (1998) Biomass allocation and light partitioning among dominant and subordinate individuals in *Xanthium canadense* stands. *Ann Bot* 82:665-673
- Anten NPR, Miyazawa K, Hikosaka K, Nagashima H, Hirose T (1998) Leaf nitrogen distribution in relation to leaf age and photon flux density in dominant and subordinate plants in dense stands of a dicotyledonous herb. *Oecologia* 113:314-324
- Arocena JM, Opio C (2003) Prescribed fire-induced changes in properties of sub-boreal forest soils. *Geoderma* 113:1-16
- Au R, Tardiff JC (2007) Allometric relationships and dendroecology of the dwarf shrub *Dryas integrifolia* near Churchill, subarctic Manitoba. *Can J Botany* 85:585-597
- Austin AT, Vivanco L (2006) Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* 442:555-558
- Badía D, Martí C (2003) Plant ash and heat intensity effects on chemical and physical properties of two contrasting soils. *Arid Land Res Manag* 17:23-41
- Beckage B, Platt WJ, Slocum MG, Panko B (2003) Influence of the El Niño southern oscillation on fire regimes in the Florida Everglades. *Ecology* 84:3124-3130

- Bennett LT, Judd TS, Adams MA (2002) Growth and nutrient content of perennial grasslands following burning in semi-arid, sub-tropical Australia. *Plant Ecol* 164:185-199
- Bergersen FJ, Peoples MB, Turner GL (1988) Isotopic discriminations during the accumulation of nitrogen by soybeans. *Aust J Plant Physiol* 15:407-420
- Berry DM, Menges ES (1997) Post-fire changes in resource limitation of Florida scrub plants. *Proceedings – Fire Effects on Rare and Endangered Species and Habitat Conference*: 197-201
- Blagodatskaya EV, Blagodatsky SA, Anderson T-H, Kuzyakov Y (2009) Contrasting effects of glucose, living roots and maize straw on microbial growth kinetics and substrate availability in soil. *Eur J Soil Sci* 60:186-197
- Blair, BC (2005) Fire effects on the spatial patterns of soil resources in a Nicaraguan wet tropical forest. *J Trop Ecol* 21:435-444
- Blair BC, Perfecto I (2008) Root proliferation and nutrient limitations in a Nicaraguan rain forest. *Caribb J Sci* 44:36-42
- Bloom RG, Mallik AU (2006) Relationships between ericaceous vegetation and soil nutrient status in a post-fire *Kalmia angustifolia*-black spruce chronosequence. *Plant Soil* 289:211-226
- Boerner REJ, Huang J, Hart SC (2009) Impacts of fire and fire surrogate treatments on forest soil properties: a meta-analytical approach. *Ecol Appl* 19:338-358
- Bond-Lamberty B, Gower ST, Wang C, Cyr P, Veldhuis H (2006) Nitrogen dynamics of a boreal black spruce wildfire chronosequence. *Biogeochem* 81:1-16
- Bonfil C, Cortés P, Espelta JP, Retana J (2004) The role of disturbance in the co-existence of the evergreen *Quercus ilex* and the deciduous *Quercus cerroides*. *J Veg Sci* 15:423-430
- Bormann BT, Sidle RC (1990) Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. *J Ecol* 78:561-578
- Bosner SP, Aarssen LW (1994) Plastic allometry in young sugar maple (*Acer saccharum*): adaptive responses to light availability. *Am J Bot* 81:400-406
- Bosner SP, Aarssen LW (2001) Allometry and plasticity of meristem allocation throughout development in *Arabidopsis thaliana*. *J Ecol* 89:72-79
- Bown HE, Watt MS, Clinton PW, Mason EG, Whitehead D (2009) The influence of N and P supply and genotype on carbon flux and partitioning in potted *Pinus radiata* plants. *Tree Physiol* 29:857-868

- Bradstock RA, Williams JE, Gill AM (2001) *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge University Press, New York
- Bret-Harte MS, García EA, Sacré VA, Whorley JR, Wagner JL, Lippert SC, Chapin III FS (2004) Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. *J Ecol* 92:635-647
- Britton AJ, Helliwell RC, Fisher JM, Gibbs S (2008) Interactive effects of nitrogen deposition and fire on plant and soil chemistry in an alpine heathland. *Environ Pollut* 156:409-416
- Brookes PC, Landman A, Pruden G, Jenkinson DS (1985) Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biol Biochem* 17:837-842
- Brown ALP, Day FP, Hungate BA, Drake BG, Hinkle RC (2007) Root biomass and nutrient dynamics in a scrub-oak ecosystem under the influence of elevated atmospheric CO₂. *Plant Soil* 292:219-232
- Brown ALP, Garland JL, Day FP (2009) Physiological profiling of soil microbial communities in a Florida scrub-oak ecosystem: spatial distribution and nutrient limitation. *Microb Ecol* 57:14-24
- Brown RB, Stone EL, Carlisle VW (1990) Soils. In: Myers RL, Ewel JJ (eds) *Ecosystems of Florida*. University of Central Florida Press, Orlando pp. 35-69
- Caffrey JM, Murrell MC, Wigand C, McKinney R (2007) Effect of nutrient loading on biogeochemical and microbial processes in a New England salt marsh. *Biogeochem* 82:251-264
- Carreira JA, Niell FX, Lajtha K (1994) Soil nitrogen availability and nitrification in Mediterranean shrublands of varying fire history and successional stage. *Biogeochem* 26:189-209
- Carter MC, Foster CD (2004) Prescribed burning and productivity in southern pine forests: a review. *Forest Ecol Manag* 191:93-109
- Cassman KG, Munns DN (1980) Nitrogen mineralization as affected by soil moisture, temperature, and depth. *Soil Sci Soc Am J* 44:1233-1237
- Cavender-Bares J, Kitajima K, Bazzaz FA (2004) Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecol Monogr* 74:635-662
- Cech PG, Kuster T, Edwards PJ, Venterink HO (2008) Effects of herbivory, fire and N₂-fixation on nutrient limitation in a humid African savanna. *Ecosystems* 11:991-1004

- Certini G (2005) Effects of fire on properties of forest soils: a review. *Oecologia* 143:1-10
- Chang SX, Handley LL (2000) Site history affects soil and plant ^{15}N natural abundances ($\delta^{15}\text{N}$) in forests of Northern Vancouver Island, British Columbia. *Funct Ecol* 14:273-280
- Chapin III FS, Matson PA, Mooney HA (2002) Principles of Terrestrial Ecosystem Ecology. Springer-Verlag, New York
- Chapin III FS, Bloom AJ, Field CB, Waring RH (1987) Plant responses to multiple environmental factors. *Bioscience* 37:49-57
- Chappell MA, Evangelou VP (2000) Influence of added K^+ on ammonium selectivity/mobility by soils with vermiculitic behavior. *Soil Sci* 11:858-868
- Chen CR, Condrón LM, Davis MR, Sherlock RR (2004) Effects of plant species on microbial biomass phosphorus and phosphatase activity in a range of grassland soils. *Biol Fert Soils* 40:313-322
- Christensen NL (1985) Shrubland fire regimes and their evolutionary consequences. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp 85-100
- Christensen NL, Muller CH (1975) Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. *Ecol Monogr* 45:29-55
- Cleary MB, Pendall E, Ewers BE (2008) Testing sagebrush allometric relationships across three fire chronosequences in Wyoming, USA. *J Arid Environ* 72:285-301
- Clemente AS, Rego FC, Correia OA (2005) Growth, water relations and photosynthesis of seedlings and resprouts after fire. *Acta Oecologica* 27:233-243
- Cleveland CC, Liptzin D (2007) C:N:P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? *Biogeochem* 85:235-252
- Cook GD (1994) The fate of nutrients during fires in a tropical savanna. *Aust J Ecol* 19:359-365
- Coomes DA, Grubb PJ (1998) A comparison of 12 tree species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. *Funct Ecol* 12:426-435
- Cornelissen T, Stiling P (2006) Responses of different herbivore guilds to nutrient addition and natural enemy exclusion. *Ecoscience* 13:66-74
- Cornelissen T, Stiling P (2008) Clumped distribution of oak leaf miners between and within plants. *Basic Appl Ecol* 9:67-77

- Covington WW, Sackett SS (1992) Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *Forest Ecol Manag* 54:175-191
- Craine JM, Morrow C, Stock WD (2008) Nutrient concentration ratios and co-limitation in South African grasslands. *New Phytol* 179:829-836
- Cruz A, Pérez B, Quintana J, Moreno J (2002) Resprouting in the Mediterranean-type shrub *Erica australis* affected by soil resource availability. *J Veg Sci* 13:641-650
- Cuevas E, Medina E (1988) Nutrient dynamics within Amazonian forests. 2. Fine root growth, nutrient availability and leaf litter decomposition. *Oecologia* 76:222-235
- D'Angelo E, Crutchfield J, Vandiviere M (2001) Rapid, sensitive, microscale determination of phosphate in water and soil. *J Environ Qual* 30:2206-2209
- D'Antonio CM, Tunison JT, Loh RK (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevational gradient in Hawaii. *Austral Ecol* 25:507-522
- D'Antonio CM, Mack MC (2006) Nutrient limitation in a fire-derived, nitrogen-rich Hawaiian grassland. *Biotropica* 38:458-467
- Daily GC, Soderqvist T, Aniyar S, Arrow K, Dasgupta P, Ehrlich PR, Folke C, Jansson A, Jansson BO, Kautsky N, Levin S, Lubchenco J, Maler KG, Simpson D, Starret D, Tilman D, Walker B (2000) The value of nature and the nature of values. *Science* 289:395-396
- Darby FA, Turner RE (2008) Below- and aboveground biomass of *Spartina alterniflora*: response to nutrient addition in a Louisiana salt marsh. *Estuaries Coasts: J CERF* 31:326-334
- Davidson EA, Reis de Carvalho CJ, Vieira ICG, Figueiredo RO, Moutinho P, Ishida FY, Primo dos Santos MT, Guerrero JB, Kalif K, Sabá RT (2004) Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. *Ecol Appl* 14:S150-S163
- Davies SJ, Myerscough PJ (1991) Post-fire demography of the Wet-mallee *Eucalyptus leuhmanniana* F.Muell. (Myrtaceae). *Aust J Bot* 39:459-66
- Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP (2002) Stable isotopes in plant ecology. *Ann Rev Ecol Syst* 33:507-509
- DaCosta EWB (1972) Variation in the toxicity of arsenic compounds to microorganisms and the suppression of the inhibitory effects by phosphate. *Appl Microbiol* 23:46-53

- Debano LF, Conrad CE (1978) The effect of fire on nutrients in a chaparral ecosystem. *Ecology* 59:489-497
- DeLuca TH, Sala A (2006) Frequent fire alters nitrogen transformations in ponderosa pine stands of the inland northwest. *Ecology* 87:2511-2522
- DeLuca TH, Nilsson M-C, Zackrisson O (2002) Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. *Oecologia* 133:206-214
- DeLucia EH, Callaway RM, Thomas EM, Schlesinger WH (1997) Mechanisms of phosphorus acquisition for ponderosa pine seedlings under high CO₂ and temperature. *Ann Bot* 79:111-120
- DeSouza J, Silka PA, Davis SD (1986) Comparative physiology of burned and unburned *Rhus laurina* after chaparral wildfire. *Oecologia* 71:63-68
- DeWilde L, Chapin III FS (2006) Human impacts on the fire regime of interior Alaska: interactions among fuels, ignition sources, and fire suppression. *Ecosystems* 9:1342-1353
- den Dubbelden KC, Knops JMH (1993) The effect of competition and slope inclination on aboveground biomass allocation of understory ferns in subtropical forest. *Oikos* 67:285-290
- Diehl P, Mazzarino MJ, Fontenla S (2008) Plant limiting nutrients in Andean-Patagonian woody species: effects of interannual rainfall variation, soil fertility and mycorrhizal infection. *Forest Ecol Manag* 255:2973-2980
- Drexhage M, Chauvière M, Colin F, Nielsen CNN (1999) Development of structural root architecture and allometry of *Quercus petraea*. *Can J Forest Res* 29:600-608
- Dunn PH, Barro SC, Poth M (1985) Soil moisture affects survival of microorganisms in heated chaparral soil. *Soil Biol Biochem* 17:143-148
- Durán J, Rodríguez A, Fernández-Palacios JM, Gallardo A (2008) Changes in soil N and P availability in a *Pinus canariensis* fire chronosequence. *Forest Ecol Manag* 256:384-387
- Durán J, Rodríguez A, Fernández-Palacios JM, Gallardo A (2009) Changes in net N mineralization rates and soil N and P pools in a pine forest wildfire chronosequence. *Biol Fert Soils* 45:781-788
- El Omari B, Aranda X, Verdaguer D, Pascual G, Fleck I (2003) Resource remobilization in *Quercus ilex* L. resprouts. *Plant Soil* 252:349-357
- Enquist BJ, Niklas KJ (2002) Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295:1517-1520

- Enquist BJ, Niklas KJ (2001) Invariant scaling relations across tree-dominated communities. *Nature* 410:655-660
- Eom A-H, Hartnett DC, Wilson GWT, Figge DAH (1999) The effect of fire, mowing and fertilizer amendment on arbuscular mycorrhizas in tallgrass prairie. *Am Midl Nat* 142:55-70
- Evans RD (2001) Physiological mechanisms influencing plant nitrogen isotope composition. *Trends Plant Sci* 6:121-126
- Evans RD, Bloom AJ, Sukrapanna SS, Ehleringer JR (1996) Nitrogen isotope composition of tomato (*Lycopersicon esculentum* Mill. Cv. T-5) grown under ammonium or nitrate nutrition. *Plant Cell Environ* 19:1317-1323
- Evans CA, Miller EK, Friedland AJ (1998) Nitrogen mineralization associated with birch and fir under different soil moisture regimes. *Can J Forest Res* 28:1890-1898
- Ewel, J, Berish C, Brown B, Price N, Raich J (1981) Slash and burn impacts on a Costa Rican wet forest site. *Ecology* 62:816-829
- Farnsworth EJ, Ellison AM (1996) Sun-shade adaptability of the red mangrove, *Rhizophora mangle* (Rhizophoraceae): changes through ontogeny at several levels of biological organization. *Am J Bot* 83:1131-1143
- Fenn ME, Poth MA, Dunn PH, Barro SC (1993) Microbial N and biomass, respiration and N mineralization in soils beneath two chaparral species along a fire-induced age gradient. *Soil Biol Biochem* 25:457-466
- Ferran A, Delitti W, Vallejo VR (2005) Effects of fire recurrence in *Quercus coccifera* L. shrublands of the Valencia region (Spain): II. plant and soil nutrients. *Plant Ecol* 177:71-83
- Field A (2009) *Discovering statistics using SPSS*, 3rd edn. SAGE
- Fisher JB, Jayachandran K (1999) Root structure and arbuscular mycorrhizal colonization of the palm *Serenoa repens* under field conditions. *Plant Soil* 217:229-241
- Flannigan MD, Amiro BD, Logan KA, Stocks BJ, Wotton BM (2005) Forest fires and climate change in the 21st century. *Mitigation Adaptation Strategies Global Change* 11:847-859
- Fox TR, Comerford NB (1990) Low-molecular-weight organic acids in selected forests of the Southeastern USA. *Soil Sci Soc Am J* 54:1139-1144
- Franco-Vizcaíno E, Sosa-Ramirez J (1997) Soil properties and nutrient relations in burned and unburned Mediterranean-climate shrublands of Baja California, Mexico. *Acta Oecol* 18:503-517

- Frank DA (2008) Ungulate and topographic control of nitrogen: phosphorus stoichiometry in a temperate grassland; soils, plants and mineralization rates. *Oikos* 117:591-601
- Frank DA, Evans RD (1997) Effects of native grazers on grassland N cycling in Yellowstone National park. *Ecology* 78:2238-2248
- Gholz HL, Fisher RF (1982) Organic matter production and distribution in slash pine (*Pinus elliotii*) plantations. *Ecology* 63:1827-1839
- Giardina CP, Sanford Jr. RL, Døckersmith IC (2000) Changes in soil phosphorus and nitrogen during slash-and-burn clearing of a dry tropical forest. *Soil Sci Soc Am J* 64:399-405
- Gilliam FS (1988) Interactions of fire with nutrients in the herbaceous layer of a nutrient-poor Coastal Plant forest. *Bull Torrey Bot Club* 115:265-271
- Gillon D, Rapp M (1989) Nutrient losses during a winter low-intensity prescribed fire in a Mediterranean forest. *Plant Soil* 120:69-77
- Gimeno-García E, Andreu V, Rubio JL (2000) Changes in organic matter, nitrogen, phosphorus and cations in soil as a result of fire and water erosion in a Mediterranean landscape. *European J Soil Sci* 51:201-210
- Goforth BR, Graham RC, Hubbert KR, Zanner CW, Minnich RA (2005) Spatial distribution and properties of ash and thermally altered soils after high-severity forest fire, southern California. *Int J Wildland Fire* 14:353-354
- Gökkaya K, Hurd TM, Raynal DJ (2006) Symbiont nitrogenase, alder growth, and soil nitrate response to phosphorus addition in alder (*Alnus incana* ssp. *rugosa*) wetlands of the Adirondack Mountains, New York State, USA. *Environ Exp Bot* 55:97-109
- Grayston SJ, Vaughan D, Jones D (1996) Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. *Appl Soil Ecol* 5:29-56
- Grogan P, Burns TD, Chapin III FS (2000) Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. *Oecologia* 122:537-544
- Guerin DN (1993) Oak dome clonal structure and fire ecology in a Florida longleaf pine dominated community. *Bull Torrey Bot Club* 120:107-114
- Güsewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. *New Phytol* 164:243-266
- Hall SA, Burke IC, Hobbs NT (2006) Litter and dead wood dynamics in ponderosa pine forests along a 160-year chronosequence. *Ecol Appl* 16:2344-2355

- Hamman ST, Burke IC, Knapp EE (2008) Soil nutrients and microbial activity after early and late season prescribed burns in a Sierra Nevada mixed conifer forest. *Forest Ecol Manag* 256:367-374
- Han Q, Kawasaki T, Nakano T, Chiba Y (2008) Leaf-age effects on seasonal variability in photosynthetic parameters and its relationships with leaf mass per area and leaf nitrogen concentration within a *Pinus densiflora* crown. *Tree Physiol* 28:551-558
- Hatten J, Zabowski D, Scherer G, Dolan E (2005) A comparison of soil properties after contemporary wildfire and fire suppression. *Forest Ecol Manag* 220:227-241
- Hawkes CV (2003) Nitrogen cycling mediated by biological soil crusts and arbuscular mycorrhizal fungi. *Ecology* 84:1553-1562
- Hawkes CV, Flechtner VR (2002) Biological soil crusts in a xeric Florida shrubland: composition, abundance, and spatial heterogeneity of crusts with different disturbance histories. *Microb Ecol* 43:1-12
- Hedin LO, Armesto JJ, Johnson AH (1995) Patterns of nutrient loss from unpolluted, old-growth temperate forests: Evaluation of biogeochemical theory. *Ecology* 76:493-509
- Henry HAL, Aarssen LW (1999) The interpretation of stem diameter-height allometry in trees: biomechanical constraints, neighbor effects, or biased regressions? *Ecol Lett* 2:89-97
- Herbert DA, Fownes JH (1995) Phosphorus limitation of a forest leaf area and net primary production on a highly weathered soil. *Biogeochem* 29:223-235
- Hernández DL, Hobbie SE (2008) Effects of fire frequency on oak litter decomposition and nitrogen dynamics. *Oecologia* 158:535-543
- Hikosaka K, Terashima I, Katoh S (1994) Effects of leaf age, nitrogen nutrition and photon flux density on the distribution of nitrogen among leaves of a vine (*Ipomoea tricolor* Cav.) grown horizontally to avoid mutual shading of leaves. *Oecologia* 97:451-457
- Hobbie EA, Colpaert JV (2003) Nitrogen availability and colonization by mycorrhizal fungi correlate with nitrogen isotope patterns in plants. *New Phytol* 157:115-126
- Hobbs NT, Schimel DS (1984) Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. *J Range Manage* 37:402-405
- Högberg P (1997) Tansley Review No. 95. ^{15}N natural abundance in soil-plant systems. *New Phytol* 137:179-203

- Holbrook NM, Putz FE (1989) Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *Liquidambar styraciflua* (Sweet gum). *Am J Bot* 76:1740-1749
- Horwath WR, Paul EA (1994) Microbial biomass. In: Weaver RW, Angle S, Bottomley P, Bezdicsek D, Smith S, Tabatabai A, Wollum A (eds) *Methods of soil analysis, part 2. Microbiological and Biochemical properties*. Soil Science Society of America, Inc., Madison pp 753-773
- Hsu PH, Jackson ML (1960) Inorganic phosphate transformation by chemical weathering in soils as influenced by pH. *Soil Sci* 90:16-24
- Huenneke LF, Clason D, Muldavin E (2001) Spatial heterogeneity in Chihuahuan desert vegetation: implications for sampling methods in semi-arid ecosystems. *J Arid Environ* 47:257-270
- Hungate BA, Dijkstra P, Johnson DW, Hinkle CR, Drake BG (1999) Elevated CO₂ increased nitrogen fixation and decreases soil nitrogen mineralization in Florida scrub oak. *Global Change Biol* 5:781-789
- Hungate BA, Hart SC, Selmants PC, Boyle SI, Gehring CA (2007) Soil responses to management, increased precipitation, and added nitrogen in ponderosa pine forests. *Ecol Appl* 17:1352-1365
- Iversen CM, Norby RJ (2008) Nitrogen limitation in a sweetgum plantation: implications for carbon allocation and storage. *Can J For Res* 38:1021-1032
- Jägerbrand AK, Alatalo JM, Chrimes D, Molau U (2009) Plant community responses to 5 years of simulated climate change in meadow and heath ecosystems at a subarctic-alpine site. *Oecologia* 161:601-610
- Jaggi RC, Aulakh MS, Sharma R (2005) Impacts of elemental S applied under various temperature and moisture regimes on pH and available P in acidic, neutral and alkaline soils. *Biol Fert Soils* 41:52-58
- James BR, Riha SJ (1986) pH buffering in forest soil organic horizons: relevance to acid precipitation. *J Environ Qual* 15:229-234
- Jenny H (1941) *Factors of soil formation*. McGraw-Hill, New York
- Jensen M, Michelsen A, Gashaw M (2001) Responses in plant, soil inorganic and microbial nutrient pools to experimental fire, ash and biomass addition in a woodland savanna. *Oecologia* 128:85-93
- Johnson AF, Abrahamson WG, McCrea KD (1986) Comparison of biomass recovery after fire of a seeder (*Ceratiola ericoides*) and a sprouter (*Quercus inopina*) species from South-central Florida. *Am Midl Nat* 116:423-428

- Johnson AF, Abrahamson WG (2002) Stem turnover in the rhizomatous scrub oak, *Quercus inopina*, from South-central Florida. *Am Midl Nat* 147:237-246
- Johnson DW, Hungate BA, Dijkstra P, Hymus G, Drake B (2001) Effects of elevated carbon dioxide on soils in a Florida scrub oak ecosystem. *J Environ Qual* 30:501-507
- Johnson DW, Hungate BA, Dijkstra P, Hymus G, Hinkle CR, Stiling P, Drake BG (2003) The effects of elevated CO₂ on nutrient distribution in a fire-adapted scrub oak forest. *Ecol Appl* 13:1388-1399
- Jonasson S, Michelsen A, Schmidt IK, Nielsen EV, Callaghan TV (1996) Microbial biomass C, N, and P in two Arctic soils and responses to addition of NPK fertilizer and sugar: implications for plant nutrient uptake. *Oecologia* 106:507-515
- Jurinak JJ, Dudley LM, Allen MF (1986) The role of calcium-oxalate in the availability of phosphorus in soils of semiarid regions – a thermodynamic study. *Soil Sci* 142:255-261
- Kalisz PJ, Stone EL (1984) The longleaf pine islands of the Ocala National Forest, Florida: a soil study. *Ecology* 65:1743-1754
- Kauffman JB, Sanford RL, Cummings DL, Salcedo IH, Sampaio EVSB (1993) Biomass and nutrient dynamics associated with slash fires in Neotropical dry forests. *Ecology* 74:140-151
- Kawamura K, Takeda H (2008) Development programmed and plastic processes of growth in the multistemmed understory shrub *Vaccinium hirtum* (Ericaceae). *Botany* 86:268-277
- Kaye JP, Hart SC (1998) Ecological restoration alters nitrogen transformations in a ponderosa pine-bunchgrass ecosystem. *Ecol Appl* 8:1052-1060
- Keeley JE (1977) Seed production, seed populations in the soil, and seedling production after fire for two congeneric pairs of sprouting and non-sprouting chaparral shrubs. *Ecology* 58:820-829
- Keeley JE, Zedler PH (1978) Reproduction of chaparral shrubs after fire: A comparison of sprouting and seeding strategies. *Am Midl Nat* 99:142-161
- Keeley JE, Keeley SC (1988) Chaparral. In: Barbour MG, Billings WD (eds) *North American terrestrial vegetation*. Cambridge University Press, New York, pp 166-207
- Kennard DK, Gholz HL (2001) Effects of high- and low-intensity fires on soil properties and plant growth in a Bolivian dry forest. *Plant Soil* 234:119-129

- Khanna PK, Raison RJ (1986) Effect of fire intensity on solution chemistry of surface soil under a *Eucalyptus pauciflora* forest. *Aust J Soil Res* 24:423-434
- Kimura M, Simbolon H (2002) Allometry and life history of a forest understory palm *Pinanga coronata* (Arecaceae) on Mount Halimum, West Java. *Ecol Res* 17:323-338
- King DA (1986) Tree form, height growth, and susceptibility to wind damage in *Acer saccharum*. *Ecology* 67:980-990
- Koerper GJ, Richardson CJ (1980) Biomass and net annual primary production regressions for *Populus grandidentata* on three sites in northern lower Michigan. *Can J For Res* 10:92-101
- Koerselman W, Meuleman AFM (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J Appl Ecol* 33:1441-1450
- Kolb KJ, Evans RD (2003) Influence of nitrogen source and concentration on nitrogen isotopic discrimination in two barley genotypes (*Hordeum vulgare* L.) *Plant Cell Environ* 26:1431-1440
- Konstantinidis P, Tsiourlis G, Xofis P (2006) Effect of fire season, aspect and pre-fire plant size on the growth of *Arbutus unedo* L. (strawberry tree) resprouts. *Forest Ecol Manag* 225:359-367
- Kozovits AR, Matyssek R, Winkler JB, Göttlein A, Blaschke H, Grams TEE (2005) Above-ground space sequestration determines competitive success in juvenile beech and spruce trees. *New Phytol* 167:181-196
- Lagerström A, Esberg C, Wardle DA, Giesler R (2009) Soil phosphorus and microbial response to a long-term wildfire chronosequence in northern Sweden. *Biogeochem* 95:199-213
- Langely JA, Drake BG, Hungate BA (2002) Extensive belowground carbon storage supports roots and mycorrhizae in regenerating scrub oaks. *Oecologia* 131:542-548
- Lewis Jr. WM (1974) Effects of fire on nutrient movement in a South Carolina pine forest. *Ecology* 55:1120-1127
- Litaor MI, Seastedt TR, Sackett LC (2008) Nutrient status in alpine soils of the Colorado front range using the nitrogen/phosphorus ratio index. *Soil Sci Soc Am J* 72:1628-1636
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD, Schabenberger O (2006) SAS for mixed models, 2nd edn. SAS Institute Inc., Cary, North Carolina

- Little S (1979) Fire and plant succession in the New Jersey pine barrens, In: Forman RTT (ed) Pine barrens: ecosystem and landscape. Academic Press, New York, pp 297-314
- Lloret F, López-Soria L (1993) Resprouting of *Erica multiflora* after experimental fire treatments. *J Veg Sci* 4:367-374
- Lufafa A, Diédhiou I, Ndiaye NAS, Séné M, Kizito F, Dick RP, Noller JS (2009) Allometric relationships and peak-season community biomass stocks of native shrubs in Senegal's Peanut Basin. *J Arid Environ* 73:260-266
- Lund M, Christensen TR, Mastepanov M, Lindroth A, Ström L (2009) Effects of N and P fertilization on the greenhouse gas exchange in two northern peatlands with contrasting N deposition rates. *Biogeosci* 6:2135-2144
- MacKenzie MD, DeLuca TH (2006) Resin adsorption of carbon and nitrogen as influenced by season and time since fire. *Soil Sci Soc Am J* 70:2122-2129
- MacKenzie MD, DeLuca TH, Sala A (2004) Forest structure and organic horizon analysis along a fire chronosequence in the low elevation forests of western Montana. *Forest Ecol Manag* 203:331-343
- MacKenzie MD, DeLuca TH, Sala A (2006) Fire exclusion and nitrogen mineralization in low elevation forests of western Montana. *Soil Biol Biochem* 38:952-961
- MacKenzie MD, McIntier EJB, Quideau SA, Graham RC (2008) Charcoal distribution affects carbon and nitrogen contents in forest soils of California. *Soil Sci Soc Am J* 72:1774-1785
- Mack MC, Treseder KK, Manies KL, Harden JW, Schuur EAG, Vogel JG, Randerson JT, Chapin FS III (2008) Recovery of aboveground plant biomass and productivity after fire in mesic and dry black spruce forests of interior Alaska. *Ecosystems* 11:209-225
- Mackensen J, Hölscher D, Klinge R, Fölster H (1996) Nutrient transfer to the atmosphere by burning of debris in eastern Amazonia. *Forest Ecol Manag* 86:121-128
- Magdoff FR, Bartlett RJ (1985) Soil pH buffering revisited. *Soil Sci Soc Am J* 49:145-148
- Main KN, Menges ES (1997) Archbold Biological Station, Station Fire Management Plan. Land Management Publ. 97-1
- Marcos E, Villalón C, Calvo L, Luis-Calabuig E (2009) Short-term effects of experimental burning on soil nutrients in the Cantabrian heathlands. *Ecol Eng* 35:820-828

- Marion GM, Black CH (1988) Potentially available nitrogen and phosphorus along a Chaparral fire cycle chronosequence. *Soil Sci Soc Am J* 52:1155-1162
- Martinelli LA, Piccolo MC, Townsend AR, Vitousek PM, Cuevas E, McDowell W, Robertson GP, Santos OC, Treseder K (1999) Nitrogen stable isotopic composition of leaves and soil: Tropical versus temperate forests. *Biogeochem* 46:45-65
- McEachern P, Prepas EE, Planas D (2002) Phytoplankton in boreal SubArctic lakes following enhanced phosphorus loading from forest fire: impacts on species richness, nitrogen and light limitation. *Lake Reserv Manage* 18:138-148
- McKinley DC, Romero JC, Hungate BA, Drake BG, Megonigal JP (2009) Does deep soil N availability sustain long-term ecosystem responses to elevated CO₂? *Global Change Biol* 15:2035-2048
- McPherson K, Williams K (1998) The role of carbohydrate reserves in the growth, resilience, and persistence of cabbage palm seedlings (*Sabal palmetto*). *Oecologia* 117:460-468
- Menges ES (1999) Ecology and conservation of Florida scrub. In: Anderson RC, Fralish JS, Baskin JM (eds) *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. Cambridge University Press, USA pp 7-22
- Menges ES (2007) Integrating demography and fire management: an example from Florida scrub. *Aust J Bot* 55:261-272
- Menges ES, Kohfeldt N (1995) Life history strategies of Florida scrub plants in relation to fire. *Bull Torrey Bot Club* 122:282-297
- Menges ES, Quintana-Ascencio PF (2004) Population viability with fire in *Eryngium cuneifolium*: deciphering a decade of demographic data. *Ecol Monogr* 74:79-99
- Merilä P, Ohtonen R (1997) Soil microbial activity in the coastal Norway spruce [*Picea abies* (L.) Karst.] forests of the Gulf of Bothnia in relation to humus-layer quality, moisture and soil types. *Biol Fert Soils* 25:361-365
- Miao S, Sindhøj K, Edelstein C (2008) Allometric relationships of field populations of two clonal species with contrasting life histories, *Cladium jamaicense* and *Typha domingensis*. *Aquat Bot* 88:1-9
- Michelsen A, Quarmby C, Sleep D, Jonasson S (1998) Vascular plant ¹⁵N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia* 115:406-418
- Molina M, Fuentes R, Calderón R, Escudey M, Avendaño K, Gutiérrez M, Chang AC (2007) Impact of forest fire ash on surface charge characteristics of andisols. *Soil Sci* 172:820-834

- Moreno JM, Oechel WC (1994) The role of fire in Mediterranean-type ecosystems. Springer-Verlag, Berlin
- Moreno JM, Oechel WC (1991) Fire intensity and herbivory effects on postfire resprouting of *Adenostoma fasciculatum* in southern California chaparral. *Oecologia* 85:429-433
- Murphy J, Riley JP (1962) A modified single solution method for determination of phosphate in natural waters. *Anal Chim Acta* 26:31-36
- Murray RB, Jacobson MQ (1982) An evaluation of dimension analysis for predicting shrub biomass. *J Range Manag* 35:451-454
- Myers RL (1990) Scrub and high pine. In: Myers RL, Ewel JJ (eds) *Ecosystems of Florida*. University of Central Florida Press, Orlando pp 150-193
- Myster RW (2006) Light and nutrient effects on growth and allocation of *Inga vera* (Leguminosae), a successional tree of Puerto Rico. *Can J For Res* 36:1121-1128
- Nadelhoffer KJ (2000) The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytol* 147:131-139
- Nadelhoffer K, Shaver G, Fry B, Giblin A, Johnson L, McKane R (1996) ^{15}N natural abundance and N use by tundra plants. *Oecologia* 107:386-394
- Niinemets Ü, Kull K (2005) Co-limitation of plant primary productivity by nitrogen and phosphorus in a species-rich wooded meadow on calcareous soils. *Acta Oecologica* 28:345-356
- Nijjer S, Rogers WE, Siemann E (2010) The impacts of fertilization on mycorrhizal production and investment in Western Gulf Coast grasslands. *Am Midl Nat* 165:124-133
- Niklas KJ (1995a) Plant height and the properties of some herbaceous stems. *Ann Bot* 75:133-142
- Niklas KJ (1995b) Size-dependent allometry of tree height, diameter, and trunk-taper. *Ann Bot* 75:217-227
- Niklas KJ (1994) *Plant Allometry; the scaling of form and process*. University of Chicago Press, Chicago
- Niklas KJ, Enquist BJ (2002a) Canonical rules for plant organ biomass partitioning and annual allocation. *Am J Bot* 89:812-819
- Niklas KJ, Enquist BJ (2002b) On the vegetative biomass partitioning of seed plant leaves, stems, and roots. *Am Nat* 159:482-497

- Niklas KJ, Enquist BJ (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *P Natl Acad Sci* 98:2922-2927
- Ohlson M, Dahlberg B, Kland T, Brown KJ, Halvorsen R (2009) The charcoal carbon pool in boreal forest soils. *Nat Geosci* 2:692-695
- Olano JM, Menges ES, Martínez E (2006) Carbohydrate storage in five resprouting Florida scrub plants across a fire chronosequence. *New Phytol* 170:99-106
- Oñate M, Munné-Bosch S (2008) Meristem aging is not responsible for age-related changes in growth and abscisic acid levels in the Mediterranean shrub, *Cistus clusii*. *Plant Biol* 10:148-155
- Paradelo R, Barral MT (2009) Effect of moisture and disaggregation on the microbial activity of soil. *Soil Till Res* 104:317-319
- Paula S, Ojeda F (2009) Belowground starch consumption after recurrent severe disturbance in three resprouter species of the genus *Erica*. *Botany* 87:253-259
- Pearson V, Read DJ (1973) The biology of mycorrhiza in the Ericaceae. I. The isolation of the endophyte and synthesis of mycorrhizas in aseptic cultures. *New Phytol* 72:371-379
- Peet M, Anderson R, Adams MS (1975) Effect of fire on big bluestem production. *Am Mid Nat* 94:15-26
- Perakis SS, Hedin LO (2002) Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature* 415:416-419
- Pérez, CA, Carmona MR, Aravena JC, Armesto JJ (2004) Successional changes in soil nitrogen availability, non-symbiotic nitrogen fixation and carbon/nitrogen ratios in southern Chilean forest ecosystems. *Oecologia* 140:617-625
- Pivello VR, Coutinho LM (1992) Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). *J Trop Ecol* 8:487-497
- Pornon A, Escaravage N (1999) Genotypic structure in clonal *Rhododendron ferrugineum* L. (Ericaceae) populations: origin and maintenance. *Plant Ecol* 141:145-150
- Powers RF (1990) Nitrogen mineralization along an altitudinal gradient: interactions of soil temperature, moisture, and substrate quality. *Forest Ecol Manag* 30:19-29
- Prieto-Fernández A, Acea MJ, Carballas T (1998) Soil microbial and extractable C and N after wildfire. *Biol Fert Soils* 27:132-142

- Qian Y, Miao SL, Gu B, Li YC (2009) Effects of burn temperature on ash nutrient forms and availability from cattail (*Typha domingensis*) and sawgrass (*Cladium jamaicense*) in the Florida Everglades. *J Environ Qual* 38:451-464
- Quintana-Ascencio PF, Menges ES, Weekley CW (2003) A Fire-Explicit Population Viability Analysis of *Hypericum cumulicola* in Florida Rosemary Scrub. *Conserv Biol* 17:433-449
- Raison RJ, Khanna PK, Woods PV (1985a) Mechanisms of element transfer to the atmosphere during vegetation fires. *Can J Forest Res* 15:132-140
- Raison RJ, Khanna PK, Woods PV (1985b) Transfer of elements to the atmosphere during low-intensity prescribed fires in three Australian subalpine eucalypt forests. *Can J Forest Res* 15:657-664
- Reich PB, Peterson DW, Wedin DA, Wrage K (2001) Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology* 82:1703-1719
- Riba M (1998) Effects of intensity and frequency of crown damage on resprouting of *Erica arborea* L. (Ericaceae). *Acta Oecol* 19:9-16
- Rice SK (1993) Vegetation establishment in post-fire *Adenostoma* chaparral in relation to fine-scale pattern in fire intensity and soil nutrients. *J Veg Sci* 4:115-124
- Robertson KM, Ostertag TE (2009) Biomass equations for hardwood resprouts in fire-maintained pinelands in the Southeastern United States. *South J Appl For* 33:121-128
- Romanyà J, Casals P, Vallejo VR (2001) Short-term effects of fire on soil nitrogen availability in Mediterranean grasslands and shrublands growing in old fields. *Forest Ecol Manag* 147:39-53
- Romme WH, Tinker DB, Stakes GK, Turner MG (2009) Does inorganic nitrogen limit plant growth 3-5 years after fire in a Wyoming, USA, lodgepole pine forest? *Forest Ecol Manag* 257:829-835
- Sah JP, Ross MS, Koptur S, Snyder JR (2004) Estimating aboveground biomass of broadleaved woody plants in the understory of Florida Keys pine forests. *Forest Ecol Manag* 203:319-329
- Saha S, Menges ES, Catenazzi A (in review) Does time since fire explain plant biomass allocation in the Florida scrub ecosystem? *Fire Ecol*
- Saha S, Strazisar TM, Menges ES, Ellsworth P, Sternberg L (2008) Linking the patterns in soil moisture to leaf water potential, stomatal conductance, growth, and mortality of dominant shrubs in the Florida scrub ecosystem. *Plant Soil* 313:113-127

- Saito L, Miller WM, Johnson DW, Qually RG, Provencher L, Carroll E, Szameitat P (2007) Fire effects on stable isotopes in a Sierran forested watershed. *J Environ Qual* 36:91-100
- Salemaa M, Sievanan R (2002) The effect of apical dominance on the branching architecture of *Arcostaphylos uva-ursi* in four contrasting environments. *Flora* 6:429-442
- Salifu KF, Timmer VR (2001) Nutrient retranslocation response of *Picea mariana* seedlings to nitrogen supply. *Soil Sci Soc Am J* 65:905-913
- Sardans J, Roda F, Penuelas J (2004) Phosphorus limitation and competitive capacities of *Pinus halpensis* and *Quercus ilex* subsp *rotundifolia* on different soils. *Plant Ecol* 174: 305-317
- Sarmiento G, Pereira da Silva M, Naranjo ME, Pinillos M (2006) Nitrogen and phosphorus as limiting factors for growth and primary production in a flooded savanna in the Venezuelan llanos. *J Trop Ecol* 22:203-212
- SAS 9.1 (2003) SAS institute Inc. Cary, North Carolina
- Schimel JP, Gullledge JM, Clein-Curley JS, Lindstrom JE, Braddock JF (1999) Moisture effects on microbial activity and community structure in decomposition birch litter in the Alaskan taiga. *Soil Biol Biochem* 31:831-838
- Schlesinger WH, Abrahams AD, Parsons AJ, Wainwright J (1999) Nutrient losses in runoff from grassland and shrubland habitats in Southern New Mexico: I. rainfall simulation experiments. *Biogeochem* 45:21-34
- Schmalzer PA (2003) Growth and recovery of oak saw palmetto scrub through ten years after fire. *Nat Area J* 23:5-13
- Schmalzer PA, Hinkle CR (1991) Dynamics of vegetation and soils of oak/saw palmetto scrub after fire: observations from permanent transects. *NASA*: 1-149
- Schmalzer PA, Hinkle CR (1992) Species composition and structure of oak-saw palmetto scrub vegetation. *Castanea* 57:220-251
- Schmalzer PA, Hinkle CR (1996) Biomass and nutrients in aboveground vegetation and soils of Florida oak-saw palmetto scrub. *Castanea* 61:168-193
- Schmidt S, Stewart GR (1997) Waterlogging and fire impacts on nitrogen availability and utilization in a subtropical wet heathland (wallum). *Plant Cell Environ* 20:1231-1241
- Schmidt S, Stewart GR (2003) $\delta^{15}\text{N}$ values of tropical savanna and monsoon forest species reflect root specialisations and soil nitrogen status. *Oecologia* 2003:569-577

- Schuur EAG, Matson PA (2001) Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia* 128:431-442
- Scogings PF, Mopipi K (2008) Effects of water, grass and N on responses of *Acacia* karroo seedlings to early wet season simulated browsing: Aboveground growth and biomass allocation. *J Arid Environ* 72:509-522
- Scott-Denton LE, Rosenstiel TN, Monson RK (2006) Differential controls by climate and substrate over the heterotrophic and rhizospheric components of soil respiration. *Global Change Biol* 12:205-216
- Scowcroft PG, Friday JB, Idol T, Dudley N, Haraguchi J, Meason D (2007) Growth response of *Acacia koa* trees to thinning, grass control, and phosphorus fertilization in a secondary forest in Hawai'i. *For Ecol Manag* 239:69-80
- Seiler TJ, Rasse DP, Li J, Dijkstra P, Anderson HP, Johnson DP, Powell TL, Hungate BA, Hinkle CR, Drake BG (2009) Disturbance, rainfall, and contrasting species responses mediated aboveground biomass response to 11 years of CO₂ enrichment in a Florida scrub-oak ecosystem. *Global Change Biol* 15:356-367
- Serrasolsas I, Khanna PK (1995) Changes in heated and autoclaved forest soils of S.E. Australia. I. Carbon and nitrogen. *Biogeochem* 29:3-24
- Sharma IK (2001) Understanding clonal diversity patterns through allozyme polymorphism in an endangered and geographically restricted Australian shrub, *Zieria baeuerlenni* and its implications for conservation. *Biochem Syst Ecol* 29:681-695
- Shen SM, Pruden G, Jenkinson DS (1984) Mineralization and immobilization of nitrogen in fumigated soil and the measurement of microbial biomass nitrogen. *Soil Biol Biochem* 16:437-444
- Sigma Plot for Windows 11.0 (2008) Systat Software, Inc. Chicago, Illinois
- Silva IA, Valenti MW, Silva-Matos DM (2009) Fire effects on the population structure of *Zanthoxylum rhoifolium* Lam (Rutaceae) in a Brazilian savanna. *Braz J Biol* 69:815-820
- Sims SE, Hendricks JJ, Mitchell RJ, Kuehn KA, Pecot SD (2007) Nitrogen decreases and precipitation increases ectomycorrhizal extramatrical mycelia production in a longleaf pine forest. *Mycorrhiza* 17:299-309
- Singh RS, Srivastava SC, Raghubanshi AS, Singh JS, Singh SP (1991) Microbial C, N and P in dry tropical savanna: effects of burning and grazing. *J Appl Ecol* 28:869-878

- Sinsabaugh RL, Lauber CL, Weintraub MN, Ahmed B, Allison SD, Crenshaw C, Cusack D, Frey S, Gallo ME, Gartner TB, Hobbie SE, Holland K, Keeler BL, Powers JS, Stursova M, Takacs-Vesbach C, Waldrop MP, Wallenstein MD, Zak DR, Zeglin LH (2008) Stoichiometry of soil enzyme activity at global scale. *Ecol Lett* 11:1252-1264
- Skyllberg U, Raulund-Rasmussen K, Borggaard OK (2001) pH buffering in acidic soils developed under *Picea abies* and *Quercus robur* – effects of soil organic matter, adsorbed cations and soil solution ionic strength. *Biogeochem* 56:51-74
- Smithwick EAH, Turner MG, Mack MC, Chapin III FS (2005a) Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. *Ecosystems* 8:163-181
- Smithwick EAH, Turner MG, Metzger KL, Balsler TC (2005b) Variation in NH_4^+ mineralization and microbial communities with stand age in lodgepole pine (*Pinus contorta*) forests, Yellowstone National Park (USA). *Soil Biol Biochem* 37:1546-1559
- Sokal RR, Rohlf FJ (1995) *Biometry* 3rd edition. Freeman, New York
- Sollins P, Glassman C, Paul EA, Swanston C, Lajtha K, Heil JW, Elliott ET (1999) Soil carbon and nitrogen: pools and fractions. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P (eds) *Standard soil methods for long-term ecological research*. Oxford University Press, Inc., New York pp 89-105
- Sousa WP (1984) The role of disturbance in natural communities. *Annu Rev Ecol Syst* 15:353-391
- SPSS 11.5 for Windows (2000) SPSS, Inc. Chicago, Illinois
- Stephens SL, Meixner T, Poth M, McGurk B, Payne D (2004) Prescribed fire, soils, and stream water chemistry in a watershed in the Lake Tahoe Basin, California. *Int J Wildland Fire* 13:27-35
- Stevens JT, Beckage B (2009) Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*) *New Phytol* 184:365-375
- Stock WD, Lewis OAM (1986) Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. *J Ecol* 74:317-328
- Takenaka A, Takahashi K, Kohyama T (2001) Optimal leaf display and biomass partitioning for efficient light capture in an understory palm, *Licuala arbuscula*. *Funct Ecol* 15:660-668
- Tanner EVJ, Kapos V, Franco W (1992) Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecol* 73:78-86

- Tate III RL, Terry RE (1980) Variation in microbial activity in histisols and its relationship to soil moisture. *Appl Environ Microbiol* 40:313-317
- Teng, Y. and V.R. Timmer. 1995. Rhizosphere phosphorus depletion induced by heavy nitrogen fertilization in forest nursery soils. *Soil Sci Soc Am J* 59:227-233
- Tessier JT, Raynal DJ (2003) Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. *J Appl Ecol* 40:523-534
- Thomas GW (1996) Soil pH and soil acidity. In: Bartels JM et al. (eds) *Methods of soil analysis Part 3 Chemical Methods*. Soil Science Society of America, Inc., Madison, Wisconsin, pp 475-490
- Todd, MCL, Adams MA, Grierson PF (2000) Mineralisation of nitrogen in a chronosequence of rehabilitated bauxite mines. *Aust J Soil Res* 38:435-451
- Toma T, Ishida A, Matius P (2005) Long-term monitoring of post-fire aboveground biomass recovery in a lowland dipterocarp forest in East Kalimantan, Indonesia. *Nutr Cycl Agroecosys* 71:63-72
- Tomkins IB, Kellas JD, Tolhurst KG, Oswin DA (1991) Effects of fire intensity on soil chemistry in a Eucalypt forest. *Aust J Soil Res* 29:25-47
- Treseder KK, Mack MC, Cross A (2004) Relationships among fires, fungi, and soil dynamics in Alaskan boreal forests. *Ecol Appl* 14:1826-1838
- Tripathi SK, Kushwaha CP, Singh KP (2008) Tropical forest and savanna ecosystems show differential impact of N and P additions on soil organic matter and aggregate structure. *Global Change Biol* 14:2572-2581
- Turner MG, Smithwick EAH, Metzger KL, Tinker DB, Romme WH (2007) Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. *P Natl Acad Sci* 104:4782-4789
- Turner MG, Tinker DB, Romme WH, Kashian DM, Litton CM (2004) Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* 7:751-775
- van Schöll L, Hoffland E, van Breemen N (2006) Organic anion exudation by ectomycorrhizal fungi and *Pinus sylvestris* in response to nutrient deficiencies. *New Phytol* 170:153-163
- van de Vijver CADM, Poot P, Prins HHT (1999) Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. *Plant Soil* 214:173-185

- Vargas R, Allen MF, Allen EB (2008) Biomass and carbon accumulation in a fire chronosequence of a seasonally dry tropical forest. *Global Change Biol* 14:109-124
- Vilà M (1997) Effect of root competition and shading on resprouting dynamics of *Erica multiflora* L. *J Veg Sci* 8:71-80
- Villani EMA, Barros NF, Novais RF, Comerford NB, Costa LM, Neves JCL, Alvarez VH (1998) Phosphorus diffusive flux as affected by phosphate source and incubation time. *Soil Sci Soc Am J* 62:1057-1061
- Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea – How can it occur? *Biogeochem* 13:87-115
- Vitousek PM, Walker LR, Whiteaker LD, Matson PA (1993) Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. *Biogeochem* 23:197-215
- Vitousek PM, Farrington H (1997) Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochem* 37:63-75
- Vora RS (1988) Predicting biomass of five shrub species in northeastern California. *J Range Manage* 41:63-65
- Wan S, Hui D, Luo Y (2001) Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecol Appl* 11:1349-1365
- Wanthongchai K, Bauhus J, Goldammer JG (2008) Nutrient losses through prescribed burning of aboveground litter and understorey in dry dipterocarp forests of different fire history. *Catena* 74:321-332
- Wassen MJ, Venterink HO, Lapshina ED, Tanneberger F (2005) Endangered plants persist under phosphorus limitation. *Nature* 437:547-550.
- Weekley CW, Menges ES (2003) Species and vegetation responses to prescribed fire in a long-unburned, endemic-rich Lake Wales Ridge scrub. *J Torrey Bot Soc* 130:265-282
- Weekley CW, Gagnon D, Menges ES, Quintana-Ascencio PF, Saha S (2007) Variation in soil moisture in relation to rainfall, vegetation, gaps, and time-since-fire in Florida scrub. *Ecoscience* 14:377-386
- Weiner J, Thomas SC (1992) Competition and allometry in three species of annual plants. *Ecology* 73:648-656
- Weiner J, Berntson GM, Thomas SC (1990) Competition and growth form in a woodland annual. *J Ecol* 78:459-469

- West GB, Brown JH, Enquist BJ (1999) A general model for the structure and allometry of plant vascular systems. *Nature* 400:664-667
- White EM, Thompson WW, Gartner FR (1973) Heat effects on nutrient release from soils under Ponderosa pine. *J Range Manage* 26:22-24
- White LL, Zak DR, Barnes BV (2004) Biomass accumulation and soil nitrogen availability in an 87-year-old *Populus grandidentata* chronosequence. *Forest Ecol Manag* 191:121-127
- Wilbur RB, Christensen NL (1983) Effects of fire on nutrient availability in a North Carolina coastal plain pocosin. *Am Midl Nat* 110:54-61
- Wilson CA, Mitchell RJ, Boring LR, Hendricks JJ (2002) Soil nitrogen dynamics in a fire-maintained forest ecosystem: results over a 3-year burn interval. *Soil Biol Biochem* 34:679-689
- Wunderlin RP, Hanson BF (2003) *Guide to the vascular plants of Florida*, 2nd edn. University Press of Florida
- Yermakov Z, Rothstein DE (2006) Changes in soil carbon and nitrogen cycling along a 72-year wildfire chronosequence in Michigan jack pine forests. *Oecologia* 149:690-700.
- Zewdie M, Olsson M, Verwijst T (2009) Above-ground biomass production and allometric relations of *Eucalyptus globulus* Labill. coppice plantations along a chronosequence in the central highlands of Ethiopia. *Biomass Bioenerg* 33:421-428

BIOGRAPHICAL SKETCH

Jennifer Schafer was born in 1979 in Columbus, Ohio. She graduated from Upper Arlington High School in 1997. Jennifer earned a Bachelor of Arts in zoology, with a minor in botany, from Miami University in May 2001. She served as an Education Intern and a Plant Ecology Intern at Archbold Biological Station in Lake Placid, Florida. Because of her love for Florida scrub ecosystems, Jennifer decided to conduct her dissertation research in the scrub preserve at Archbold Biological Station. Jennifer is a Buckeye and a Gator.