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**Cover Photograph:** Abundance and cover of *Serenoa repens* (Saw Palmetto) was negatively correlated with phosphorus in soil in fire-dependent pine rocklands of Everglades National Park. Photograph © Suzanne Koptur.

# CARIBBEAN NATURALIST

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## Ecosystem Responses to Prescribed Fire Along a Chronosequence in a Subtropical Pine Rockland Habitat

Bryan M. Dewsbury<sup>1,2</sup>, Suzanne Koptur<sup>1,\*</sup>, and James W. Fourqurean<sup>1</sup>

**Abstract** – *Pinus* (Pine) rockland forests are oligotrophic, subtropical habitats whose primary-producer community structure is typically maintained by periodic fire. Contemporary urbanization and mechanized agriculture have reduced this habitat to a fraction of its former range in subtropical South Florida. Most studies of pine rocklands have focused on the timing and intensity of required periodic fire. However, we were specifically interested in the relationships between the soil and foliar biogeochemistry of the plant community and how they might change during secondary succession following fire. Utilizing techniques common in studies of seagrass ecosystems, we employed a chronosequence approach based on the records of prescribed burns at Long Pine Key in Everglades National Park to compare the abundance of dominant species and chemistry of foliage and soil from the year following fire to 7 years after a burn. The return of the community to previous coverage after fire was rapid due to resprouting, and the primary-producer structure returned to its pre-fire state within a year and a half after burning. Some shrub species followed a discernible pattern of increase or decrease in relation to phosphorus changes compared across the chronosequence. Specifically, the abundance and cover of *Serenoa repens* (Saw Palmetto) was negatively correlated with phosphorus over the sampling period. The results suggest that during succession, though overall species distribution in these systems might not be controlled by nutrients, certain species may serve as indicators for biogeochemical regime shifts over limited temporal scales. The complexity of the plant community in terrestrial habitats is perhaps better described with traditionally employed vegetation analyses, but we suggest that further work could demonstrate that soil- and foliar-nutrient content of key species may be useful as a proxy for successional stage in pine rocklands and other fire-prone terrestrial communities.

### Introduction

The impetus to understand ecosystems has prompted ecologists to examine and evaluate many properties of communities—plant species, individual plants, litter, and soil—to find proxies for time-since-disturbance. In temperate and tropical hardwood forests, canopy cover and light reaching the forest floor are correlated with forest stature and community maturity. Soil-nutrient content may change during succession from low to progressively higher through the changing seres from groundcover, to shrubs, to softwood trees, and then hardwood trees. For plant species present in this community for a period of time, foliage nutrients may change in response to changing soil conditions, as has been observed in plants of

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the seagrass community following disturbance (Fourqurean et al. 2005). We undertook this study to determine if we could find correlations to indicate the time-since-disturbance in a terrestrial, fire-successional community endemic to South Florida and the Caribbean.

*Pinus* (pine) rocklands are upland, oligotrophic, fire-dependent habitats, dominated in southern Florida by *Pinus elliottii* (Slash Pine), which grows with a number of tropical and temperate woody species on mid- to late-Pleistocene limestone rock (Osmond et al. 1965, Snyder et al. 1990). Pine rocklands are distinct from other pine and tropical dry forests, which are fire-sensitive, in that they have a very limited range and are subject to frequent fires (Otterstrom et al. 2006). Rather than the more common situation in which dominant tree species are keystone primary producers (Williams et al. 2007), pines in these subtropical rocklands are foundation species (O'Brien et al. 2008). Accumulated organic matter from litter-fall may be ignited by lightning or humans, creating fires that release nutrients trapped in the litter and vegetation as well as maintaining forest structure and species composition typical of a fire-dependent ecosystem. If the fire interval is too long, an over-accumulation of fuel can result in more intense burns than the species typical of pine rocklands can tolerate (Snyder et al. 2005); ecosystem consequences include a longer recovery time when adult trees, seedlings, and even seeds in the seedbank are killed, thus eliminating sources of regenerating pines following fire (Fisher 2008). The buildup of organic matter and nutrients in vegetation and litter in the absence of fire can ultimately favor late-succession species, resulting in a completely different ecosystem structure and function (Loope and Dunevitz 1981, Nguyen 2011). Left undisturbed for 20 years or more, pine rocklands undergo succession to hardwood hammock communities with remnant pines (Alexander 1967, Harley 2012, Robertson 1953).

In southern Florida, pine rockland ecosystems are considered an endangered habitat because their area has been vastly reduced by anthropogenic activities over the last century (Koptur 2006, Snyder et al. 1990). Lands formerly occupied by pine rocklands have undergone rapid urbanization since the middle of the 20<sup>th</sup> century and are now occupied by homes and businesses, with some areas having been rock-plowed to provide land for agriculture (Koptur 2006, O'Brien 1998). Pinelands and hardwood hammocks (both found on higher elevations rangewide) have been reduced to about 3% of their historical acreage (Bergh and Wisby 1996). The fragmentation of the remaining pine rocklands poses challenges to land managers charged with their conservation; changes in community structure—due to exotic plant invasions, for example—disrupt the availability and type of fuel for periodic burns (Possley et al. 2014, Snyder et al. 2005). Additionally, pine rockland fragments are often located adjacent to urbanized areas, which limits or entirely eliminates fire as a management tool due to proximity of human habitation.

Studies of pine rockland ecosystems have focused primarily on the periodicity and intensity of fire and its role in shaping the structure of the plant community. Less is known about the temporal biogeochemical changes between burns, and their potential role in influencing the recovering plant community. Pine rockland

communities are generally phosphorus-limited ecosystems (Taylor and Woods 1981) found on slightly elevated limestone rock through which nutrients are easily leached. Fire has different effects on nitrogen and phosphorus—the 2 main nutrients that affect primary productivity—and these effects can be differentiated even further according to burn intensity (Saha et al. 2009). Organic nitrogen is lost rapidly in burns; the overall volume of organic nitrogen loss is directly proportional to organic matter loss. The remaining nitrogen exists primarily in inorganic form. Organic nitrogen steadily increases as plants re-sprout and microbial activity by symbiotic and free-living nitrogen-fixing bacteria increases (Nguyen 2011, Wan et al. 2001). Phosphorus availability is highly dependent on pH concentration due to its differential adsorptive capacities with cations; high pH makes phosphorous unavailable in carbonate soils. Decreases in pH after fire therefore make phosphorus available for re-sprouting seedlings (Nguyen 2011, Zhou and Li 2001).

During post-fire recovery, nitrogen and phosphorus availability in the soil increase rapidly, then decrease fairly soon as plants re-sprout or seedlings germinate and establish new recruits that grow until the next burn. Rapid recovery of aboveground biomass has been documented, showing species distribution and abundance returning to a pre-fire state within a year of burning (Sah et al. 2006). Although the general ecosystem response to fire is well documented, the species-specific responses to the biogeochemical changes that occur during the time between burns are not as well known. Even less is known about how the plant community and its associated biogeochemistry might change over the years following a fire. In this study, we used space-for-time substitution to examine changes across the chronosequence to answer a number of questions relating to the biogeochemistry and plant-community structure of a pine rockland ecosystem. Our major objective in this study was to identify an ecological indicator, other than organic matter accumulation, that represented the system's relative stage of succession (and thus relative position in the burn cycle). We tested the hypothesis that differences in soil and foliage-nutrient composition of a plant species in the fire-successional pine rockland community correspond to time-since-fire, and that these patterns can be elucidated using the chemical analysis of particular sentinel plant species from the community. Because many of the perennial species in this habitat are long-lived, their presence may not be changed by fire, but others may be more or less abundant depending on the frequency and severity of fire. We focused on common species typical of this forest type, assessed the chemistry of their foliage, and compared it with nutrient levels in the surrounding soil to see if there were associations over time.

## Methods

### Study site

We carried out our study in 2012 on Long Pine Key, an extensive pine rockland habitat in Everglades National Park, Homestead, FL. Long Pine Key had been divided into multiple sectors with different burn schedules, following a plan devised by scientists and managers [(National Park Service 2010). Park managers

have recorded the year burned, intensity, and size of burn for all sectors. We used their dataset to create a chronosequence where, for the purposes of our study, we considered all parts of the habitat as functionally equal. We assumed that more recently burned areas would become structurally similar to areas less recently burned if left for the same period of time. We chose replicates of 3 sites for each of the following burn years: 2003, 2005, 2007, and 2010 (Table 1). At each site, we used park-provided coordinates that corresponded with the fire's point of origin as starting points for sampling and ensured that the area sampled was representative of the effects of that fire. We collected data on species composition, species cover, soil nitrogen and phosphorus, and foliar nitrogen and phosphorus.

### Species composition and cover

We ran three 25-m transects—to the north, west, and east—from the point of origin, and randomly sampled ten 1-m<sup>2</sup> quadrats along each transect (Table 1). To determine species cover, we used a modified Braun Blanquet technique (Fourqurean et al. 2002) that assigned relative cover to each sampled species. Both observers present identified species, each investigator assigned a Braun Blanquet score corresponding to each species, and we averaged the 2 scores. The Braun Blanquet cover score we assigned referred to the percentage of the soil that was blocked from view by the species' foliage. In this system 0.5 meant sparse coverage, 1 = 0–5%, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, and 5 = >75%. We calculated average coverage scores for every identified species, and summed their average coverage scores for each site. Taxonomy (Table 2) follows Wunderlin and Hansen (2011) and the Atlas of Florida Vascular Plants (<http://florida.plantatlas.usf.edu>).

### Soil nutrients

We collected 5-cm<sup>3</sup> samples of soil in duplicate vials for nitrogen and phosphorus analysis. Because pine rocklands have little soil, we collected our samples from fissures and holes in the rocky substrate. We took 2 samples near the endpoints

Table 1. Location of sites used for the chronosequence analysis in Everglades National Park and their corresponding GPS coordinates. Because there was only 1 large 2010 burned site, we chose 3 sampling sites at random located at least 200 m from each other within the large burn plot.

Site (code)	Year last burned	Latitude	Longitude
PR4	2003	25.419088281	-80.706913837
PR17	2003	25.414442121	-80.687897915
PR24	2003	25.408190494	-80.659491504
PR3	2005	25.395085251	-80.663116106
PR5	2005	25.404518114	-80.712512189
PR13	2005	25.397652609	-80.684982641
PR8	2007	25.420938847	-80.703991466
PR14	2007	25.396311849	-80.624495424
PR23	2007	25.393534900	-80.640662400
PR2010A	2010	25.381707	-80.671797
PR2010B	2010	see caption	
PR2010C	2010	see caption	

of each transect for a total of 6 samples per site. In the laboratory, we determined percent nitrogen content using a Carlo-Erba CHN analyzer (Fisons NA1500, OEA Laboratories, Charlotte, NC) and percent phosphorus content with an acid hydrolysis extraction followed by a colorimetric analysis (Fourqurean et al. 1992). We used 20–25-mg sub-samples of for each procedure.

### Foliar nutrients

We investigated foliar nutrient concentrations of 2 common and ubiquitous species, *Sabal palmetto* (Cabbage Palmetto) and *Serenoa repens* (Saw Palmetto) at the different burn sites. In the field, we randomly chose 3 mature plants in each transect, and removed about half of a single leaf from each selected individual at each site, choosing the uppermost, fully expanded, mature leaf. In the lab, we dried the samples, ground them into a fine powder, and took sub-samples for percent nitrogen and phosphorus analysis as described above for soil samples.

### Statistical analysis

We performed canonical correspondence analysis (PC-ORD) to examine patterns in vegetation change over the chronosequence. The first matrix contained mean cover values for 23 species at each of 12 sites (3 in each burn year); the second

Table 2. Species encountered during pine rockland vegetation sampling and the abbreviations used in CCA plot (first four letters of generic and specific epithets). \* symbolizes exotic species

Name	Abbreviation	Family	Common name
<i>Ardisia elliptica</i> Thunb.*	ardielli	Myrsinaceae	Shoebuttton Ardisia
<i>Ardisia escallonioides</i> Schiede & Deppe ex Schlttdl. & Cham.	ardiesca	Myrsinaceae	Marlberry
<i>Byrsonima lucida</i> (Mill.) DC.	byrsluci	Malpighiaceae	Locustberry
<i>Chrysobalanus icaco</i> L.	chryiac	Chrysobalanaceae	Cocoplum
<i>Chrysophyllum oliviforme</i> L.	chryoliv	Sapotaceae	Satinleaf
<i>Cladium jamaicense</i> Crantz	cladjama	Cyperaceae	Sawgrass
<i>Guettarda elliptica</i> Sw.	guetelli	Rubiaceae	Hammock Velvetseed
<i>Guettarda scabra</i> (L.) Vent.	guescab	Rubiaceae	Rough Velvetseed
<i>Ilex cassine</i> L.	ilexcass	Aquifoliaceae	Dahoon
<i>Jacquemontia curtissii</i> Peter ex Hallier f.	jacqcurt	Convolvulaceae	Pineland Clustervine
<i>Metopium toxiferum</i> (L.) Krug & Urb.	metotoxi	Anacardiaceae	Poisonwood
<i>Morinda royoc</i> L.	moriroyo	Rubiaceae	Mouse Pineapple
<i>Myrica cerifera</i> L.	myriceri	Myricaceae	Wax Myrtle
<i>Myrsine cubana</i> A. DC.	myrscuba	Myrsinaceae	Myrsine
<i>Persea borbonia</i> (L.) Spreng. var. <i>borbonia</i>	persborb	Lauraceae	Red Bay
<i>Pinus elliottii</i> Engelm.	pinuelli	Pinaceae	Slash Pine
<i>Pluchea baccharis</i> (Mill.) Pruski	plucbacc	Asteraceae	Rosy Camphorweed
<i>Randia aculeata</i> L.	randacul	Rubiaceae	White Indigoberry
<i>Sabal palmetto</i> (Walter) Lodd. ex Schult. & Schult.f.	sabapalm	Arecaceae	Sabal Palm
<i>Schinus terebinthifolia</i> Raddi*	schitere	Anacardiaceae	Brazilian Pepper
<i>Serenoa repens</i> (W. Bartram) Small	sererepe	Arecaceae	Saw Palmetto
<i>Sideroxylon salicifolia</i> (L.) Lam.	sidesali	Sapotaceae	Willow Bustic
<i>Tetrazygia bicolor</i> (Mill.) Cogn.	tetrnico	Melastomataceae	Tetrazygia

contained 4 burn years (and a third contained mean soil-phosphorous levels). To better visualize the separation among years in the graph (Fig. 1), we eliminated the outlier species—2 exotic species, *Schinus terebinthefolia* (Brazilian Pepper) and *Ardisia elliptica* (Shoebutton Ardisia), the dominant Slash Pine and the understory species *Ilex cassine* (Dahoon) and *Pluchea carolinensis* (Rosy Camphorweed). To test for differences in species cover and abundance among different sites in the chronosequence, we used a one-way analysis of variance (ANOVA) with burn year as the independent variable. We analyzed the sites for differences in the dependent variables: total species cover, individual species cover, species diversity, and sediment and foliar nutrient concentrations. We employed Bonferroni-corrected significance levels for multiple comparisons.

## Results

### Species composition and cover

All sites contained the plant species that characterize South Florida pine rockland communities (Gunderson 1994); we encountered 23 species in the vegetation sampling (Table 2). Because the CCA showed no significant trend with soil phosphorous, we present only results for vegetation and year of burn, which show

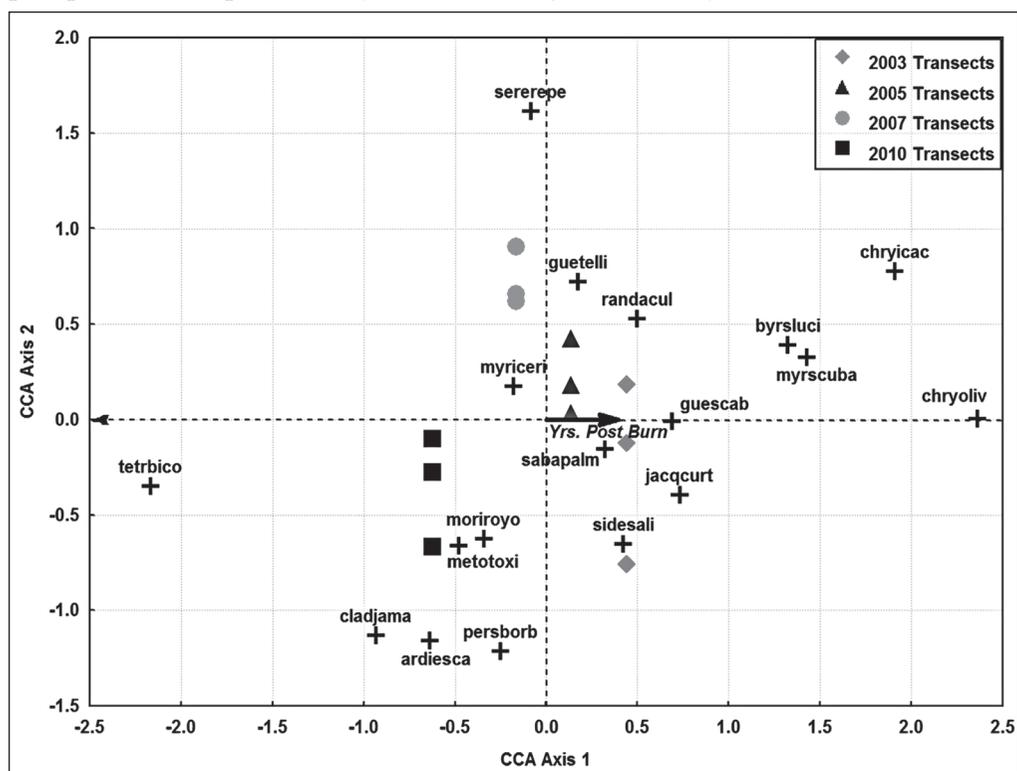


Figure 1. Canonical correspondence analysis of 23 species in 4 burn years (2003, 2005, 2007, 2010), measured in 2012, testing the hypothesis that plant-community structure changes significantly with time-since-fire. Species abbreviations given in Table 2. Several species were not plotted to allow better resolution for this figure (see methods).

separation of the burn years, along the 2 axes (Fig. 1). Axis 1 explained 40% of the variance, and axis 2 added very little. Some woody species were more abundant at sites with the longest post-burn recovery time (e.g., *Byrsonima lucida* (Locust-berry), *Chrysobalanus icaco* (Cocoplum), *Chrysophyllum oliviforme* (Satinleaf), *Myrsine cubana* (Myrsine), and *Guettarda* spp.(velvetseeds).

### Soil nutrients

Phosphorus varied significantly among the burn years. In the year immediately after fire, phosphorus concentration was 0.064% (Fig. 2). Phosphorus concentrations were significantly lower in the subsequent years, but increased slightly in the sites that were the longest time since burn ( $P < 0.05$ ; Table 3). Nitrogen concentrations also decreased, but not significantly, with time since fire, and followed the same trend as phosphorous concentrations. The 2003 burned sites, however, had nitrogen concentrations that were as high as the sites that were most recently burned (Fig. 2). There was no significant correlation between phosphorus and nitrogen concentrations (Pearson  $C = 0.83$ ,  $P = 0.17$ ).

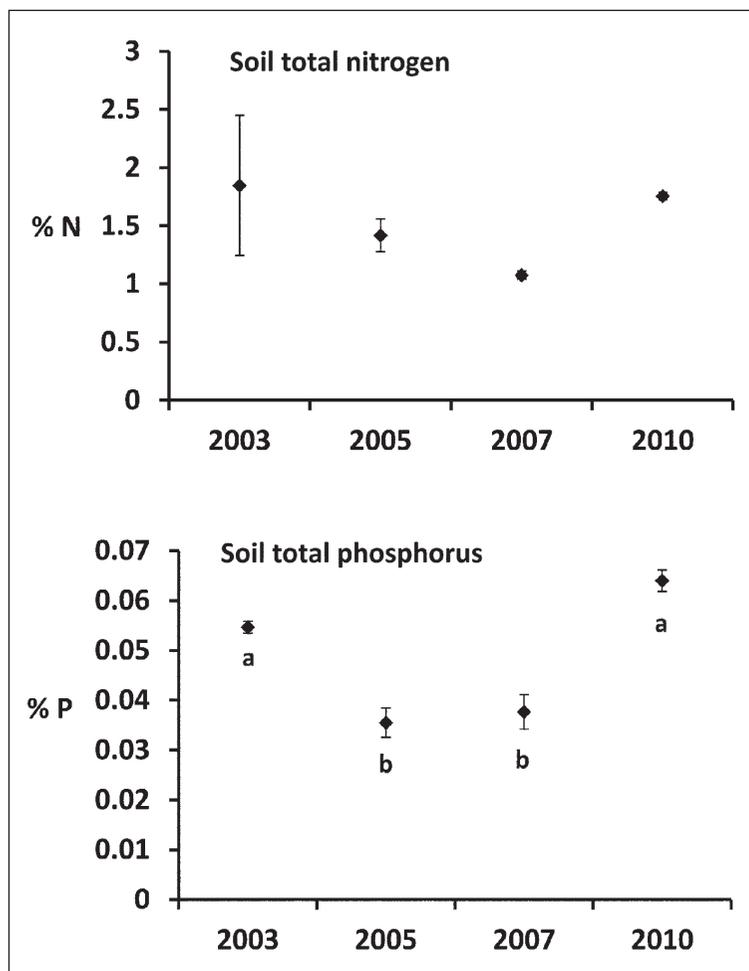


Figure 2. Change in nutrient concentrations in soil during the burn years. Soil nitrogen (above) and phosphorous (below).

**Foliar nutrients**

Nitrogen did not vary between burn years for either Cabbage Palm or Saw Palmetto. Foliar concentration of nitrogen was higher in Cabbage Palm (1.74%) than in Saw Palmetto (1.45%). There was no significant difference in foliar phosphorus among burn years for Cabbage Palm or Saw Palmetto (Fig. 3); patterns were the same, but differences were more extreme for Cabbage Palm.

Table 3. Results of one-way ANOVA using burn year as the independent variable. \* indicates significant differences among burn years.

Variable	F	P
Phosphorus		
Soil total	2.899*	<0.050*
Saw Palmetto total	3.534*	0.054*
Sabal Palm total	2.082	0.181
Nitrogen		
Soil total	0.084	0.981
Saw Palmetto total	1.453	0.298
Sabal Palm total	0.149	0.927

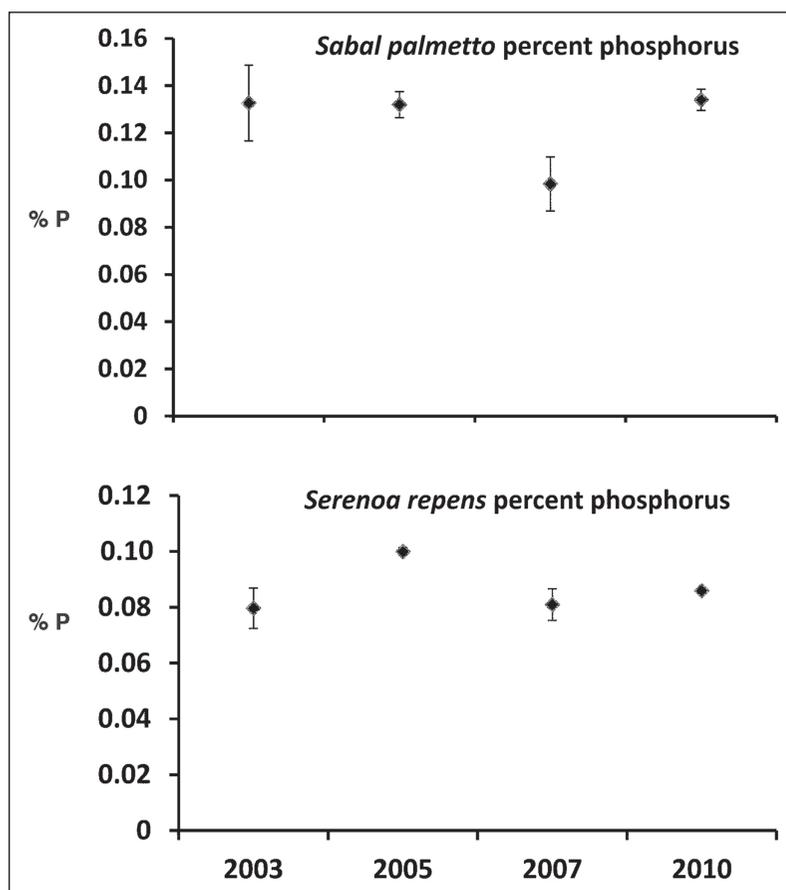


Figure 3. Change in foliar tissue phosphorus concentration of Saw Palmetto and Sabal Palm during the chronosequence sampling period.

## Discussion

Using a chronosequence approach, we demonstrated that time-since-burn had a significant effect on the plant-community structure and soil biogeochemistry of pine rockland ecosystems in South Florida. In this region, typical fire-return intervals range from 3 to 10 years (Snyder et al. 1990), and regular burns have been conducted in the Long Pine Key in Everglades National Park for more than 50 years. Understory structure returned to pre-burn condition within 2 years of a burn, but different species recovered at different rates, perhaps in concert with the relative availability of phosphorus in the soil. This differentiated response was largely unaffected by soil-nitrogen concentrations, even though these concentrations showed the same trends with burn-year as did phosphorus. In calcareous pine rockland soils, the ability of plants to utilize nitrogen may be limited by phosphorous availability.

The rapid recovery of vegetation after fire in pine rockland ecosystems is well documented because fire plays a pivotal role in the release of stored carbon and nutrients that aid the resprouting of pine rockland plants (Snyder et al. 2005) as well as flowering (Gunderson et al. 1983, Koptur 2006). While overall species cover quickly recovers to pre-burn levels, species composition may differ depending on time-since-burn. Because post-burn recovery patterns may vary by species, plant community structure and function may differ even if overall cover is regained. *Cladium jamaicense* (Sawgrass) responded quickly after fire, while woody species such as *Byrsonima lucida* (Locustberry), *Randia aculeata* (White Indigoberry), and Saw Palmetto took several years to respond. As total vegetation coverage of the system increased, the relative abundance of White Indigoberry and Saw Palmetto decreased. Sawgrass increased in abundance as total species cover increased, which may be typical of perennials with extensive vegetative reproduction (but see Ponzio et al. 2004).

Traditional management of fire-controlled ecosystems typically encompasses a mixture of fuel monitoring, invasive species removal, and protection of habitat from human development (Snyder et al. 2005). Fuel monitoring relies on being aware of the build-up of organic matter, and the temporal scale over which fuel accumulation takes place (Sah et al. 2006). The current approaches to systematically manage burn cycles are rooted in many years of studies, but relatively few studies have looked at species-specific responses that may affect the post-burn plant-distribution patterns in the community (some exceptions being Hiers and Mitchell 2007, Liu et al. 2005, Menges and Root 2004, O'Brien 1998, Schafer et al. 2013, Slapcinsky et al. 2010, Spier and Snyder 1998). Understanding biogeochemical changes and how they affect aboveground community structure post-fire may help better predict, on a local scale, the various stages of succession and provide an additional tool to determine burn cycles that will help managers achieve the desired results. In our study, the nutrient patterns exhibited in the soil corresponded to the nutrient pattern in Cabbage Palm foliage, suggesting that this species may act as an indicator for the overall nutrient status of the system. Biomass has proven a reliable indicator of time-since-fire (McNab et al. 1978, Sah et al. 2006). Because overall vegetative cover and diversity increase fairly rapidly after fire in pine rocklands,

total species abundance may not necessarily be a sufficient indicator of successional stage. Organic matter accumulation, which could indicate relative successional stage (increasing over time), can be an even less accurate measure, as differences in species evenness can affect the amount and type of organic matter present (Ross et al. 2003).

Our study also highlighted another important ecological consideration. The concentration of phosphorus, a highly limiting nutrient in wet Everglades ecosystems (Taylor and Woods 1981) may also play a role in shaping plant-community structure. In our experiment, we focused on the relationship of nutrients and species with a significant presence through all the burn years, but those are not the only species whose abundance and distribution are affected by this nutrient. The burning of aboveground plant material releases nutrients to the soil, stimulating regrowth and flowering (Alexis et al. 2012, Michalzik and Martin 2013, Schafer and Mack 2010).

Though many studies have shown that fire frequency, fuel load, and herbaceous plant diversity are strongly related, we suggest that pine rockland management might also utilize nutrient analysis to maintain the correct periodicity of prescribed fire and to monitor the changes that occur within the community between burn years. With more studies of this type, we may be able to use nutrient changes to better understand species distribution, successional stage, and ultimately the conditions that allow for adequate preservation of pine rockland community structure. We hope that our study will encourage others to explore the potential for nutrient content of soil and foliage as indicators of time-since-fire, and test their utility in other fire-successional ecosystems.

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