FIRE EFFECTS ON NITROGEN CYCLING IN NATIVE AND RESTORED CALCAREOUS WETLANDS

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ABSTRACT

Fire is an important natural process and management tool in the Florida Everglades, but few studies have examined its effects on nutrients; nitrogen (N) in particular has received little attention across the whole Everglades system. In this study, we investigated fire effects on the N cycle in both a high-phosphorus (P) restored wetland and a low-P reference calcareous wetland (marl prairie) in the Hole-in-the-Donut region of the southern Everglades. Potential N mineralization, denitrification, extracellular enzyme activities, and periphyton N_2 fixation rates were measured immediately (two days), one month, and one year after a prescribed burn. Results showed differing responses of N cycle processes between the two sites: N availability increased immediately after the fire at the low-P reference site, but did not increase immediately at the high-P restored site. We also saw a greater increase in denitrification immediately after the fire in the reference site (118% increase) compared to only 20% increase in the restored site. Periphyton N_2 fixation in the restored site tended to be stimulated, but was inhibited in the reference site after the fire. The underlying mechanisms for these changes are not clear, but fire residues (ash and char) may directly and indirectly affect the N cycle. These findings have implications for management of fire intensity in natural and P-impacted sites.

INTRODUCTION

Fire has great influences on nutrient cycles in ecosystems by changing the form, distribution, and amount of nutrient, as well as by changing plant species composition (Raison 1979, Bissett and Parkinson 1980, Dumontet *et al.* 1996, Grogan *et al.* 2000, Brown *et al.* 2004, Certini 2005). The effect of fire on the nitrogen (N) cycle is highly important because N, like phosphorus (P), is often a limiting nu-trient for primary productivity. Compared to P, the N cycle is more complex and involves various processes. For example, N can be easily lost through denitrification, ammonification, and volatilization. Since N is important for plants, many studies have focused on the available N status before and after fire, trying to understand the effects of the fire on subsequent primary production.

Fire can affect nutrient cycles within a system in various ways. Combustion differential-

ly affects elemental composition of fuel through volatilization of carbon compounds and N as ammonia (NH_3) and nitrogen oxides (NO_x), while P compounds largely remain in the ash and char residues (Hogue and Inglett 2012). The transfer of heat to the soil increases soil temperature and affects the physical, chemical, and biological soil properties (Neary *et al.* 1999). For example, elevated temperatures can kill soil microbes, decompose organic matter, and change N forms (Raison 1979).

The particulate residues left by fire are also an important pathway for nutrients to return back to or redistribute in the ecosystem after the fire (Zackrisson *et al.* 1996, Qian *et al.* 2009). Fire residues contain small amounts of inorganic and organic N that directly serve as a N source (Qian *et al.* 2009, Hogue and Inglett 2012). Both ash and charcoal can also exert an indirect influence on N availability through modification of the pH and the cation exchange capacity (Raison 1979, Glaser *et al.* 2002). Indirectly, P in fire residues can also stimulate N processes, such as N_2 fixation and nitrification, and N mineralization, especially in P-limited ecosystems (Eisele *et al.* 1990; White and Reddy 1999, 2000). Charcoal with its great adsorptive surface can also enhance nitrification, leading to elevated nitrate levels (Zackrisson *et al.* 1996; Wardle *et al.* 1998; DeLuca *et al.* 2002, 2006).

Studies on prescribed fire have mostly focused on forests, grasslands, and prairies (Ojima *et al.* 1994, Blair 1997, Grogan *et al.* 2000, Castaldi and Aragosa 2002, Zackrisson *et al.* 2004), while comparatively few have focused on wetlands (Battle and Golladay 2003). However, fire and hydrology together are important elements in wetland management (Lockwood *et al.* 2003) where fire is used to control the spread of invasive species in both coastal and inland wetlands (Kirby *et al.* 1988). For example, the Florida Everglades is regarded as a fire-dependent landscape (Beckage *et al.* 2005), and reestablishing a more natural hydrology and fire regime is a key component of successful restoration (Lockwood *et al.* 2003).

Numerous fire projects have been conducted in a diversity of landscapes across the Everglades, such as the River of Grass prescribed fire plan for the wet prairie and sawgrass marsh ecosystems, the Pinelands burn plan, the mangrove-marsh ecotone fire project, and the fire project in Water Conservation Area 2A (WCA 2A) of the northern Everglades (Spier and Snyder 1998, Beckage *et al.* 2005, Qian *et al.* 2009). However, while most of these projects have focused on restoring native plant species, little is known about the fire effects on nutrient biogeochemistry, let alone on the N cycle that has been ignored across the whole Everglades ecosystem (Miao and Sklar 1998, Miao and Carstenn 2006, Qian *et al.* 2009, Inglett *et al.* 2011).

To bridge the gap between our knowledge of fire, the N cycle, and wetland restoration, a case study on the N responses to fire at restored and reference wetlands was conducted in the Everglades National Park. Based on the literature, we proposed the following hypotheses: 1) fire would increase N availability, in particular that of nitrate; 2) higher nitrate levels would lead to increased denitrification rates; and 3) fire would increase N_2 fixation because of the possible elevation of available P after fire.

METHODS

Study Site and Sampling Methods

The study site was located in the Hole-in-the-Donut (HID) of Everglades National Park, Florida, USA (Figure 1). Two sampling sites were selected in this study. One site was used extensively for agriculture with subsequent nutrient enrichment and was restored by topsoil removal (Res2000; Inglett and Inglett 2013), while the other was a native marl prairies ecosystem that had not been disturbed by humans (Reference; Figure 1). Plant species at Res2000 were dominated by *Andropogon* spp., *Muhlenbergia* spp., and *Baccharis halimfolia* L.; while the dominant species at the reference site included *Muhlenbergia* spp. and *Cladium*
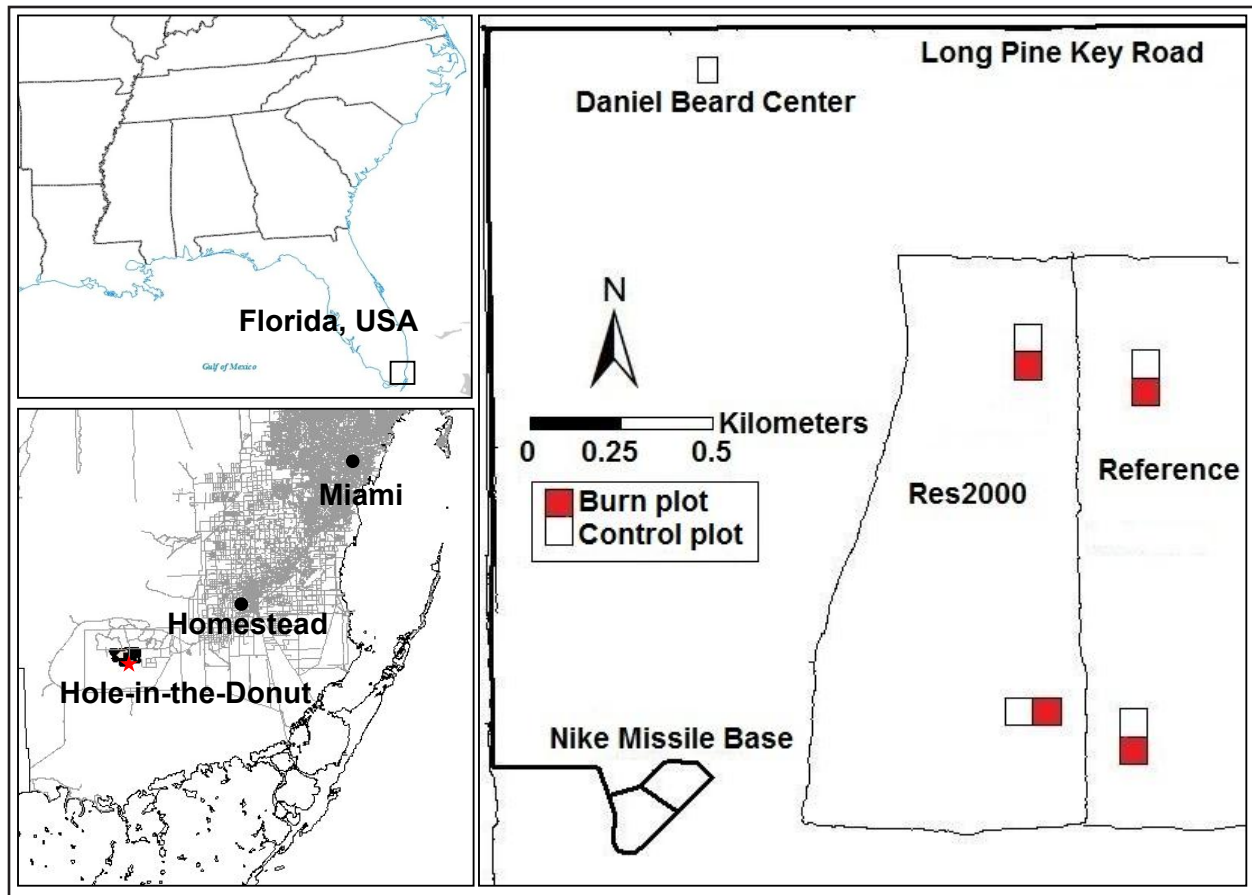
Figure 1. Location of the study site within the Everglades National Park in South Florida, USA.

jamaicense (Crantz). The removal of soil in the restored sites resulted in comparatively shallower soil depth (average 2.3 cm) in these areas relative to that of the reference site (average 10.3 cm).

At each of the Res2000 and Reference sites, two locations corresponding to high and low elevation areas were selected. At each of these four locations, three treatment (burned) and three control (unburned) 10 m × 30 m plots were identified. Fire encroachment into the control areas was prevented by removing the vegetation within a 2-meter buffer zone surrounding each of the plots. Within each sampling plot, a 2 m × 2 m grid system was devised (75 grid cells) and used to randomly sample each of the plots before and after the fire.

The prescribed fire occurred on 4 May 2010. Based on prescription parameters, all

fire weather observations taken during the firing period were either in preferred or acceptable ranges except for shaded fine dead fuel moistures. Recorded relative humidity was lowest in the morning with a value of 55 %, which was within the preferred range of 45 % to 75 %. In the afternoon, at the hottest hour of the day, the heat index value was 36 °C. Wind direction was predominantly from the south or south southeast, but occasionally switched to all directions except north. Exposed fine dead fuel moistures were lowest at noon with values of 8 %, which was within the acceptable range of 5 % to 10 %. The prescribed fire was completed through a combination of burning out from control lines, burning around research plots, and aerial ignition. Observed head fire rates of spread near the research plots ranged from 5 m min^{-1} to 10 m min^{-1}, depending on the density and continuity

of grassy fuels. Flame lengths from grassy fuels were usually 2.5 m to 3.6 m.

We collected samples one month before the fire (8 to 10 April 2010), and two days (6 and 7 May 2010), one month (10 and 11 June 2010), and one year (25 and 26 May 2011) after the fire. Samples of surface soil (0 cm to 5 cm or to the bedrock) were taken using a sharpened steel tube, and periphyton biomass samples were taken by hand. All samples were sealed in plastic bags and kept on ice until their return to the laboratory, where the samples were refrigerated at 4 °C until subsequent analysis.

Periphyton samples were kept intact (periphyton mat) and inspected to remove large organic debris (plant litter) and soil. Soil samples were sieved to remove roots and rock fragments greater than 2 mm diameter. Fresh periphyton was used to determine nitrogenase activity, while sieved soil samples were used in the determination of all soil microbial and enzyme related parameters. A subsample of sieved soil was oven dried at 105 °C for three days and ground using a mortar and pestle for moisture content and total nutrient determinations. Periphyton moisture content and nutrients were determined using the sample used for nitrogenase activity, which was oven dried at 65 °C for three days and ball milled.

Biogeochemical Analysis

Extractable inorganic nitrogen. Extractable and exchangeable NH_4^+ and NO_3^- was determined by extracting soil samples (1 g dry weight equivalent) with 25 ml of 2.0 M KCl for 1 h (Mulvaney 1996). The samples were then centrifuged and the supernatant filtered through Whatman 41 and analyzed for NH_4-N (EPA method 350.1 [USEPA 2012]) and NO_3-N (EPA method 353.2 [USEPA 2012]). Microbial biomass C and N (MBC and MBN, respectively) were determined using the chloroform fumigation-extraction technique (Brookes *et al.* 1985). The extraction efficiency factors

for MBC and MBN in the study were 0.37 and 0.42, respectively.

Denitrification enzyme assay (DEA). This method was modified from Smith and Tiedje (1979), using the acetylene block technique (yielding N_2O production) and adding sufficient NO_3^- and carbon source. Triplicate, 5 g wet soil samples were sealed with rubber septa stoppers in 30 ml tubes; 3 ml distilled deionized (DDI) water were added to the tube and purged with N_2 to maintain anaerobic conditions. Two milliliters of acetylene gas (C_2H_2; approximately 10 % headspace) was injected into the tubes to block the conversion from N_2O to N_2, and the tubes were then shaken for 1 h to disperse the gas. After shaking, a DEA solution (0.202 g KNO_3 L^{-1}, 0.25 g chloramphenicol L^{-1}, and 0.360 g $C_6H_{12}O_6$ L^{-1}) purged with oxygen-free N_2 gas was added to the tubes. Samples were shaken and incubated at room temperature. Headspace gas was collected at 1 h intervals for about 5 h. The potential denitrification rate was calculated from the steepest portion of curve produced when cumulative N_2O evolution was plotted against time. The sampled gas was injected in a Shimadzu GC-14-A ECD gas chromatograph (Shimadzu Corporation, Kyoto, Japan) equipped with an electron capture detector (ECD) and Porapak Q column (Waters Associates, Inc., Milton, Massachusetts, USA). The operation temperatures for the column, injection port, and detector were set at 70 °C, 120 °C, and 230 °C, respectively. A 10 ppm standard concentration gas (Scott Specialty Gases, Inc., Plumsteadville, Pennsylvania, USA) was used to calibrate the measurement, and results were reported as N_2O-N produced per gram of dry weight soil, per hour.

Extracellular enzyme activities. Two N-related enzymes, (i.e., N-acetyl-β-D-glucosaminidase [NAG, EC 3.2.1.30] and Leucine aminopeptidase [LAP, EC 3.4.11.1]), were measured using fluorogenic enzyme substrate

(Hoppe 1983). Methods were modified from Sinsabaugh *et al.* (1997) to optimize the substrate concentrations in soil samples with fluorogenic substrates 4-Methylumbelliferyl N-acetyl-β-D-glucosaminide (MUF-N) for NAG, and L-leucine 7-amido-4-methyl coumarin (AMC) for LAP. Enzyme substrates MUB-N and AMC produce fluorochrome methylumbelliferone (MUF) and aminomethylcoumarin (AMC) once they are hydrolyzed by the enzyme NAGase and LAPase, respectively. The fluorescence of samples and standards was measured at an excitation of 350 nm and an emission of 450 nm using a Bio-Tek Model FL600 fluorometric plate reader (Bio-Tek Instruments, Inc., Winooski, Vermont, USA). The potential enzyme activity was expressed in μmol MUF g^{-1} dw h^{-1} released or μmol AMC g^{-1} dw h^{-1} released.

Nitrogenase activity (N_2 fixation). We used the acetylene reduction (AR) assay described by Liao and Inglett (2012). Wet periphyton (5 g) was placed into 42 ml, screw-capped culture tubes (Kimax™, Kimble Chase Life Sciences and Research Products LLC, Vineland, New Jersey, USA) with an open-top cap containing a teflon-lined, silicone septa (0.125 cm thick). Acetylene gas (generated by adding water to CaC_2 in an evacuated serum bottle) was added to each tube (4 ml; ~10 % headspace) and the tubes were gently shaken to evenly distribute the gas in the sample. Tubes containing samples and blanks containing only injected C_2H_2 were incubated at a constant temperature (27 °C) for up to three hours under either light (~900 μmol m^{-2} s^{-1} photosynthetically active radiation [PAR]) or dark conditions. After incubation, tubes were vigorously shaken to equilibrate gas phases, and gas samples (4 ml) were taken from each tube and stored in evacuated 3.5 ml Exetainers™ (Labco International, Houston, Texas, USA.) Gas samples were analyzed for ethylene using a GC-8A (Shimadzu Corp., Kyoto, Japan) gas chromatograph equipped with a flame ionization detector (110 °C) and a Porapak N column (80 °C). Two standard gases (1 ppm and 10 ppm) were used to calibrate the measurement. Nitrogenase was then expressed as nmol C_2H_4 g^{-1} dw h^{-1}.

Statistical Analysis

Data were analyzed with JMP v.8© statistical software (SAS Institute, Inc., Cary, North Carolina, USA). For pre-fire data, one-way analysis of variance (ANOVA) was used to compare the difference in measured parameters between the restored and reference sites. For post fire data, the factors of site and sampling time were fixed and separate one-way analyses for the different sites and dates were performed. Regressions between different parameters were performed using the linear least-squares method. All results were reported as significant when $P < 0.05$. Data were log transformed when necessary to improve normality.

RESULTS

Fire effects on extractable inorganic nitrogen. Both restored and reference sites showed an increase in extractable NO_x-N and NH_4-N two days after the fire (Figure 2). The increase of extractable inorganic N was greater at the reference site (i.e., approximately twice that of the control plots) compared to the restored site (i.e., only 20 % to 40 % higher than the control plots); and only at the reference site was the difference statistically significant ($P < 0.05$). At longer time scales (one month to one year after the fire), the extractable NO_x-N remained higher in the burn plots than in the control plots for the reference site (Figure 2), but the extractable NH_4-N at both restored and reference sites dropped to levels below that of the control plot one month after the fire (Figure 2).
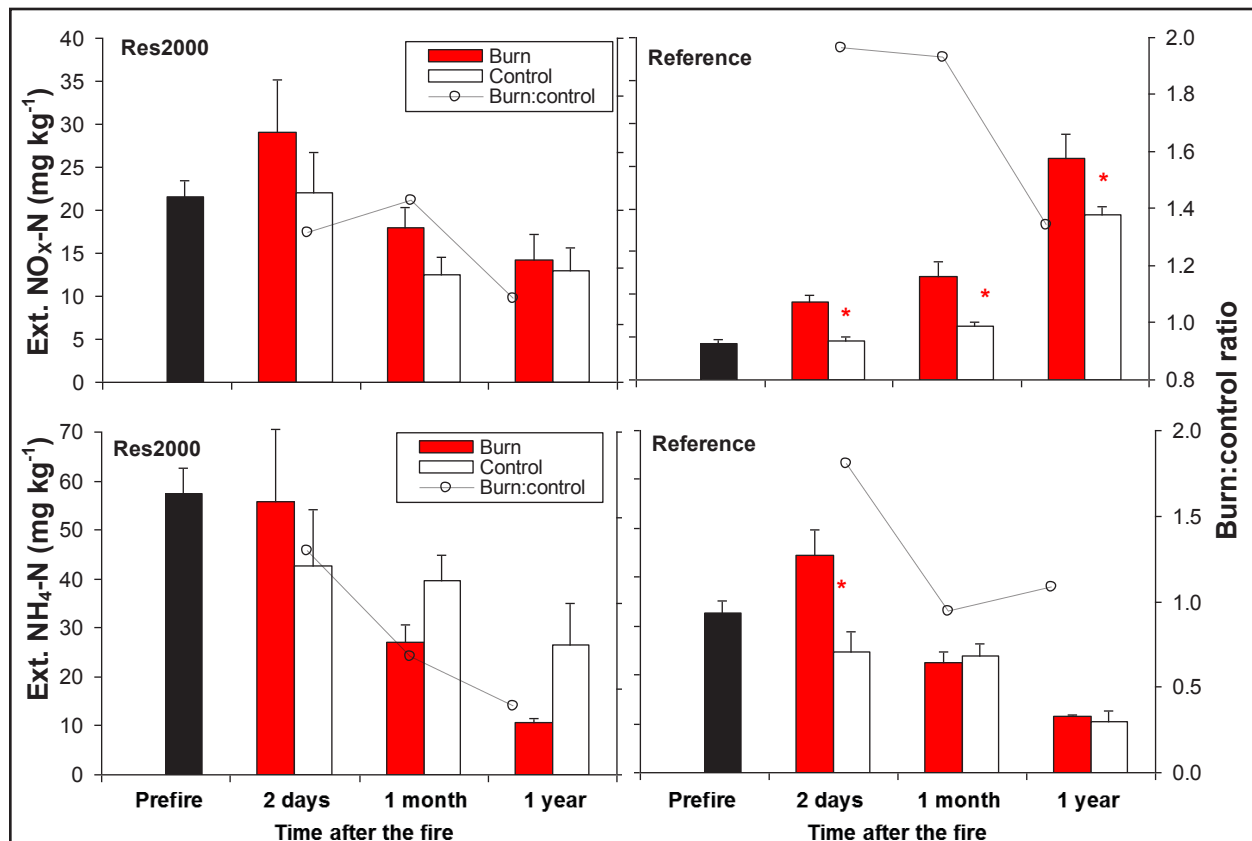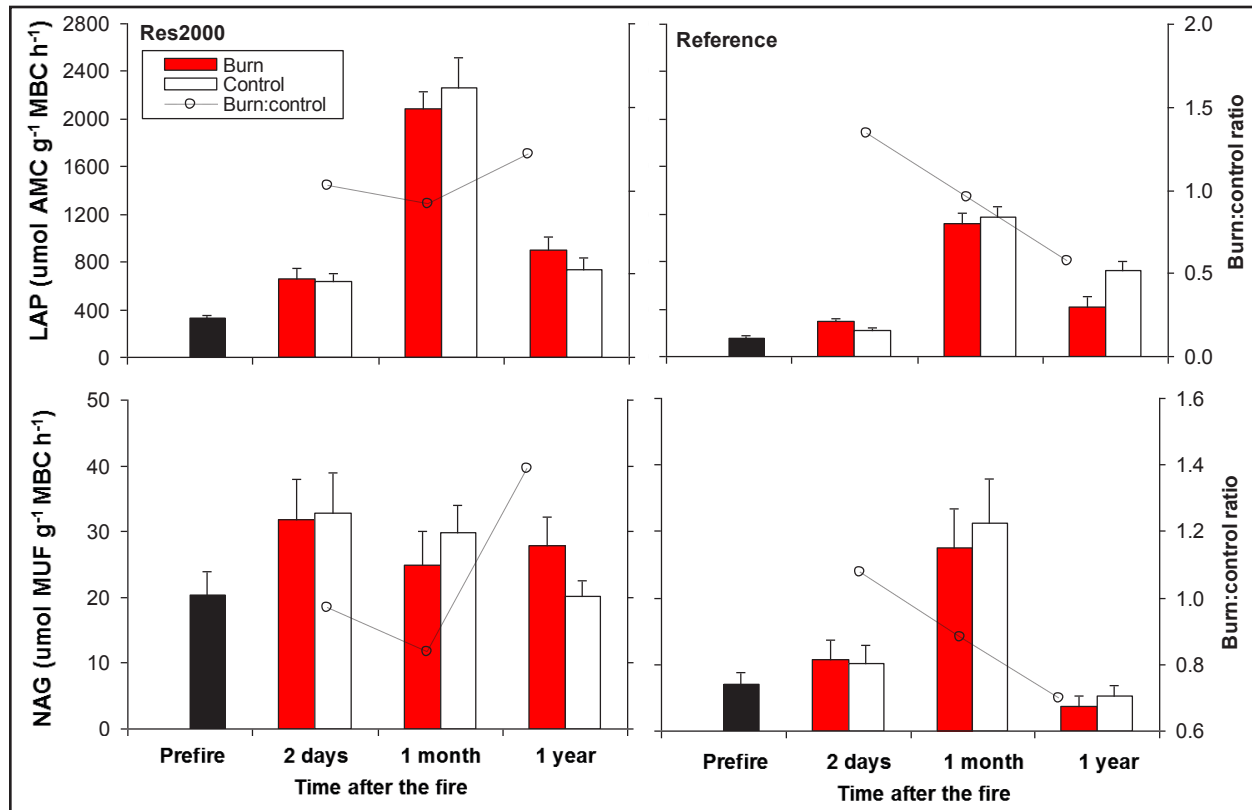
Figure 2. Changes of the extractable NO_x-N and NH_4-N of the soil in the burn plots and control plots in the restored wetlands (Res2000) and reference wetlands two days, one month, and one year after the fire. The black bar represents the value before fire. The star (*) denotes significant difference between the burn plots and control plots ($P < 0.05$).

Fire effects on extracellular enzyme activities. The two N-related enzymes (i.e., LAP and NAG) responded to the fire similarly at each specific site, but responded differently between sites (Figure 3). In the restored site, the LAP and NAG did not change appreciably up to one month after the fire, but after one year, they increased by 20 % and 40 %, respectively, relative to the control plots. In contrast with the restored site, the enzyme activities in the burn plots at the reference site were significantly greater than those in the control plots immediately (two days) after the fire, but after one month, the enzyme activities returned to or even fell below the control levels.

Fire effects on denitrification. Both the restored and reference sites showed similar responses of denitrification (measured as DEA)

to the fire (Figure 4). Immediately after the fire, approximately 20 % higher DEA rates were observed in the burn plots compared to the control plots at the restored site. For the reference site, the DEA rates at the burn plots were up to twice the values in the control plots. After one year, DEA rates in the burn plots had returned to the levels in control plots.

Fire effects on periphyton N_2 fixation. The responses of periphyton N_2 fixation to the fire differed between the restored and reference sites. At the restored site, N_2 fixation rates slightly decreased immediately after the fire, but then increased to as high as twice those in the control plots one year after the fire. In contrast, at the reference site, the rates fell below the control levels after one year (Figure 5).

Figure 3. Changes of LAP and NAG in the burn plots and control plots in the restored wetlands (Res2000) and reference wetlands two days, one month, and one year after the fire. The black bar represents the value before fire.

## DISCUSSION

Responses of Nitrogen Availability to the Fire

Most studies consistently suggest that fire can increase the availability of soil NH_4^+ and NO_3^- (Wan and Lao 2001). NH_4^+ is a direct product of the combustion, which is adsorbed by the soil, thus increasing the concentration of NH_4^+. In this project, higher extractable NH_4-N was observed two days after the fire in the burn plots at both restored and reference sites. The release of NH_4^+ from organic matter could also be further oxidized to NO_2^- and then NO_3^- (Hobbs and Schimel 1984, Blank and Zamudio 1998). Covington *et al.* (1991) found that NO_3^- was not immediately affected, but one year after burning, concentrations had become dramatically higher than the pre-fire level. In this study, however, both the restored

and reference sites saw an immediate increase in NO_x-N two days after the fire, and in the reference site, the increased NO_x-N lasted for one year.

The elevation of N availability may be the result of deposition of ash with high concentrations of nutrients. Grogan *et al.* (2000) investigated the effect of natural ash deposition on post-fire ecosystem N cycling by removing the surface ash layer from field plots within one week of a wildfire in a Californian Bishop pine (*Pinus muricata* D. Don) forest. They characterized the influence of ash on plant, soil, and microbial N pools during the first growing season after fire and found that ash deposition during wildfires can enhance soil N availability to plants and facilitate ecosystem N retention. A recent explanation for the increase of the available N in forest ecosystems was the influence of charcoal on soil N dynam-
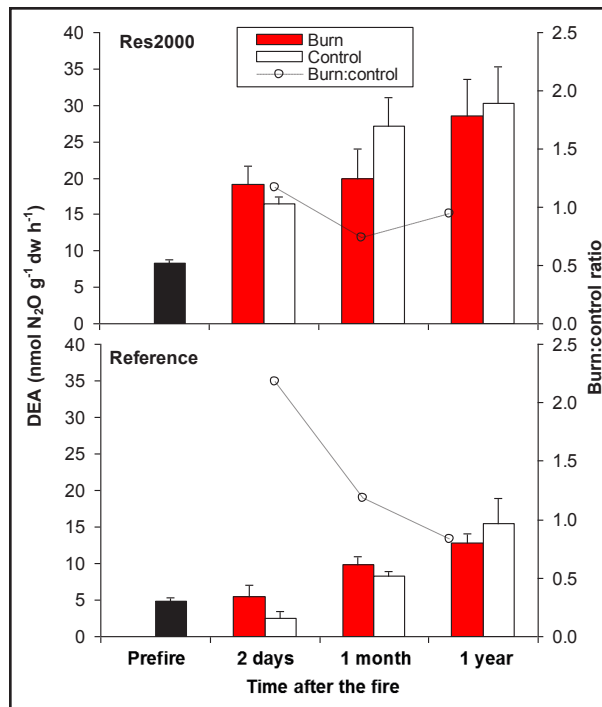
Figure 4. Changes of denitrification enzyme activities (DEA) in the burn plots and control plots in the restored wetlands (Res2000) and reference wetlands two days, one month, and one year after the fire. The black bar represents the value before fire.
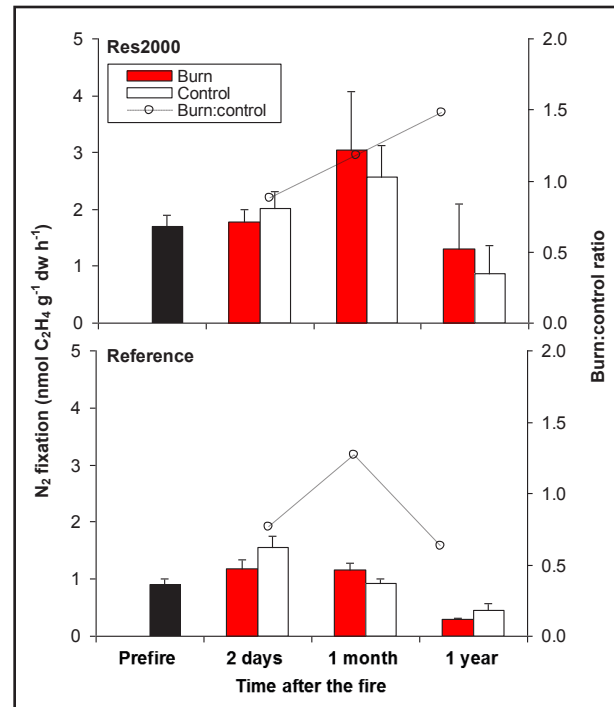
Figure 5. Changes of N_2 fixation rates in the burn plots and control plots in the restored wetlands (Res2000) and reference wetlands two days, one month, and one year after the fire. The black bar represents the value before fire.

ics and, in particular, nitrification (DeLuca *et al.* 2006). In their study, DeLuca and Sala (2006) found that charcoal significantly increased nitrification and the NO_3^- concentration in the soils. Despite these studies, there are few reports on wetland ecosystems. Qian *et al.* (2009) simulated fire in the Water Conservation Area (WCA)-2A in the Everglades through muffle furnace combustion but focused only on the effects of ash on phosphorus. Hogue and Inglett (2012) characterized fire residues (ashes) created by both muffle furnace and flame combustion, observing an increase of available N in char residues after the simulated fire.

In addition, burning can increase extractable P through combustion and heating of organic matter, and pH increases caused by ash also can cause the release of ortho-P bound by iron and aluminum (DeBano and Klopatek 1988). Hogue and Inglett (2012) showed that

charcoal formed after burning at low temperature in the HID marl prairie ecosystem contained more bicarbonate extractable P. For the low-P reference site, the addition of P through ash or charcoal could stimulate N mineralization and further increase N availability, similar to the results of White and Reddy (1999, 2000) and Inglett *et al.* (2007) in which P loading led to increased N mineralization in Everglades wetland soil.

Previous studies of the effects of fire on N mineralization in prairie and grasslands have resulted in conflicting results, with fire either causing a decrease (Ojima *et al.* 1994; Blair 1997; Turner *et al.* 1997, 2007), an increase (Aranibar *et al.* 2003, Boerner and Brinkman 2003), or having no effect on N mineralization (Raison 1979). The results depend on different ecosystems and fire behavior; accordingly, various mechanisms were proposed to explain the observations. For example, Bell and Bin-

kley (1989) pointed out that N mineralization from soil organic matter is enhanced after fire due to elevated soil temperature, while Vance and Henderson (1984) concluded that N mineralization decreased after a burn because of the poor substrate quality. Stock and Lewis (1986) also considered that these conflicting results may be attributed to the use of different methods to determine N mineralization. In this study, we measured potential soil N mineralization (PMN) using a 10-day anaerobic incubation method. We saw slightly increased PMN after the fire at the low-P reference site compared to the high-P restored site, although the responses were not significant (data not shown).

Effects of Fire on Extracellular Enzyme Activities

It is important to study the effects of fire on the activity of soil microorganisms and enzyme systems because these are responsible for mineralization processes and nutrient availability (Saa *et al.* 1993). Moreover, microbial biomass and enzyme activities are affected by management practices and can be used as sensitive indicators of ecological stability (Ajwa *et al.* 1999, Vazquez *et al.* 2003). The two N-related enzymes measured in this study, LAP and NAG, are inducible enzymes that are synthesized or activated when needed. LAP activities were significantly positively related with PMN (Figure 6), indicating that LAP activity can be used as a reliable index of N mineralization in soils. NAG activity, in this study, decreased one month after the fire in the restored and reference sites.

These results agreed with Boerner *et al.* (2008) who observed reductions in chitinase activity after fire in North American forest ecosystems. They considered these reductions to be the result of the deposition of more labile organic matter following fire. Other than nutrients, the response of N acquisition enzymes could depend on fire intensity or sever-

ity (Boerner *et al.* 2000). For example, during low-severity fires (as in grassland type systems like the HID), little heat is transferred downward, minimizing the direct effect of heat on microbial death and, thus, resulting in no significant short-term change in the enzyme activities.

Fire Effects on Denitrification

Few studies have focused on the influence of fire on denitrification. Our results showed that there was no significant difference in potential DEA rates between the burned and control plots, which was similar to the results of Castaldi and Aragosa (2002) in that DEA did not change significantly immediately after fire (i.e., seven days after the fire) in a Mediterranean shrubland. They considered that other factors, such as water content, would affect denitrification more than the fire. In this study, the slight increase of DEA two days after the fire could be caused by the increase of NO_3^- content, especially for the reference site in which a significantly positive correlation between NO_X-N and DEA was observed (Figure 6). No significant correlation existed between the NO_X^- and DEA in the restored sites (Figure 6), which may have been reflective of the higher N demand in the soils of these areas.

Fire Effects on Periphyton N_2 Fixation

It is anticipated that P inputs will have a stimulatory effect on N_2 fixation by periphyton (Inglett *et al.* 2004, Liao and Inglett 2012); however, we were only able to observe increased fixation rates in the restored site after one year (Figure 5). This result was similar to that of Zackrisson *et al.* (2004) that showed, in northern boreal forests in Sweden, the N_2 fixation rates increased linearly with time since fire. They attributed the increase to the degree of colonization by cyanobacteria and site factors such as presence of available N. In this study, it is likely that ash deposition from the
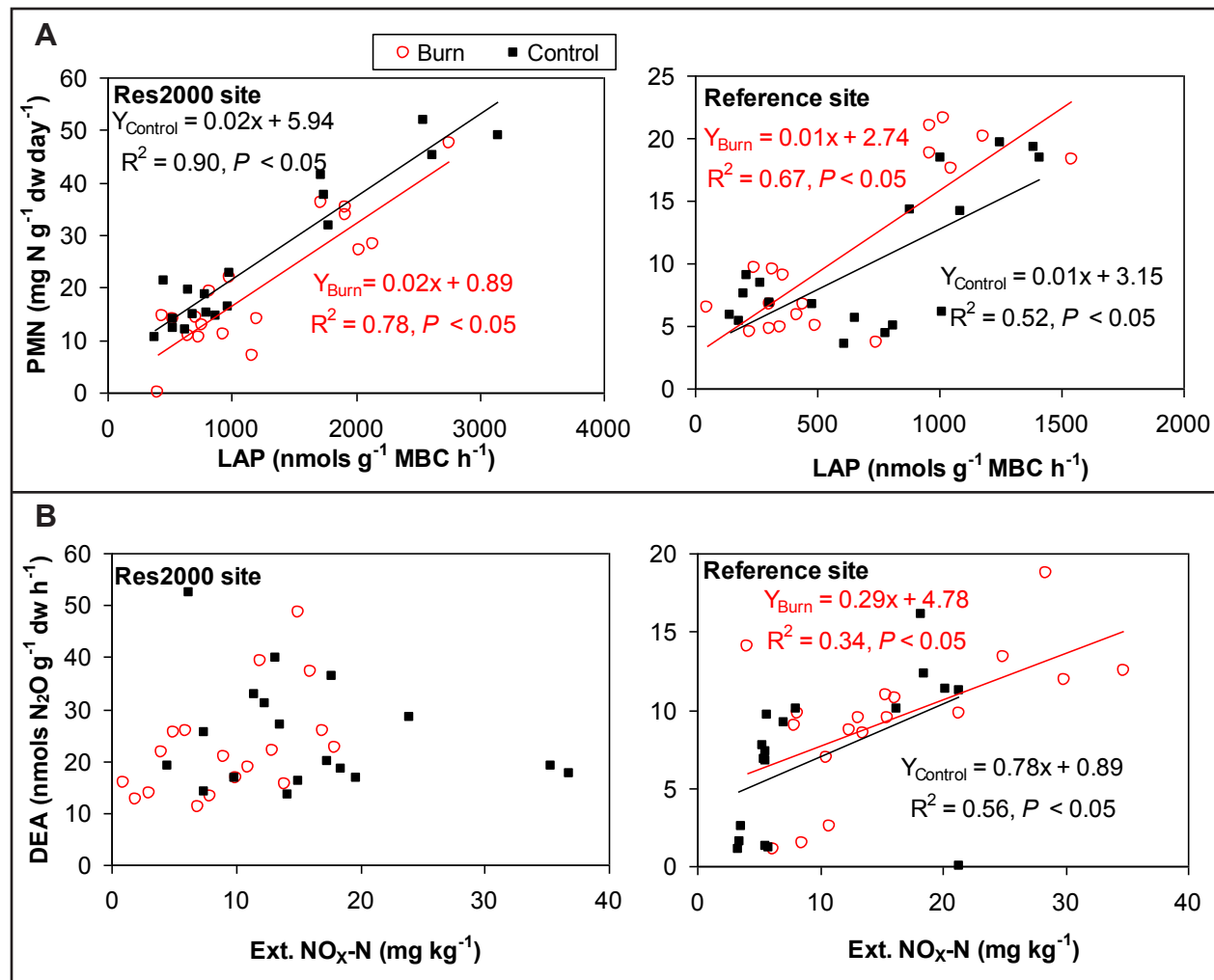
Figure 6. (A) Correlation between nitrogen mineralization (measured as potentially mineralizable nitrogen, PMN) and Leucine aminopeptidase (LAP), and (B) correlation between extractable nitrite/nitrate (Ext. NOX-N) and denitrification (measured as potentially denitrification rates DEA) two days, one month, and one year after the fire in the restored (Res2000) and reference wetlands.

fire elevated P levels in the restored site (Hogue and Inglett 2012). This pulse of new P may have enhanced the N limitation already present in these sites, thus resulting in stimulated periphyton N_2 fixation.

In contrast, at the reference site, the nitrogenase activities only slightly increase one month after the fire and reduced below their control levels one year after the fire. DeLuca *et al.* (2002) pointed out that since fire increased the availability of N and reduces the presence of *P leurozium schreberi* and associated N-fixing symbionts, it is likely that the N_2 fixation rates by *P. schreberi* would decrease

following the fire. Another study related to nitrogenase response to the fire was done in mountain shrub and grassland communities during two years following fire (Hobbs and Schimel 1984). They found that nitrogenase activity was depressed by fire one year after the burn in the mountain shrub community, and they considered that the elevation of the soil inorganic N levels in burn plots may contribute to the depression in nitrogenase activity. This explanation is plausible in the reference site in which we did see increases of extractable NO_X^- one year after the fire.

Implications for Restoration Management

In this study, we found that fire exerted different influences on the N cycle in sites of different P status. In P-limited ecosystems like the reference site in this study, a small amount of P addition through ash can stimulate N mineralization and nitrification, while for the restored site with high P, the P deposition from ash does not greatly affect the N cycle. Another fire residue, charcoal, has also been reported to elevate the nitrification and N availability (DeLuca *et al.* 2002, 2006). Since fire intensity decides the proportion of charcoal and ash (Qian *et al.* 2009, Hogue and Inglett 2012), it would be helpful for land managers to know which form contributes more to the increase of N availability when deciding on a high- or low-intensity fire plan.

Fire volatilizes N but can simultaneously increase the short-term availability of residual soil N (Vitousek and Howarth 1991). The increase of inorganic N is likely a significant influence on the regrowth of native plant species, the invasion of exotic plant species, and ultimately, the site recovery potential (Dalrymple *et al.* 2003, Rau *et al.* 2007). For the HID res-

toration, the young restored sites are more N-limited, while the native reference site is limited more by P. The long-term goal for the restoration is to shift from N limitation in the recently restored sites to a more P-limited condition similar to the reference site (Inglett and Inglett 2013). Frequent fire causes addition of P and losses of N in excess of replacement by N_2 fixation, and is probably a significant cause of N limitation in terrestrial ecosystems (Vitousek 1982). Therefore, it is important to decide whether a high- or low-frequency burning cycle should be applied in the restored site to speed up the restoration process.

Overall, this type of research is important to help identify the impacts of fire on the N cycle as it relates to the availability of P. Future research should focus on the relationships between fire intensity and severity, abundance and form of fire residues, as well as the long-term effect of particular fire regimes (low or high frequency). This information is crucial to better understand the function of fire in the natural ecosystem and the balance between N and P leading to the reestablishment of native wetlands with low nutrients, such as the Everglades.

ACKNOWLEDGMENTS

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