THE IMPACT OF FIRE ON PHOSPHORUS AND THE RESTORATION OF SUBTROPICAL CALCAREOUS WETLANDS

By

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To my loving wife, Amanda

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LIST OF ABBREVIATIONS

APA	Alkaline phosphatase activity
Bis P	Bis-4-methylumbelliferyl-phosphate
C	Carbon
DDI	Distilled deionized water
DON	Dissolved organic nitrogen
ENP	Everglades National Park
HID	Hole-in-the-Donut
HNPB	High nutrient plant biomass
LNPB	Low nutrient plant biomass
MBP	Microbial biomass phosphorus
MUF P	4-methylumbelliferyl-phosphate
N	Nitrogen
P	Phosphorus
Pi	Inorganic phosphorus
Po	Organic phosphorus
Ref	Reference site
Res00	Restored in 2000 site
SE	Standard Error
TC	Total carbon
TN	Total nitrogen
TP	Total phosphorus
TP_i	Total inorganic phosphorus
TP_o	Total organic phosphorus

Abstract of Thesis Presented to the Graduate School
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Fire is a critical regulator of biogeochemical cycles in approximately 40% of the earth's land surface. Fire is known to increase the abundance of desired plant species in wetlands, however, it also releases phosphorus stored in plant biomass and soil organic matter which may further exacerbate the problem of phosphorus (P) enrichment in these systems. To evaluate the potential negative impacts fire may have on P limited wetlands, two wetlands, one undergoing restoration efforts after P enrichment and the other containing low P concentrations were evaluated both before and up to one year after a prescribed fire.

The sites undergoing restoration from P loading contained woody and undesirable plant species, allowing for a greater storage of P in plant biomass. All sites recorded an increase in P after the fire; however, overall soil P storage was not greatly altered. Conversely, storage of extractable P was doubled after the fire and did not diminish greatly up to one year later. Periphyton may have played a critical role in the initial uptake and storage of P and most likely contributed to the observed release of P over time. Measured phosphatase activity and biomass nutrient ratios indicated that P limitation persisted after burning except at the most enriched site. This may indicate

that while fires do increase P availability, an overall shift away from P limitation will most likely not occur except in sites of high P enrichment.

During muffle and lab combustion of both plant biomass types, carbon and nitrogen (N) were volatilized (>99%), while P remained in high concentrations in the residues. It was also found that of the N and P remaining in flame combustion residues, only 5% N and 50% P was extractable. These results are in contrast with similar muffle furnace residues where 95% N and 90% P remaining was readily extractable. Because the flame combustion was most like an actual field fire, we concluded this method was more appropriate for mimicking field fire residues in the laboratory. These results can be adapted to fire impact models to predict potential nutrient enrichment that may occur after a fire-event.

CHAPTER 1
INTRODUCTION

Fire is an important ecological regulator in many ecosystems worldwide (Bond et al., 2005). Estimates have found that approximately 40% of the earth's land surface is regularly impacted by fire events (Chapin et al., 2002). While climate is traditionally regarded as the main regulator of ecosystem characteristics and biogeochemical cycles (Whitaker, 1975), fire has the capability of shifting or permanently altering these systems to a greater degree than climate (Bond et al., 2005; DeSantis et al., 2011). Global incidences of fire are predicted to increase as climate changes occur (Westerling et al., 2006; Krawchuck et al, 2009). As a result, it is essential to understand all impacts fire has on an ecosystem.

Characteristics of fire-events can be altered by a variety of parameters such as fuel load quantity and quality, moisture content, ambient air temperature, wind speed and direction, and ignition source (Ryan, 1991; USGS, 2001; Certini, 2005). The most apparent impact caused by a fire is the combustion and charring of vegetation. Both C and N contained in plant biomass are lost in large quantities due to volatilization (Gioavannini et al., 1988; Fisher and Binkley, 2000) while most P remains within plant residual ash and char. The reamaining P after a fire is often thought to be readily available (Saa et al., 1998; Galang et al., 2010; Qian et al., 2009).

Besides the release of macronutrients, mainly P, from plant biomass, cations are also released into the soil affecting soil pH while reduction/oxidation reactions may alter cation exchange capacity (Nye and Greenland, 1960; Khanna and Raison, 1986; Macadam, 1987). Soil organic matter, like plant biomass, is often converted into inorganic forms due to the increased heat from a fire, releasing and altering stored

nutrients. When soil temperatures become high enough, denaturing and sterilization of soil microbial communities can occur (DeBano, 1998).

While most research on wildfires has occurred in forest and shrublands (DeBano and Conrad, 1978; Aranibar et al., 2003; Certini, 2005; Boerner et al., 2005; Lagerström et al., 2009; Fonda and Binney, 2011), approximately 80% of the global fire adapted ecosystems are dominated by herbaceous plant species (Flannigan et al., 2009). Of these systems, grasslands and savannahs are most studied while little attention is given to the impact of fire within wetlands. Despite this lack of attention, however, the role of fire is critical for preventing the loss and degradation of many wetlands (Egler, 1952; Robertson, 1953; Craighead, 1971).

As it alters nutrient forms and availabilities, fire can have important consequences for wetland systems, particularly those involving impacts from nutrients. Wetlands fires that have been studied have been shown to increase the amount of P in the water column, periphyton, plant biomass and soil (Vazquez et al., 1991; Saa et al., 1998; Miao and Carstenn, 2005; Qian et al., 2009; Galang et al., 2010). Within most freshwater wetlands, P is the dominant limiting nutrient and small additions of P are known to significantly alter biogeochemical process. Increased primary productivity of both plants and microbes from P pulses can result in the release of greenhouses gases, which are normally stored in wetlands. Decomposition rates of organic matter have also been linked with P enrichment, where increased P results in lower phosphatase activity and increased C degrading enzymes (Chauhan et al., 1981; Wright and Reddy, 2001; Penton and Newman, 2007)

Because these findings indicate that increases in P lead to shifts in biogeochemical cycles and potentially decreased organic P storage, concern arises about the impacts of fire on many wetland restoration efforts. Reducing ecosystem impacts from nutrient enrichment is most often the key focus in most wetland restoration efforts. Nutrient enrichment occurs readily within wetlands because of their low-lying elevation and the flow of water, rich in P and other elements, entering these systems. Naturally most freshwater wetlands are oligotrophic and when excess nutrients enter, shifts in soil microbial and vegetation communities can occur. In order to stop these changes from occurring, the storage or removal of P is necessary. While P and its role in biogeochemical cycles in the context of restoration have been studied, little focus has been given to the impact of fire and wetland restoration.

The Florida Everglades: A Fire adapted Ecosystem

Field sampling was conducted in a calcareous subtropical wetland within the Everglades National Park (ENP) in southern Florida, USA. The region sampled was located between the Taylor and Shark River Sloughs in an area of the ENP know as the Hole-in-the-Donut (HID) (Fig. 1-1). These marl prairie wetlands are fire-adapted and depend on fire to maintain herbaceous species dominance (Miao and Carstenn, 2006; Miao et al., 2009). Egler (1952) famously summed up the importance of fire in the Everglades by saying “the herbaceous Everglades and the surrounding pinelands were born in fires [and] they can survive only with fires.” Because fire is important to the historical shaping of the Everglades, prescribed fires have become a major component to the restoration efforts and modeling within the Everglades (USGS, 2004). While fire promotes the dominance of herbaceous plant species (Rundell, 1981), it also increases

P availability (Vazquez et al., 1991; Saa et al., 1998) which could hinder restoration efforts.

Like most freshwater wetlands, the Everglades is sensitive to P additions, and so one of the major goals for restoration in these HID sites is reducing P availability. Agricultural practices at the HID have left some soils containing 5x the amount of naturally occurring P (natural = 200 mg P kg^{-1}) and removal through storage is key to achieving restoration (Smith et al., 2011). Fire is used as a tool in the HID to remove invasive species that have become dominant in part due to increased soil P concentrations. However, past studies have shown increases in soil P after fire events, which could greatly impact restoration efforts. In the short-term, fire will remove the invasive plants but if fire increases P in the soil and short (3 – 5 yr) fire frequency is not maintained at these sites, fire could be detrimental to long-term restoration.

Because fire naturally occurs in these wetlands and it removes undesirable plant species, it is a key component in management practices at the HID. However, few fire studies have been performed on wetlands therefore the potential impact of nutrient enrichment is largely unknown. Of the studies that have observed the effect of fire on wetlands, none have addressed wetland fires on seasonally flooded wetlands. A total of four sites within the HID were chosen, two P enriched and two with natural P concentrations. Both high and low elevations were chosen in order to measure the impact of hydroperiods have on fire-events and their ecosystem impacts.

Objectives

The central hypothesis of this study was that fire in wetlands will add bioavailable P from above-ground biomass altering biogeochemical cycles and perhaps shifting ecosystems away from P limitation. It is expected that plant biomass will greatly

influence the combustion rates and nutrient forms added to these soils after fire. The following objectives were developed in order to study this hypothesis:

- Measure P storage pools both immediately and one-year after a fire-event and compare them with pre-burned conditions
- Characterize plant biomass residues after combustion to determine how they impact nutrient additions after a fire.

Thesis Format

Chapter 2 examines the impacts of fire on P storages in both nutrient rich and unimpacted subtropical calcareous wetlands. The amount of P added from above-ground plant biomass was estimated and P storage pools were measured both above and below ground. Indicators of bioavailable P enrichment such as nutrient ratios and phosphatase enzymes activities were used to estimate the impact of fire. In Chapter 3, plant biomasses from both nutrient rich and unimpacted wetlands were muffle furnace and lab fire combusted. Residues were analyzed for their remaining nutrients (total and extractable) in order to assess what additions would occur after a wetland fire. Chapter 4 presents a synthesis of the findings and conclusions within this thesis, as well as their implications.

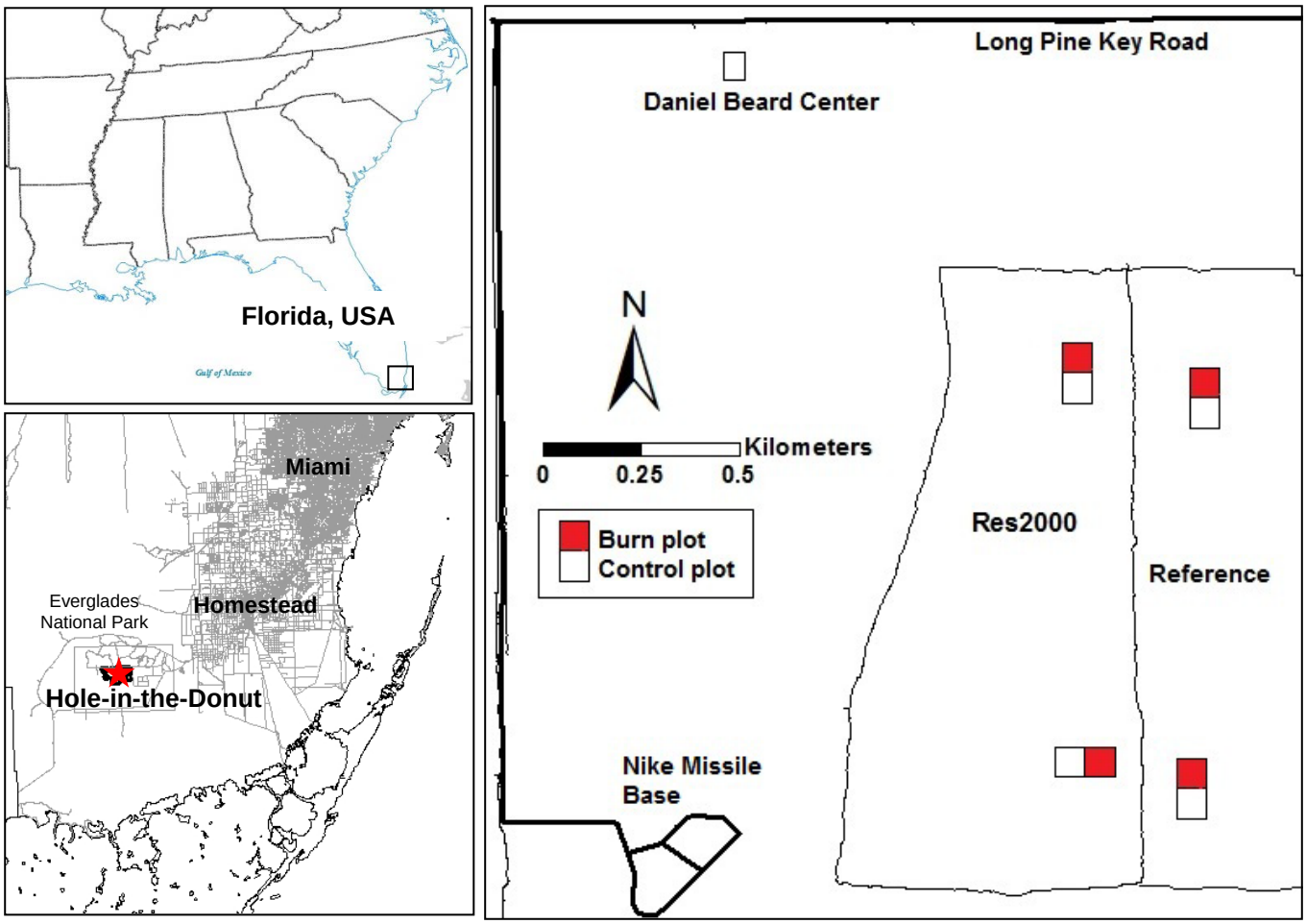


Figure 1-1. The location of the Hole-in-the Donut sites within the Everglades National Parks. The four sampling sites are shown with high elevation sites being the two northern sites. Restored2000 sites were restored through soil removal down to bedrock in 2000. Reference sites had no history of significant human disturbance.

CHAPTER 2
IMMEDIATE AND LONG TERM IMPACTS OF FIRE ON PHOSPHORUS AVAILABILITY IN HERBACEOUS DOMINATED CALCAREOUS WETLANDS

Field Fire Introduction

Fire, natural or prescribed, is important to the presence and function of grasslands, prairies, shrublands, boreal forests and other ecosystems (Bond et al., 2005). While temperature and precipitation are traditionally regarded as one of the main regulators of vegetation presence and distribution (Whitaker, 1975), fire is capable of suppressing or promoting vegetation types to the same degree as climate (Bond et al., 2005; DeSantis et al., 2011). Similarly, as climate affects biome vegetation, it also regulates the frequency of natural fires. Expected shifts in climate have also been predicted to increase the global occurrence of natural fires (Westerling et al., 2006; Krawchuck et al., 2009). Consequently, the need for a better understanding of the impacts fire has on vegetation and soil nutrients is critical to a more accurate depiction of ecosystem characteristics and biogeochemistry, both present and future.

While most research on wildfires has occurred in terrestrial biomes (Certini, 2005; Boerner et al., 2005), fire can be a dominant ecosystem driver in wetlands (Egler, 1952; Robertson 1953, Craighead, 1971). The most common cause of fires is a combination of drought and lightning strikes. In wetlands, fire is critical in maintaining vegetation communities by reducing the amount of woody vegetation and converting organic forms of nutrients (N, P and metals) into inorganic and more bioavailable forms (Cade-Menun et al., 2000) and simultaneously removing stored C and N due to volatilization (Fisher and Binkley, 2000).

The most apparent alteration caused by a fire in any biome is the combustion and charring of vegetation. The severity of a fire can be altered by a variety of parameters

but most significant is the fuel load or plant biomass type, quality and quantity (USGS, 2001). The time needed for plant biomass to recover after a fire-event is dependent upon vegetation type. Grass and shrublands can take less than 3 years for regrowth, while forests may take several decades (Wetzel et al., 2001). In this manner, effects of fire can be either short-term (impact of combustion) or long-term (changes in species and regrowth), both of which can have consequences on ecosystem nutrient cycling and bioavailability (Rundell, 1981; Woodmansee and Wallach, 1981).

The initial combustion of a fire is capable of modifying soil physical, chemical and biological properties (Certini, 2005). Deposition of combusted residues results in a direct alteration of chemistry and nutrient availability. Ash is characteristically enriched in P after the volatilization of most C and N compounds. Ignition of live plant biomass does not occur until 350°C or higher depending on plant moisture content (Saito, 2001; Ward 2001). In wetland ecosystems, high moisture content can create patchiness in burns and incomplete biomass combustion (Bond and Van Wilgen, 1996). Incomplete combustion or combustion under limited oxygen can lead to the creation of char residues (Nocentini, 2011) composed of stable aromatic C structures which can complex with other nutrients and be added to the soil (Baldock and Smernik, 2002; Czimczik et al., 2002).

Fire induced temperature can drastically result in reduction of microbial populations (DeBano, 1998). Soil pH often increases after a fire due to the denaturation of organic acids and the release of cations (in ash) from combusted plant biomass (Macadam, 1987). In calcareous soils, carbonates are highly resistant to increased temperatures, resulting in little change in soil pH (Rabenhorst, 1988; Úbeda et al.,

2005). Any increase in pH from base saturation that usually occurs after a fire (Macadam, 1987) could cause coprecipitation of phosphate and carbonates present (Dodd, 2003; Otsuki and Wetzel, 1972).

Within many oligotrophic, freshwater wetlands, P is extremely limiting, and any additional pulse of P has the ability to alter the structure of microbial and plant communities. Because of the conversion of organic P to ash and char P forms, there is generally an observed increase in P availability after a fire (Miao and Carstenn, 2005). For this reason, the production of ash and char in a fire can be a major driver on wetland species composition and overall productivity. Despite this importance of fire, however, there are few studies to document the role of fire in wetland P biogeochemistry.

With the potential to alter, P biogeochemistry, fire is extremely important in wetlands restoration efforts. In wetlands and other aquatic systems, one of the major goals in maintaining and restoring historical vegetation communities is establishing low nutrient levels, and in freshwater systems, low or P limiting conditions. Fire has been a key factor in the prevention of woody species and the establishment of herbaceous species dominance (Egler, 1952; Davis, 1991; Wetzel, 2001; USGS, 2004; Ponzio et al., 2004). But while the effects of fire on vegetation are well studied, the role of fire in altering and nutrients is not fully explored in the context of restoration. In this regard, there are few studies to determine the effect on P biogeochemistry potentially altering the nutrient status of these systems.

The purpose of this study was to assess the changes in P resulting from a fire in two herbaceous wetland ecosystems of varying nutrient status. Our specific objectives

were: (i) to determine the amount of P added to the soil through combustion, (ii) assess the changes in P storages and forms after a fire, (iii) and to determine how long the fire effects last within these sites.

Materials and Methods

Site Description

Sites chosen for field sampling were wetlands where P additions are known to cause shifts in biogeochemical cycles (Inglett et al., 2011). In general, sampling ecosystems to determine the impact of fire is done after a fire-event by comparing burned areas with neighboring unburned areas. This experiment involved a prescribed fire, therefore, pre-fire sampling occurred within the same post-fire sampling plots removing any error that may occur by sampling neighboring sites. Temperatures at both 1 cm above and below soil surface (1 s interval) were measured between pre and immediate post burn sampling trips in order to determine the intensity of the burn and its potential impact above and below soil surface.

Field sampling was conducted in a calcareous wetland within the Everglades National Park (ENP) in southern Florida, USA. Sampling sites were located between the Shark and Taylor Slough in a region known as the Hole-in-the Donut (HID). This region is a fire-adapted prairie wetland currently undergoing restoration processes (Ewel et al., 1982). Two of the sites chosen for sampling were used extensively for agriculture and subsequently are nutrient enriched and undergoing restoration (Res00) while the other two sites sampled have not been disturbed as extensively by humans (Ref) and thus have naturally occurring nutrient concentrations are present (Fig. 1-1). Elevation has been shown to impact the restoration processes in these sites (Inglett et al., 2010), therefore elevations were treated as separate sites (High and Low),

accounting for 4 total sampling sites. The two enriched sites have gone through extensive restoration efforts including complete removal of soil to remove excess nutrients (Dalrymple et al., 2003).

Soil and Vegetation Sampling

Samples of surface soil (0-5 cm or bedrock), periphyton and plant biomass were taken at 4 HID sites corresponding to high and low elevation areas in each of the Res00 and Ref areas. Each of the 4 sampling sites had 3 burned and 3 control 10x30m plots. Two-meter buffer zones surrounded each of the control plots. Within each plot, a 2x2 m grid system was devised (75 grid cells) and used to randomly sample each of the plots on 4/8/2010, 5/6/2010, 6/10/2010, and 1/25/2011. The first sampling trip (4/8/2010) occurred prior to the fire event while the remaining trips occurred approximately 2 d, 1 mo and 12 mo after the burn.

During sampling, care was taken to not walk frequently in the plots in order to not disturb the vegetation or compact the soil. Samples were collected for both concentration measurements as well as storage calculations. For concentration measurements, periphyton samples were removed from the soil and stored in plastic sample bags before the soil underneath was sampled (0 – 5 cm or 0 – bedrock). Soil was collected in triplicate with three 2x2m squares randomly selected for each replicate prior to sampling. Within each 2x2 square, 3 – 5 samples were taken and composited accounting for a range of 9 – 15 samples for each soil replicate. This accounts for a range of 9 – 15 samples for each composite replicate of soil and periphyton. For storage calculations, four replicates of plant (live and dead), periphyton and litter biomass were sampled before and after the prescribed burn using $1m^2$ plots in order to

determine areal P storage. Soil depth was estimated using 24 measurements taken at 2 m intervals along two grid lines in each replicate plot.

Soil and periphyton samples were kept on ice for transport to the laboratory. Field moist soil samples were sieved using a 2 mm mesh and then stored at field-collected moisture content in polyethylene containers at 4°C until further analysis. Immediately after sieving the soil, a subsample of soil was dried (3 d at 105°C) to determine moisture content and then hand ground using a mortar and pestle for total nutrients. Plant biomass samples and periphyton samples were cleaned to remove any soil that may have been attached after sampling. The plant biomass samples were also separated into live and dead plant material (litter had been separated previously in the field). The plant biomass and periphyton samples were then oven dried (65°C for 72 h), and hand ground in a mortar and pestle for nutrient analysis.

Bulk density (BD) was determined in triplicate composite samples of three individual cores (3.6 cm dia.) for each of the burned and control plots at each of the different sites. In the lab, soil was passed through a 2 mm mesh sieve and dried at 105°C for 72 hours to determine the total dry weight. Calculated volumes of rocks and roots, using water displacement, were removed from the overall core volume when calculating BD. Soil pH was measured using a 1:2 (g:v) ratio of soil to DDI water using approximately 10 g of soil.

Chemical Analysis

Total phosphorus (TP) in soil, litter, plant biomass (live and dead) and periphyton was measured by loss-on-ignition (LOI) (Jackson, 1985). Briefly, ashed samples were dissolved in 6.0 M hydrochloric acid (HCl) (Anderson, 1976) followed by colorimetric

analysis of PO_4^{3-} using a Shimadzu UV-160 spectrophotometer in accordance with US EPA method 365.1 (USEPA, 1993).

Total soil inorganic P (TP_i) was measured by weighing wet weight equivalent to 0.5 g dry weight soil into 50 mL centrifuge tubes with 25 mL 1.0 M HCl added. The HCl was added in increments of 5 mL due to the violent release of CO_2 that occurs when calcareous soils are acidified. The tubes were shaken horizontally on low for 3 h and then centrifuged at 6000 rpm for 10 m. After this the solution was filtered through a 0.45 μm membrane filter and stored at room temperature until it was analyzed colorimetrically (US EPA Method 365.1). Because this gave TP_i of the soil, total organic P (TP_o) was determined as the difference between TP and TP_i.

Total N and C for soil was measured by weighing 33 mg dried, hand ground soil into 10x10 mm tin capsules. Each capsule was rolled into a ball while wearing gloves and then analyzed for TN and TC by combustion in a Flash EA 1112 series TN and TC soil analyzer. The TN and TC in the litter, plant biomass (live and dead), and periphyton were analyzed on a mass spectrometer. These dried, hand ground samples were weighed out in 2 – 3 mg increments in 4x6 mm tin capsules in the same way as the soil samples.

Microbial biomass P, N and C (MBP, MBN, and MBC) were measured the using chloroform extraction method (Sparling et al., 1990; Brookes et al., 1985). Briefly, the process involves the determination of total P, N, and C on extracts (0.5 M $NaHCO_3$ (pH = 8.5) for P (Hedley et al., 1982) or 0.5 M K_2SO_4 for C and N) of soils incubated with and without added chloroform. Total OC in the MBC extractants was measured using a Shimadzu TOC analyzer (EPA Method 415.1) while both MBN and MBP were analyzed

on a Technicon Autoanalyzer (EPA Method 351.2 and 365.1). The difference in P, N, and C between the fumigated and non-fumigated samples was assumed to equal MBP, MBN and MBC and extraction efficiency coefficients were applied to MBC and MBN (Sparling et al., 1990; Brookes et al., 1985).

Soil phosphatase enzymes were measured using a modified method previously described by Marx et al. (1994) and Sinisabaugh et al., (1997). Two different substrates, 4-methylumbelliferyl phosphate and Bis-4-methylumbelliferyl phosphate, which are mono- and di-ester phosphates, respectively, were chosen. Each was made in an 8.5 pH buffer to measure alkaline phosphate activity. Soil was added to scintillation vials in a 1:100 (g:v) dilution using DDI water and placed horizontally onto a fixed-speed shaker at 280 osc/min for 1 h. Shaking was used to help prevent lysing of microbial cells during homogenization. Substrates were added to each sample slurry and incubated for 2 h in the dark at room temperature in 96-well plates. After the incubation, fluorescence was measured in the plates using a BioTek Model FL600 fluorometric plate reader (Bio-Tek Instruments, Inc. Winooski, VT) at excitation of 350nm and emission of 450nm (Hoppe, 1983) and corrected for any quenching interference that may have occurred from the soil matrix.

Areal P storage (m^{-2}) was determined using average site BDs and soil depths, plant biomass from the vegetation plots, and measured P concentrations. In the soil, analyzed P fractions included bioavailable P_i and P_o ($NaHCO_3$-TP,SRP), MBP, and total inorganic (HCl-P_i) and organic P (TP – HCl-P_i). Vegtation and periphyton P storages were calculated before and immediately after the burn by sampling four 1 m^2 plots at each site where all plant biomass (live and dead), periphyton, and litter was collected

and an average mass was determined on an areal basis. Average concentrations measured later in the laboratory for each were then calculated on an areal basis using the dried mass.

Statistical Analysis

All statistics were run using JMP® 7.0.2 (SAS® Institute Inc., 2007). Overall trends over time and seasonal patterns were analyzed using a fit model multifactor ANOVA across all parameters. Individual parameters for each time period that appeared significant were also analyzed using t-tests to determine significant differences between burn and control plots during each sampling event. Regressions were used in order to determine correlations between measured parameters. A significance level of $P<0.05$ was used throughout the experiment.

Results

Pre-Fire Site Conditions

Plant species found at both Res00 High and Low were very similar prior to the burn with *Andropogon glomeratus* identified as a dominant plant at these sites (Serra, 2011). The Res00 High elevation site was also dominated with *Muhlenbergia capillaris* and *Baccharis halmifolia,* while the Low site was also dominated by *Centilla asiatica*. Little difference was found between High and Low elevations at Ref where the two dominant plants found were *Muhlenbergia capillaris* and *Cladium jamaicense* with the low site having some *Centilla asiatica*.

The amount of plant biomass (live, dead and liter; g m^{-2}) found at each site was significantly different between the sites. The Res00 and Ref High sites had the most plant biomass with 553±19 and 365±48 g m^{-2} respectively. Both Res00 and Ref Low sites had significantly lower plant biomass with 195±31 and 285±42 g m^{-2}, respectively.

Prior to the burn, below-ground storage of P was significantly higher at the Res00 sites when compared to Ref (Figs. 2-1 and 2-2), with most of this P being stored in the soil organic pool. Microbial biomass accounted for approximately 8-15% of organic P storage while 1.5-2.0% was stored as bioavailable P_o. The storage of TP_i at these sites was often significantly lower than TP_o and accounted for 25-45% below-ground P storage. Of this TP_i, 4 – 9% was measured to be bioavailable; a significantly higher portion when compared to the bioavailable P_o found in the soils.

The relative abundance of P_i to P_o was highest in the Res00 site and was influenced by elevation changing from 1:1 to 1:3 from high to low elevation. This significant change along the elevation gradient found at the Res00 site affected the quantity of P stored in microbial biomass and bioavailable forms, but expressed as a percent of TP_i or TP_o, no significant storage change occurred across elevation. Microbial biomass P and bioavailable P_o accounted for 8.5 and 1.5% of TP_o, respectively, while bioavailable P_i was approximately 4% of TP_i. No significant differences in storage were found between the two Ref sites. The TP_i to TP_o ratio was 1:3 while the percents of bioavailable P_i, P_o, and MBP to their respective $TP_{i/o}$ fractions was 8, 2, and 15% respectively.

The below-ground storage of P at the Res00 site was found to be double that measured at Ref (11 g P m^{-2} versus 5 g P m^{-2}), with no significant difference caused by the change in elevation. The amount of above-ground P stored at these sites was significantly lower than the amount in below-ground ranging from 53 to 81 mg P m^{-2}. No significant difference was measured between elevations at the Ref sites where above-ground P storage was 53 and 55 mg P m^{-2} while the Res00 site stored 63 and 81 mg P

m^{-2} at the Low and High elevations, respectively. The percent of total above-ground P stored in periphyton biomass at these sites was measured to be 54 – 61% except for the Res00 High site where only 23% of above-ground P stored in periphyton. The Res00 High site was also unique from the others by storing 31% of above-ground P in litter. Both Res00 and Ref stored a significantly higher amount of P in litter at the higher elevations; 3 and 1.3 mg P m^{-2} at Ref High and Low and 29 and 3 mg P m^{-2} at Res00, respectively.

Immediate Post-Fire Conditions

During the fire, temperatures above the soil were recorded to reach 450°C for several seconds and then returned to baseline temperatures after only a few minutes (Data not shown). After the prescribed burn, a substantial amount of plant biomass (live and dead plant) and litter were combusted. The higher elevation sites of Res00 and Ref lost approximately 88% and 96% plant biomass in the fire while at lower elevations approximately 65% and 94% plant biomass combusted, respectively. The temperature recorded at 1 cm depth for each of these sites did not increase above normal baseline (approximately 30°C) temperatures during the burn nor was a significant decrease in SOM (estimated from LOI) observed.

Significant increases in soil TP (mg kg^{-1}) were measured in the burn plots at all of the sites within the first month after the fire; however, a significant change in below-ground P storage did not coincide with this finding. These contradictory results were most likely attributed to slight differences in soil TP concentrations between burn and control plots prior to the burn. While increases in soil P were expected, there was not enough P in above ground biomass to significantly increase soil TP storage of

concentrations. At the Res00 sites, storage of TP_i increased while TP_o decreased; a trend also observed the Ref High site. No significant increase in bioavailable P_i storage was observed immediately after the fire while bioavailable P_o storage doubled. Storage of MBP did not experience any significant change but the fire increased averages. Similarly, the fire did not significantly lower phosphatase activity as would be expected after a pulse of P.

Similar to soil TP storage, no significant change in periphyton TP (mg kg^{-1}) was observed immediately after the fire while a 50% or more increase in periphyton P storage (mg m^{-2}) occurred. Again these data are contradictory and imply an increase in mass of periphyton after the burn. Most likely this was observed not because of the fire but rather because pre-sampling took place approximately 1 month prior to the fire-event, and periphyton mass had increased during that time. Plant Biomass (live and dead) and litter experienced significant losses of stored P due to the high combustion rates that occurred during the fire. When not considering periphyton, all sites lost significant amounts of above-ground stored P.

One-Year Post-Fire Conditions

Below-ground P storage approximately one year after the fire was not significantly different from pre-burn conditions at any of the sites. Both Ref sites had measured shifts in TP_i and TP_o with gains in TP_o storages coupled with decreases in TP_i; this pattern was only significant at the Ref High site. All sites had higher average P storages in MBP and bioavailable P_i one year after the burn.

Storage of above-ground P was still greatly impacted by the fire one year later. The amount of P stored in live and dead plant biomass at the Res00 sites was greater than that prior to the burn. Litter P storage was equal to pre-burn conditions at the Low

site while it was significantly lower at the High site. At both Ref sites, P storage in plant biomass (live and dead) had increased since immediately after the fire but were still not equivalent to pre-burn P storage numbers. A decrease in periphyton P storage from immediately after the burn occurred at both Ref and Res00 High sites making Ref High equivalent to and Res00 High significantly lower than pre-burn P storages. Both Low sites still had elevated P storage in the periphyton one year after the burn. This coupled with plant biomass (live and dead) and litter, made the Low sites have significantly higher P storage one year after the fire while both High sites experienced significant losses.

Discussion

Estimation of P Added to the Soil

The combustion efficiency and temperatures reached during a fire are highly dependent on plant biomass present. Larger fuel loads can reach hotter temperatures while elevated fuel moisture can reduce combustion rates and cause less efficient smoldering of plant biomass (Ryan, 1991; Urbanski et al., 2009). For ignition of plant materials to occur, temperatures of at least 350°C must be reached, however woody vegetation or plants with higher moisture content could need higher temperatures for ignition (Saito, 2001; Ward, 2001).

Moisture contents did not appear to reduce combustion rates between these sites. Ref High and Low contained the same dominant species, *Muhlenbergia capillaries* and *Cladium jamaicense*, with similar plant biomass (live, dead and litter) moisture contents (17 and 14% respectively). Studies suggest this would result in slightly lower combustion rates at the higher sites, but instead, the High site combusted slightly more plant biomass (96 versus 94%). Oppositely, Res00 sites did contain significantly

different moisture contents in plant biomass; 34 at High and 24% at Low. Along with higher moisture content at Res00 High, the dominance of more woody vegetation such as *Baccharis halmifolia* was present. High moisture content along with the presence of woody vegetation would normally indicate that the High site should combust less. This was not observed, instead Res00 High combustion was 88% while the Low site was 65 percent. Since moisture content and vegetation dominance did not appear to hinder combustion, it was assumed that instead spatial plant distribution caused the observed combustion rates. Ref site plant biomasses were significantly more compacted, with less spatial variability than Res00 sites, causing little difference between combustion rates (Bond and Van Wilgen, 1996). Because of the differences in plant biomass types (Table 2-1) and significantly greater fuel load at Res00 High (Fig. 2-1), the Res00 sites combustion rates were significantly different.

Through the combustion of plant biomass, large quantities of P are potentially released into soil. The estimations of post-fire P addition were dependent mainly on two factors. First, soil P concentrations greatly influenced storages in plant biomass determining the potential P addition for each site. Soils containing greater quantities of P have a greater amount of P within the above-ground biomass pools (vegetation and periphyton). Second, vegetation type and spatial variability significantly influenced combustion rates and the amount of P released from the plant biomass P pool. Both Res00 sites contained higher concentrations of P in the soil and subsequently plant biomass stored more P; 62 and 27 mg P m^{-2} at the High and Low sites, respectively. Ref High and Low sites contained significantly less P in the soil but these sites contained more biomass on an areal basis, therefore, P stored in plant biomass here

was not significantly different from the Res00 Low site; 25 and 21 mg P m^{-2} for High and Low.

If complete combustion had occurred at these sites the total above-ground P storage would equal the potential amount of P that would be added to the soils. However, uniform combustion rarely occurs during a fire (Bond and Van Wilgen, 1996), and did not occur at these sites.

Based on the efficiency of combustion, P addition from plant biomass at the Res00 High and Low were 55 and 17 mg P m^{-2}, while Ref High and Low were 24 and 21 mg P m^{-2}, respectively. The estimations did not include periphyton, which accounted for approximately half of above-ground P storage at Res00 Low and both Ref sites. This was not included in the estimation because periphyton appeared to have grown in the time between our pre- and immediate post burn sampling due to several rain events. Therefore an estimation of loss of P from periphyton was not possible after this burn-event. In the future, pre-burn sampling should take place closer to the fire-event to prevent this error.

For example, Raison et al. (1985) found that P remaining in ash after a fire is directly proportional to the vegetation type and nutrient concentrations present within the burn site. Fuel loads high in woody materials can reach burn temperature of 1000°C or higher (Brown and Davis, 1973) and are capable of volatilizing P (Weast, 1980) and losing up to 60% of the combusted P (Raison et al., 1985). Woody plant biomass types also contain significantly higher P (mass) and have been found to add 100 mg P m^{-2} after a fire event (Giardina et al., 2000). Fuels found in wetlands contain significantly less woody plants than most terrestrial ecosystems and are instead rich in

grass species. Therefore, based on plant biomass storages and combustion rates in these sites the estimated P addition at Res00 High and Low were 55 and 17 mg P m^{-2} while Ref High and Low were 24 and 19 mg P m^{-2}. These additions are comparable with known atmospheric deposition ranges found in these sites (20–80 mg P m^{-2} yr^{-1}). However, these estimated additions occurred over the course of minutes rather than hours suggesting that some impact should occur on P biogeochemical cycles in the short-term. Because these additions were not significantly higher than what could happen naturally over time, any alterations may not be severe in the long term.

Fire Effects on P Storage

When comparing both soil and periphyton P concentrations and storages the results appear to contradict one another. Soil TP concentrations increased significantly after the fire while P storage did not. While increases in soil TP concentrations were expected from the estimated P additions, significant increases TP would not be possible even if all above ground P was added to the soil (this does not mean significant changes in P fractions could not occur). The measured significance in soil TP was most likely due to the burn sites being slightly higher in soil TP prior to the burn; which occurred at every site. Slight variations in soil depth after the fire also contributed to the significant difference in TP soil concentrations not being reflected in soil TP storage. . Similarly, periphyton P concentrations did not change after the fire while P storage increased significantly. These results imply an increase in the periphyton mass immediately after combustion. While an increase in periphyton is expected after a fire, it should not have occurred so soon after the fire event (Miao and Carstenn, 2006), therefore, periphyton must have grown in the month between the pre- and immediate

post-burn sampling trips causing a false positive result of increased periphyton mass after combustion.

Periphyton does however, have a high affinity for P and much of the released P from the plant biomass may have been absorbed by periphyton before reaching the soil. Daoust and Childers (2004) found that calcareous periphyton mats are extremely sensitive to any P addition rapidly absorbing added P. Periphyton is often used as an indicator of nutrient enrichment in wetlands due to its rapid response (day to weeks) to P addition (Gaiser et al., 2005). Fire-events in the Everglades often occur at the beginning of the wet season right as periphyton communities are beginning to become reestablished after the dry season. Because of this, and the lack of other vegetation restricting light (Cronk and Mitsch, 1994; Inglett et al., 2004), fire-events and P additions at this time in the year can perhaps impact periphyton more than soil.

While much of the bioavailable P_i immediately released from the fire could have been absorbed by periphyton for growth, storage and concentrations of bioavailable P_o increased significantly in soil after the burn (Fig. 2-5). Two possible sources of this increase include: bioavailable P_o released from plants which did not completely combust and P_o released from soil organic P pools that may have been denatured at high temperatures during the fire (Saá et al., 1998). Soil temperatures, however, did not increase significantly during the burn (Data not shown) and likewise, TP_o storage was not significantly affected. As a result, the most likely source of bioavailable P_o was from plant biomass that did not undergo complete combustion (Saá et al., 1998).

When complete combustion of plant biomass does not occur, char is often the remaining product. While it is widely accepted that charring of plant material occurs

during prescribed burns and wildfires, its effects have rarely been addressed (Nocentini et al., 2010). Characterization of char is difficult due to the wide variability of materials and temperatures in which it is produced. One variable that is constant during the creation of char is the need for smoldering plants under low oxygen conditions (Schmidt and Noack 2000). Char created under more intense fires will have higher aromaticity (Knicker et al. 1996, Czimczik et al. 2002, Almendros, Knicker and Gonzalez-Vila 2003) and can be more recalcitrant than some soil minerals (Certini et al. 2007, Marschner et al. 2008; Singh and Cowie, 2008). In wetlands, char residues may considered less stable because of the low temperatures at which they were created. Because of this, a slower release of bioavailable P from char was expected and resulted in the longer than expected timeframe of elevated bioavailable P (Figs. 2-4 and 2-5).

While the estimated amount of P added to the soil after the fire was only equivalent to 0.6 and 1.2% of soil P at the Res00 and Ref sites, a significant proportion of this material appeared to be readily available. All of the sites experienced significant increases in concentrations and storage of bioavailabe P because of the fire. The data support the conclusion that P was added through both complete and incomplete combustions of plant biomass, creating ashed (bioavailabel P_i) and charred (bioavailable P_o) plant residuals. This combination of materials may have resulted in P additions occurring in these soils not only immediately but also up to one year after the burn (Fig. 2-3).

Soil Indicators of Bioavailable P Enrichment

Phosphorus enzyme activity and TP_i have often been found to have inverse relationships in wetlands (Newman and Reddy, 1993; McLatchey and Reddy, 1998). Because of this, P enzyme activity is often used as an indicator of P enrichment. For

this reason, when bioavailable P enrichment occurs following a fire event, the activation of phosphomonoesterase and phopshodiesterase should be repressed (Spiers and McGill, 1979; Newman et al., 2000). While significant increases in soil TP concentrations were observed at the 2- or 30-day samplings at every site, the 30-day diesterase enzyme activity was the only measured occurrence of APA being significantly lowered by the burn (Fig. 2-6). Two possible explanations for the lack of change in APA after the burn are (i) other nutrients such as C, N, and K increased in availability in larger quantities making P more limiting and/or (ii) some enzymes that were bound before the prescribed burn were released into the soil.

With regard to other nutrients remaining after a fire, C and N that are not volatilized often remains in simpler forms which are more available for microbial and plant use. This can decrease the impact of the P pulse if enough C and N are made available to maintain P limitation. Similarly, any impact by a pulse of P could be diminished through an increase base saturation, which occurs often after fires (Macadam, 1987). Úbada et al. (2005) have found significant increases in available K after a fire while Tomkins et al. (2005) have also found the same increase in K, Mg and Ca up to two years after a fire event. High pH of these calcareous soils would be beneficial for phosphates to complex with these cations making any P added quickly unavailable.

Conversely, enzyme activity can be reduced when complexed with phenolic or humic compounds (Wetzel, 1991; Chróst, 1991). When Ca and Mg ions are released after a fire, they can break these complexes by binding with the phenolic or humic compounds, releasing the enzymes into the soil (Chua, 2001). Harrison (1983) found

that TP_i and APA had a high positive correlation when soil P concentrations were less than 50 mg P kg^{-1}. In these sites, all of the soil TP concentrations are higher than 50 mg P kg^{-1} but the lower TP_i values found at the Ref sites did correlate stronger with APA than the two restored sites (R^2=0.2571 and R^2=0.1752 respectively). While TP and bioavailable P increased at the sites after the prescribed fire, APA of the soil still suggests that P may be limiting.

McLatchey and Reddy (1998) have found that within microbial biomass, the mass MBC:MBP ratio of >20 is more indicative of P limitation. The MBC:MBP mass ratio never measured below 50 at the Res00 sites or 100 at the Ref sites suggesting that the P addition was not large enough to shift the microbial community away from P limitation. This further confirms the results that measured APA did not decrease because a large enough P pulse did not occur.

Another indicator often used to determine nutrient limitation within wetlands is by measuring nutrient ratios in plant and microbial biomass. While the previous two indicators, microbial nutrient ratios and enzyme activity, are useful for determining nutrient limitation in the soil, they are quickly altered and may not be appropriate for determining nutrient limitation in an entire ecosystem. N:P ratios in vegetation are considered indicators of long term nutrient limitation and are more often used to assess ecological scale nutrient limitation (Tessier and Raynal, 2003). Daoust and Childers (1999) have found that molar N:P ratio of live plant biomass in the Everglades can accurately determine either N or P limitation where >36 indicates P limitation and <30 N limitation (mass ratio equivalents are 16 and 14 respectively).

At all of the sites, mass N:P ratios in live plant biomass decreased in the burn plots after the fire (Table 2-3). This effect was observed for up to 4 months after the burn and 8 months after the burn at the Res00 High site. Despite the fact that bioavailable P was increased by the fire and N:P plant ratios decreased, plant biomass remained P limited in all but the Res00 High site. Eight months after the fire, the Res00 High plant biomass exhibited N:P ratios between N and P limitation (13±1.5) and then after 1 year it exhibited N limitation (10±1.5) suggesting enough P may have been added to switch to N limitation but further sampling would need to be done to determine how long this affect, only measured in plant biomass, occurred.

Long-term P Storage Effects

Fire-events not only provide pulses of P in the short-term but can also alter the nutrient balance and cycling at sites overall (Rundel, 1981; Woodmansee and Wallach, 1981). In ecosystems such as forests, where P addition from a fire is larger than that of grasslands (Giardina et al., 2000), P pulses have been measured up to several years after the fire-event. The quick pulse of P added to these sites can increase P present but may not be enough to significantly alter soil P fractions or storages. The lack of response from additional P after a fire has been previously observed (Galang et al., 2010).

Much of the bioavailable P_i that was released from plant biomass may have been absorbed by calcium-rich periphyton. This P absorption mechanism may improve long-term storage of P in calcareous wetlands. During the dry season, as periphyton dries out, much of it becomes a part of the soil (O'Hare, 2008; Inglett et al., 2011). Depending on the formation of P complexes and their stability within the periphyton, the

addition of P could be bioavailable or in the form of a stable mineral such as calcite (Dodd, 2003). It is most likely that in the Ref sites as periphyton decomposed and its P storage decreased, the form of P released was bioavailable. This resulted in the pulse of bioavailable P_i observed only at the one-year sampling after the fire and decreases in phosphatase enzyme activities (Figs. 2-4 and 2-6).

Another form of long-term P storage besides periphyton, could have been the char created through incomplete plant biomass combustion (Nocentini et al., 2010). At these sites, elevated bioavailable P concentrations were not significant until one year after the fire at the Res00 Low site (Figs. 2-3 and 2-4). This site achieved the lowest complete combustion; therefore, the most stable char would have been at this site. Char created from woody biomass also has the ability to permanently store P in the soil as black C, but the char created from these plant biomasses appear to slowly release bioavailable P_o over time.

While bioavailable P was added to these sites after combustion and increases were seen up to one year later, soil biogeochemical indicators do not suggest that nutrient limitations have shifted dramatically due to the fire. Live plant biomass N:P ratios at all of the sites decreased due to the increase in P but only at the Res00 High site did the ratio suggest a shift to N limitation one year after the fire. This site contained the largest amount of plant biomass and the largest potential P addition (Figs. 2-1 and 2-2). These data suggest that wetland sites dominant in native vegetations will not be significantly impacted, while fire at sites containing high P containing species may hinder P storage and restoration efforts. Fire has been shown to successfully remove unwanted species such as *Typha spp.* from nutrient enriched wetland (Ponzio

et al., 2004), however the presence of woody species, as found at Res00 High, may not respond as positively to restoration through fire.

Field Fire Conclusions

In this study the two herbaceous wetland ecosystems of varying nutrient status were sampled before and up to one year after a prescribed fire. The measurement of above- and below-ground P storages, as well as different biogeochemical indicators was measured to assess the effect of fire within these systems. Estimated P addition from the combustion of these herbaceous plant biomasses was equivalent to atmospheric deposition ranges (20 – 80 mg P m^{-2} yr^{-1}) with the highest additions of P at the sites with most plant biomass. While this is a small amount of P, the release of P occurred during one fire-event rather than over a year. The addition of P was most likely higher than estimated because periphyton released P after combustion, estimations of which could not be calculated due to fluctuation in periphyton mass between the pre and 2 d post fire sampling trips. Based on previous research, most P remaining was assumed to be available; however, P pulses were observed up to one year after the fire indicating the possibility of the creation of unstable char residues slowly releasing bioavailable P over time. Bioavailable and microbial P pools were the only storages significantly altered by the fire, while TP, TP_i, and TP_o appeared to have been unaffected. These elevations in labile soil P were most evident immediately after the fire but persisted up to one year later indicating that fires in calcareous wetlands could potentially have long-term impacts by increasing P availability.

The significant increase in bioavailable P one year after the fire, especially at the Ref sites, highlights the importance of understanding how different plant biomasses are combusted during a fire-event and the forms of nutrients remaining in combustion

residues. It was observed that plant communities and species structures greatly affected the combustion rates during the burn, therefore it is reasonable to assume plant communities and species structures will impact the amount and forms of nutrients remaining after combustion. If combustion is less efficient, smoldering occurs and the creation of char can occur, which can store or release nutrients over time prolonging the impact of a fire-event. Similarly, periphyton may also alter impact of fire in calcareous, prairie wetlands when periphyton is dominant. It was observed in this study that much of the P released during biomass combustion was potentially utilized by the periphyton and not added directly to the soil after the fire. Calcium enriched periphtyon, such as those at these sites, has the ability to increase long-term storage of P and further research should be done to better understand the role of periphyton during a drained wetland fire.

These conclusions have implications for restoration efforts in grasslands and wetlands where fire is used as a management tool for the removal of non-herbaceous plant species. The presence of non-herbaceous plant species in these systems is often due to nutrient enrichment, mainly P, and concern is warranted about the increase in available P that occurs after a fire-event. In these sites little else other than labile pools were altered and biogeochemical indicators did not indicate a shift in P limitation within these sites, with the exception of Res00 High. Res00 High was enriched with higher amounts of P when compared to the other sites in this study and N:P ratios one year after the fire indicated a shift to N limitation within the system. Caution should, therefore, be used when prescribing burns to highly P enriched grassland or wetlands because the increase in available P may hinder restoration efforts. Further research

should be done at Res00 High to determine the longevity of N limitation, if it is permanent or temporary. These findings also warrant the implementation of similar studies on grassland and wetlands that are more P enriched than these sites to determine if fire may be detrimental to restoration, as seen at the highest P enriched site in this study.

Table 2-1. Site sampling dates, locations, elevations, and basic characteristics, mean (SE). (pH, moisture content, Loss-on-Igntion, total N, C, and P).

Site	Transect	Burn Treatment	Sampling Date	Latitude	Longitude	Elevation m	pH	MC	LOI	TN	TC	TP
								------- % -------		------- g kg^{-1} -------		mg kg^{-1}
Res00	**High**	Burn	4/8/10	W80.67449	N25.38153	0.7	8.2 (0)	44.2 (0.5)	20.1 (2.1)	7.1 (0.5)	159 (4)	755 (77)
		Burn	5/6/10				8.1 (0)	45.5 (2.3)	16.5 (1)	7 (0.4)	161 (4)	713 (60)
		Burn	6/10/10				8.3 (0)	42.7 (1.8)	18.2 (1.1)	6.9 (0.3)	159 (4)	776 (39)
		Burn	5/25/11				7.7 (0)	34.5 (12)	20.2 (0.7)	8.2 (0.3)	171 (3)	796 (11)
		Control	4/8/10				8.2 (0)	43.6 (1.6)	17.9 (2.2)	7.6 (0.5)	165 (7)	700 (7)
		Control	5/6/10				8.2 (0)	46.8 (0.9)	14.6 (1.3)	6.3 (0.2)	154 (2)	577 (14)
		Control	6/10/10				8.4 (0)	48.2 (1.5)	29.6 (7.1)	7.4 (0.1)	163 (5)	664 (119)
		Control	5/25/11				7.8 (0)	21.5 (6.8)	20.1 (0.7)	8.1 (0.3)	168 (4)	710 (39)
Res00	**Low**	Burn	4/8/10	W80.67372	N25.37235	0.5	8.1 (0)	44.8 (0.7)	21 (0.5)	7.3 (0.4)	154 (3)	492 (38)
		Burn	5/6/10				8 (0)	44.5 (0.9)	17.6 (1.2)	7.5 (0.3)	157 (3)	471 (59)
		Burn	6/10/10				8.2 (0)	48.1 (0.7)	25.1 (4.6)	7.6 (0.2)	154 (3)	460 (11)
		Burn	5/25/11				7.9 (0)	29.7 (7.1)	23.1 (2.2)	8.2 (0.2)	163 (4)	496 (6)
		Control	4/8/10				8.2 (0)	47.9 (2)	20 (1.6)	7.7 (0.6)	161 (3)	456 (10)
		Control	5/6/10				7.9 (0)	41.6 (2.3)	14.9 (1.2)	7.1 (0.4)	155 (2)	382 (34)
		Control	6/10/10				8.3 (0)	52.2 (1.2)	22.8 (3)	9.1 (1.4)	186 (28)	410 (6)
		Control	5/25/11				7.8 (0)	20 (2.3)	19.2 (1.4)	8.5 (0.7)	165 (4)	509 (35)
Ref	**High**	Burn	4/8/10	W80.67205	N25.38092	0.8	8.4 (0)	37.6 (2.5)	11 (0.9)	6.4 (0.5)	157 (2)	140 (6)
		Burn	5/6/10				8.3 (0)	38.8 (0.9)	13.3 (2.1)	6.7 (0.4)	156 (2)	133 (6)
		Burn	6/10/10				8.4 (0)	40.9 (2.8)	10.9 (1)	6.2 (0.3)	153 (1)	149 (25)
		Burn	5/25/11				8 (0)	21.4 (3.8)	11.9 (0.2)	6.6 (0.3)	160 (3)	141 (8)
		Control	4/8/10				8.4 (0)	37.9 (0.6)	10.5 (1.3)	7 (0.1)	158 (2)	119 (3)
		Control	5/6/10				8.3 (0)	37.5 (1)	14.7 (2.4)	5.2 (0.3)	149 (1)	97 (3)
		Control	6/10/10				8.5 (0)	40.1 (1.2)	13 (0.7)	6 (0.3)	153 (2)	144 (11)
		Control	5/25/11				8.1 (0)	15.3 (2.2)	13.1 (1)	7 (0.1)	162 (1)	145 (8)
Ref	**Low**	Burn	4/8/10	W80.67232	N25.37174	0.6	8.3 (0)	42.5 (1.3)	13.2 (0.7)	7.5 (0.3)	157 (2)	140 (11)
		Burn	5/6/10				8.2 (0)	37.4 (0.7)	13.8 (1.4)	6.7 (0.4)	154 (3)	139 (6)
		Burn	6/10/10				8.3 (0)	46.6 (4.8)	14.6 (0.6)	6.9 (0.2)	155 (1)	139 (4)
		Burn	5/25/11				8 (0)	24.1 (11.5)	13.5 (0.2)	6.5 (0.2)	155 (1)	139 (3)
		Control	4/8/10				8.3 (0)	41.5 (0.8)	13.2 (1.2)	7.3 (0.1)	156 (3)	134 (5)
		Control	5/6/10				8.2 (0)	36.4 (0.7)	11.2 (0.8)	6.1 (0.2)	149 (1)	106 (7)
		Control	6/10/10				8.5 (0)	40.7 (0.7)	14.7 (1.8)	6 (0.2)	150 (1)	128 (9)
		Control	5/25/11				8 (0)	30.2 (10.1)	11.4 (0.6)	6.3 (0.2)	156 (2)	120 (2)

Table 2-2. Total P in periphyton and soil, mean (SE), and measured P fractions an parameters (total inorganic and organic P, microbial biomass P, and monoesterase and diesterase P activities).

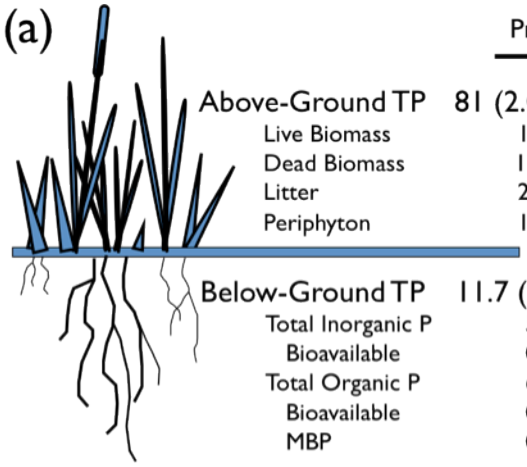
Site	Transect	Burn Treatment	Sampling Date	Periphyton TP	Soil TP	TP_i	TP_o	MBP	MUF P	Bis P
				---------- mg kg^{-1} ----------					mmol MUF g^{-1} MBC h^{-1}	
Res00	**High**	Burn	4/8/10	397 (34)	755 (77)	356 (65)	398 (32)	40.1 (3)	702 (46)	715 (100)
		Burn	5/6/10	439 (17)	713 (60)	386 (35)	362 (28)	43.7 (4)	3090 (357)	1406 (266)
		Burn	6/10/10	448 (96)	776 (39)	433 (18)	366 (47)	42.1 (3)	2189 (411)	775 (99)
		Burn	5/25/11	397 (53)	796 (11)	391 (66)	339 (18)	48.5 (1)	3965 (1375)	1437 (459)
		Control	4/8/10	313 (60)	700 (7)	338 (31)	343 (21)	44.5 (5)	740 (165)	622 (141)
		Control	5/6/10	329 (50)	577 (14)	270 (40)	396 (52)	45.2 (2)	2833 (219)	1150 (93)
		Control	6/10/10	387 (28)	664 (119)	268 (70)	287 (30)	55.7 (4)	3071 (175)	1483 (92)
		Control	5/25/11	324 (62)	710 (39)	356 (72)	237 (55)	45 (4)	3501 (346)	1380 (135)
Res00	**Low**	Burn	4/8/10	81 (7.4)	492 (38)	127 (10)	365 (30)	29.3 (1)	1386 (283)	1087 (147)
		Burn	5/6/10	114 (15)	471 (59)	136 (30)	411 (16)	41.8 (2)	2390 (795)	674 (163)
		Burn	6/10/10	153 (28)	460 (11)	173 (25)	317 (34)	36.8 (2)	2787 (306)	1003 (122)
		Burn	5/25/11	125 (5.5)	496 (6)	135 (11)	305 (34)	36.9 (2)	6113 (1178)	2536 (528)
		Control	4/8/10	91 (4.7)	456 (10)	117 (22)	317 (51)	37 (6)	1480 (193)	1269 (81)
		Control	5/6/10	114 (8.2)	382 (34)	147 (24)	194 (76)	42.6 (2)	2454 (472)	734 (232)
		Control	6/10/10	129 (4.7)	410 (6)	174 (59)	292 (83)	44 (3)	2325 (114)	960 (40)
		Control	5/25/11	125 (24)	509 (35)	107 (4)	295 (31)	34.6 (5)	6741 (1730)	2738 (557)
Ref	**High**	Burn	4/8/10	67 (5.3)	140 (6)	35 (5)	348 (34)	13.1 (1)	1003 (171)	823 (87)
		Burn	5/6/10	96 (3.4)	133 (6)	47 (3)	343 (33)	25.3 (1)	3653 (515)	1494 (252)
		Burn	6/10/10	99 (8.1)	149 (25)	23 (1)	282 (45)	18.7 (2)	2292 (122)	1003 (113)
		Burn	5/25/11	95 (4.4)	141 (8)	16 (5)	295 (28)	20.7 (2)	5697 (1485)	1499 (446)
		Control	4/8/10	67 (7.2)	119 (3)	32 (1)	443 (17)	14 (1)	1726 (442)	1168 (37)
		Control	5/6/10	90 (10)	97 (3)	36 (3)	389 (27)	16.5 (3)	3424 (428)	1198 (142)
		Control	6/10/10	70 (16)	144 (11)	24 (3)	411 (46)	18.7 (3)	2584 (336)	1022 (95)
		Control	5/25/11	86 (4.1)	145 (8)	19 (1)	301 (27)	22.9 (2)	6670 (847)	2793 (242)
Ref	**Low**	Burn	4/8/10	57 (4.9)	140 (11)	41 (17)	85 (9)	15.3 (1)	1158 (191)	1177 (147)
		Burn	5/6/10	79 (5.3)	139 (6)	26 (15)	61 (5)	19.9 (3)	3672 (648)	1251 (169)
		Burn	6/10/10	75 (5.8)	139 (4)	29 (7)	113 (11)	18.2 (2)	2395 (195)	839 (32)
		Burn	5/25/11	78 (2.4)	139 (3)	11 (2)	70 (12)	16 (2)	10737 (2773)	3483 (901)
		Control	4/8/10	58 (5.3)	134 (5)	47 (20)	125 (6)	14 (2)	1083 (108)	1189 (69)
		Control	5/6/10	76 (3.2)	106 (7)	36 (6)	126 (6)	16.2 (2)	2608 (388)	921 (147)
		Control	6/10/10	72 (4.0)	128 (9)	16 (1)	128 (2)	17.4 (1)	2663 (312)	976 (74)
		Control	5/25/11	79 (1.4)	120 (2)	10 (2)	110 (2)	19.1 (1)	12101 (674)	4064 (295)

Table 2-3. Mass ratios, mean (SE), for soil, microbial biomass and litter from all sites.

Site	Transect	Burn Treatment	Sampling Date	Soil			Microbial Biomass			Litter		
				C:N	C:P	N:P	C:N	C:P	N:P	C:N	C:P	N:P
				mass ratio								
Res00	**High**	Burn	4/8/10	22.4 (1.2)	214 (18)	9.5 (0.5)	8.8 (0.3)	80 (3.3)	9.1 (0.5)	59 (6)	2901 (305)	51 (8.7)
		Burn	5/6/10	23.1 (1)	230 (25)	10.1 (1.5)	8.8 (0.8)	83 (3.1)	9.7 (1.1)	51 (2.3)	1837 (196)	37 (4.9)
		Burn	6/10/10	22.9 (0.5)	206 (15)	9 (0.8)	7.8 (0.4)	84 (8.5)	10.7 (0.5)			
		Burn	5/25/11	20.9 (0.6)	215 (0)	10.3 (0.3)	9.7 (0.4)	95 (4.5)	9.7 (0.2)	84 (3.5)	2427 (168)	29 (2.8)
		Control	4/8/10	21.8 (1)	236 (8)	10.9 (1)	8.8 (0.8)	88 (9.9)	9.9 (0.6)			
		Control	5/6/10	24.7 (1)	268 (6)	10.9 (1)	8.6 (0.3)	84 (1.4)	9.7 (0.3)			
		Control	6/10/10	21.9 (0)	258 (38)	11.8 (2)	7.6 (0.9)	71 (9.7)	9.3 (0.3)			
		Control	5/25/11	20.7 (0)	238 (10)	11.5 (0)	10 (0.6)	93 (6)	9.3 (0.1)			
Res00	**Low**	Burn	4/8/10	21.2 (1)	316 (18)	14.9 (1)	11.9 (0.1)	108 (4.5)	9 (0.4)	53 (12)	4051 (344)	85 (16)
		Burn	5/6/10	21 (1)	346 (48)	16.4 (2)	9.3 (0.4)	95 (4.5)	10.2 (0.1)	56 (5.4)	1877 (293)	34 (5.9)
		Burn	6/10/10	20.3 (0)	335 (12)	16.5 (1)	9 (0.6)	97 (1.9)	10.8 (0.6)			
		Burn	5/25/11	19.9 (1)	327 (6)	16.5 (1)	11 (0.5)	109 (4.2)	9.9 (0.6)	65 (5.1)	3946 (222)	61 (4.4)
		Control	4/8/10	20.9 (1)	353 (14)	17 (2)	11.3 (1.4)	96 (9.7)	8.6 (0.7)			
		Control	5/6/10	21.9 (1)	411 (30)	18.7 (0)	9 (0.5)	86 (6)	9.7 (0.6)			
		Control	6/10/10	20.6 (0)	453 (65)	22 (3)	10.5 (0.5)	90 (2.6)	8.6 (0.3)			
		Control	5/25/11	19.7 (1)	326 (17)	16.6 (1)	12.6 (1.1)	102 (9)	8.3 (1.2)			
Ref	**High**	Burn	4/8/10	24.7 (1.6)	1125 (44)	45.8 (2)	14.2 (1.1)	195 (8.7)	13.9 (1.6)	62 (1.2)	6641 (186)	107 (3.2)
		Burn	5/6/10	23.4 (1)	1179 (37)	50.5 (0.7)	11.3 (0.2)	104 (7.6)	9.2 (0.8)	34 (5.1)	2396 (299)	74 (13)
		Burn	6/10/10	25 (0.9)	1079 (156)	43 (5.2)	12.4 (1.1)	146 (7.1)	11.9 (0.5)			
		Burn	5/25/11	24.2 (0.8)	1144 (51)	47.3 (1.4)	13.4 (2)	152 (23.9)	12 (2.8)	81 (2.8)	7083 (853)	88 (13)
		Control	4/8/10	22.8 (0)	1336 (42)	58.7 (2)	18 (2.2)	175 (15.1)	9.8 (0.4)			
		Control	5/6/10	28.7 (1)	1527 (34)	53.4 (3)	13.2 (1.2)	137 (9)	10.5 (1.1)			
		Control	6/10/10	25.8 (1)	1077 (77)	41.7 (2)	13.2 (0.7)	150 (10.6)	11.4 (0.7)			
		Control	5/25/11	23.2 (0)	1119 (58)	48.2 (2)	13.7 (1)	118 (1.4)	8.7 (0.6)			
Ref	**Low**	Burn	4/8/10	20.9 (1)	1128 (86)	54.5 (7)	17.2 (0.6)	166 (7)	9.7 (0.4)	71 (2.9)	6249 (395)	89 (8.7)
		Burn	5/6/10	23.1 (1)	1113 (61)	48.5 (3)	11.4 (0.7)	136 (8.6)	11.9 (0.8)	38 (7.4)	2786 (114)	79 (18)
		Burn	6/10/10	22.6 (1)	1120 (32)	49.5 (2)	12.8 (0.3)	157 (13.5)	12.2 (0.8)			
		Burn	5/25/11	23.8 (0)	1116 (20)	47 (0)	15.2 (2.9)	145 (11.3)	9.9 (1.2)	93 (2.9)	9742 (1011)	106 (13)
		Control	4/8/10	21.5 (1)	1161 (35)	54.2 (3)	17.5 (1.7)	173 (1)	10 (0.9)			
		Control	5/6/10	24.4 (0)	1417 (116)	58.3 (6)	13.3 (0.3)	155 (2.7)	11.7 (0.2)			
		Control	6/10/10	25 (1)	1181 (75)	47.2 (3)	13.7 (0)	157 (4.9)	11.4 (0.4)			
		Control	5/25/11	24.9 (1)	1297 (25)	52.1 (2)	12.8 (0.8)	122 (2.2)	9.6 (0.4)			

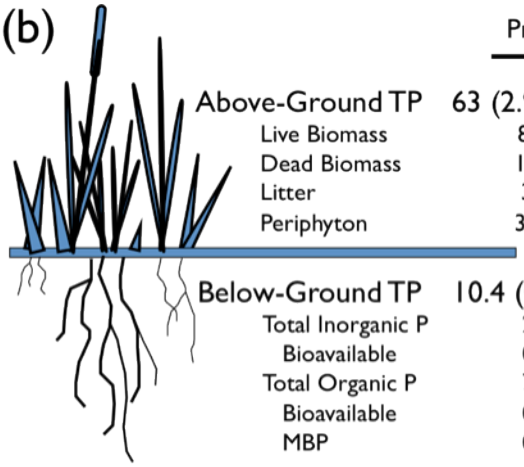
Table 2-4. Storage of P in above-ground plant biomass and nutrient mass ratios in live plant biomass, mean (SE).

Site	Transect	Burn Treatment	Sampling Date	Live	Dead	Litter	Live Plant Biomass		
							C:N	C:P	N:P
				---------- mg kg^{-1} ----------			---------- mass ratio ----------		
Res00	**High**	Burn	2/8/10	420 (26)	166 (36)	149 (13)	42 (2.8)	1037 (72)	25 (0.3)
		Burn	5/6/10	773 (102)	434 (44)	246 (32)	31 (1.9)	566 (84)	18 (2.2)
		Burn	7/7/10	565 (41)	389 (25)		42 (0.4)	757 (52)	18 (1.4)
		Burn	1/25/11	583 (28)	165 (19)		57 (9.1)	731 (34)	13 (1.5)
		Burn	5/25/11	474 (36)	156 (9.4)	178 (12)	101 (16.7)	926 (65)	10 (1.5)
		Control	7/7/10	463 (46)	350 (174)		52 (2.8)	970 (105)	19 (2.2)
		Control	1/25/11	685 (72)	209 (47)		49 (11.6)	642 (64)	14 (1.7)
Res00	**Low**	Burn	2/8/10	416 (95)	154 (27)	103 (8.6)	34 (1.8)	1349 (477)	41 (16)
		Burn	5/6/10	327 (94)	326 (40)	241 (33)	37 (5.5)	1691 (442)	46 (11)
		Burn	7/7/10	369 (37)	169 (20)		48 (3)	1233 (123)	26 (1.3)
		Burn	1/25/11	523 (25)	128 (12)		37 (1.7)	832 (49)	22 (1.1)
		Burn	5/25/11	324 (12)	207 (13)	107 (5)	60 (1.6)	1386 (49)	23 (1.4)
		Control	7/7/10	370 (19)	256 (16)		38 (1.4)	1194 (64)	31 (0.5)
		Control	1/25/11	634 (105)	125 (19)		33 (1.4)	717 (109)	22 (2.6)
REF	**High**	Burn	2/8/10	145 (32)	56 (21)	66 (2.1)	58 (1.8)	4010 (1488)	70 (27)
		Burn	5/6/10	761 (300)	216 (9.8)	164 (21)	32 (4.5)	665 (274)	20 (3.8)
		Burn	7/7/10	322 (17)	153 (n/a)		41 (1.5)	1360 (75)	33 (1.8)
		Burn	1/25/11	244 (7.9)	46 (3.1)		65 (3.1)	1789 (61)	28 (0.7)
		Burn	5/25/11	195 (6.9)	66 (5.6)	63 (7.6)	54 (2.4)	2267 (88)	42 (0.9)
		Control	7/7/10	216 (7.7)	59 (3.9)		49 (2.3)	2047 (70)	42 (2)
		Control	1/25/11	220 (20)	48 (6.5)		103 (13.6)	2045 (214)	20 (2)
REF	**Low**	Burn	2/8/10	141 (19)	64 (4.5)	71 (4.6)	54 (1.8)	3255 (403)	61 (9)
		Burn	5/6/10	358 (8.9)	196 (7.9)	139 (9.7)	36 (3.2)	1157 (34)	32 (5.8)
		Burn	7/7/10	283 (16)	299 (31)		47 (9.7)	1548 (95)	36 (4.9)
		Burn	1/25/11	227 (16)	39 (5.8)		65 (6)	1940 (154)	30 (0.8)
		Burn	5/25/11	164 (11)	64 (2.6)	46 (5.6)	62 (2.3)	2683 (184)	43 (2.2)
		Control	7/7/10	182 (8)	59 (6.1)		56 (0.6)	2438 (91)	44 (1.2)
		Control	1/25/11	228 (21)	44 (7.5)		58 (4)	1977 (188)	34 (1)



(a)

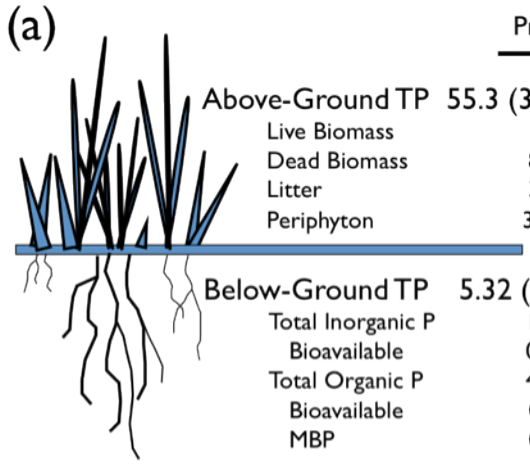
	Pre-Fire	Post-Fire (2day)	Post-Fire (1year)
Above-Ground TP	81 (2.0) mg m^{-2}	46 (2.9) mg m^{-2}	66 (3.4) mg m^{-2}
Live Biomass	15.81^{b}	0.12^{c}	37.40^{a}
Dead Biomass	17.04^{ab}	9.47^{b}	19.12^{a}
Litter	29.10^{a}	4.76^{b}	4.45^{b}
Periphyton	18.80^{b}	31.95^{a}	5.19^{c}
Below-Ground TP	11.7 (1.2) g m^{-2}	11.0 (1.0) g m^{-2}	12.5 (1.6) g m^{-2}
Total Inorganic P	5.39^{a}	5.92^{a}	5.95^{a}
Bioavailable	0.21^{a}	0.22^{a}	0.27^{a}
Total Organic P	6.29^{a}	5.11^{a}	6.55^{a}
Bioavailable	0.10^{b}	0.20^{a}	0.10^{b}
MBP	0.62^{b}	0.70^{a}	0.76^{a}



(b)

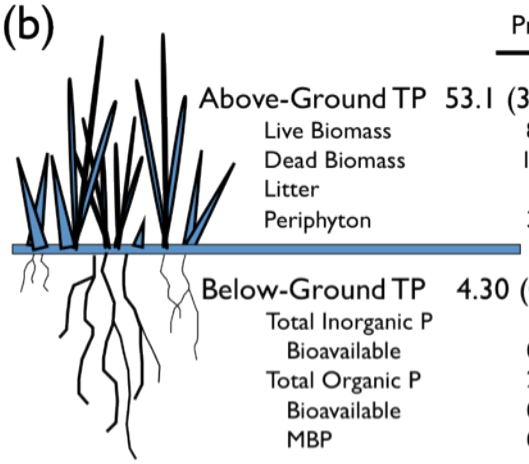
	Pre-Fire	Post-Fire (2day)	Post-Fire (1year)
Above-Ground TP	63 (2.9) mg m^{-2}	66 (5.0) mg m^{-2}	93 (3.1) mg m^{-2}
Live Biomass	8.21^{ab}	2.16^{b}	12.03^{a}
Dead Biomass	15.14^{a}	8.61^{a}	17.85^{a}
Litter	3.05^{a}	3.67^{a}	3.03^{a}
Periphyton	36.46^{b}	51.15^{ab}	59.81^{a}
Below-Ground TP	10.4 (0.7) g m^{-2}	10.0 (1.3) g m^{-2}	10.5 (0.2) g m^{-2}
Total Inorganic P	2.69^{a}	3.11^{a}	2.87^{a}
Bioavailable	0.12^{b}	0.09^{b}	0.22^{a}
Total Organic P	7.75^{a}	6.91^{a}	7.67^{a}
Bioavailable	0.12^{b}	0.21^{a}	0.12^{b}
MBP	0.62^{b}	0.89^{a}	0.78^{ab}

Figure 2-1. Total P storage of above and below ground fractions for both Res00 High (a) and Res00 Low (b) sites. Total P, mean (SE), is shown in mg m^{-2} for above ground and g m^{-2} for below ground. Letters indicate significant differences analyzed using Tukey's HSD test.



(a)

	Pre-Fire	Post-Fire (2day)	Post-Fire (1year)
Above-Ground TP	55.3 (3.9) mg m^{-2}	58.9 (1.4) mg m^{-2}	42.9 (1.8) mg m^{-2}
Live Biomass	13.7^{a}	0.01^{b}	8.14^{ab}
Dead Biomass	8.22^{a}	1.23^{b}	3.91^{ab}
Litter	3.04^{a}	1.06^{b}	0.69^{b}
Periphyton	30.23^{b}	56.68^{a}	30.12^{b}
Below-Ground TP	5.32 (0.2) g m^{-2}	5.02 (0.3) g m^{-2}	5.33 (0.3) g m^{-2}
Total Inorganic P	1.32^{ab}	1.32^{a}	0.62^{b}
Bioavailable	0.12^{ab}	0.12^{b}	0.19^{a}
Total Organic P	4.00^{ab}	3.24^{b}	4.72^{a}
Bioavailable	0.08^{b}	0.18^{a}	0.10^{b}
MBP	0.50^{b}	0.96^{a}	0.79^{a}



(b)

	Pre-Fire	Post-Fire (2day)	Post-Fire (1year)
Above-Ground TP	53.1 (3.6) mg m^{-2}	73.5 (3.7) mg m^{-2}	72.4 (4.6) mg m^{-2}
Live Biomass	8.94^{a}	0.13^{b}	6.62^{a}
Dead Biomass	10.41^{a}	0.93^{b}	3.61^{b}
Litter	1.29^{a}	1.39^{a}	0.52^{a}
Periphyton	32.5^{b}	71.04^{a}	61.6^{a}
Below-Ground TP	4.30 (0.8) g m^{-2}	4.15 (0.4) g m^{-2}	4.21 (0.6) g m^{-2}
Total Inorganic P	1.34^{a}	1.14^{a}	0.35^{a}
Bioavailable	0.09^{a}	0.05^{a}	0.12^{a}
Total Organic P	2.96^{a}	3.01^{a}	3.86^{a}
Bioavailable	0.06^{b}	0.12^{a}	0.05^{b}
MBP	0.46^{a}	0.61^{a}	0.47^{a}

Figure 2-2. Total P storage of above and below ground fractions for both Ref High (a) and Ref Low (b) sites. Total P, mean (SE), is shown in mg m^{-2} for above ground and g m^{-2} for below ground. Letters indicate significant differences analyzed using Tukey's HSD test.

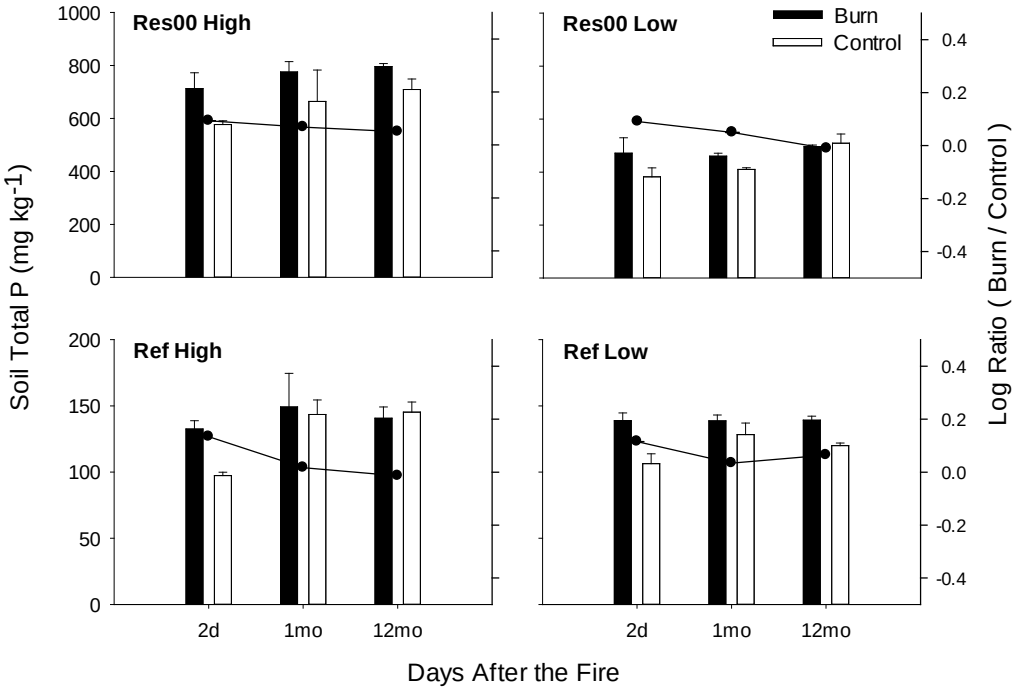


Figure 2-3. Total soil P, mean (SE), for both burn (black) and control (white) plots sampled on 5/6/2010 (2d), 6/10/2010 (1 mo) and 5/25/2011 (12 mo) at each of the four sites. Log ratios of burn divided by control also shown (line) on the right axis.

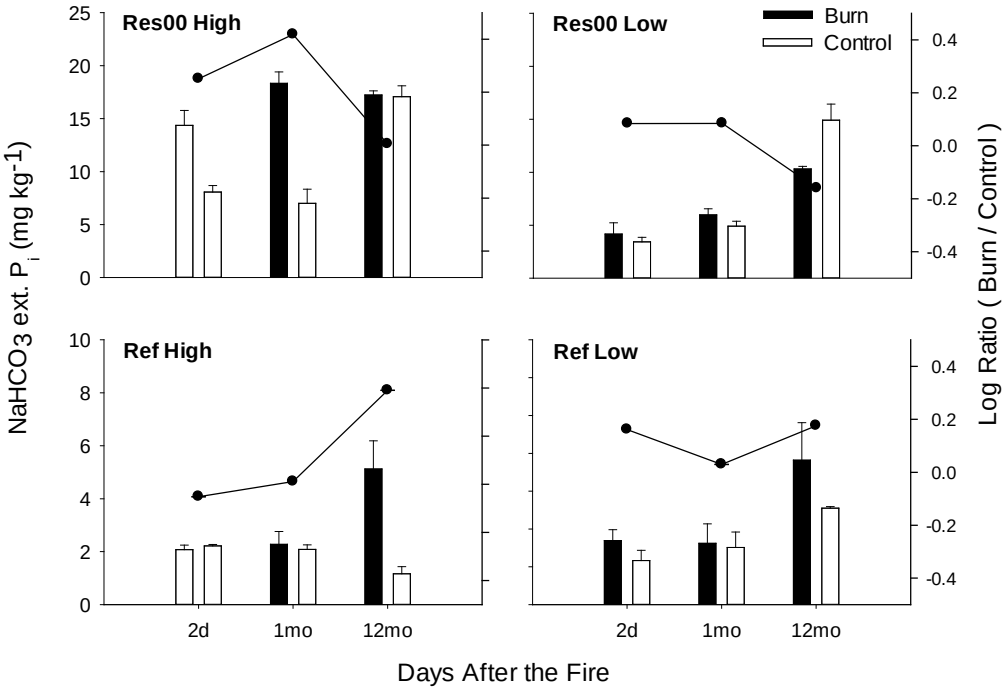


Figure 2-4. Soil bioavailable P_i, mean (SE), for both burn (black) and control (white) plots sampled on 5/6/2010 (2d), 6/10/2010 (1 mo) and 5/25/2011 (12 mo) at each of the four sites. Log ratios of burn divided by control also shown (line) on the right axis.

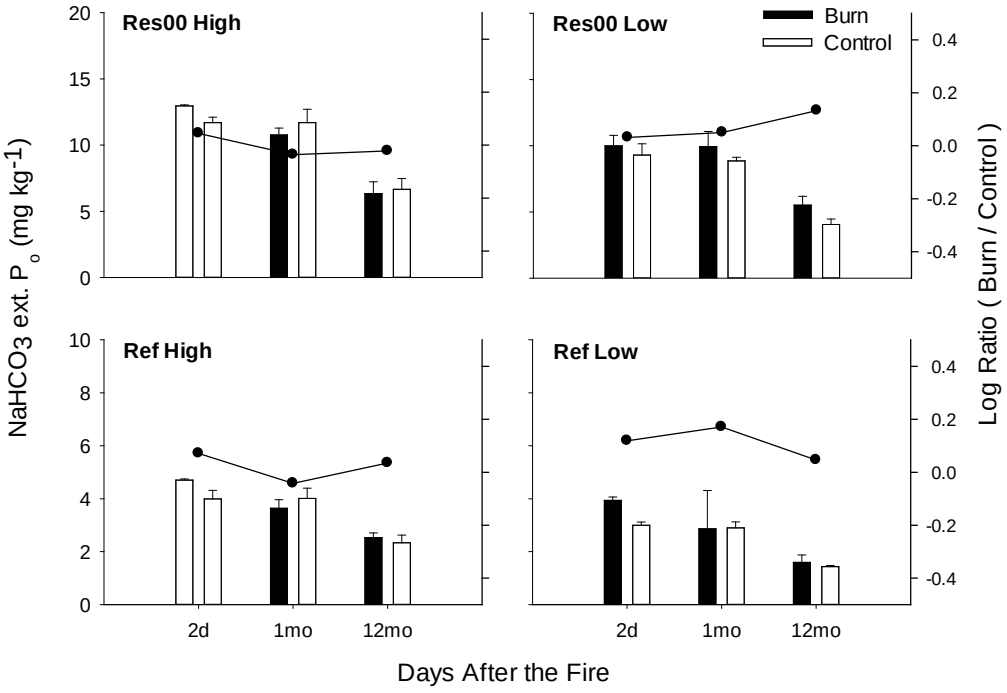


Figure 2-5. Soil bioavailable P_o, mean (SE), for both burn (black) and control (white) plots sampled on 5/6/2010 (2d), 6/10/2010 (1 mo) and 5/25/2011 (12 mo) at each of the four sites. Log ratios of burn divided by control also shown (line) on the right axis.

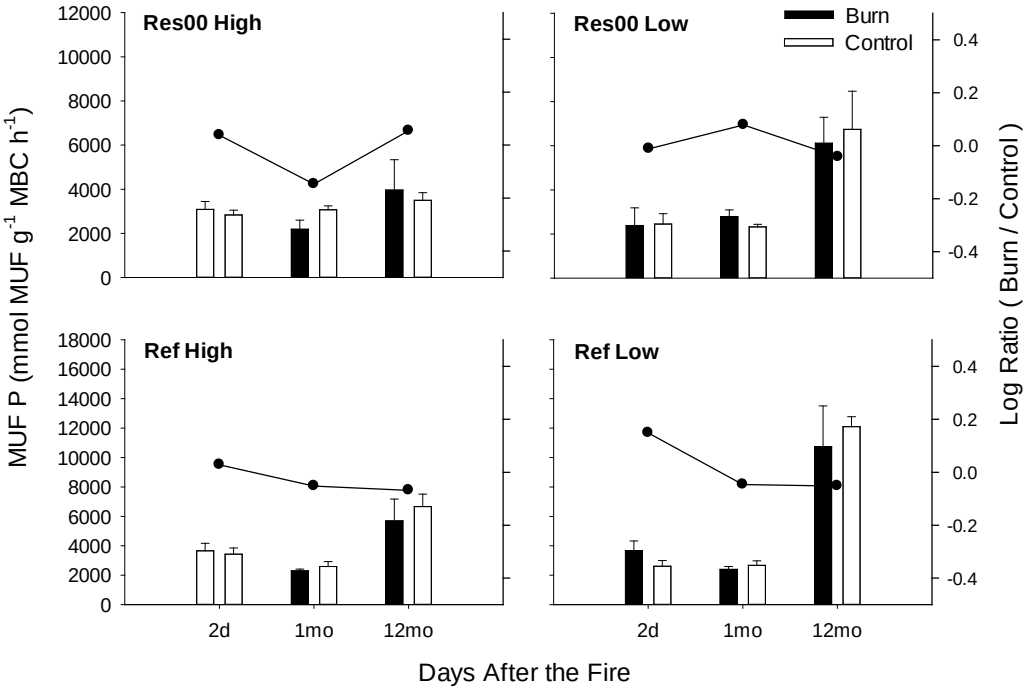


Figure 2-6. Soil alkaline phosphatase activity, mean (SE), for both burn (black) and control (white) plots sampled on 5/6/2010 (2d), 6/10/2010 (1 mo) and 5/25/2011 (12 mo) at each of the four sites. Log ratios of burn divided by control also shown (line) on the right axis.

CHAPTER 3
INFLUENCE OF COMBUSTION TEMPERATURES ON NUTRIENT RELEASE IN HERBACEOUS WETLAND VEGETATION

Lab Fire Introduction

Fire is an important ecological regulator in many ecosystems worldwide (Bond et al., 2005). Estimates have found that approximately 40% of the earth's land surface is regularly impacted by fire events (Chapin et al., 2002). While climate is traditionally regarded as the main regulator of ecosystem characteristics and biogeochemical cycles (Whitaker, 1975), fire has the capability of shifting or permanently altering these systems to a greater degree than climate (Bond et al., 2005; DeSantis et al., 2011). Global incidences of fire are also predicted to increase as climate changes occur (Westerling et al., 2006; Krawchuck et al, 2009), therefore, it is essential to understand the functional impacts of fire on ecosystems.

Characterization of fire-events can be altered by a variety of parameters such as fuel load quantity and quality, moisture content, ambient air temperature, wind speed and direction, and ignition source (Ryan, 1991; USGS, 2001; Certini, 2005). The most apparent impact caused by a fire is the combustion and charring of vegetation. Both C and N contained in plant biomass are lost in large quantities due to volatilization (Gioavannini et al., 1988; Fisher and Binkley, 2000) while most P, assumed to be readily available, is known to remain within plant residual ash and char. Besides the release of macronutrients from plant biomass, cations are also released into the soil affecting soil pH and cation exchange capacity (Nye and Greenland, 1960; Khanna and Raison, 1986; Macadam, 1987). Soil organic matter, like plant biomass, is often

converted into inorganic forms due to the increased heat from a fire, releasing and altering stored nutrients. When soil temperatures become high enough, denaturing and sterilization of soil microbial communities can occur (DeBano, 1998).

Extensive research on soil and vegetation communities after a fire exists (Giovannini et al., 1990; Saa et al., 1994; Giardina et al., 2000; Knicker et al., 2005; Certini, 2005; Boerner et al., 2005). In contrast to the studies of system-level response after a fire, few studies have directly assessed nutrients and their availability in plant biomass residues after combustion (Badia and Marti, 2003; Qian et al., 2009). Studies have found large pulses of bioavailable P in soil after fire, as well as, increased P concentrations within soil microbes and vegetations communities (Vazquezt et al., 1991; Blank et al., 1994; Saa et al., 1998; Galang et al., 2010). Other studies have concluded that the release of cations from combusted plant biomass complexes with available nutrients left in ashed plant biomass reducing the impact of the release of nutrients caused by fires (Raison et al., 1985; Gray and Dighton, 2006; Qian et al., 2009). While it is recognized that complete combustion creates ash high in P, K, and Ca (Rasion et al., 1985), incomplete combustion of plant biomass can also lead to the creation of char, containing more C and N.

Recently, much attention has been focused on biochar, a subgroup of materials in the black carbon continuum (Warnock et al., 2007). In nature, biochar is created by a lack of oxygen leading to incomplete combustion of plant biomass (Nocentini et al., 2010). This byproduct can be more stable than some soil minerals and has the ability to store C and other nutrients such as P for prolonged periods of time (Knicker et al., 1996;

Czimzik et al., 2002; Almendros et al., 2003). Thus, the presence of char material can directly affect the availability of other nutrients released during combustion.

Much of the available literature has focused on woody instead of herbaceous plant materials because of their higher likelihood to not fully combust. Herbaceous plant species are thinner and often dryer than woody species (Ryan, 1991). They have lower ignition temperatures and their lag time for smoldering is only 1 h compared to upwards of 1,000 h for most trees (Mutch, 1970; Rogers et al., 1986; Brown and Davis, 1973; Saito, 2001). Also, approximately 80% of the global fire-adapted ecosystems are dominated by herbaceous plant biomass (Flannigan et al., 2009). Even though herbaceous species are not ideal for generating stable char residues, dense compaction of plant biomass in grasslands can generate positive conditions for char residues by suppressing oxygen flow leading to incomplete combustion. The byproduct may not be as stable char residues created from thick woody species but could potentially retain nutrients longer than ash.

Most research on ash and char from combusted plant biomass has been done within the laboratory. These studies have used muffle furnaces at different temperatures and duration with varying oxygen levels to create ash and/or char (Galang et al., 2010; Mukherjee et al., 2011). Plant species used for these experiments are often singular in species (Gray and Dighton, 2006; Qian et al., 2009). Natural fires however, involve multiple plant species causing patchiness or non-uniformed combustion followed by non-uniform residues (Bond and Van Wilgen, 1996); a result not capable of achieving within a muffle furnace. Muffle furnace combustion is also not capable of combusting plant biomass at high temperatures for a short period of time in

the same manner field combustion occurs. Because of this, lab fire combustions will also be done in an attempt to mimic field fire combustion. It is also known that plant species combust differently (Rogers et al., 1986; Mutch, 1970), therefore, two different herbaceous biomasses compositions will be studied.

Within this experiment, two different herbaceous plant biomass groups were combusted in order to study the composition and availability of nutrients within combusted plant residues. These biomasses contained species with both differing structure and beginning nutrient concentrations in order to study what impact this may cause. Furthermore, a range of temperatures and two different combustion types, traditional muffle furnace as well as flame ignition, were performed for each biomass group.

Materials and Methods

Plant Biomass Description

Two herbaceous plant biomass groups were collected from a herbaceous, grass-dominated, seasonally-flooded wetland within the northern area of the Everglades National Park (Fig. 1-1). Portions of this prairie wetland were used extensively for agriculture, which has led to two distinct plant biomass compositions throughout the HID. Plant biomass 1 (High Nutrient Plant Biomass; HNPB) was collected from soil rich in legacy P with dominant plant species *Andropogon glomeratus* and *Ludwigia spp.* Plant biomass 2 (Low Nutrient Plant Biomass; LNPB) was collected in P-limited soils, not used for agriculture with dominant species *Muhlenbergia capailaries* and *Cladium jamaicense*. The sampling of both HNPB and LNPB occurred in April 2010 and contained live and dead plant tissues as well as litter present within 1 m^2 plots (4 replicates each).

Laboratory Plant Processing and Combustion

Both HNPB and LNPB were cleaned for removal of any residual soil and periphyton and stored at 4°C after collection from the field. As moisture content can influence combustion (Menaut et al., 1993), both the HNPB and LNPB were equilibrated to approximately 7.5% moisture content, corresponding to the optimal moisture content of plant biomass for prescribed burning (Ryan, 1991). This was achieved by first removing all moisture from the plant biomass (5 d @ 65°C) and subsequently enclosing dried samples for 24-48 h at room temperature (23ºC) inside an airtight container containing a paper towel moistened with an amount of water sufficient to increase the plant moisture content to 10% (if all of the water was absorbed by the plant biomass). The plants were reweighed and observed to only absorb approximately 7.5% of this water.

Muffle furnace combustion (2 h) of both HNPB and LNPB (2-3 cm cut lengths) were done in triplicate for 2 h at 200, 250, 300, 350, 400, 450, and 550°C, similar to the method of Qian et al. (2009). This method of combusting plant biomass has been seen in many studies due to its ease of standard replication. We felt that this may not, however, properly reflect the creation of ash and/or char in prescribed fires, which can reach temperatures within this range chosen, but not for the duration of elevated temperature in the muffle furnace (Jensen et al., 2001). Using the same biomass materials, laboratory fires were created by igniting the plant biomass in 8x11x2 tins in amounts of 5, 10 and 25g in order to achieve different intensities and produce different nutrient forms and availabilities to compare with the range found in the muffle furnace combustion.

Three-foot high walls of aluminum foil were constructed around 3 sides of the tin in order to block wind and create repeatable burning conditions. Datalogging thermocouples were placed in the middle of the burning litter to record temperature readings every second and monitor the intensity and duration of the fire. Weights before and after muffle furnace and laboratory fires were recorded in order to determine loss on ignition of fires for both HNPB and LNPB.

Analytical Methods

The pH of the ash and/or char residual was measured using a 1:50 (w:v) dilution (Qian et al., 2009). Total nutrients (C, N and P) were analyzed on the initial plant biomass material and the ash and/or char after both flame and muffle furnace combustion. Total P (TP) of initial and combusted materials was analyzed by placing samples in a muffle furnace at 550°C for 4 h and then dissolving the resulting ash in 6 M HCl and filtering the solution (Whatman 41). The filtrate was then analyzed using a Shimadzu spectrophotometer in accordance with EPA method 365.1. Total C and N were analyzed on a Flash EA 1112 series TN/TC analyzer.

Extractable P and N forms were measured on the NPB and HNPB ash residuals. The extractable P forms were labile or bioavailable forms represented by extraction with water (DDI) and 0.5 M HCO_3 (pH = 8.5) (Hedley et al., 1982; Cross and Schlesinger, 1995) which have been used in previous studies (Hartshorn et al., 2009). Both labile P_i and P_o were measured using these extracts with P_o being calculated as the difference between measured P_i and TP of the extracts (Hartshorn et al., 2009). The extractable N forms measured were TKN, NO_3, and NH_4 using 1 M KCl as the extractant. DIN and DON were calculated from these KCl extracts (DON = TKN – NH_4; DIN = NO_3 + NH_4).

Statistical Methods

All statistics were run using JMP® 7.02 (SAS® Institute Inc., 2007). Non-parametric one-way ANOVA's followed by Tukey's HSD test were used to measure significant difference between muffle furnace temperature, lab fire intensities and plant biomass types (Gray and Dighton, 2006). The significance level of $P<0.05$ was used throughout the experiment.

Results

Initial Plant Biomass Materials

Significant differences were observed between the HNPB and LNPB when analyzed for total and extractable nutrients prior to muffle furnace or lab fire combustion (Table 3-1). Total C and P were significantly higher in the HNPB in comparison to LNPB. Total N concentrations were not significantly different between the two materials (5.3 ± 0.1 and 8.1 ± 1.2 mg kg^{-1} for LNPB and HNPB), but the HNPB had significantly greater ext. TKN (960 ± 79 mg kg^{-1}) and ext. NH_4 (125 ± 25 mg kg^{-1}) than the LNPB (605 ± 74 and 6.8 ± 0.3 mg kg^{-1} respectively). Extractable P_i and P_o were also significantly higher in the HNPB (135 ± 14 and 41 ± 7.1 mg kg^{-1}) than LNPB (61 ± 3.5 and 18 ± 2.9 mg kg^{-1}).

Muffle Furnace Combustion

It was visually observed after the combustion of the LNPB and HNPB in the muffle furnace that the range of temperatures chosen for this experiment resulted in very different end products of ash and/or charred plant biomass. At the lower end of the temperature range (200°C), the plant biomass contained no ash and was charred only slightly with mostly brown plant material still present. At 300°C, the material still lacked white ash, but was almost completely black, charred plant biomass. As temperatures

increased above 450°C, the presence of charred plant biomass decreased until white ash made up approximately all of what was left after muffle furnace combustion.

Both HNPB and LNPB followed the same trend of mass loss with increasing combustion temperature. Approximately 50% of mass was lost at 200°C, with 80% from 300-350°C, and >98% at temperatures of 400°C and above. Both combusted materials also experienced an increase in measured pH with increased temperature ranging in value from 6 to 11.5. The measured TP and TC concentrations of both materials behaved almost inversely with TC (g kg^{-1}) decreasing and TP (mg kg^{-1}) increasing as incubation temperatures increased (Fig. 3-1). TN behaved differently with a peak in concentration at 350°C (Fig. 3-1) followed by a decline at higher temperatures.

Similar to the pattern observed by TN, Bioavailable P (DDI and $NaHCO_3$ ext.) peaked between the 300-400°C combustion temperatures. Bioavailable P_i $NaHCO_3$ ext. (Fig. 3-2) peaked at 400°C while DDI ext. peaked at 300 or 350°C depending on the plant biomass (Fig. 3-2). Bioavailable P_o $NaHCO_3$ ext. (Fig. 3-2) did not experience a peak at any temperature while DDI ext. peaked between 200 and 300°C (Fig. 3-2). For both plant biomasses types, extractable NH_4^+ and TKN displayed the same pattern as TN with the highest measured concentrations at the 350°C incubation combustion temperature while extractable NO_3^- peaked at 400°C (Fig. 3-3). The pattern of extractable NH_4^+ concentrations reflects much closer the pattern of TN concentrations than TKN or NO_3^-.

Lab Fire Combustion

By changing the amount of plant biomass being consumed during combustion in the lab fire, we were successful in altering the intensity of the fires (Fig. 3-4). The

recorded average temperatures for the high, medium and low intensity fires for the LNPB were approximately 520, 460 and 350°C respectively. Temperatures for the HNPB fires were slightly lower reaching 440, 420 and 380°C, for each of the different fire intensities. Not only were the recorded temperatures different for these intensities but, the heat duration was much longer for the higher intensity fire. The HNPB, while not reaching as high of temperatures as the LNPB, did on retain elevated temperatures longer than the LNPB.

Even with recorded differences in intensities between the lab fires, significant differences in the mass lost due to combustion were not measured between the low, medium and high intensities for each of the plant biomass types, nor were significant differences measured between the LNPB and HNPB at each of the intensities. The pH of the lab fire combusted materials were not significantly different at any of the intensities or between the LNPB and HNPB with an average value of 10.8 ± 0.1.

Despite the significant differences in the intensities of the lab fires for HNPB and LNPB biomass types, there were few significant differences in total nutrients remaining in the residual materials after combustion (Fig. 3-5). The low intensity fires exhibited some variation in measured total nutrient concentrations with slightly less C and N being volatilized. Unlike the total nutrients, which experienced minor measured differences in nutrient concentrations, the extractable N and P only had slight variations in measured concentrations. Both bioavailable P_i and P_o $NaHCO_3$ ext. measured higher than DDI ext. P forms in residual materials (Fig. 3-6). DDI ext. P_o differed from other labile P forms by decreasing as the lab fire intensity increased. Extractable NH_4^+ was significantly higher in the LNPB at the high intensity lab fire (Fig. 3-7) while NO_3 had

elevated concentrations in the low intensity lab fire (Fig. 3-7). TKN did not experience any significant change with regards to lab fire intensity (Fig. 3-7).

Discussion

Muffle Furnace Implications

Because herbaceous plant biomasses combust at lower temperatures, field fires dominated by these types of species do not achieve temperatures far outside the range chosen for this muffle furnace combustion experiment. However, this muffle furnace temperature range would be inappropriate if woody plant species were being studied. Temperatures necessary to combust woody plant species can be 1100°C or higher (Brown and Davis, 1973). The biomasses used in this experiment, while significantly different in nutrient content, both behaved as herbaceous species during combustion as seen in previous work with similar biomass types(Qian et al., 2009).

During muffle furnace combustion, total nutrient concentrations displayed similar patterns in both HNPB and LNPB (Fig. 3-1). As seen in previous studies volatilization of C and N begin around 200°C (Giovannini et al., 1988) following almost complete combustion of C and N occurring after temperatures of 400°C (Marion et al., 1991). In both materials, C volatilized quicker (>99% loss at 400°C) while N loss was approximately 50% until almost all C was lost and then N quickly volatilized. This caused the N concentration peak in both HNPB and LNPB. Because leaf morphology differed, LNPB experienced lower C combustion rates at lower temperatures while HNPB experienced less mass loss at higher muffle temperatures. Because combustion of both HNPB and LNPB yielded similar concentrations, macronutrient masses remaining after muffle furnace combustion were dependent upon beginning nutrient

amounts (Table 3-1), with HNPB containing more C, N, and P after combustion. While the total C,N, and P concentrations were similar after muffle furnace combustion, the extractable forms differed between HNPB and LNPB.

Both HNPB and LNPB lost N mass at similar rates with most volatilized above 400°C (Fig. 3-9), however, the extractable forms of inorganic N remaining in combusted residues differed with biomass type. Both biomass types had insignificant amounts of extractable N before 350°C combustion and after 400°C, HNPB favored the release of extractable NO_3 while LNPB contained more NH_4. While shifts in the forms of extractable inorganic N depended on plant biomass so little inorganic N remained (<0.5μg per g combusted) that the difference measured here would not significantly alter soil or water biogeochemical cycles after a fire. In both plant biomasses, approximately 90% remaining N, after 400°C muffle furnace combustion, remained as DON. Previous studies have documented almost complete volatilization of N after combustion (Neary et al., 1999) with remaining N forms being readily available (Prieto-Fernandez et al., 1993; Serrasolsas and Khanna, 1995). While most N remaining after combustion was readily available DON, the peak mass remaining after combustion at 300°C for HNPB and LNPB were approximately 300 and 100 μg DON g^{-1} initial biomass. Based on previous literature on N leaching in wetlands (Reddy et al., 2001; Malecki et al., 2004), this pulse of DON would not be enough to alter biogeochemical cycles unless above ground plant biomass (m^{-2}) was abundant.

As found with extractable N forms, HNPB and LNPB yielded differing forms of available P after muffle furnace combustion. Extractable P peaked at 400°C (Fig. 3-6), which corresponds with similar findings in muffle furnace combustion with P_i peaks also

at 400°C (Sertsu and Sanchez, 1978) and 460°C (Giovannini et al., 1990). While previous studies have measured extractable P after muffle combustion, none with the exception of Qian et al. (2009) have performed both DDI and bioavailable extractions on combusted herbaceous materials. In this approach, it was determined in this study that while both HNPB and LNPB resulted in similar conversion of P to labile forms (Fig. 3-8), the HNPB bioavailable P was slightly less available than LNPB bioavailable P. LNPB resulted in almost the same amount of DDI-P as with $NaHCO_3$-P while HNPB had very little DDI-P. The lower DDI-P in HNPB could be due to the release of cations, which has been shown to occur after combustion (Khanna and Raison, 1986; Macadam, 1987; Ubada et al., 2005; Tomkins et al., 2005), being higher in HNPB combusted material in comparison with LNPB. This difference in extractable P was only experienced until 400°C where enough cations were released to lower bioavailable P, as seen in previous studies (Blank et al., 1994; Qian et al., 2010).

Laboratory Fire Implications

In contrast with muffle furnace combustion, remaining concentrations of C, N, and P did not differ between burn intensities after lab fire combustion (Fig. 3-1). Temperature profiles indicated that altering fuel loads for both HNPB and LNPB resulted in different combustion intensities (temperature and duration; Fig. 3-4). Even though different intensity combustions for HNPB and LNPB was successfully achieved, little difference in total nutrient concentrations were observed between biomass type and combustion intensity. The exception to this was the low intensity combustion of LNPB where the maximum temperature recorded was less than 400°C and likely C had not fully volatilized from the material.

In general, concentrations of C, N, and P remaining after lab fire combustion for both HNPB and LNPB were similar to those found between 300 and 400°C after muffle furnace combustion. While recorded temperatures during lab fire combustion were hotter than 300 and 400°C, lab fire combustion temperatures most likely experienced a host of temperatures and durations similar to field fires (Bond and Van Wilgen, 1996). Variability in intensity during lab fire combustion was also apparent by visually observing the combusted residues. Lab fire combustion residues of both HNPB and LNPB results in both black charred biomass and white ashed biomass while residues from muffle furnace combustion were uniform, resulting in brown, then black, then gray, then white materials as combustion temperatures increased. Because concentrations were similar in both HNPB and LNPB across different fuel loads, it can be concluded that the total mass of C, N and P remaining after lab fire combustion of these herbaceous materials was highly dependent upon initial nutrient concentrations.

Extractable N concentrations after lab fire combustion were significantly different from those found after muffle furnace combustion in both HNPB and LNPB. As seen with total nutrients, the intensity of lab fire combustion did not affect residues as greatly as it did within muffle furnace combustion with the exception of extractable NO_3^- and NH_4^+ in the LNPB. After the low intensity burn, NO_3^- concentrations were higher than the medium or high intensity burns (Fig. 3-7). These concentrations suggest that although maximum temperatures of this combustion reached approximately 350°C (Fig. 3-4), the concentration of remaining NO_3^- reflected muffle furnace combustion somewhere below 200°C (Fig. 3-3). This implies that overall combustion of this material was extremely low. Similarly, extractable NH_4^+ from the LNPB yielded in higher

than expected concentrations after the high intensity burn. This increase in extractable NH_4^+ did not reflect an increase in N the combustion residues but rather an increase in the amount of extractable N.

Extractable N accounted for less than 10% of the remaining N after combustion (Fig. 3-9), implying that while peak temperatures were high during lab fire combustion, the combustion rates were not uniform and overall combustion was more similar to muffle furnace temperatures below 350°C (Fig. 3-7). These results indicate that the amount of N remaining in combustion residues in the field may be higher than muffle furnace combustion of similarly high temperatures would predict. While most of this remaining N was not measured as readily available, it is also expected to be less recalcitrant (Preito-Fernandez et al., 1993; Serrasolsas and Khanna, 1995). If N is limiting after a fire, this remaining N could be made available through enzymatic hydrolysis.

Similar to the extractable N results after lab fire combustion, extractable P results were different from muffle furnace extractable P. No differences in HNPB or LNPB were measured between burn intensities for $NaHCO_3$-P with approximately 1000 mg P kg^{-1} combustion residue(Fig. 3-6); much lower than the high temperature muffle furnace results (Fig. 3-2). While differences were not observed in $NaHCO_3$-P between HNPB and LNPB, they were with DDI-P (Fig. 3-6). HNPB had the highest amount of DDI-P at the low intensity burn, which corresponds with the muffle furnace DDI data trend (Fig. 3-2). As combustion temperature increased DDI-P decreased, especially in the HNPB. However, in the LNPB DDI-P peaked at the high intensity burn, when it was predicted to be the lowest due to increased release of cations at the higher combustion (Blank et al.,

1994). Because the high intensity burn had the most biomass, the probability of lower oxygen concentrations in the center of the burn is greater and may have resulted in less efficient combustion, or smoldering, of the plant biomass. While peak temperatures were the highest, if smoldering occurred in these samples, less cations may have been released resulting in more DDI-P than expected. This may have also explained the increased extractable NH_4 measured in the LNPB at the high intensity burn (Fig. 3-7).

Comparing Muffle and Lab Fire Combustions

Using muffle furnace approaches to recreate residues similar to that of field fires has been done in previous studies (Baldock and Smernik, 2002; Qian et al., 2009). The primary reason for this is that the collection of combustion residues after a field fire can be difficult (Galang et al., 2010). In most cases, field combustion residue C, N, and P concentrations are measured and then these values are extrapolated onto a curve of muffle furnace combustions similar to those done in this experiment (Qian et al., 2009). We attempted to reconcile the characteristics of materials created through flame combustion with the characteristics of materials created at different temperatures in the muffle furnace. In this manner, we hoped to validate lab fire combustion concentrations were extrapolated onto the muffle furnace graphs using linear lines between each concentration. Because lab fire intensities did not significantly alter total nutrient concentrations or forms, all lab fire combustion results were used to estimate muffle furnace equivalent temperatures for HNPB and LNPB. This extrapolation provided further evidence that lab fire combustion results in dissimilar residues than muffle combustion (Fig. 3-11).

While the overall results of extrapolating lab fire combustion results onto muffle furnace combustion results showed how the two combustion types yielded different

residues, it does not prove that one method is better than the other for mimicking plant biomass combustion in a lab. When only extrapolating total C, N and P to muffle furnace temperature, as other studies have done, it appears that muffle furnace combustion can in fact mimic lab fire combustion. However, lab fire combustion residues appeared (visually) differently than muffle furnace residues. Muffle furnace combustion created more homogeneous residues of either ash or char remaining. In contrast lab fire combustion yielded residues which appeared more like material present after a field fire, with a gradient of both ash and char material. Lab fire combustion also experienced non-uniformed heating similar to a grassland field fire, where temperatures reached slightly higher temperatures than those in the muffle furnace, but for a much shorter timescale (Fig. 3-4). Because the results for HNPB and LNPB reached max temperatures above those in the muffle furnace but were often more similar to mid-range muffle temperature results, it is also assumed that the lab fire combustion experienced a host of temperatures with differing durations which more closely resembles how a field fire undergoes combustion (Ryan, 1991; Bond and Wilgen, 1996; Urbanksy et al., 2009). These reasons suggest that of the two combustion methods used in this experiment, the lab fire combustion was better at mimicking how the HNPB and LNPB would combust in a field fire.

Lab Fire Conclusions

The comparison of muffle and lab fire combustions of two contrasting herbaceous plant biomasses was used to assess the dominant nutrient forms after combustion. Total nutrient concentrations after muffle furnace combustion were not significant from each other when comparing HNPB and LNPB. This was because the combustion rates of C and N in herbaceous species are similar despite the fact that each biomass had

significantly different initial nutrient concentrations. However, the forms of nutrients remaining after muffle combustion were dependent upon the initial nutrient status of the material. This was especially true in regard to available P where most available P remaining in LNPB was DDI extractable. Both HNPB and LNPB final forms of N after lab fire combustion were mainly DON, however the mass N remaining was so small that this addition of available N to a system after a fire would most likely have negligible effects.

It was also evident in this study that muffle furnace combustion could not mimic field fire as well as the lab fire combustion technique. Unlike the muffle furnace results, concentrations of HNPB and LNPB were similar across different intensities implying herbaceous plant biomasses combust similarly and final mass of C, N, and P is dependent upon initial concentrations. Both HNPB and LNPB final form of N after lab fire combustion was mainly non-extractable, with DON accounting for the little amount of extractable N present. Similar to the muffle combustion results, the mass of N remaining was so small that little effect would be seen from this after a fire. In contrast with N, volatilization of P did not occur and based on lab fire combustion results, LNPB while containing less P (mass) in the combustion residue, contained more available P than the HNPB. This result is attributed to the release of more cations in the HNPB dampening the effect of more P present in this plant biomass. Caution should be applied to these results because important factors such as plant biomass moisture content or wind were not taken into account during lab fire combustion.

Further research on the lab fire combustion technique to mimic field fires should address other factors that also influence combustion (e.g., moisture content; Ryan,

1991). Increased moisture content can increase the ignition point of plant biomasses and increase smoldering of plant biomass (Saito, 2001; Ward, 2001). It is also known that different plant species vary in their flammability (Rogers et al., 1986; Mutch, 1970) and while plant biomasses used in this experiment are typical herbaceous species found in many grassland and wetlands there are a host of other species that were not measured in this experiment that may behave differently. Some nutrient enriched grasslands or wetlands contain woody plant biomass, which was not studied in this experiment and could potentially alter the combustion of herbaceous species when included.

These conclusions have implications not only for determining what nutrients are made available during the combustion of herbaceous plant species, but can also be applied to a larger ecosystem scale to determine potential changes in biogeochemical cycles or restoration efforts. Up to 50% of remaining P was observed to be bioavailable after combustion while the remainder could be slowly of not available. This could increase the occurrence of non-herbaceous species growth in grasslands and wetlands; species that fire normally suppresses and their presences are normally undesirable. In oligotrophic wetlands, a pulse of available P can cause eutrophication and/or hinder restoration efforts of reducing nutrient availability (Zedler, 2000; Burns and McDonnel, 2003). Being able to approximate the amount of available nutrients after herbaceous plant biomass combustion when given initial nutrient concentrations can allow for modeling the potential impacts of fire on an ecosystem. In major systems where these plant biomasses are present, such as the Everglades, Florida, modeling of fire effects

on P biogeochemical cycles has only recently begun and much more data is necessary to accurately predict the impact of plant biomass combustion (Tian et al., 2010).

Table 3-1. Means (SE) of total nitrogen (TN), total carbon (TC), total phosphorus (TP), as well as dominant plant species of both High Nutrient Plant Biomass (HNPB) and Low Nutrient Plant Biomass (LNPB)

	units	LNPB	HNPB
Plant Species		Cladium Jamaicense Muhlenbergia capillaris	Andropogon glomeratus Ludwigia spp. Typha domingensis
TN	g kg-1	5.3 ± 0.1	8.1 ± 1.2
TC	g kg-1	444 ± 4.3	410 ± 10
TP	mg kg-1	97 ± 4.6	192 ± 6.3

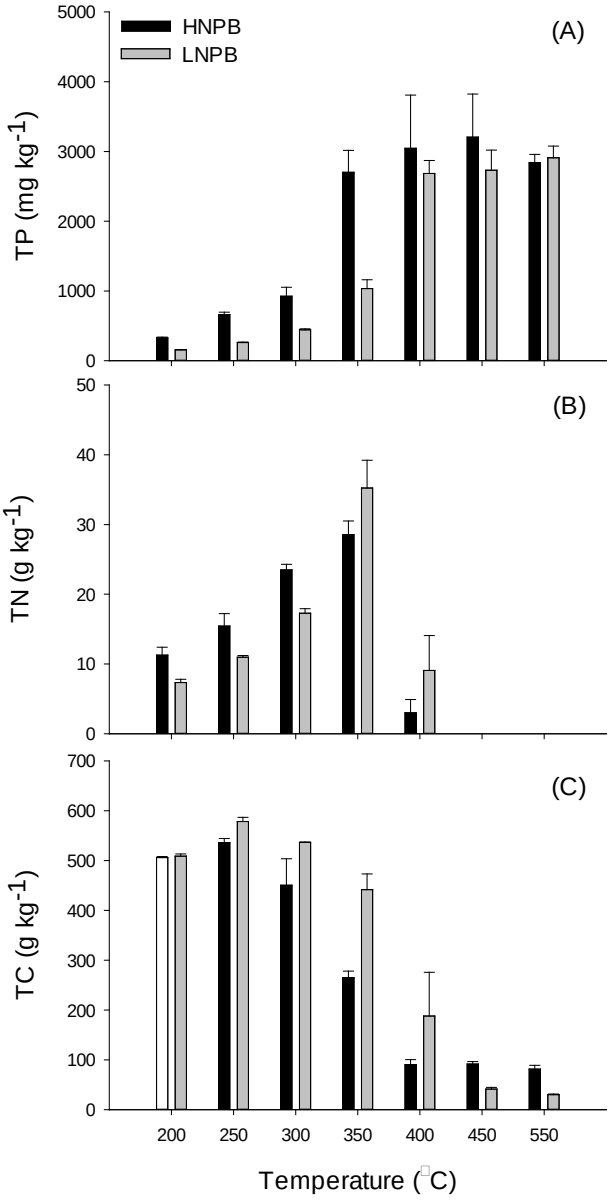


Figure 3-1. Total C, N and P, mean (SE), in remaining residues after muffle furnace combustion for both HNPB (black) and LNPB (gray).

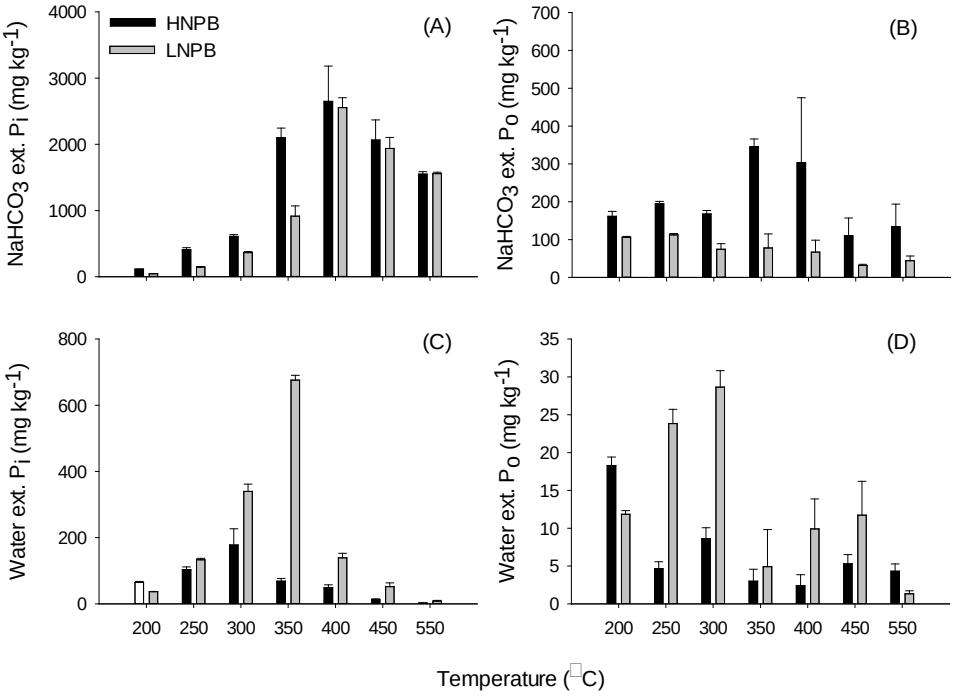


Figure 3-2. Extractable organic and inorganic P, mean (SE), in remaining residues after muffle furnace combustion for both HNPB (black) and LNPB (gray).

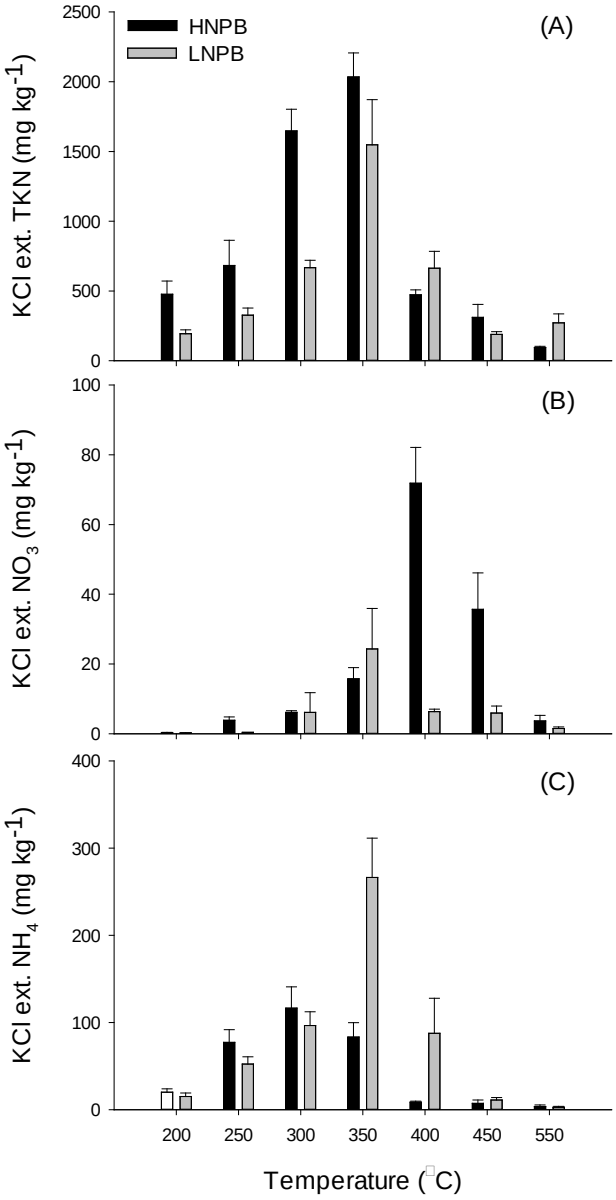


Figure 3-3. Extactable N concentrations, mean (SE), in remaining residues after muffle furnace combustion for both HNPB (black) and LNPB (gray).

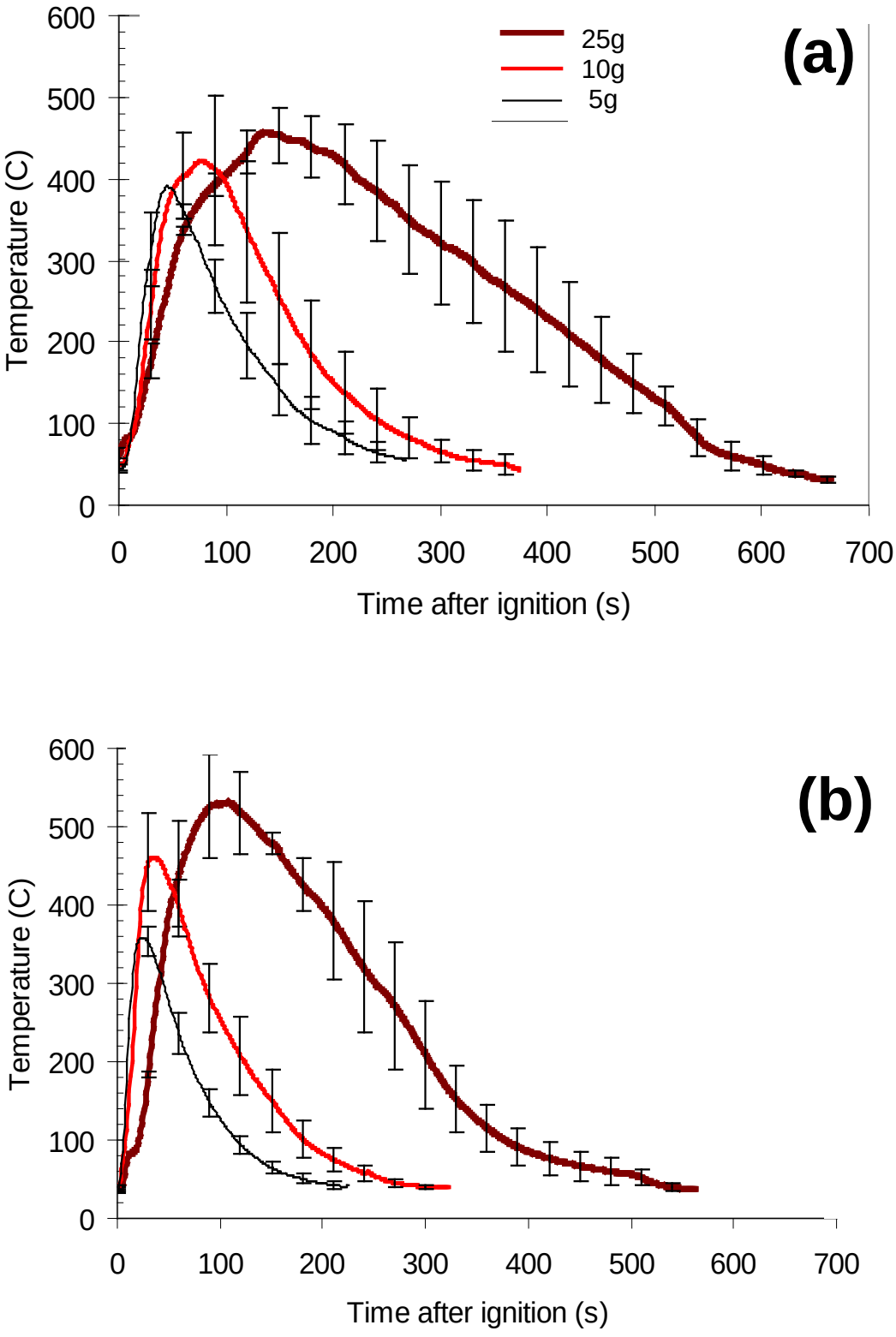


Figure 3-4. Measured peak temperatures, mean (SE), during lab fire combustion for both HNPB (a) and LNPB (b) for all three burn intensities.

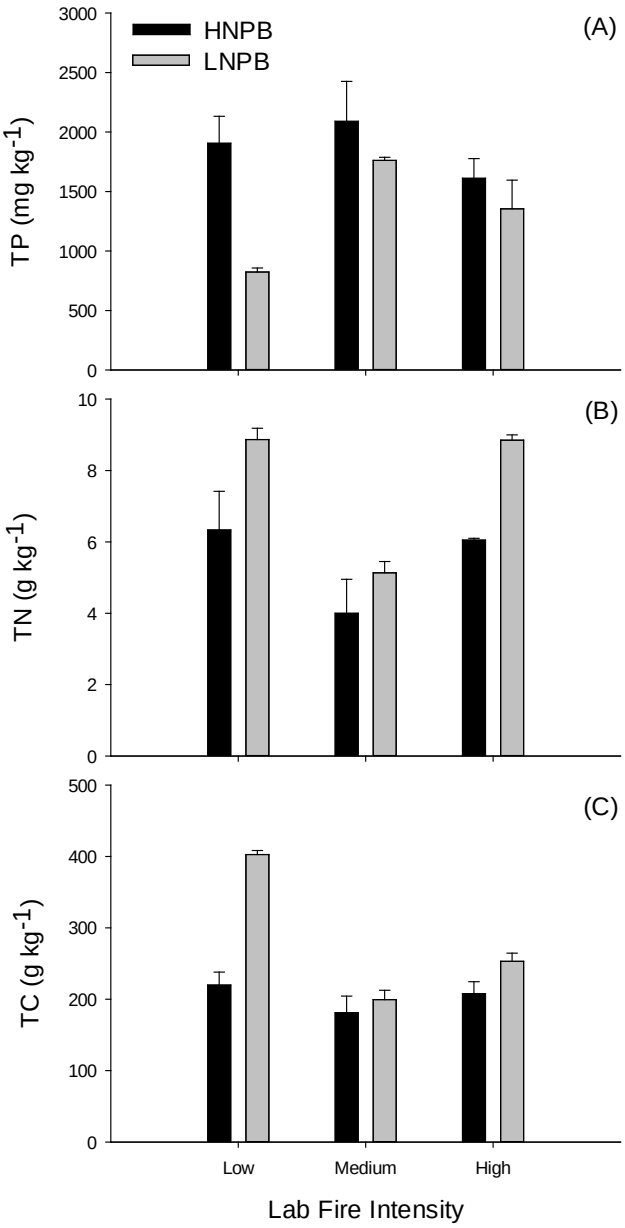


Figure 3-5. Total C, N and P, mean (SE), in remaining residues after lab fire combustion for both HNPB (black) and LNPB (gray).

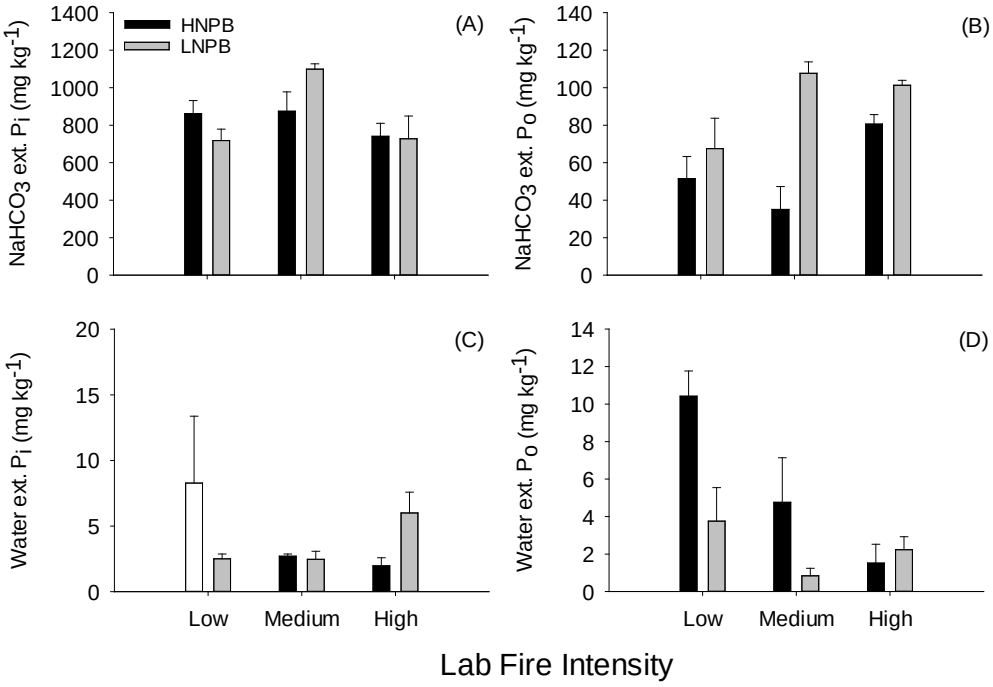


Figure 3-6. Extractable inorganic and organic P, mean (SE), in remaining residues after lab fire combustion for both HNPB (black) and LNPB (gray).

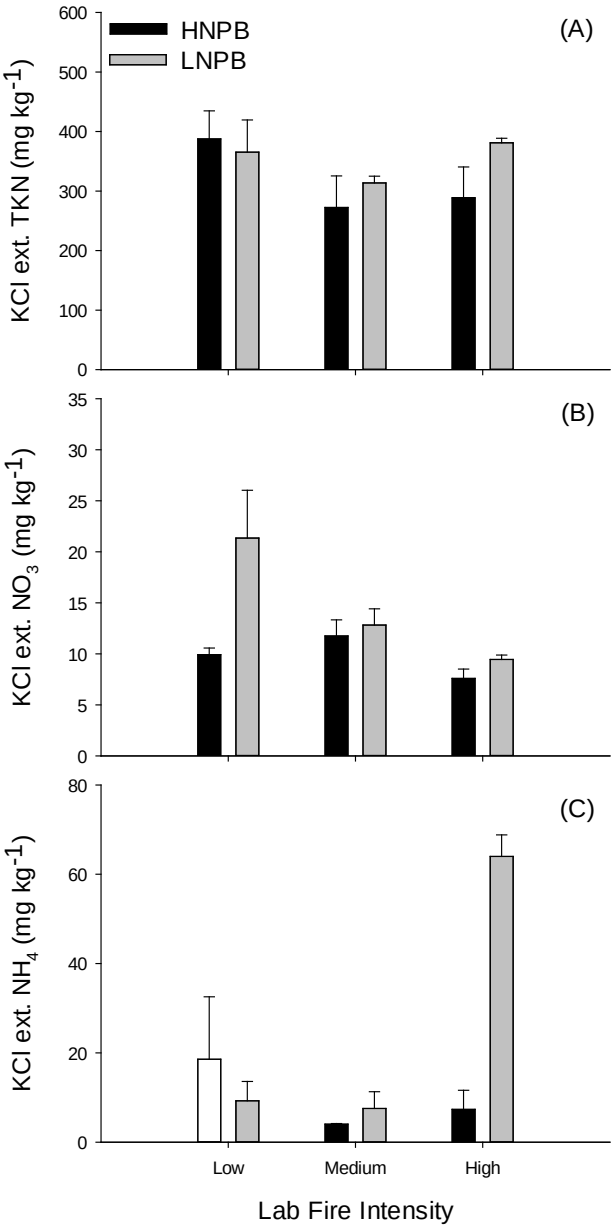


Figure 3-7. Extractable N, mean (SE), in remaining residues after lab fire combustion for both HNPB (black) and LNPB (gray).

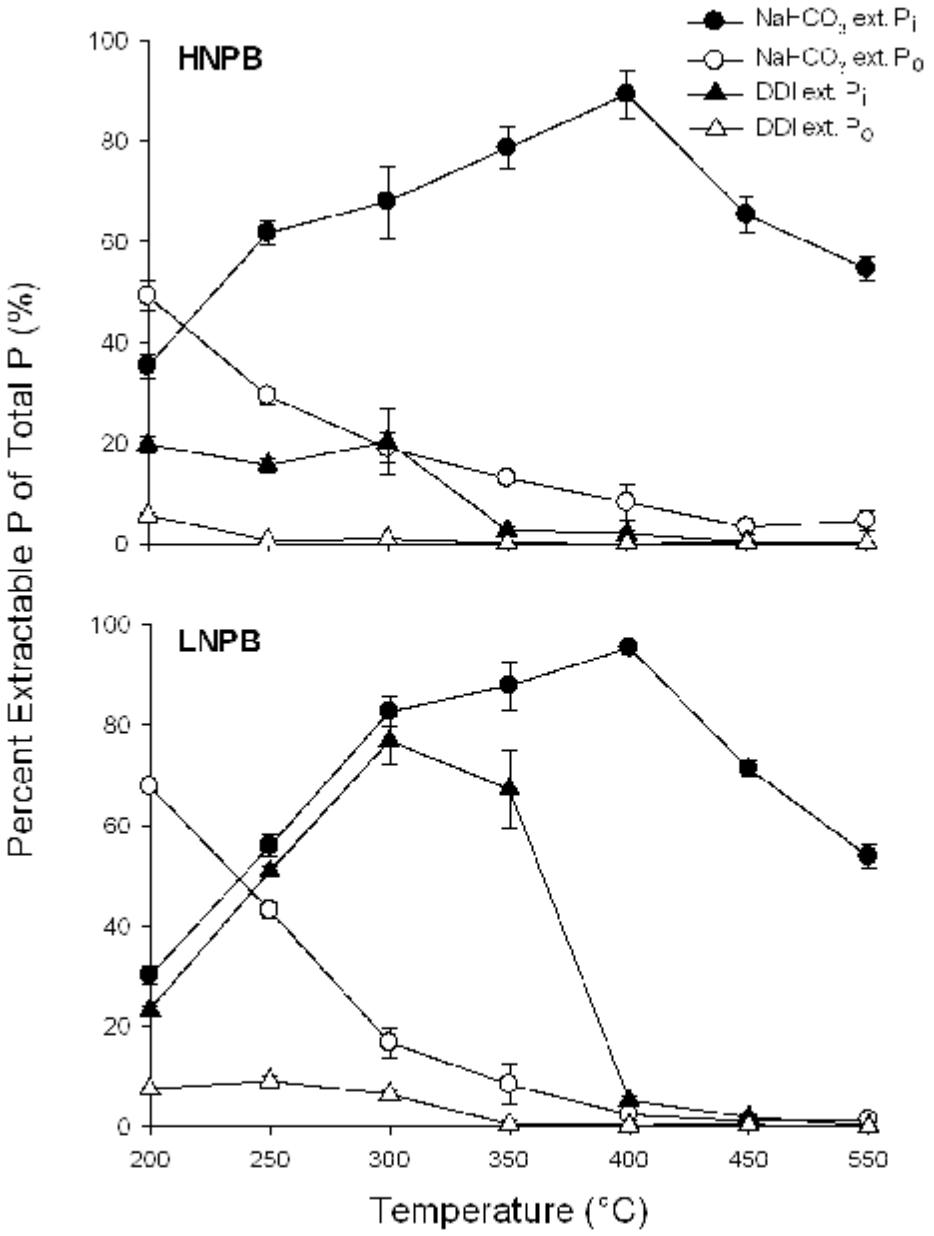


Figure 3-8. Extractable P, mean (SE), remaining after muffle furnace combustion as a percentage of remaining total P.

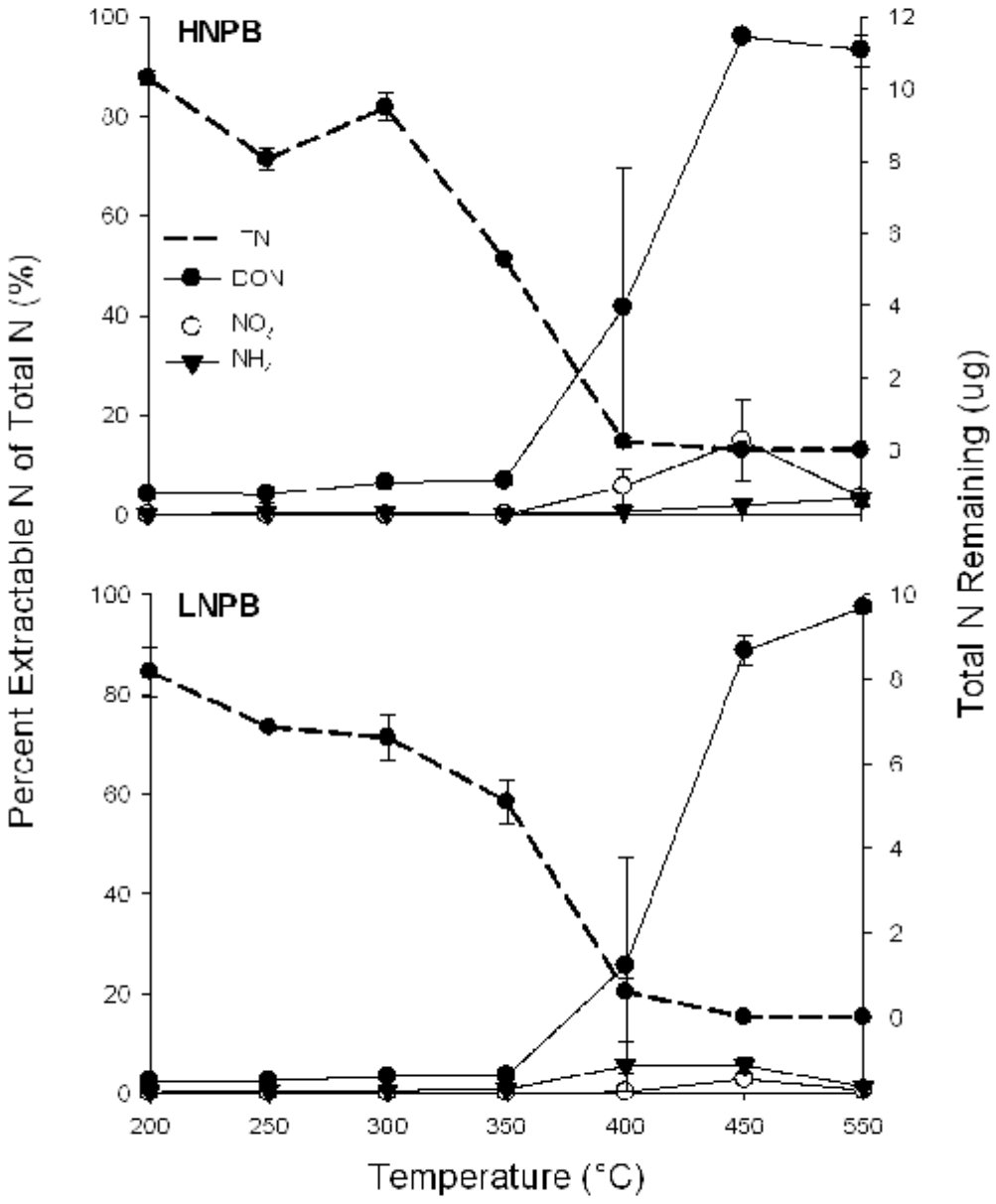


Figure 3-9. Extractable N, mean (SE), remaining after muffle furnace combustion as a percentage of remaining total N.

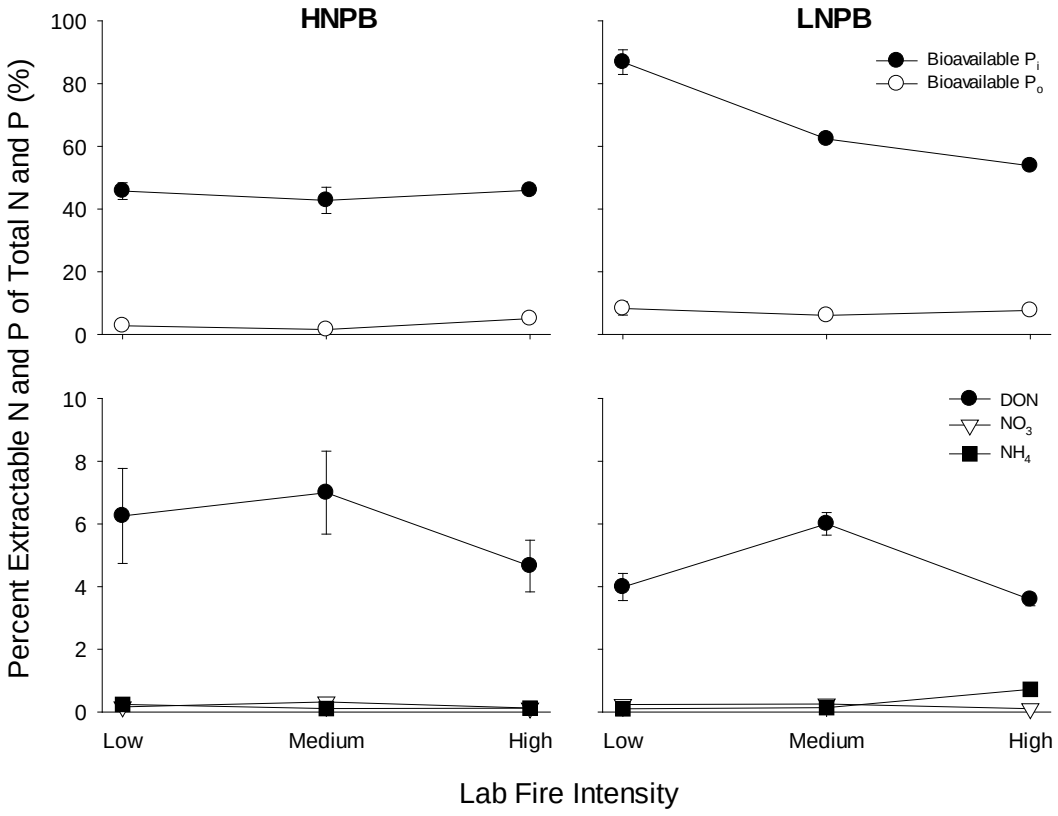


Figure 3-10. Extractable P and N, mean (SE), remaining after muffle furnace combustion as a percentage of remaining total P and N.

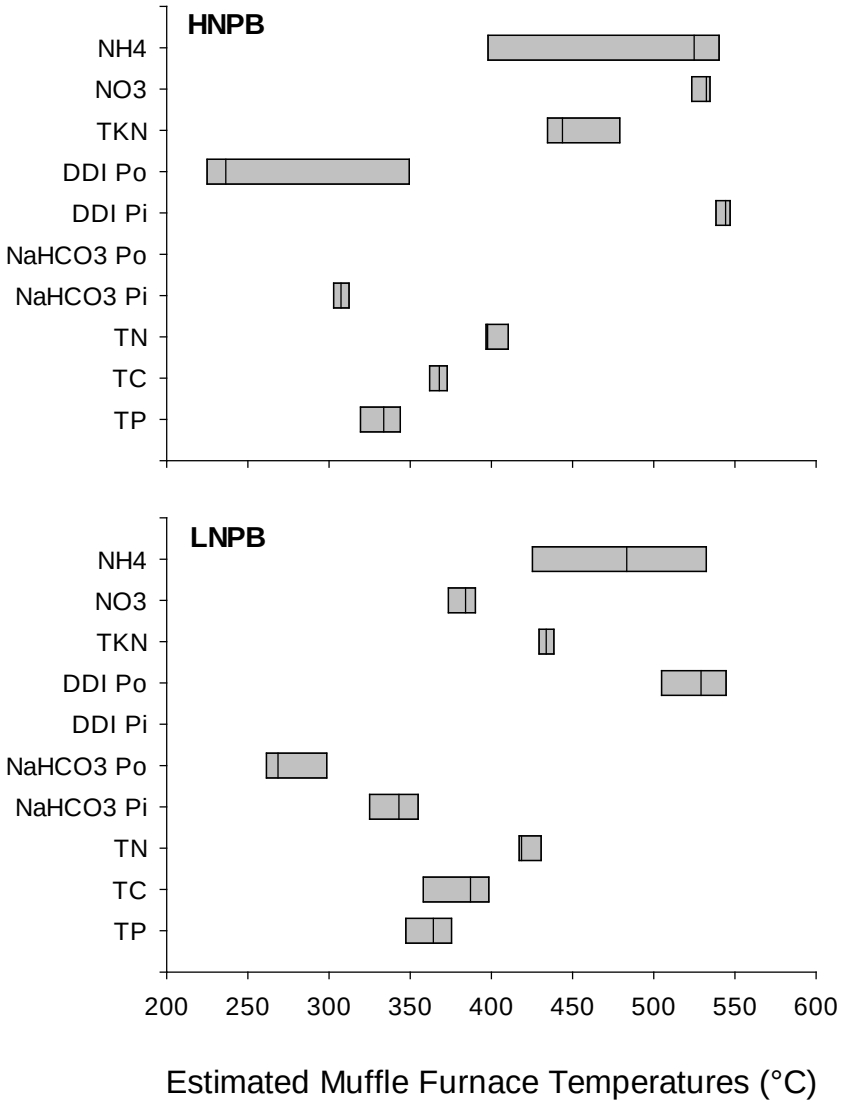


Figure 3-11. Estimated muffle furnace temperatures extrapolated from lab fire combustions.

CHAPTER 4
SYNTHESIS AND CONCLUSIONS

Fire is a dynamic ecosystem driver on grasslands and wetlands throughout the world. In this study, we examined the degree to which fire can shape herbaceous dominated wetland ecosystems. We accomplished this by exploring fire and its effect on the P cycle in a seasonally flooded calcareous marl wetland within the Everglades National Park, Florida. Fire is important in shaping ecosystems communities within the Everglades; however, fire in this and other wetlands is poorly studied. In this thesis we assessed a field fire and attempted to elucidate the final forms of nutrients remaining in combustion residues from herbaceous plant biomass.

After monitoring the burned and control plots in the HID up to one year after a fire event, we observed an increase in soil P labile pools. Estimated P additions at the native sites were dependent upon the amount (300 g m^{-2}) of above ground biomass present during the fire. Periphyton also appeared to be an important source and storage of P in these sites; however, the sampling approach used in this study may have prevented. These sites experienced a pulse in P following the fire which altered labile P pools up to one year after the fire. Above ground P storage in plant biomass had also not recovered in terms of biomass one year after the fire while N:P ratios were slightly lower. Based on these patterns we can conclude fire is a driving force in this system.

In the restored areas of the HID, fire resulted in the same pattern of increased P availability but to an even greater degree. Above ground biomass at these sites contained greater quantities of P before combustion leading to greater P deposition when compared to the native reference sites. Different plant biomass types also led to

lower combustion rates at these sites potentially causing the creation of char residues capable of storing or slowly releasing P into the soil over time. The estimated P addition at these sites was greater and indicators such as N:P ratio in live plant biomass indicated that one year after the fire, the system had shifted to N limitation. Maintaining P limitation is a key component to restoration of these sites and a large pulse of available P may have negatively affected restoration. However, caution should be used in assessing the long-term ramifications of this P pulse because this study only sampled these sites up to one year after a fire event.

Assessing combustion product residues is important to understanding nutrient forms and availabilities after a field fire. In this experiment, we used a comparison of muffle and lab fire combustion techniques on two herbaceous plant biomass types to determine the availability of nutrients after combustion. A range of three intensity burns under lab fire combustion on both biomass types revealed that remaining total nutrients after combustion varied little with changes in intensity. Lab fire combustion burn intensity differences did, however, result in slight differences in available inorganic N forms with the majority of available N remaining was DON. Available P after lab fire combustion was also similar across the three intensities with upwards of 50% P remaining in labile forms.

In contrast with lab fire combustion, muffle furnace combustion did not result in similar residues after combustion at different intensities. Combustion of plant biomass in a muffle furnace occurs at a steady temperature and resulted in more homogenous compositions of ash or char residues. At the mid range temperatures (300 - 400°C) muffle furnace combustion did result in total nutrient concentrations similar to those

remaining in residues after lab fire combustion. However, based on the differences in the extractable nutrients in materials from each of the two methods, the muffle furnace could not duplicate the conditions (likely temperature ranges and durations) present during flame combustion.

The results from the lab fire combustion experiment can be applied to measured field biomass fuel loads in order to estimate what the combustion materials added to the sites after the field fire (Table 4-1). These estimates can be used to explain results seen in the field from nutrient additions we were only able to estimate without the lab fire combustion experiment. Performing this combustion technique to characterize residues of other dominant plant species could potentially be used to build a database of predicted residue compositions. This data could be applied to current models used to determining system effects of fire in the Everglades as well as other wetland or grassland ecosystems.

The synthesis of these results from both field and lab fires indicate that fire can significantly impact nutrient biogeochemical cycles in herbaceous dominated wetlands. The degree to which this impact occurs is largely dependent upon plant biomass type and fuel load. Plant biomass types containing high amounts of P and N will release more available nutrients following combustion and have a greater potential of changing ecosystem biogeochemical processes. The production of char appears to be important at these sites and depending on biomass type, can slowly release available nutrients long after a fire event. Because fire is effective as a management tool in these systems, much more information is necessary to fully understand the effects of fire on achieving restoration goals, such as promoting a state of P limitation.

Further research is necessary to determine the full extent of the effects of fire on nutrient availability in similar sites. In this experiment non-herbaceous plant biomass types were not abundant; however, they are frequently present in wetlands. Therefore, more fire studies should be conducted to determine the impact of fire on ecosystems containing non-herbaceous plant species. Also, the potential of periphyton to capture and store nutrients following fire was not directly addressed in this experiment. However, periphyton did appear to utilize much of the available nutrients after the fire thus further research is warranted to determine the forms and complexes of P created by periphyton. Moisture content is another key variable affecting both the degree of combustion process and the characteristics of the nutrients remaining in combustion residues. Better chemical characterization of plant biomass residues should also be done including techniques such as NMR and XRD to analyze the structure and mineralogy of remaining plant biomass residues. Further analysis of plant biomass residues, using more advanced techniques, can better establish the impact of fire in nutrient availability and storage

The findings of this study have implications for other systems where fire is a component, either natural or prescribed. Lab fire combustion results can be applied to current models used to predict both long and short term impacts of fire on nutrient cycles and larger ecosystem processes such as species composition and productivity. In this manner, findings of this work can have an important role in our understanding of fire and its impacts on biogeochemical cycles, especially in the context of global climate change.

Table 4-1. Estimation of nutrients added after the field fire from Chapter 2 based on lab fire combustion results from Chapter 3.

		Res00 High	Res00 Low	Ref High	Ref Low
TC	g m^{-2}	7.26	2.96	12.80	10.33
TN	g m^{-2}	0.20	0.08	0.32	0.26
TP	g m^{-2}	0.06	0.02	0.03	0.02
$NaHCO_3$-P_i	mg m^{-2}	37.9	30.6	29.5	12.0
$NaHCO_3$-P_o	mg m^{-2}	1.83	0.75	3.89	3.14
DDI-P_i	mg m^{-2}	0.19	0.08	0.14	0.11
DDI-P_o	mg m^{-2}	0.25	0.10	0.09	0.08
DON	mg m^{-2}	11.43	4.65	14.08	11.37
NO_3^-	mg m^{-2}	0.35	0.14	0.67	0.54
NH_4^+	mg m^{-2}	0.45	0.18	0.91	0.74

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BIOGRAPHICAL SKETCH

Benjamin Hogue was born in Atlanta, Georgia to Gerald and Natalie Hogue. Four years later he was blessed with a younger sister Laura and they grew up in Atlanta until relocating with their parents to Orlando, Florida in 2001. After grade school, Ben attended the University of Florida and received a BS in Environmental Science. In 2008, prior to his senior year of being an undergraduate, he married the love of his life Amanda Crane Hogue. That same year, he met Dr. Patrick Inglett through a mutual friend and was given a part time position in his laboratory. That year of working for and being mentored by Dr. Inglett led to an offer of a MS working position under Dr. Patrick Inglett at the University of Florida from 2009 to 2011. This thesis is a result of some of the research that followed.