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ARTICLE

Freshwater Ecology

Fire intensity and ecosystem oligotrophic status drive relative phosphorus release and retention in freshwater marshes

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Abstract

Ecosystems have been shaped by fire for millions of years. Many oligotrophic ecosystems rely on fire for biogeochemical cycling and maintenance of key processes. However, it is uncertain how fire intensity interacts with nutrient limitation to drive differential responses in postfire biogeochemical cycling and ecosystem recovery. In this study, we compare pre- and postfire carbon and nutrient pools in two adjacent wetlands characterized by either lower or higher phosphorus (P) inputs and thus different levels of P limitation. Carbon (C), nitrogen (N), and P pools and litter and root decomposition rates were measured starting 1 year prefire until 1 year postfire in lower-P (LP) and higher-P (HP) freshwater marshes of the Florida Everglades. Dominant vegetation biomass and vegetation composition were monitored as well. Fire energy release was measured to link the causal mechanism, heat transfer, to nutrient fluxes. We observed temporary increases in surface water, periphyton, and leaf tissue P concentrations in both wetland types following fire. Soil P increased and soil C:P and N:P ratios decreased postfire in the LP wetland but did not change in the HP wetland. Prefire soil P was greater in the HP than the LP wetland, but did not differ 1 month or 1 year postfire. Vegetation structure and composition were marginally affected by fire. Fire intensity was highly variable within both wetlands. Increasing fire intensity correlated with increasing accumulation of soil organic matter in the LP wetland, and with increases in decomposition rates in both wetland types, between pre- and postfire. Litter and root decomposition rapidly increased with increasing fire intensity, but seemed to stabilize after a certain fire intensity threshold was reached. Our results indicate that fire can temporarily ease P limitation in oligotrophic wetlands, by affecting soil nutrient stoichiometry and organic matter processing, while maintaining vegetation community composition. Further, we identified fire dosing, expressed as the fire radiative energy release, to be an effective control of postfire biogeochemical cycling. Hence, nutrient management should be incorporated into burn prioritization tools and, when applying prescribed fires, natural resource managers should also consider how fire attributes, such as fire intensity, impact nutrient cycling and other soil processes.

KEYWORDS
decomposition, Everglades marl, fire energy release, oligotrophic wetlands, organic matter, soil stoichiometry

INTRODUCTION

For millions of years, fire has been driving the evolution of many fire-prone ecosystems (Bond & Keeley, 2005). Interactions of fire with soil and vegetation systems are characterized by strong feedbacks. Soil and vegetation serve as fuels and fuel substrate, enabling fire to ignite and spread. Fire in turn shapes soil formation processes (Santín & Doerr, 2016) and influences the composition and structure of vegetation communities (Gordijn & O'Connor, 2021; Higgins et al., 2007; Watts et al., 2012). For these reasons, fire management can have profound ecological impacts on fire-prone ecosystems (Hiers et al., 2021). Hence, mechanistic studies are necessary to reveal how fire characteristics interact with environmental variables (hydrology and nutrient availability) in maintaining ecosystems and in driving postfire ecosystem recovery (Butler et al., 2018; Kominoski et al., 2022; O'Brien et al., 2018).

Fire transforms fuels (i.e., biomass, necromass, and soil organic matter) into ashes, which, based on the combustibility of the vegetation and the attributes of the fire (González-Pérez et al., 2004; Hatten & Zabowski, 2009; Qian et al., 2009), can exhibit a range of chemical and physical properties, causing distinct effects on ecosystem biogeochemical cycling, including increasing soil pH and nutrient pools, or changing physical properties such as soil texture and water repellency (Bodí et al., 2014). Fire can be a determinant factor for carbon (C), nitrogen (N), and phosphorus (P) cycles in fire-prone ecosystems (Boerner, 1982; Butler et al., 2018; Knicker, 2007; Wan et al., 2001). Often, as a result of vegetation burning, a reduction in ecosystem C and N is observed because of the volatilization of these elements at relatively low temperatures (Bodí et al., 2014; Boerner, 1982; Wan et al., 2001), while an increase in soil and litter P and a decrease in C:P and N:P ratios are observed at the same time (Butler et al., 2018). Thus, fire has been indicated as an important recurring disturbance that can ease P limitation of oligotrophic ecosystems (Boerner, 1982; Butler et al., 2018).

Fire attributes are also critical in determining the fate of C and nutrients subsequent to the event. In particular, fire intensity affects the loss of organic matter, loss of nutrients, and the chemical properties of the ashes produced (Bodí et al., 2014; Hatten & Zabowski, 2009; Qian et al., 2009). Laboratory burning of Everglades (Florida, USA) plant species revealed that the amounts of available P in ashes are related to fire intensity and that sawgrass (*Cladium jamaicense* Crantz), the most ubiquitous and representative plant species of the Everglades wetlands, has significant potential to release available P when burned (Qian et al., 2009). Although fires in dry ecosystems directly impact the soil, often causing losses of organic matter and inhibition of soil microorganism activity (Hatten & Zabowski, 2009; Pressler et al., 2019; Turetsky et al., 2015), wetland fires often occur with water above the soil surface, especially during prescribed fires (e.g., Miao et al., 2010). As a result, wetland fires likely trigger a priming effect in the soil due to enhanced root productivity, stimulated by plants' death and N volatilization (Johnson & Matchett, 2001), and the addition of organic material and mineralized nutrients to the soil (Cleveland et al., 2002; Kuzyakov et al., 2000).

Fire is an essential component of Everglades wetlands, where it has shaped vegetation patterns and topography for millennia (Noss, 2018). In Everglades National Park (ENP), prescribed fire and fire suppression have historically been applied for the preservation of fire-adapted vegetation communities, to control the expansion of invasive species, and to minimize the risks of severe wildfires that burn peat soils during extreme drought (Nocentini, Kominoski, Sah, Redwine, et al., 2021; Smith et al., 2001; Turetsky et al., 2015). More recently, prescribed fire is also being considered as a tool to manage nutrient cycling (Nocentini, Kominoski, & Sah, 2021; Nocentini, Kominoski, Sah, Redwine, et al., 2021). The Everglades was a vast P-limited oligotrophic ecosystem that has been reduced in area by 50% in the last century (Davis & Ogden, 1994). Agriculture and urbanization are the primary drivers of Everglades degradation, resulting in a landscape characterized by a mosaic of conditions, spanning from oligotrophic to highly P-enriched, also based on hydrology, soil type, and vegetation (Noe & Childers, 2007). Given this condition, drivers of biogeochemical cycling, such as fire, are likely to produce distinct effects in wetlands characterized by different degrees of degradation, with concentrations of soil C and nutrients as key factors controlling response to fire (Nocentini, Kominoski, & Sah, 2021).

In this study, we conducted a field experiment designed to assess the effects of a prescribed fire on biogeochemical cycling in wetland ecosystems. Fire was applied with varying intensity in two adjacent wetlands characterized by similar soil type and hydrology, but which differed in their level of P limitation. Specifically, our goals were to: (1) quantify changes in organic matter content of soil, in the C, N, and P concentrations of soil, live organisms (plant and algae), and surface water, and in litter and root decomposition rates between pre- and postfire; (2) understand if fire effects on biogeochemistry were transient or lasted until 1 year postfire; (3) quantify differences in fire effects between lower-P (LP) and higher-P (HP) wetlands; (4) relate any of the changes measured between pre- and postfire with fire intensity; and (5) characterize potential shifts in wetland vegetation structure or composition postfire. We predicted similar short-term increases in P concentrations in the surface water and live organism tissues in both the LP and the HP wetland. We predicted larger increases in P concentration and larger decreases in C:P and N:P ratio in soils in the LP wetland compared with the HP wetland following fire (Boerner, 1982; Nocentini, Kominoski, & Sah, 2021). We also hypothesized that the predicted changes in soil chemistry would last until 1 year postfire only in the LP wetland, compared with transient changes in the HP wetland. We predicted an increase in soil organic matter content following fire due to the turnover of dead plants' roots and to increased root productivity (Johnson & Matchett, 2001), and an increase in litter and root decomposition rates due to the pulse on nutrient-rich ashes (Cleveland et al., 2002). Finally, within the limits imposed on fire by the presence of water above the soil surface, we predicted that increasing fire intensity would return to the soil increasing amounts of nutrient-rich, particularly P-rich, ashes (Bodí et al., 2014; Qian et al., 2009), which would trigger increasing decomposition rates (Cleveland et al., 2002). Although fire effects on nutrient cycling have been extensively studied (Boerner, 1982; Butler et al., 2018; Wan et al., 2001), this is a unique study that aims to test the ability of fire to ease P limitation of oligotrophic wetlands. Our recent work (Nocentini, Kominoski, & Sah, 2021) found differential effects of fire and wetland hydroperiod on soil chemistry at the regional scale, whereby in short-hydroperiod wetlands soil P concentration was higher with time since last fire corresponding to 2–15 years, and soil C and N concentrations were highest in long-hydroperiod wetlands irrespective of fire history. Here, we focused on the mechanisms of postfire wetland nutrient cycling at the ecosystem scale. Importantly, we related nutrient cycling and organic matter processing to fire intensity, an attribute that can be challenging to measure, but appears to be a critical determinant of the ecological effects of fire management. Relating fire energy release to biogeochemical cycling has been suggested as a path forward for improving our mechanistic approach to quantify biophysical fire effects (O'Brien et al., 2018). Previous studies have explored this relationship in laboratory settings (Hatten & Zabowski, 2009; Qian et al., 2009; Smith et al., 2016), have related field-measured fire energy release to fire severity, expressed as fuel consumption (Kremens et al., 2012), or have related a postfire assessment of fire severity to biogeochemical cycling (Boulanger et al., 2011; Brown et al., 2014). Here, we address a knowledge gap using a novel approach to relate field-measured fire energy release to nutrient cycling and organic matter processing in freshwater marsh ecosystems.

METHODS

Study site and experimental design

Our experiment was conducted in oligotrophic sawgrass-dominated wetlands along the eastern boundary of ENP, in South Florida (Homestead, 25°24′ N, 80°33′ W). Wetlands in this region are characterized by marl soils, which are shallow (often less than 10 cm; Osborne et al., 2011) and C-poor compared with the peat soils that characterize longer hydroperiod areas of the Everglades. The differentiation between peat and marl soils is correlated with localized changes in elevation that led to the development of a landscape of sloughs and ridges with species composition and carbon accumulation processes defined by either longer or shorter annual hydroperiods. Marl soils are the driest within ENP and remain inundated for 10%–60% of the year, while peat soils areas are inundated 60%–100% of each year (Osborne et al., 2011).

We selected two sites separated by 4.8 km along Aerojet Canal for the study based on their P availability. One site was located halfway along the canal while the second one at the end of the canal, and both were located on the canal's western side (Figure 1). The entire study area is an oligotrophic wetland containing individual marshes displaying a wide range of P limitation. Even though both sites still fell on the oligotrophic side of the full spectrum of trophic levels, while the first site was characterized by severe P limitation, typical of the historic Everglades, the second site was receiving more P inputs, which made it moderately P-enriched. The two study sites were then designated as LP and HP, respectively. The HP site received more

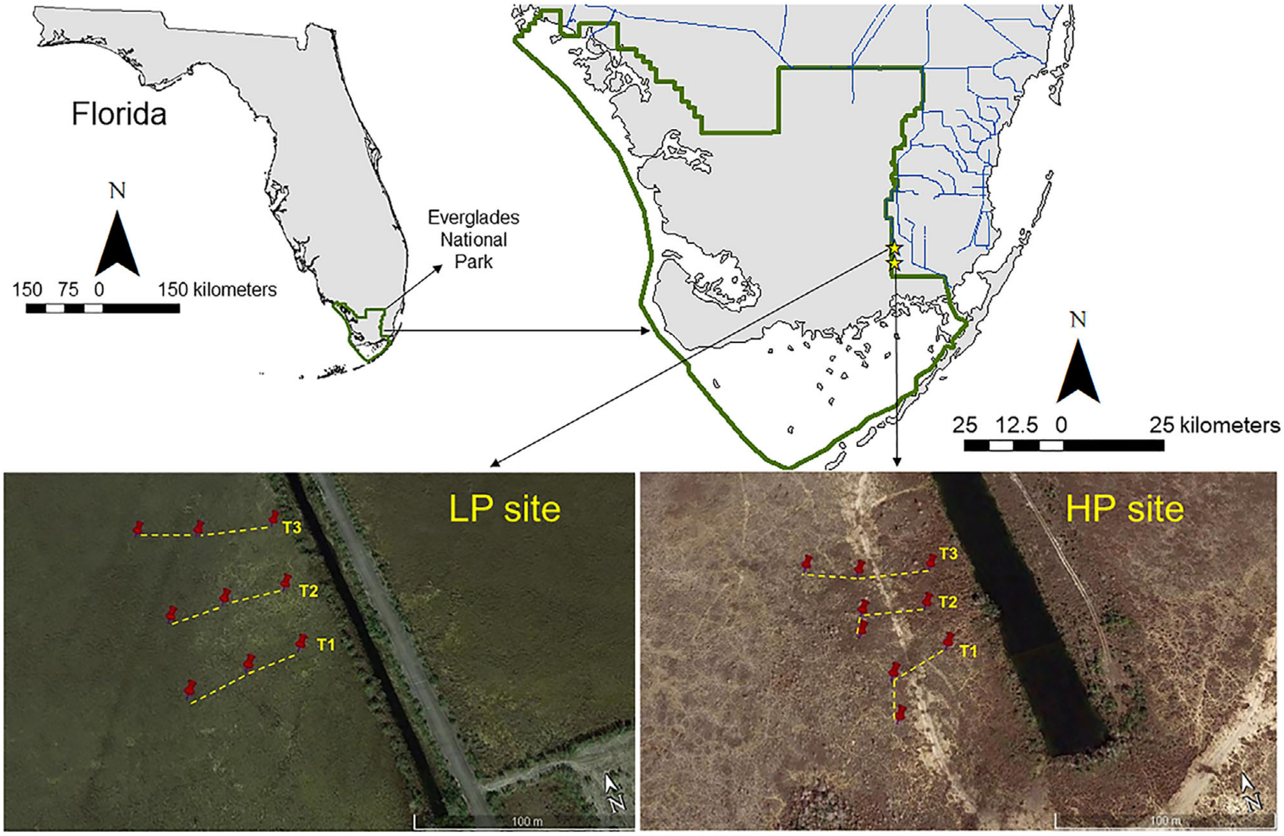

FIGURE 1 Position of the lower-P (LP) and higher-P (HP) sites used for the experiment relative to Everglades National Park boundaries in South Florida, and the three transects (T1, T2, and T3) set up at each site.

P contributions (i.e., anthropogenic P) from upstream areas, which were transported to the site by the waters of the canal. This difference in P availability was evident by looking at the difference in vegetation composition between the two sites: while LP was completely dominated by sawgrass (*C. jamaicense* Crantz), HP was also characterized, especially in close proximity of the canal, by other species such as spikerush (*Eleocharis cellulosa* Torr.), lanceleaf arrowhead (*Sagittaria lancifolia* L.), and pond apple (*Annona glabra* L.). Both of our experimental sites were also characterized by the presence of periphyton, an association of algae, bacteria, fungi and microfauna, that forms thick mats that cover limestone sediments, coat the submerged stems of macrophytes, or form rafts floating in the water, which is also an important and ubiquitous base of the Everglades wetland food web (Trexler et al., 2015).

At both sites, we established three transects, each composed of three sampling plots (2 sites × 3 transects × 3 plots = 18 total plots); the area of each plot was 9 m^2 (3 × 3 m). The transects were oriented perpendicular to the canal and were set at a distance of about 50 m from each other, while the sampling plots within each transect were about 30 m from each other (Figure 1). Transects were designed at both experimental sites in order to account for spatial variability in longitudinal (plots closer to or further from the Aerojet Canal) and latitudinal directions. We selected two separate wetlands, the LP and HP one, to ensure that all plots were on the footprint of the prescribed fire and that plots within the same treatment (i.e., oligotrophic status) were not differing in other important soil and ecosystem characteristics. Although the conditions of our field experiment did not allow for a completely randomized experimental design and our spatial replication violates assumptions of inferential statistics (Hurlbert, 1984), the ecosystem scale of our experiment was essential for understanding ecosystem-level responses to differences in oligotrophic status and fire intensity. In addition, plots within each of the two wetlands that were separated by at least 30 m were characterized by highly variable fuel loads, which resulted in correspondingly variable fire intensities, hence reducing the risk of spatial autocorrelation (Bataineh et al., 2006).

The prescribed fire

The experimental plots were included in a large operational prescribed fire conducted on 18 February 2020 and managed by the ENP Fire Cache Crew in collaboration with the South Florida Water Management District (SFWMD) Land Management Team. Prescribed fire is used extensively throughout the park for a variety of objectives. This fire was intended to treat 245 km^2 of an Everglades wetlands mosaic, with several goals, including hazardous fuels reduction, maintaining habitat diversity, reducing fuels around fire-sensitive vegetation types, reducing the cover of invasive *Schinus terebinthefolius*, and stimulating nutrient recycling. Fire weather during the burn period was typical of conditions that would produce low to moderate fire behavior with a maximum temperature of 28°C, minimum humidity of ~70%, and winds out of the east ranging from 11 and 19 km h^{-1}. While the majority of the burn unit was ignited from a helicopter with supplemental airboat and hand ignitions in the experimental plots, relatively low fuel amounts were available for burning due to the presence of standing water. This resulted in a very patchy burn, characterized by a mosaic dominated by unburned vegetation, consistent with the objectives of the prescription (Figure 2). The experimental plots were ignited by hand, though again, the patchy available fuels and standing water resulted in a high variability in vegetation consumption within and around the plots.

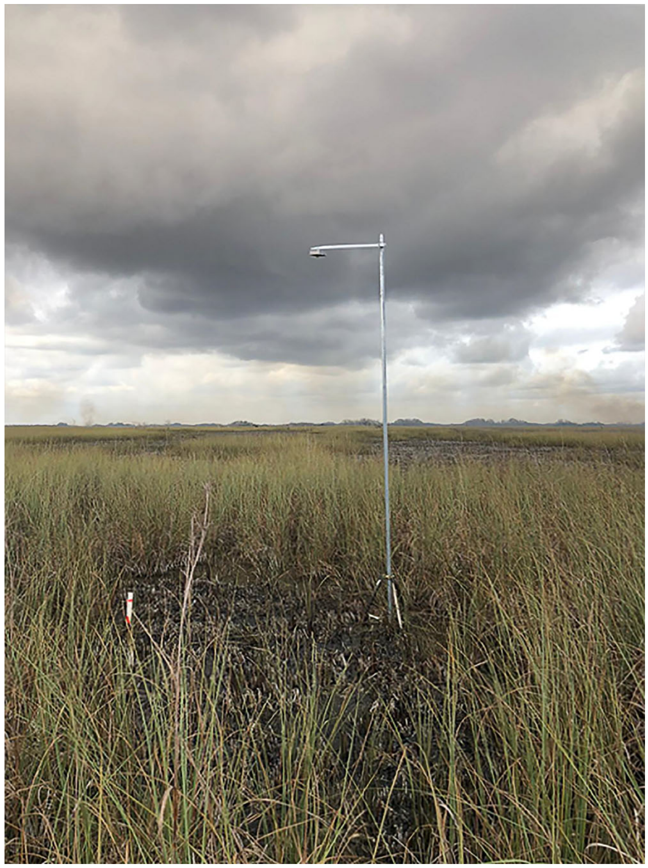

FIGURE 2 One of the infrared radiometers, set up on top of a tripod, at one of the experimental plots of the lower-P site, pictured after the prescribed fire carried out on 18 February 2020 in the eastern marl wetlands of the Everglades (Florida, USA). Infrared radiometers were used to measure fire radiative power and energy, which we used to express fire intensity. In this picture, the patchiness, which characterized the entire fire, is clearly visible. Photo credit: Andrea Nocentini.

Plant composition, biomass, and chemistry

Between September 2018 and March 2021, every three months, we visually assessed sawgrass and other plant species areal cover (%) in each plot. Within a 1 × 1 m subplot, we also counted the number of live and dead plants of each species, and the height and diameter of $n = 15$ random sawgrass culms in order to estimate aboveground biomass using previously derived allometric relationships between culm height, diameter, and biomass (Childers et al., 2006).

From each plot, two sawgrass plants (including roots) were collected twice before fire (December 2018 and December 2019) and twice after fire (May 2020 and March 2021); all samples were stored at 4°C until processing. Leaves and fine (≤2 mm diameter) roots were oven-dried at 40°C for 72 h. Dried subsamples were ground using an 8000D ball mill (SPEX SamplePrep, New Jersey, USA) and analyzed for C, N, and P concentrations. Estimating C and N concentrations in collected samples involved the use of a CE Flash 1112 elemental analyzer (CE Elantech, New Jersey, USA), following standard procedures. Phosphorus concentrations were determined from a dry-oxidation acid hydrolysis extraction followed by a colorimetric analysis of phosphate using a UV-2450 spectrophotometer (Shimadzu, Kyoto, Japan).

Sawgrass was selected for the collection of aboveground biomass and leaf and root chemistry because it was the only or the dominant vegetation at most plots and was only scarcer at a few plots closest to the Aerojet Canal at the HP site. Sawgrass is the dominant wetland macrophyte across the Everglades and is estimated to be present in 70% of Everglades wetlands (Scheidt et al., 2021).

Surface water physicochemistry

Between September 2018 and March 2021, every three months, three measures of local surface water depth were taken at each plot, as the distance between the soil surface and the surface of the aboveground water layer (e.g., in case of no aboveground water, the recorded water depth would be 0 cm). A YSI Pro1030 multiparameter probe (Yellow Springs, Ohio, USA) was employed to measure the surface water pH as well. From each plot, two (filtered and unfiltered) surface water samples were collected twice before fire (December 2018 and December 2019) and twice after fire (February 2020 and March 2021). All samples were collected into high-density polyethylene bottles, and one sample at each plot was filtered through a 0.45-μm nylon membrane filter (Whatman, Inc.). Unfiltered samples were stored at 4°C until analysis, and filtered samples were frozen. The unfiltered samples were analyzed for total organic C (TOC), and total N (TN) and total P (TP), while filtered samples were analyzed for dissolved organic C (DOC), dissolved inorganic N (DIN), and soluble reactive phosphorus (SRP), the latter constituting a measure of orthophosphate (PO_4^{3-}), directly available to organisms such as algae and plants. Total organic C/DOC was determined by introducing the sample into a combustion tube and oxidizing it to form CO_2, which was detected by a nondispersive infrared (NDIR) detector, part of a Shimadzu TOC-V Analyzer (Kyoto, Japan). TN was determined through conversion to nitric oxide, reaction with ozone, and detection of the chemiluminescent emission by a photomultiplier tube. TP was determined by oxidizing and hydrolyzing all of the phosphorus-containing compounds to SRP. Analysis for inorganic filtered nutrients, ammonia/ammonium as N (NH_3/NH_4-N), nitrite as N (NO_2-N), nitrate and nitrite as N (N + N), and SRP as P, was simultaneously performed by wet chemical analysis using a four-channel rapid flow analyzer based on standard Environmental Protection Agency procedures.

Periphyton chemistry

From each plot, one periphyton sample was collected twice before fire (December 2018 and December 2019) and twice after fire (March 2020 and March 2021). Periphyton was grabbed floating from the water surface or, when the system was dry (March 2020), from the soil surface. Samples were frozen until analysis. Periphyton, after being cleaned from dead plant material and rocks, was oven-dried at 40°C for several days until moisture completely evaporated. Samples were then ground and analyzed for TC, TN, and TP concentrations.

Soil bulk density, organic matter, and chemistry

From each plot, two soil cores (54 mm diameter) down to 20 cm soil depth were collected one time before fire (December 2018) and twice after fire (March 2020 and March 2021); all samples were stored at 4°C until analysis. At the time of sampling, the exact depth of each soil core was recorded (since in several occasions the soil was shallower than 20 cm) in order to derive the volume needed for bulk density calculation. Upon return to the laboratory, the fresh mass of the soil sample and of subsamples, collected after homogenization of the soil core, was obtained, then subsamples were oven-dried at 40°C for 120 h before dry mass measurement. Soil bulk density was calculated as the ratio between the dry mass of the sample and its volume, and it was used to convert soil C and nutrient concentrations to amounts per unit of soil volume. Dried soil subsamples were then ground and analyzed for TC, TN, and TP concentrations. Ash-free dry mass for the calculation of soil organic matter content was measured by combusting dried and ground subsamples at 500°C in a muffle furnace for 4 h, and then by subtracting the ashed mass to the total mass of subsamples; soil organic matter content was expressed as percentage of the total soil mass.

Litter and root decomposition

Air-dried sawgrass root and leaf material collected at the LP and HP sites were used to study the decomposition rates in the soil. The material, divided into litter (leaf), coarse roots (>2 mm diameter), and fine roots (≤2 mm diameter), was placed into 1 mm-mesh nylon bags; each bag contained ~3 g (leaf litter), ~5 g (coarse roots), or ~1 g (fine roots) of dry mass. Before deployment, subsamples were placed in the oven at 60°C for 72 h to estimate residual moisture content. Within each experimental plot, one fine root and one coarse root decomposition bag was placed in the soil, at a 20 cm soil depth. Similarly, within each experimental plot, one leaf litter bag was placed on the soil surface, homogenized with the rest of the litter. Each bag was tied with a fishing line to a marker stick and to a weight that prevented it from floating. All decomposition bags were incubated in the soil for 1 year before the burn treatment (January 2019 to December 2020), then new bags, filled with recently collected litter and root material, were placed after the burn for another year (March 2020 to March 2021). After each 1-year period of incubation, litter bags were retrieved from the soil, leaf and root litter were rinsed over a sieve, oven-dried at 60°C for 72 h, and weighed. The difference in mass between deployment date and retrieval date allowed us to calculate decomposition rates. Decomposition rates, expressed as k, were estimated using a linear regression of the ln-transformed fraction of dry mass remaining versus time (Benfield, 2006). The model is given by the following equation:

$$M_t = M_0 \times e^{-kt} \tag{1}$$

where M_0 is the initial mass, M_t is the mass on a given sampling day, and t is the time of incubation in days.

The k coefficient is a standard measure of decomposition rates, which allows comparison of results among distinct studies; higher values of k indicate faster decomposition rates.

Fire behavior measurements

The day before experimental burns, metal poles (3 m height) supported by tripods were placed at the edge of six plots along two transects of both LP and HP sites. A crossbar, equipped with an infrared radiometer and a HOBO datalogger (Onset Computer Corporation, Massachusetts, USA), was mounted on top of the poles to align the radiometer field of view with the plot center. Dataloggers were launched about 1 h before the burn and set up with a data acquisition resolution of 1 Hz. The radiometers had a 50° field of view, which covered a 6.15 m^2 circular area and measured fire radiative flux density in the experimental plots (Kremens et al., 2012; O'Brien et al., 2016). Only one instrument failed to deploy, so we were able to successfully collect fire radiative energy in five plots of the six plots at the LP site and in all the plots at the HP site. Fire intensity was expressed as fire radiative energy density (in megajoules per square meter), the time integral of the fire radiative flux density (in watts per square meter) in the plot; the former is an effective measure of the total amount of organic matter consumed (Keeley, 2009).

Data analysis

For all statistical analyses, we used R version 3.6.0 (R Core Team, 2021).

We performed a two-way ANOVA, testing for differences in the concentrations of C, N, and P in the different ecosystem compartments (i.e., surface water, sawgrass leaf and root tissues, periphyton, and soil), as effected by two factors: fire (i.e., time: pre- and postfire) and wetland oligotrophic status (i.e., site: LP and HP). Two-way ANOVA was chosen as variance was homogeneous among sampling dates and between sites (Levene test $p > 0.05$). The two-way ANOVA was followed by Tukey post hoc test for pair-wise comparisons.

We also tested for Pearson's correlations between fire intensity and the changes measured in the concentrations of C, N, and P in the different ecosystem compartments between the last prefire sampling (December 2019) and the first postfire sampling (February and March 2020).

All data collected during this study were made publicly available and accessible through publication on the Environmental Data Initiative repository (Nocentini & Kominoski, 2021).

RESULTS

Fire behavior

All the $n = 18$ experimental plots burned to some degree during the prescribed fire. Measured fire intensity, expressed as the integral of the radiative energy released by the fire, varied between 1.02 and 0.003 MJ m^{-2}, and was 0.34 ± 0.32 and 0.32 ± 0.38 MJ m^{-2} at the LP and HP sites, respectively (Figure 3).

Surface water depth and fire effects on sawgrass biomass and vegetation composition

Peak surface water depth was lower at the end of wet season (South Florida wet season extends from 1 May to 31 October) 2019 than at the end of wet seasons 2018 or 2020 at both sites (Figure 4a). The prescribed fire was carried out with relatively low surface water depth (14 ± 1 and 15 ± 1 cm at the LP and HP sites, respectively) in February 2020.

Sawgrass biomass peaked at both sites in December 2018, reaching 330 ± 40 and 213 ± 46 g m^{-2} of dry biomass at the LP and HP sites, respectively (Figure 4b). Sawgrass biomass was instead lower in the following season (261 ± 37 and 145 ± 26 g m^{-2} of dry biomass at the LP and HP sites, respectively, in December 2019). One year after the fire, sawgrass biomass reached prefire levels at the LP site, whereas it was still lower than prefire levels at the HP site (248 ± 42 and 88 ± 20 g m^{-2} of dry biomass, respectively, in December 2020).

Vegetation composition remained stable throughout the course of the experiment at both sites. The LP site was characterized by pure sawgrass stands, and no other species was observed in the plots before or after fire. By contrast, we observed spikerush and lanceleaf arrowhead in addition to sawgrass at the HP site, which were mostly present in the plots closer to the canal. While prefire spikerush and lanceleaf arrowhead represented 30% and 5% of plant relative abundance at the HP site, during postfire they represented 33% and 11%, respectively, due to a reduction in sawgrass cover.

Fire effects on surface water chemistry

Surface water TOC and TN varied in time (Table 1), but their variation did not seem related to any fire effect. All measured prefire surface water TP concentrations were lower than the concentration measured 1 year postfire at

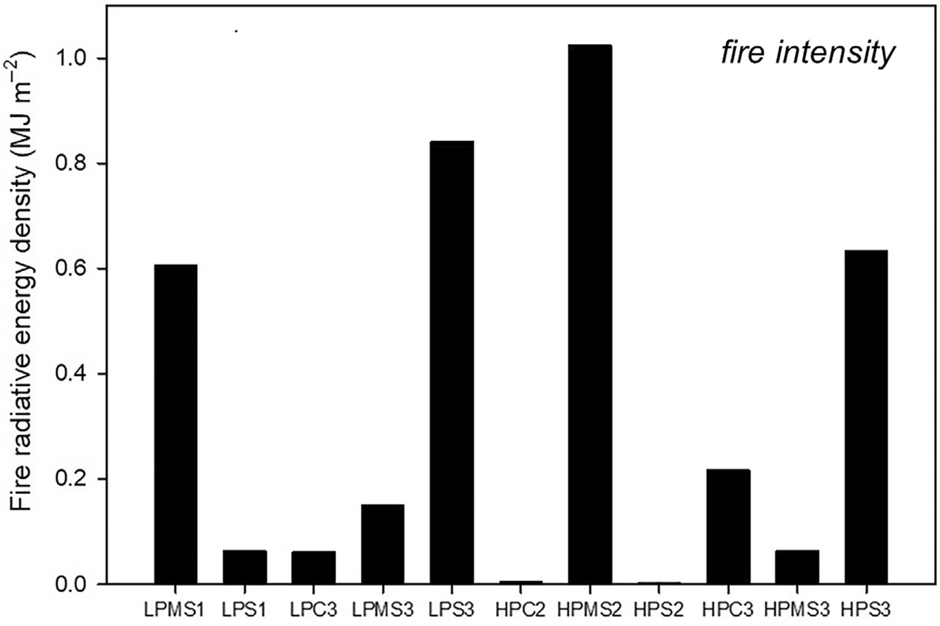

FIGURE 3 Fire intensity, here expressed as fire radiative energy density (in megajoules per square meter), for each of the 11 plots where radiometer data were collected on 18 February 2020, during the prescribed fire carried out in the eastern marl wetlands of the Everglades (Florida, USA). The first two letters in the plot name identify the site (lower P [LP] or higher P [HP]), while the number identifies the transect number (1–3).

the HP site (Table 1). The reason for this difference seems to be the periodical P loading from the canal rather than a fire effect. We observed an increase in surface water DOC and DIN at the LP site between the samples collected a few weeks prefire and those collected 3 days postfire (Figure 5a,b), and we also observed the presence of SRP in the surface water at both sites 3 days postfire (Figure 5c), which had not been detected a few weeks prefire. Surface water pH marginally increased at the HP site postfire (Appendix S1: Figure S1).

Fire effects on organismal chemistry

Sawgrass leaf N concentration was higher 3 months postfire than prefire at the HP site, whereas it did not change at the LP site (Table 2). Sawgrass leaf P concentration increased 3 months postfire compared with prefire at both sites, but returned to prefire concentration 6 months postfire and did not change afterwards (Table 2; Appendix S1: Figure S2A).

Sawgrass fine root C concentration did not change throughout the course of the experiment at both sites, while sawgrass fine root N concentration was lower 3 months postfire than prefire or 1 year postfire at both sites, and sawgrass fine root P concentration was higher 3 months postfire than prefire or 1 year postfire at the LP site (Table 3; Appendix S1: Figure S2B).

Periphyton mats C, N, or P concentrations were higher 1 month postfire at the HP site than prefire, 1 year postfire, or at the LP site (Table 4; Appendix S1: Figure S3).

Fire effects on soil organic matter and chemistry

Soil C amounts were not different between sites or between sampling dates throughout the course of the experiment (Figure 6a). Soil N and P amounts were higher 1 month and 1 year postfire than prefire at the LP site, whereas they did not change throughout the course of the experiment at the HP site (Figure 6b,c). Although soil C amounts did not differ between the two sites prefire, soil N and P amounts were higher at the HP than at the LP site prefire. However, 1 month and 1 year postfire, soil N and P amounts were similar at the two sites. Soil C:N ratio decreased 1 month postfire at both sites, but returned to prefire values 1 year postfire (Figure 7a). Soil C:P and N:P ratios decreased 1 month postfire and remained lower 1 year postfire than prefire values at the LP site, while they did not change at the HP site throughout the course of the experiment (Figure 7b,c). Although soil C:P and N:P ratios were higher at the LP than at the HP site prefire, they did not differ anymore between the two sites 1 month and 1 year postfire. The effect of fire on the differences in soil stoichiometry between the two sites was underlined by a significant interaction of fire with wetland oligotrophic status in the two-way ANOVA model (Figure 7b,c). Soil organic matter content was lower at the LP than at the HP site prefire, but did not differ anymore between the two sites 1 month and 1 year postfire, due to a higher increase at the LP site relative to the HP site (Figure 8).

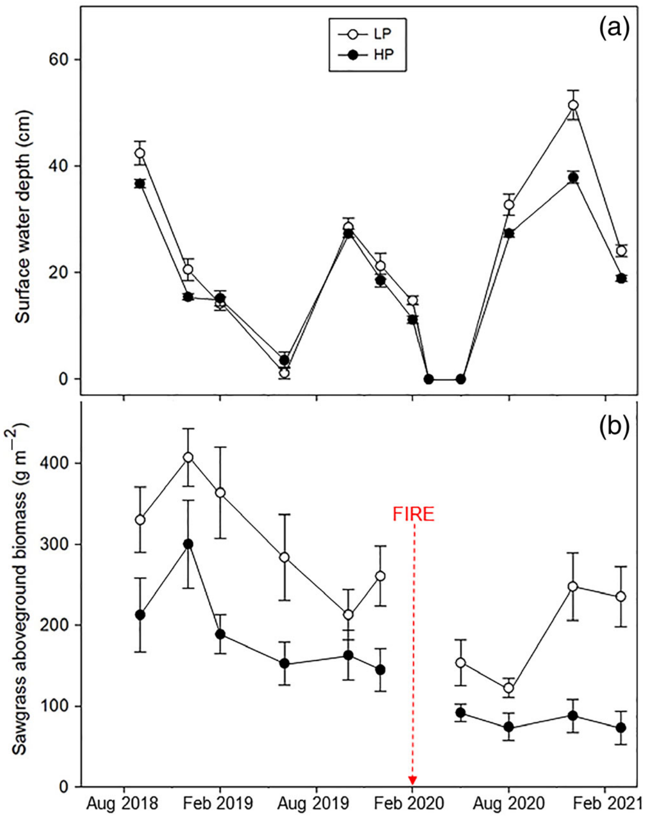

FIGURE 4 Surface water depth and sawgrass (*Cladium jamaicense* Crantz) aboveground biomass measured at different times, before and after fire, between September 2018 and March 2021 at the lower-P (LP) and higher-P (HP) sites in the eastern marl wetlands of the Everglades (Florida, USA). The prescribed fire was carried out on 18 February 2020.

Initial exploration of the relationship between fire intensity and changes in nutrient concentrations was limited by the number of sampling plots where fire intensity information was collected. So, although correlations were only marginally significant ($p < 0.10$), the increases in soil N and P concentrations between pre- and postfire at the LP site seemed to linearly increase with increasing fire intensity (Figure 9a,c). The increase in organic matter content at the LP site between pre- and postfire significantly correlated with fire intensity ($p < 0.05$; Figure 9e).

Fire effects on organic matter decomposition

We observed an increase in organic matter breakdown rates postfire compared with prefire. In particular, litter decomposition rates increased more substantially at the HP site, whereas fine root decomposition rates increased more substantially at the LP site (Table 5). Conversely, no change in coarse root decomposition rates was observed between pre- and postfire. The increases in fine root decomposition rates (Figure 10a) and in litter decomposition rates (Figure 10b) measured at the LP and HP plots, respectively, correlated logarithmically with fire intensity. Decomposition rates rapidly increased with small increases in fire intensity until a threshold of radiative energy released by the fire between 0.1 and 0.2 MJ m^{-2} was reached, after which decomposition rates barely increased, even with large increases in fire intensity. The lower number of data points from the LP site compared with the HP site (Figure 10) is due to the fact that in one of the five plots where radiometer data were collected, we were not able to collect the fine root decomposition bag postfire; the presence of surface water until late in the season and the growth of thick benthic periphyton mats prevented us from recovering it. We placed decomposition bags on the soil surface in plots postburn to avoid the consumption of litter material by fire, and for this reason the

TABLE 1 Concentrations (in parts per million; mean ± SD) of total organic carbon (TOC), total nitrogen (TN), and total phosphorus (TP) in surface water, measured at different times before and after fire at the lower-P (LP) and higher-P (HP) sites in the eastern marl wetlands of the Everglades (Florida, USA).

	Surface water TOC		Surface water TN		Surface water TP	
Date	LP site	HP site	LP site	HP site	LP site	HP site
Dec 2018	8.7 ± 0.4	8.6 ± 0.3	1.0 ± 0.3	0.9 ± 0.1	0.018 ± 0.01	0.021 ± 0.02
Dec 2019	9.2 ± 0.1	9.4 ± 0.1	0.7 ± 0.03	0.8 ± 0.04	0.020 ± 0.01	0.023 ± 0.004
Feb 2020 (21)	9.3 ± 0.3	7.8 ± 0.4	0.9 ± 0.1	1.0 ± 0.7	0.033 ± 0.003	0.031 ± 0.01
Mar 2021	9.6 ± 0.1	10.5 ± 0.8	1.0 ± 0.1	1.2 ± 0.2	0.026 ± 0.003	0.039 ± 0.003

Note: The prescribed fire was carried out on 18 February 2020. Two-way ANOVA results: surface water TOC (time, $p < 0.001$; site, p = ns; time:site, $p < 0.001$), surface water TN (time, $p < 0.01$; site, p = ns; time:site, p = ns), surface water TP (time, $p < 0.001$; site, p = ns; time:site, p = ns); ns, not significant (when $p > 0.05$).

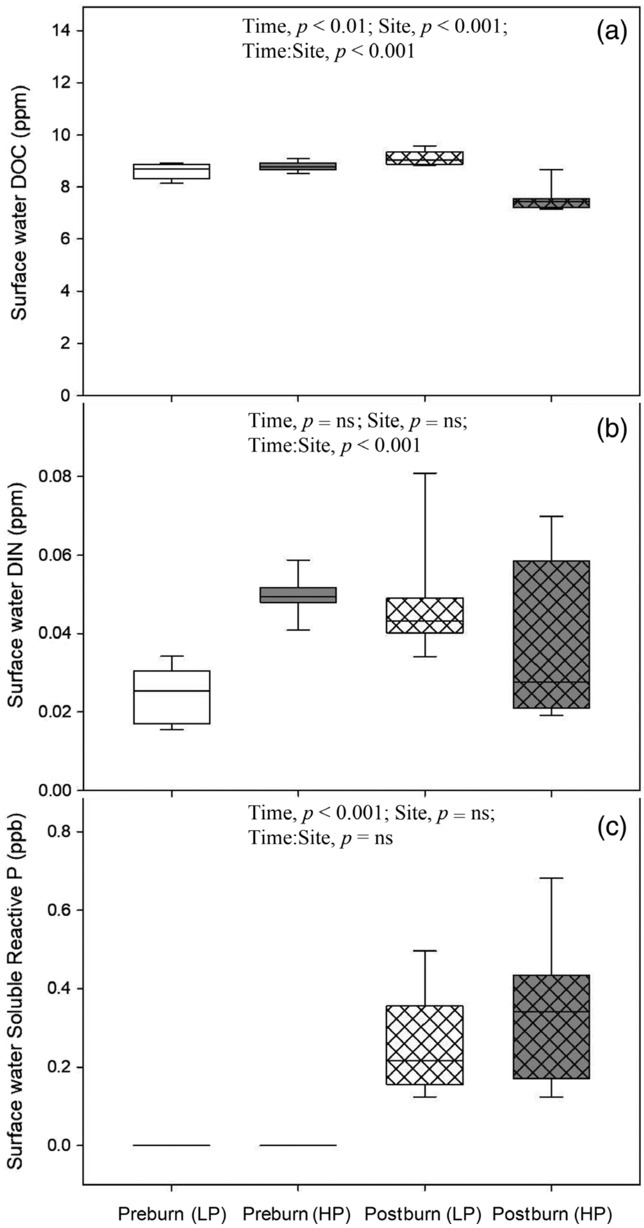

FIGURE 5 Surface water dissolved organic carbon (DOC), dissolved inorganic nitrogen (DIN), and soluble reactive phosphorus concentrations measured within a few weeks preburn and again 3 days postburn at the lower-P (LP) and higher-P (HP) sites in the eastern marl wetlands of the Everglades (Florida, USA). Two-way ANOVA results are reported within each sub-figure; ns, not significant (when $p > 0.05$).

potential effect of fire radiant heat on decomposition rates was not included in the results presented here.

DISCUSSION

Fire eases wetland oligotrophic status

As expected, we observed changes in the cycling of nutrients triggered by the prescribed fire carried out in the eastern marl wetlands of the Everglades. The measured increases were only temporary in some of the nutrient pools, while other nutrient increases lasted until the end of the experiment, 1 year postfire. Our observations are in line with previous studies that have found increases in nutrient concentrations in the surface water (Brown et al., 2014; Miao et al., 2010), in the periphyton mats (Miao et al., 2010), in macrophyte leaf tissues (Christensen, 1977), and in the soil (Butler et al., 2018) following fire.

Fire released P regardless of ecosystem oligotrophic status: some of the observed changes occurred in the same direction at both LP and HP marshes, whereas other changes occurred at one or the other site only. However, the legacy of fire was greater in the LP than the HP wetland, as soil P amounts at the LP site were still higher 1 year postfire than prefire, and, importantly, similar to the P amounts at the HP site, whereas they were significantly lower prefire. The increase in soil P at the LP site resulted in lower soil C:P and N:P ratios, which also remained lower than prefire until the end of the experiment, 1 year postfire. An increase in periphyton mats P concentration was detected only at the HP site, in contrast with our expectations that a transient increase in P would occur at both sites. This result could strengthen the hypothesis that, in more oligotrophic wetlands, characterized by lower amounts of soil P, mechanisms to retain P in the soil might be occurring following fire (Boerner, 1982); mechanisms to retain nutrients characterize both N- and P-limited ecosystems (Dijkstra & Adams, 2015). Possibly, postfire phosphorus retention at the LP site occurred through precipitation as calcium (Ca) phosphate, as these oligotrophic wetlands are characterized by high calcareous periphyton biomass, which releases dissolved Ca in the water column, or through sorption of phosphate by organic matter complexed with iron and aluminum (Reddy et al., 1999), although there is low probability for this latter mechanism to have occurred due to trace quantities of iron and aluminum present in Everglades soils (Scheidt et al., 2021). Whichever the mechanisms, which should be addressed in future research, soils from more oligotrophic wetlands are likely further from their P retention maximum and have greater potential to accumulate P (Reddy et al., 1999). Conversely, in HP wetlands, soils are likely closer to their P retention maximum, and therefore the P recycled by the fire might be temporarily retained in other ecosystem compartments, such as periphyton mats, or be exploited by plant species that require high amounts of P for growth. For example, lanceleaf arrowhead, a plant species whose abundance is regulated by P availability (Daoust & Childers, 1999), expanded at the HP site postfire. Similarly, in Florida intermittent wetlands, soil P did not increase postfire, and the nutrient-rich ashes released were promptly used to boost

TABLE 2 Concentrations (mean ± SD) of carbon (C; in milligrams per gram), nitrogen (N; in milligrams per gram), and phosphorus (P; in micrograms per gram) in sawgrass (*Cladium jamaicense* Crantz) leaves, measured at different times before and after fire at the lower-P (LP) and higher-P (HP) sites in the eastern marl wetlands of the Everglades (Florida, USA).

	Leaf C		Leaf N		Leaf P	
Date	LP site	HP site	LP site	HP site	LP site	HP site
Dec 2018	488 ± 4	490 ± 3	8.5 ± 1.0	7.8 ± 1.1	204 ± 48	214 ± 29
Dec 2019	471 ± 27	464 ± 30	8.2 ± 1.5	7.4 ± 1.0	254 ± 39	235 ± 41
May 2020	465 ± 29	462 ± 26	9.2 ± 1.2	9.6 ± 1.4	351 ± 83	332 ± 61
Mar 2021	487 ± 4	487 ± 3	9.8 ± 1.0	8.3 ± 0.8	242 ± 45	209 ± 47

Note: The prescribed fire was carried out on 18 February 2020. Two-way ANOVA results: leaf C (time, $p < 0.001$; site, $p =$ ns; time:site, $p =$ ns), leaf N (time, $p < 0.001$; site, $p < 0.05$; time:site, $p =$ ns), leaf P (time, $p < 0.001$; site, $p =$ ns; time:site, $p =$ ns); ns, not significant (when $p > 0.05$).

TABLE 3 Concentrations (mean ± SD) of carbon (C; in milligrams per gram), nitrogen (N; in milligrams per gram), and phosphorus (P; in micrograms per gram) in sawgrass (*Cladium jamaicense* Crantz) fine roots (with diameter ≤2 mm), measured at different times before and after fire at the lower-P (LP) and higher-P (HP) sites in the eastern marl wetlands of the Everglades (Florida, USA).

	Fine root C		Fine root N		Fine root P	
Date	LP site	HP site	LP site	HP site	LP site	HP site
Dec 2018	459 ± 15	463 ± 11	8.2 ± 0.8	9.0 ± 1.0	220 ± 85	264 ± 84
Dec 2019	463 ± 26	477 ± 59	9.5 ± 2.4	9.6 ± 2.0	222 ± 28	297 ± 75
May 2020	445 ± 32	445 ± 23	7.0 ± 0.9	6.9 ± 0.9	345 ± 178	286 ± 94
Mar 2021	459 ± 36	470 ± 19	9.0 ± 0.6	9.5 ± 1.0	220 ± 44	260 ± 64

Note: The prescribed fire was carried out on 18 February 2020. Two-way ANOVA results: fine root C (time, $p =$ ns; site, $p =$ ns; time:site, $p =$ ns), fine root N (time, $p < 0.001$; site, $p =$ ns; time:site, $p =$ ns), fine root P (time, $p < 0.001$; site, $p =$ ns; time:site, $p =$ ns); ns, not significant (when $p > 0.05$).

TABLE 4 Concentrations (mean ± SD) of carbon (C; in milligrams per gram), nitrogen (N; in milligrams per gram), and phosphorus (P; in micrograms per gram) in the periphyton mats, measured at different times before and after fire at the lower-P (LP) and higher-P (HP) sites in the eastern marl wetlands of the Everglades (Florida, USA).

	Periphyton C		Periphyton N		Periphyton P	
Date	LP site	HP site	LP site	HP site	LP site	HP site
Dec 2018	216 ± 12	228 ± 4	9.1 ± 0.9	10.7 ± 0.4	60 ± 10	91 ± 25
Dec 2019	205 ± 24	230 ± 7	8.5 ± 1.1	10.7 ± 0.7	59 ± 16	119 ± 21
Mar 2020	208 ± 9	273 ± 43	10.1 ± 1.2	18.8 ± 5.4	85 ± 19	249 ± 100
Mar 2021	208 ± 6	209 ± 4	7.7 ± 0.5	7.9 ± 0.5	50 ± 10	89 ± 34

Note: The prescribed fire was carried out on 18 February 2020. Two-way ANOVA results: periphyton C (time, $p < 0.001$; site, $p < 0.001$; time:site, $p < 0.001$), periphyton N (time, $p < 0.001$; site, $p < 0.001$; time:site, $p < 0.001$), periphyton P (time, $p < 0.001$; site, $p < 0.001$; time:site, $p < 0.001$); ns, not significant (when $p > 0.05$).

plant recovery (Kominoski et al., 2022). However, at our sites, apart from a reduction of sawgrass aboveground biomass and small increases in the cover of spikerush and lanceleaf arrowhead at the HP site, we did not observe any strong effect of fire on vegetation composition, structure, or tissue chemistry, demonstrating the resiliency and adaptation to fire of these wetlands (Pellegrini et al., 2015).

The manner in which nutrient retention mechanisms function following fire is nevertheless probably dependent on the magnitude of the disturbance events: some disturbances may have a strong impact on the ecosystem, disrupting the ecological linkages that allow its established dynamics to function (Jordan & Herrera, 1981). The prescribed fire at our experimental sites occurred with standing water, but if the fire had occurred with dry soil and low fuel moisture, we would likely have observed consumption of soil and litter organic matter, and losses of nutrients from the soil, litter, and aboveground mass through increased ash convection and volatilization of elements, as a result of a more severe burn (Neary et al., 1999; Ruiz et al., 2013). Although at our experimental sites fire intensity was limited by the wet conditions, we still measured a decrease in soil N:P ratio postfire at the LP site, which likely meant that N, which volatilizes at low temperatures compared with P

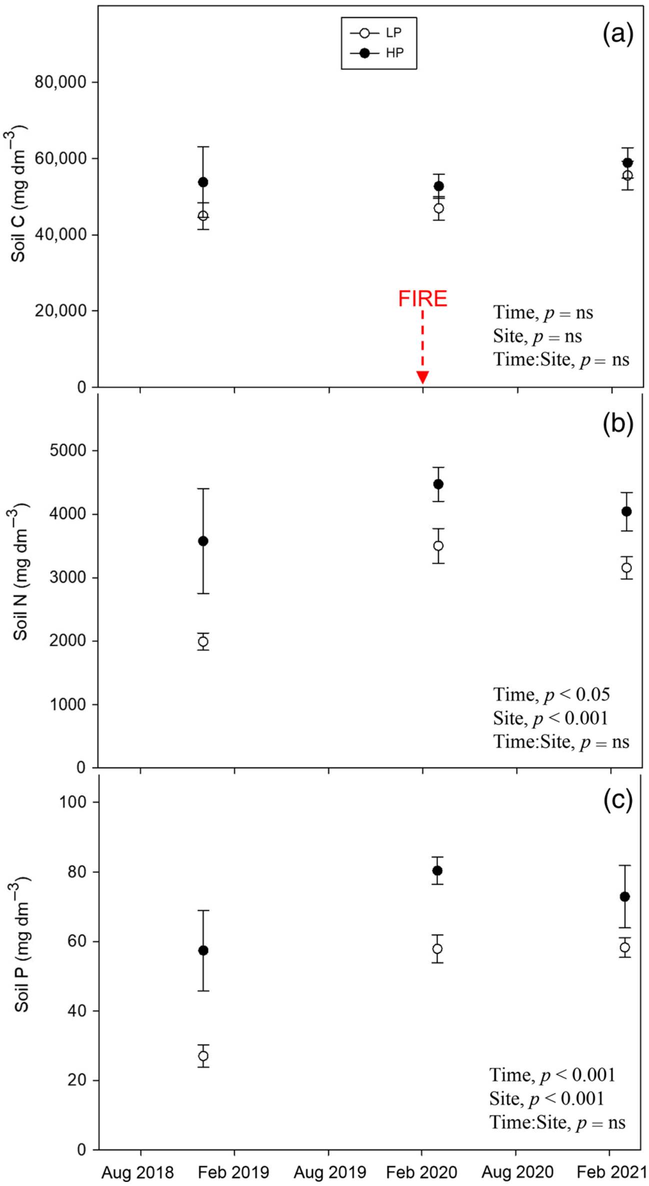

FIGURE 6 Soil carbon (C), nitrogen (N), and phosphorus (P) amounts per unit of soil volume measured one time prefire and two times postfire at the lower-P (LP) and higher-P (HP) sites in the eastern marl wetlands of the Everglades (Florida, USA). The prescribed fire was carried out on 18 February 2020. Two-way ANOVA results are reported within each sub-figure; ns, not significant (when $p > 0.05$).

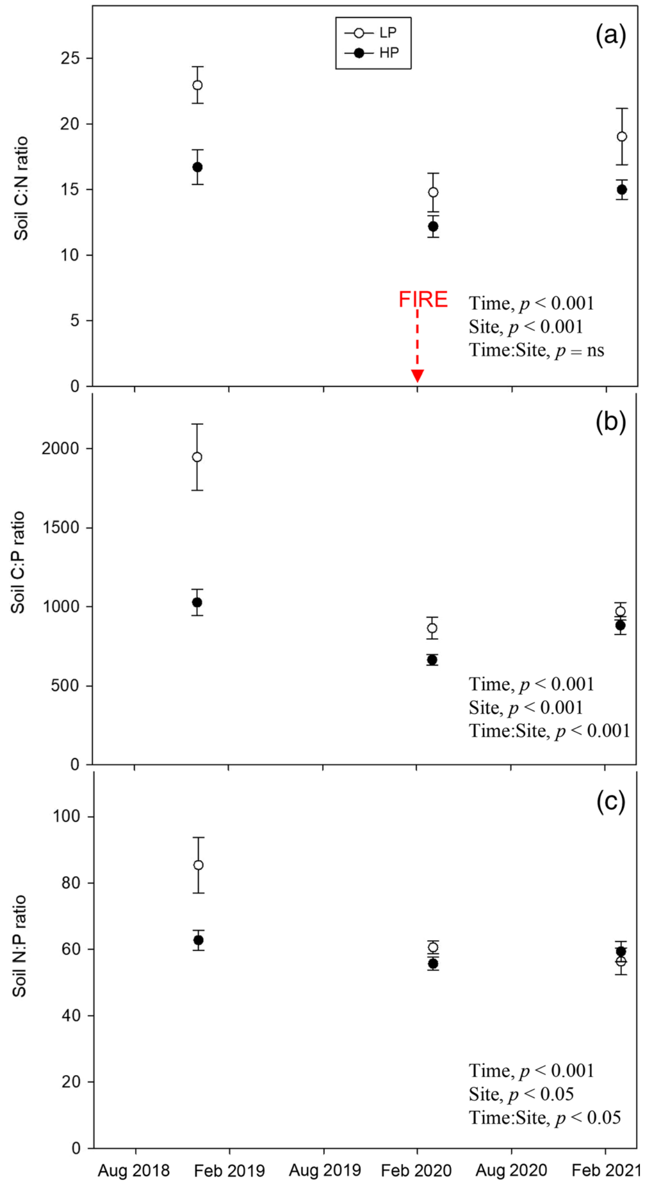

FIGURE 7 Soil C:N, C:P, and N:P mass ratios calculated using the concentrations of carbon (C), nitrogen (N), and phosphorus (P) measured in the soil one time prefire and two times postfire at the lower-P (LP) and higher-P (HP) sites in the eastern marl wetlands of the Everglades (Florida, USA). The prescribed fire was carried out on 18 February 2020. Two-way ANOVA results are reported within each sub-figure; ns, not significant (when $p > 0.05$).

(Bodí et al., 2014), was in part lost to the atmosphere, thus resulting in a disproportionate amount of mineralized P compared with N in the fire ashes (Butler et al., 2018). It is understood that hydrology plays a critical role in fire ecology, particularly in wetland ecosystems (Osborne et al., 2013): hydrological conditions during the fire event affect fire intensity, severity, and patchiness of the burn (Noss, 2018), and hydrological conditions postfire drive biogeochemical cycling by affecting the fate of the ashes (Kominoski et al., 2022; Nocentini, Kominoski, & Sah, 2021), and postfire vegetation recovery (Kominoski et al., 2022). During our experiment, hydrologic conditions, monitored by measuring surface water depths every three months, were similar in the two oligotrophic marshes, and, at the same time, the region was not affected by any other typical disturbance such as hurricanes, which may have introduced additional, confounding effects on postfire biogeochemical cycling.

The temporary increase in soil organic matter, measured 1 month postfire, could be attributed to increased postfire root productivity (Johnson & Matchett, 2001) and

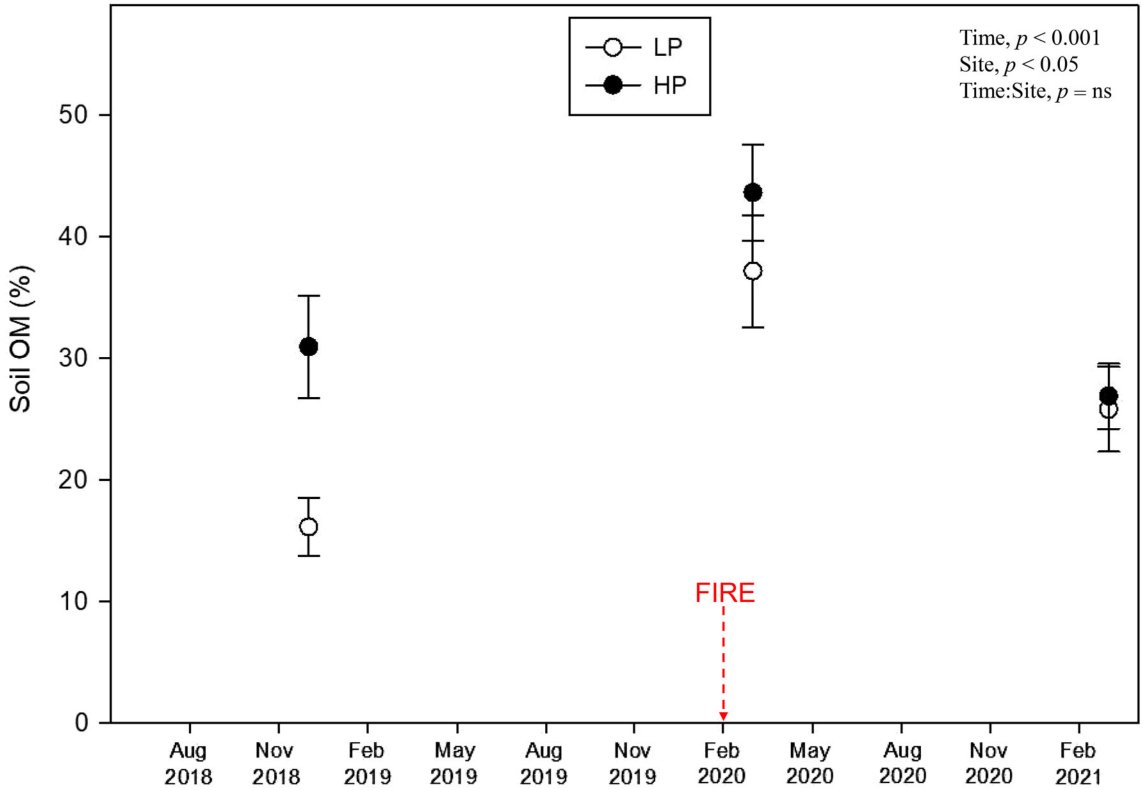

FIGURE 8 Soil organic matter (OM) content measured one time prefire and two times postfire at the lower-P (LP) and higher-P (HP) sites in the eastern marl wetlands of the Everglades (Florida, USA). The prescribed fire was carried out on 18 February 2020. Two-way ANOVA results are reported within the figure; ns, not significant (when $p > 0.05$).

turnover, or to the pulse of dead (but not charred) plant parts added to the litter and soil by the fire, which can trigger rapid changes in soil processes (Kuzyakov et al., 2000). At the same time, organic matter decomposition rates increased in the year postfire. Globally, contrasting responses of soil microorganisms and fauna to fire were found in a meta-analysis that analyzed 131 empirical studies (Pressler et al., 2019): fire reduced microorganism abundance by up to 96%, nematode abundance by 88%, but had no significant effect on soil arthropods. However, these findings came from dry ecosystems such as forests, grasslands, and shrublands, while in wetland ecosystems, when fire occurs with standing water, the soil is shielded from direct fire impacts. Furthermore, while frequent fire seems to slow down litter decomposition rates (Brennan et al., 2009; Butler et al., 2019; Hopkins et al., 2020), the effect of single fire events on organic matter decomposition varies from slowing down to enhancing breakdown rates, depending on factors such as fire intensity, rainfall regimes, and vegetation type (Boulanger et al., 2011; Davies et al., 2013; González-Pérez et al., 2004; Throop et al., 2017). In particular, the flammability of the vegetation determines the biodegradability of the fire products: plants characterized by high combustibility produce highly refractory organic materials, such as black carbon, while, conversely, plants characterized by low autocombustibility do not get charred but rather killed and dried, and return to the soil biodegradable C-forms (Bodí et al., 2014; González-Pérez et al., 2004). The increase in surface water DOC postfire measured at the LP site did not correlate with fire intensity (data not shown), supporting the hypothesis that part of the fuel C was not volatilized or charred, but released in the surface water in more degradable and soluble forms. Further, in wetlands, surface water preserves large amounts of organic matter in the litter and the surface soil layers, which are not subject to any direct fire impact (and therefore do not get charred), but that can indirectly be affected by increased microbial activity stimulated by the pulse of nutrient-rich ashes (Cleveland et al., 2002; Kuzyakov et al., 2000).

Nutrient cycling and organic matter processes respond to fire intensity

Investigations of the causal mechanisms of fire effects require quantifying fire behavior in meaningful ways (O'Brien et al., 2018). We chose to measure fire radiative energy density as the dose (sensu Smith et al., 2016) driving the postfire nutrient responses. Although our

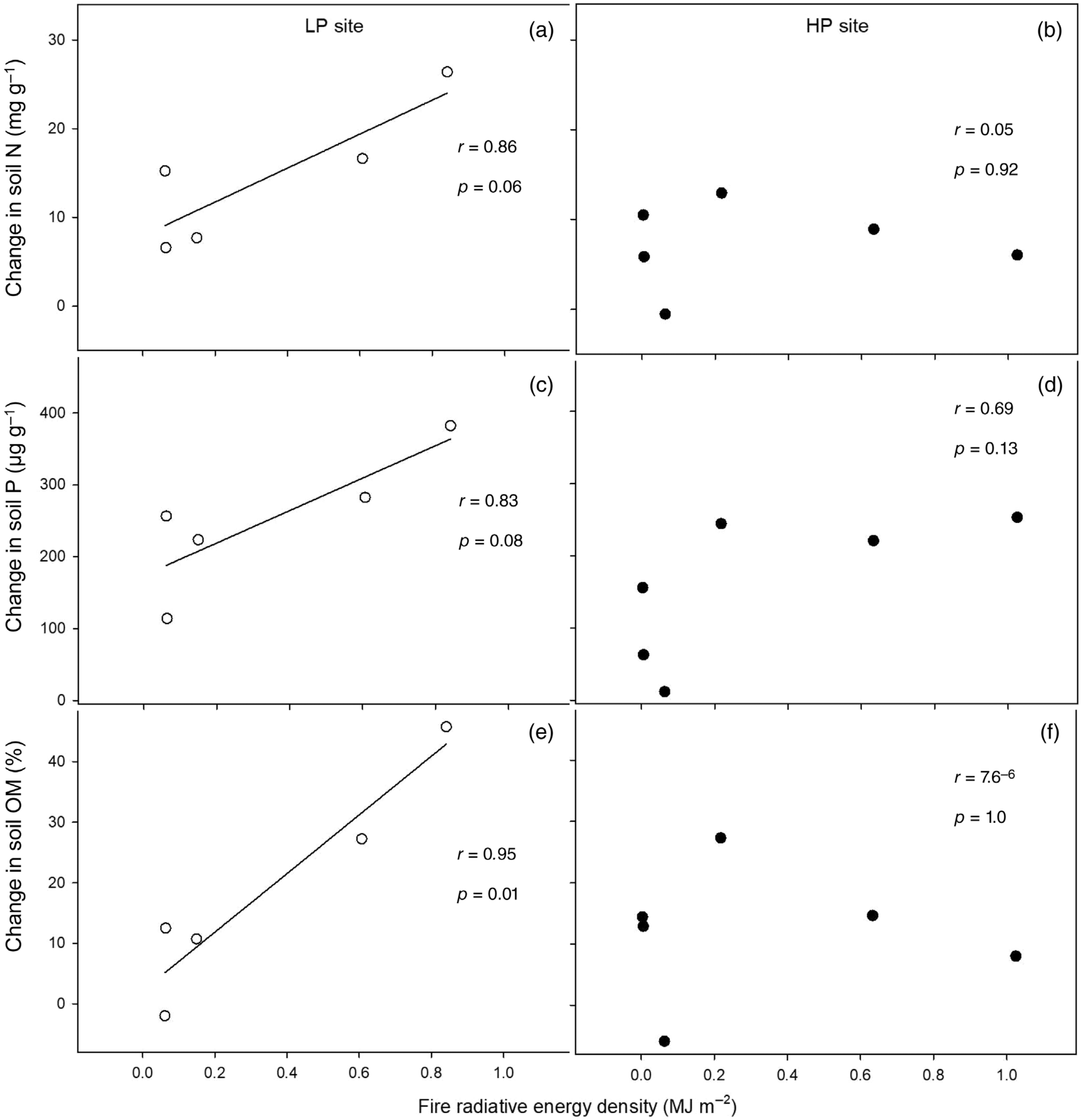

FIGURE 9 Correlations between fire intensity (expressed as the integral of radiative energy) and the change in soil nitrogen (N) and phosphorus (P) concentrations, and in soil organic matter (OM) content measured between prefire and postfire at the experimental plots of the lower-P (LP) and higher-P (HP) sites. We fit a linear function to the regressions and calculated Pearson's correlation coefficient (*r*) and statistical significance (*p*).

experiment captured only the relatively low end of the fire intensity potential of the site due to the wet conditions during the burn, increasing fire intensity increased soil organic matter and appeared to linearly increase nutrients added to soils. However, in contrast to our predictions, linear increases in soil nutrients and organic matter with increasing fire intensity were only detected at the LP site; as discussed above, this difference may be the result of fast nutrient uptake by lanceleaf arrowhead and periphyton at the HP site. We also found that minimal increases of fire intensity were needed to cause a substantial increase in organic matter decomposition, until a certain dose of fire intensity was reached. Fire intensity was found to affect the chemical properties of sawgrass

TABLE 5 Decomposition rates (k day^{-1}; mean ± SD) of sawgrass (*Cladium jamaicense* Crantz) litter and fine root material, measured pre- and postfire at the lower-P (LP) and higher-P (HP) sites in the eastern marl wetlands of the Everglades (Florida, USA).[a]

	Litter breakdown rate		Fine root breakdown rate		Coarse root breakdown rate	
Time period	**LP site**	**HP site**	**LP site**	**HP site**	**LP site**	**HP site**
Prefire	0.0090 ± 0.0003	0.0093 ± 0.0004	0.0031 ± 0.0002	0.0034 ± 0.0003	0.0069 ± 0.00004	0.0070 ± 0.0001
Postfire	0.0095 ± 0.0011	0.0104 ± 0.0009	0.0036 ± 0.0002	0.0037 ± 0.0004	0.0072 ± 0.0001	0.0070 ± 0.0001

Note: Litter and roots were incubated on the soil surface or belowground, respectively, for 1 year before collection and calculation of breakdown rates.
[a]Two-way ANOVA results: litter breakdown rate (time, $p < 0.01$; site, $p < 0.05$; time:site, $p =$ ns), fine root breakdown rate (time, $p < 0.01$; site, $p =$ ns; time:site, $p =$ ns), coarse root breakdown rate (time, $p =$ ns; site, $p =$ ns; time:site, $p =$ ns); ns, not significant (when $p > 0.05$).

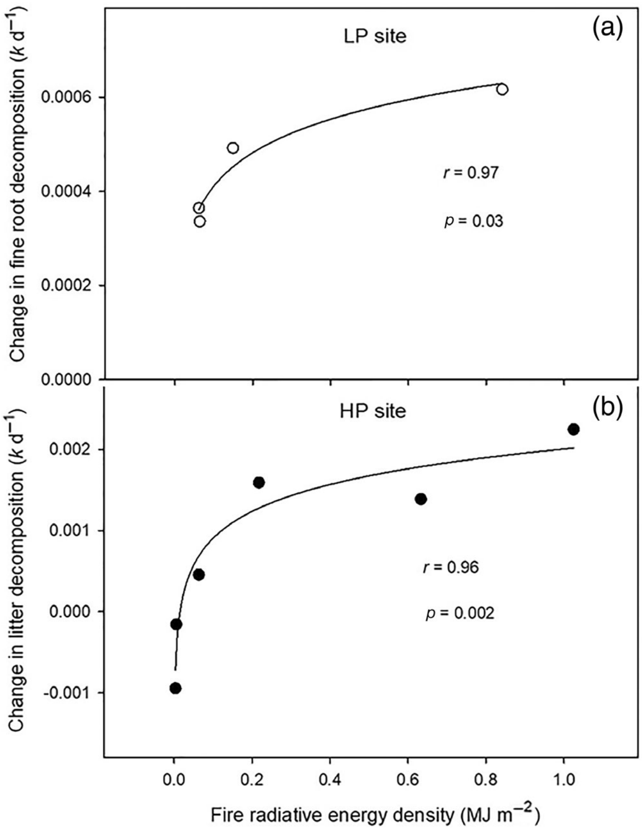

FIGURE 10 Correlations between fire intensity (expressed as the integral of radiative energy) and the change in fine root or litter decomposition rates measured between prefire and postfire at the experimental plots of the lower-P (LP) and higher-P (HP) sites, respectively. We fit a logarithmic function to the regressions and calculated the correlation coefficient (r) and statistical significance (p).

ashes: although sawgrass releases large amounts of available P-rich ashes, increasing fire intensity reduces the availability of ash P, while volatilizing N (Qian et al., 2009). Hence, we suggest that, as low intensity fires return to the soil more available P forms whereas high intensity fires return to the soil more passive P forms and affect more strongly N:P ratios, the fire return interval to achieve soil nutrient reloading of oligotrophic wetlands should not only be based on the soil and vegetation types (Nocentini, Kominoski, & Sah, 2021), but also on the attributes of the prescribed fire applied. We propose that there should be an inverse proportionality between return interval and intensity of prescribed fires: as fire intensity decreases, a shorter fire return interval should be applied, as the P returned to the soil will likely be removed and utilized more readily by living organisms, and, in general, the ecological effects triggered by the disturbance will be milder.

Coupling fire and nutrient management in ecosystems

Fire is an essential component of many oligotrophic wetlands and, as such, understanding its ecological and biogeochemical effects informs the preservation, management, and restoration of these ecosystems. With the present study, we learned that oligotrophic wetlands, characterized by shallow soils with low C and nutrient concentrations, benefit from fire by retaining in the soil the P contained in the ashes, and we therefore identified fire as a mechanism to ease P limitation in these wetlands. In our previous study, soil P reloading by fire was found to be effective for about 15 years in marl soil wetlands, which, irrespective of fire intensity, is then the suggested fire return interval to achieve this particular goal (Nocentini, Kominoski, & Sah, 2021). However, in the HP wetland, characterized by similar soils, we did not measure any P increase in the soil, but we found that the P contained in the ashes was allocated to other ecosystem compartments, such as periphyton biomass or high P-demanding macrophytes. Neither of the two wetlands shifted vegetation structure or composition following fire. Fire is thus a disturbance that, in many fire-prone ecosystems, has a fundamental role in regularly consuming vegetation and recycling nutrients, while maintaining vegetation communities, that no other disturbance (e.g., herbivores, floods, and hurricanes) can replace to the same degree (Bond & Keeley, 2005). Moreover, we learned that the physical dose of fire, measured here as energy release, applied in wetlands is a key factor in regulating the ecological outcomes of fire disturbances: small differences in fire intensity may result in significantly different changes to soil stoichiometries, and organic matter production and processing. Therefore, knowledge of ignition patterns and of the interactions among fire, weather, and fuel types are a critical asset for natural system fire managers (Furman, 2018). Controlling for these attributes as part of the application of prescribed fires will allow managers to apply known fire energy doses that, together with the appropriate fire return intervals, can be used to achieve the desired natural resource objectives (Hiers et al., 2021). Defining the physical thresholds of fire intensity that may result in distinct fire return intervals seems likely to be a useful course of study for future projects, as we hypothesize that there will likely be some thresholds that apply across many fire-prone ecosystems and others that are specific to individual ecosystems or plant communities. Continuing to link fire behavior to a number of fundamental ecological mechanisms, be they biogeochemical, microbial, or species-specific, should provide us with evidences for or against applying any one threshold to an individual fire management program. Observations of fire intensity are currently challenging to obtain, but we anticipate that expanded use of new technologies (e.g., use of drones and remote sensing) should rapidly enhance our ability to define many more fire intensity thresholds, triggering specific biological cascades.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Nocentini & Kominoski, 2021) are available from the Environmental Data Initiative Data Portal: https://doi.org/10.6073/pasta/b202c11db7c64943f6b4ed9f8c17fb25.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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