Phosphorus Release from Ash and Remaining Tissues of Two Wetland Species after a Prescribed Fire

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Dead plant tissues and ash from a prescribed fire play an important role in nutrient balance and cycling in the Florida Everglades ecosystem. The objective of this study was to assess the dynamic changes in total phosphorus release (TPr) from ash or tissues of either cattail (*Typha domingensis* Pers.) or sawgrass (*Cladium jamaicense* Crantz) to water. Natural-dead (senesced-dead) and burning-dead (standing-dead due to a prescribed fire) cattail and sawgrass were collected from highly (H) and moderately (M) impacted zones in the Florida Everglades. This experiment was conducted by incubation and water-extraction of the materials in plastic bottles for 65 d at room temperature (24 ± 1°C). Results showed that 63 to 88%, 17 to 48%, 9 to 20%, and 13 to 28% of total P (TPp) were released as TPr from cattail and sawgrass ash, cattail tissues from the H zone, cattail tissues, and sawgrass tissues from the M zone, respectively. TPp means total P of plant tissues, whereas TPr is total P release from the tissues or ash. Most of the TPr was released within 24 h after burning. The quick release of TPr observed in this experiment may help explain the P surge in the surface water immediately following a fire in the marsh. These findings suggest that prescribed burning accelerates P release from cattail and sawgrass. They also imply that it is very important to keep the water stagnant in the first 24 h to maximize the benefits of a prescribed fire in the Everglades.

The Everglades is a vast, freshwater wetland in South Florida; it is called "the river of grass" in tribute to sawgrass (*Cladium jamaicense* Crantz) dominance (Douglas, 1947; Christopher and Richards, 2001). Anthropogenic activities such as urban and agricultural development have had negative impacts on the Florida Everglades ecosystem for more than a century (Sklar et al., 2005). This has led to significant ecosystem changes in hydrology, fire frequency, biotic diversity, and nutrient biogeochemistry (Noe et al., 2001). Phosphorus (P) enrichment is one of the dominant factors altering the Everglades ecosystem as it is a historically P-limited and oligotrophic freshwater wetland, and consequently, sensitive to small alterations in P concentrations (Noe et al., 2001). Increases in P flux to the Everglades from agricultural and urban runoff (Davis, 1994) have resulted in increased growth of cattail (*Typha domingensis* Pers.) in traditionally sawgrass-dominated landscapes (Qian et al., 2004). Sawgrass is a perennial and native sedge that covers 70% of the Everglades (Loveless, 1959). The sawgrass root system distributes vertically and hence grows on banks or inclines. It can tolerate low-nutrient stress but has low photosynthetic rates (Kuhn et al., 2002).

Alternatively, cattail is an erect herb up to 3 m tall with sword-shaped leaves and a horizontal root system (Barkley, 1986). Cattail is an invasive plant in the Everglades because its photosynthetic rate is greater than that of sawgrass (Miao and DeBusk 1999); specifically, excess of water and nutrients result in the taller cattail plants replacing sawgrass. During the last century, thousands of hectares of the historically sawgrass-dominant and oligotrophic Everglades have been replaced by cattail populations, which are common indicator plants of P-enriched habitats (Miao and Sklar, 1998). To maintain sawgrass communities in the Everglades, cattail and sawgrass interactions were examined along a gradient of long-term nutrient additions, altered hydroperiod, and fire (Richardson et al., 2008a). However, little is known regarding the P transformations that occur during Everglades prescribed burns. Previous studies have found that fire

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Abbreviations: H, highly impacted zone; HC, cattail in highly impacted zone; M, moderately impacted zone; MC, cattail in moderately impacted zone; MS, sawgrass in moderately impacted zone; MW, marsh water from moderately impacted zone; ND, natural-dead (or senesced-dead); PP, particulate phosphorus; SD, standing-dead (or burning-dead); SRP, soluble reactive phosphorus; TPp, total phosphorus in plants; TPr, released total phosphorus.

significantly influences vegetation patterns and P bioavailability in the Everglades (Wu et al., 1996; Smith and Newman, 2001; Qian et al., 2009). Therefore, it is essential to evaluate the effects of fire on P nutrient bioavailability, particularly release from ash and remaining plant tissues after the burn. However, fire is a difficult process to experimentally manipulate, especially at a landscape scale (Wu et al., 1996). The ash containing both soluble and insoluble phosphates is extremely mobile in situ but primarily deposited ex situ. Thus, it is difficult to accurately monitor the dynamic changes in P bioavailability at the field scale.

Prescribed fire is often performed during dry season, but the area still has standing water to avoid burning sediment. The plant tissues in the area are burned and may have different P composition because of differences in their physiological status. In general, burning-dead tissues contain more total P (TPp) than natural-dead tissues (Miao et al., 2009) because remobilized P is absorbed before the tissues die (Marschner, 1995). Therefore, P release should also be different. Release of P may be accomplished through the dissolution of combined inorganic P from ash or microbial mineralization of leaf organic matter. This process may be species dependent as well. There is, however, limited information available on the dynamic release of total P (TPr) from either the natural- or burning-dead tissues of both cattail and sawgrass. Thus, the present study examined dynamic changes in P released from ash and from natural- or burning-dead tissues of cattail and sawgrass.

The objectives of this study were to (i) determine the release in TPr in forms of soluble reactive P (SRP) and particulate P (PP) from ash or directly from the tissues of cattail from both the heavily impacted (H) and moderately impacted (M) zones or sawgrass from the M zone; (ii) quantify the effects of prescribed fire on the TPr release from both cattail and sawgrass tissues and ash; and (iii) compare the TPr release of ash to the TPr release of senesced-dead and burning-dead tissues of cattail and sawgrass.

Materials and Methods

Materials

This study was designed and conducted in a laboratory simulation at air-conditioned room temperature (24 ± 1°C) in the Tropical Research and Education Center, University of Florida, Homestead, FL. The plant materials were collected using an imbalanced factorial design with three independent factors: plant materials, species, and habitats. Three types of materials were used in the analysis: ash, senesced-dead tissues, and burning-dead tissues after a prescribed fire (Table 1). Two species were used: cattail (*T. domingensis*; C) and sawgrass (*C. jamaicense*; S) naturally grown in two habitats: the H and M zones of Water Conservation Area 2A within the northern Everglades. As there was no sawgrass located at H zone, only sawgrass tissues collected from M zone were used. Thus, the study included a total of 10 different materials (9 treatments + 1 control [no ash or plant materials]). The H zone with 1000 to 2000 mg P kg soil^{-1} is located at 26°34′ N, 80°37′ W and the M zone with 600 to 1000 mg P kg soil^{-1} at 26°32′ N, 80°38′ W. Additional site information can be found in Qian et al. (2009).

Nonburned senesced-dead and burning-dead tissues of cattail were collected from both of the H and M zones while those of sawgrass were collected from the M zone following a prescribed fire (Table 1) on 20 July 2008 and 13 Aug. 2008. The tissues were air-dried for 3 mo and then cut into 1-cm lengths to fit the plastic bottles before treatment.

After a prescribed fire in the wetland ecosystem, not everything was totally burned. To produce ash of the two species, both senesced-dead and burning-dead tissues were collected for either cattail or sawgrass. Laboratory-produced ash was used instead of natural ash to study the difference in P release between the two different species because the natural ash could be a mixture of burning different species growing in the same area. The ash used in this study was produced by burning the collected senesced-dead and burning-dead tissues of cattail from the H zone (HC) or M zone (MC) or of sawgrass from the M zone (MS). Based on a previous study (Qian et al., 2009), the burning condition was 400°C in a muffle furnace oven with natural (21%) oxygen supplied for 2 h. Cattail ash of HC was produced by burning 1.5 g of senesced-dead cattail tissues and 1.5 g of burning-dead tissues both from the H zone. Similarly, cattail ash of MC and sawgrass ash of MS were created by burning 1.5 g of senesced-dead tissues and 1.5 g of burning-dead tissues of corresponding species all from the M zone.

Thirty 500-mL wide-mouthed plastic bottles (Rubbermaid Servin' Saver, Cat. No. 3093, Newell Rubbermaid, Atlanta, GA) were used in this study. Ashes from burning 3.0 g of dead tissues or either 3.0 g of cut senesced-dead or 3.0 g of burning-dead plant tissues were placed into individual bottles. Then 400 mL of marsh water collected from either the H or M zone was added to the bottle containing the ash or cut tissues from the corresponding H or M zone. The bottles with the ash or tissues were incubated and extracted in the dark at air-conditioned room temperature (24 ± 1°C) for 65 d. Control treatment was prepared using marsh water from the M zone without ash or tissues. All of the treatments were conducted in triplicate.

Table 1. Descriptions of treatments of the incubation experiment following prescribed fire in the Everglades, Florida.

No.	Identity†	Habitat	Species	Incubation water source
		Ash		
1	HC	H	Cattail	H
2	MC	M	Cattail	M
3	MS	M	Sawgrass	M
		Senesced-dead tissues		
4	HC	H	Cattail	H
5	MC	M	Cattail	M
6	MS	M	Sawgrass	M
		Burning-dead tissues		
7	HC	H	Cattail	H
8	MC	M	Cattail	M
9	MS	M	Sawgrass	M
		Marsh water		
10	MW	M	No plants	M

† H, highly impacted zone; HC, cattail in H; M, moderately impacted zone; MC, cattail in M; MS, sawgrass in M; MW, marsh water from M.

Sampling and Sampling Time

Ten milliliters of liquid was collected from each of the bottles at 0, 2, 8, 12, 24, 48, 72, 96, 120, 168, 336, 504, 672, 840, 1008, 1176, 1344, and 1560 h (65 d). A 5-mL aliquot was filtered through a 0.2-μm membrane filter (Part 4192, Pall Corporation, East Hills, NY) for SRP analysis. The remaining 5-mL unfiltered aliquot was digested for TPr analysis. Additional corresponding marsh water was added to replace the loss of water due to sampling to maintain the solution at a constant volume of 400 mL throughout the incubation period.

Sample Digestion

A 5-mL aliquot of unfiltered subsample was digested with sulfuric acid and ammonium persulfate in an autoclave at 125°C and 1.03 to 1.38 × 10^5 Pa for 30 min. Digestion of plant tissues and ash was based on a method by Hanlon et al. (1994). Briefly, 200 mg of oven-dry plant tissue or of oven-dry ash was placed in a muffle furnace at 500°C for 5 h. The resulting ash was placed in 50-mL volumetric flasks, dissolved with 2 mL 6.0 M hydrochloric acid (HCl), diluted to volume with deionized water and filtered through a Whatman No. 41 filter paper (VWR LabShop, Batavia, IL).

Determination of Calcium, Magnesium, and Phosphorus

Calcium and Mg were analyzed at 422.7 or 285.2 nm with an air-acetylene flame using an AA-6300 (Shimizu, North America, Atlanta, GA). Phosphorus concentrations were analyzed using an Automated Discrete Analyzer (AQ2+, SEAL Analytical, Hanau, Germany) based on USEPA Method 365.1 (USEPA, 1983).

Calculation of Soluble Reactive Phosphorus, Particulate Phosphorus, Total Phosphorus Released, or Unreleased Phosphorus

The solution was diluted by 3% for every sampling from the second to the last sampling because 10 mL of marsh water from either the H or M zone was supplemented to replace the volume in each corresponding bottle after every sampling. Due to the Everglades' extremely oligotrophic condition, the USEPA determined that an annual or longer term mean of 10 μg P L^{-1} (parts per billion, or ppb) would protect the Everglades flora and fauna (Payne et al., 2003). Therefore, 10^3 μg P L^{-1} is used instead of mg P L^{-1} for the convenience to compare the P concentration in the water with the criterion. The true P concentration $[P]_t$ for SRP or TPr was calculated as follows.

$$[P]_{ti}\left(10^3\ \mu g\ L^{-1}\right)=\left([P]_{ri}-C\times\frac{10}{400}\right)\left(\frac{400}{390}\right) \quad [1]$$

where $[P]_{ti}$ represents the ith true P concentration (10^3 μg L^{-1}), $[P]_{ri}$ is the ith reading of P concentration from the equipment, and $i \geq 2$ and ≤18 because the solution was gradually diluted since the second sampling and sampled 18 times. C is the concentration of either SRP or TPr in the marsh water either from the H or M zone. The values for C are 0.110 and 0.011 for SRP for the H and M zones, respectively, and 0.156 and 0.038 10^3 μg L^{-1} for TPr for the H and M zones, respectively, and 400/390 is the dilution factor.

The total amount of phosphorus released is:

$$P_{ta}\left(10^3\ \mu g\right)=\frac{[P]_{r18}\times 400+\sum_{i=1}^{17}\left([P]_{ri}\times 10\right)}{1000} \quad [2]$$

where P_{ta} is SRP (10^3 μg) when $[P]_{ri}$ or $[P]_{r18}$ is the reading of the subsample without digestion or TPr (10^3 μg) when the $[P]_{ri}$ or $[P]_{r18}$ is the reading of the subsample with digestion. $[P]_{ri}$ and $[P]_{r18}$ are the ith and 18th P reading of P concentration from the analysis. Ten (10) is the volume (mL) of sampling solution. Four hundred (400) is the volume of extraction water in the bottle. One thousand (1000) is the conversion factor from milliliters to liters.

Particulate P (PP) is referred to as

$$PP = TPr - SRP \quad [3]$$

In this study, the PP is from two sources: the ash or dead tissues and newly formed during the incubation period. Equation [3] is used to calculate PP concentrations from different sources.

Unreleased P is defined and calculated as follows:

$$\text{Unreleased P} = TPp - TPr \quad [4]$$

Statistical Analysis

The data were analyzed in one-way and two-way ANOVA using the General Linear Model method (SAS Institute, 2009). Results for the two-way ANOVA are not shown if there is not significant interaction between two factors. Results were considered significant at $p < 0.05$. After running the SAS program, the critical ranges ($LSD_{2,\ 0.05}$) of Duncan's Multiple Range Test were used to detect the difference between two means (Hubbard, 2001). Based on criteria for evaluating the goodness of fit by Chimney and Pietro (2006), the curves of best fit were produced using dynamic fitting by Sigmaplot 10.1 (Systat Software, Inc., Chicago, IL). Additionally, to conveniently compare the release difference between the ash and tissues of both species, the data of the TPr releases were calculated from 10^3 μg L^{-1} into 10^3 μg TPr kg^{-1} dried tissues or 10^3 μg TPr kg^{-1} ash. The latter were then converted into 10^3 μg TPr kg^{-1} dried tissues from 10^3 μg TPr kg^{-1} ash.

Results

Changes in Released Total Phosphorus Concentration

For the ash, the actual concentration of TPr released from HC was significantly greater than that from either MC or MS ($p < 0.01$), but there was no significant difference in the TPr released from MC and MS ash (Fig. 1). All of the curves showed a sharp increase in the first 24 h of incubation followed by a small increase thereafter. The mean TPr concentrations over the entire incubation period (Fig. 1) were 1.88, 1.23, and 1.18 × 10^3 μg L^{-1} for HC, MC, and MS, respectively. Therefore, overall the ash from cattail biomass released 52.8% more TPr in the H zone than in the M zone. The mean TPr value from the 18 sampling events from the M zone water was 40 μg L^{-1}, about twice as much as the mean SRP value (19 μg L^{-1}) in the same marsh water. They are both negligible compared with the TPr and SRP released from the ash or tissues and are not presented.

For cattail tissues, each of the senesced-dead tissues from the H and M zones and the burning-dead tissues from the corresponding zones showed a sharp release in TPr in the first 12 h

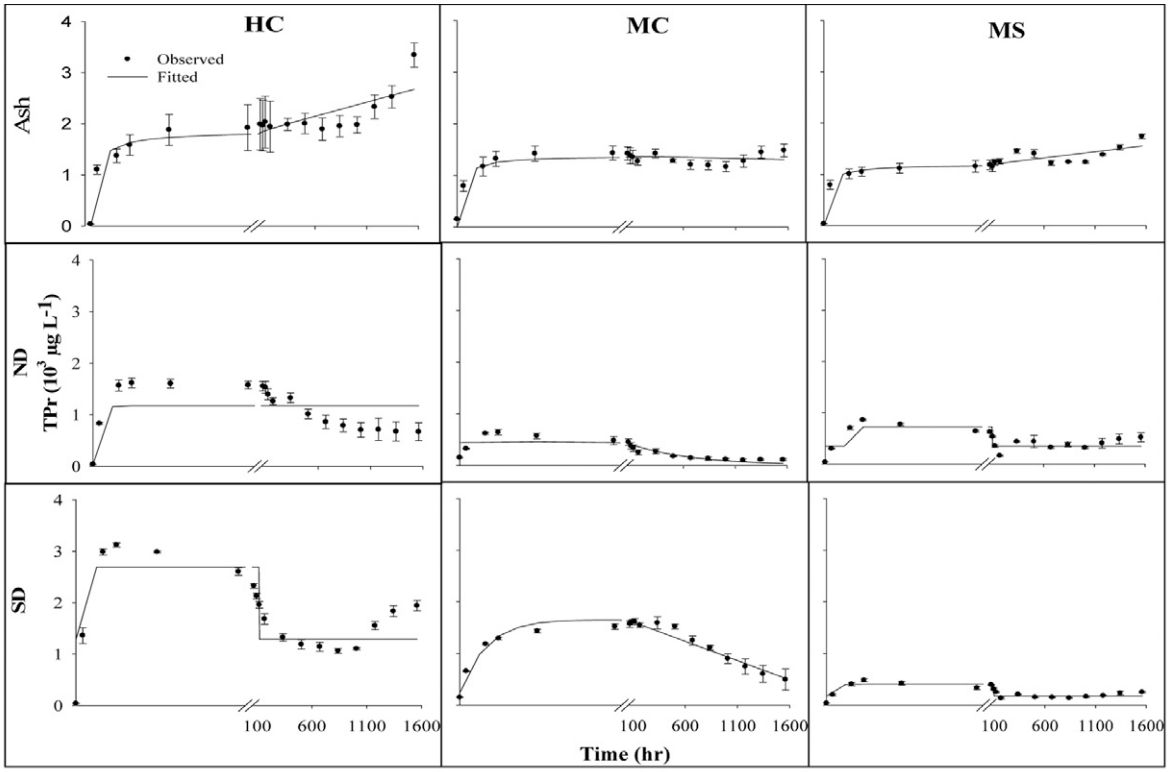

Fig. 1. Actual concentrations (10^3 μg L^{-1}) of total phosphorus (TPr) released from ash, senesced-dead plants, and burning-dead plants collected from the Water Conservation Area 2A, the Everglades, Florida. To better show the changes in the first period of time, the *x*-axis has a break at Hour 50. HC, cattail in highly impacted zone; MC, cattail in moderately impacted zone; MS, sawgrass in moderately impacted zone; ND, senesced-dead, namely, natural-dead; SD, burning-dead, namely, standing-dead; TPr, total phosphorus released from ash or dead plant tissues.

(Fig. 1). Among the four treatments, the burning-dead tissues at HC demonstrated the greatest changes: TPr dropped about 66% between 12 and 840 h and decreased to as low as 1.06 × 10^3 μg L^{-1}, and then increased by 83% between 840 and 1560 h, reaching up to 1.94 × 10^3 μg L^{-1} by 1560 h.

The burning-dead tissues in MC had significantly greater TPr concentration than the senesced-dead tissues in MS at $p < 0.01$. The latter produced a significantly greater TPr concentration than either the MC senesced-dead tissues or MS burning-dead tissues at $p < 0.01$. However, there was no significant difference in TPr concentration between the MC senesced-dead tissues and the MS burning-dead tissues.

Changes in Concentrations of Soluble Reactive Phosphorus

Actual concentration of SRP released from the ash of cattail tissues collected from the H zone was significantly greater than that from cattail tissues or sawgrass tissues from the M zone (Fig. 2). The means of the 18 sampling events were 1.85, 1.21, and 1.09 × 10^3 μg L^{-1} for HC, MC, and MS, respectively. The mean SRP released from HC was 53 and 70% greater than that of MC and that of MS during the incubation. However, SRP released from both species from the M zone did not differ significantly. All of the three curves followed a saturation pattern and reached their corresponding maxima at 1008 h (42 d), 336 h (14 d), and 504 h (21 d) for HC, MC, and MS, respectively.

The cattail tissues from either the H zone or M zone differed significantly with regard to their release rates of SRP ($p < 0.01$) (Fig. 2). The mean concentrations were 530, 150, and 140 μg L^{-1} for natural-dead tissues of each of HC, MC, and MS, respectively. The corresponding values for burning-dead tissues of each of HC, MC, and MS were 1.08, 0.75, and 0.76 × 10^3 μg L^{-1}, respectively. The burning-dead tissues of cattail in the H zone released 104% more SRP than the senesced-dead ones during the incubation period. The burning-dead tissues of cattail in the M zone released 400% more SRP than the senesced-dead ones. All of the dead tissues had the highest SRP release at 12 h except the MC burning-dead tissues that peaked at 120 h. The maximum SRP values from each of HC, MC, and MS senesced-dead tissues, and the HC, MC, and MS burning-dead tissues were 1.05, 0.53, 0.75, 2.20, 1.20, and 0.33 × 10^3 μg P L^{-1}, respectively.

Different species had a similar SRP release pattern from either the senesced-dead or the burning-dead tissues in the M zone. The SRP release was highest at 12 h and then sharply declined at 24 h except for the MC burning-dead tissues, which had the highest SRP release at 120 h (5 d) followed by a significant gradual decline at 840 to 1344 h. The mean SRP release from the MC burning-dead tissues was significantly greater than those observed from each of the other three types of dead tissues in the M zone including both the senesced-dead from MC and MS and the burning-dead from MS at $p < 0.01$ (Fig. 2).

Total Phosphorus Released from the Ash and Tissues

In this study, ash formation rates of the dead tissues were 17.8 and 16.9% for cattail in the H and M zones and 19.8% for sawgrass in the M zone. Their corresponding TPr releases were 2518 ± 317, 1179 ± 166, and 1178 ± 60 × 10^3 μg P kg^{-1} ash. The TPr released from the three types of ash ranged from 199 to 448 × 10^3 μg kg^{-1} in dried tissues. From the ash treatment, the HC released a signifi-

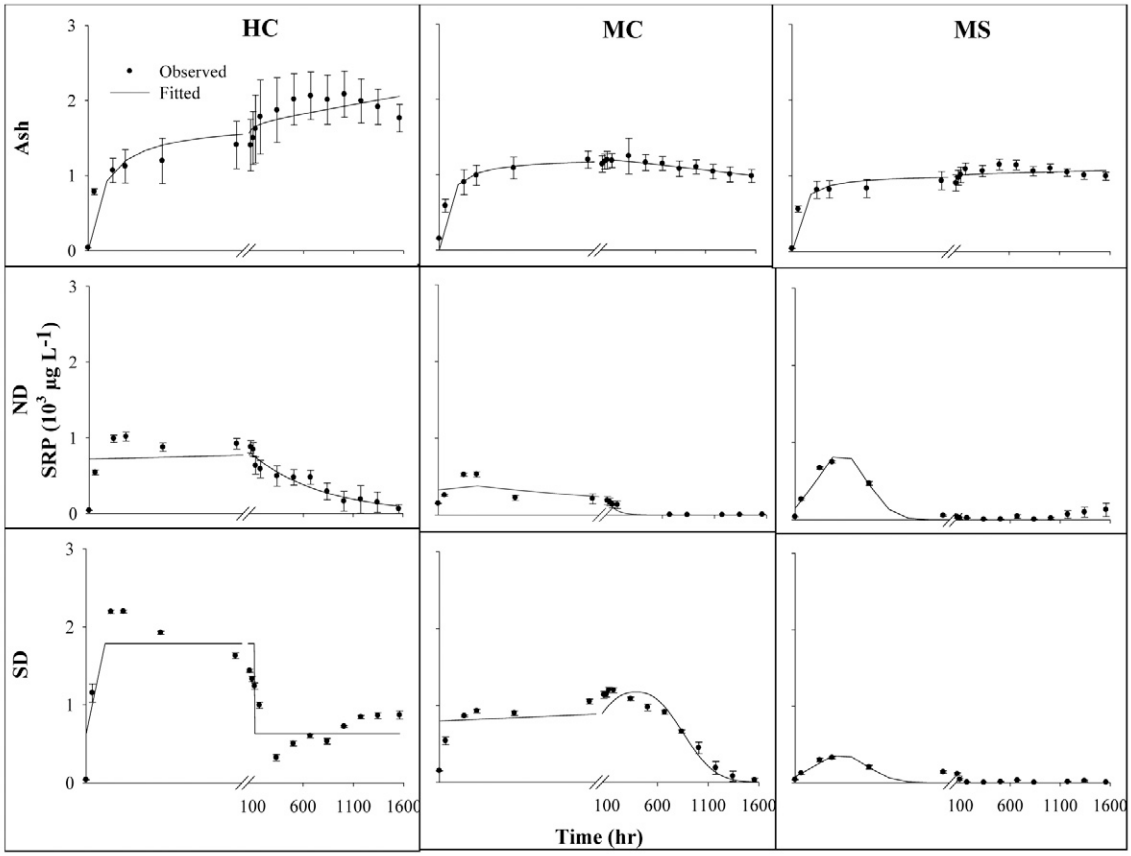

Fig. 2. Actual concentrations (10^3 µg L^{-1}) of soluble reactive phosphorus (SRP) released from ash; natural-dead plants; and burning-dead plants collected from the Everglades, Florida. To better show the changes in the first period of time, the *x*-axis has a break at Hour 50. HC, cattail in highly impacted zone; MC, cattail in moderately impacted zone; MS, sawgrass in moderately impacted zone; ND, senesced-dead, namely, natural-dead; SD, burning-dead, namely, standing-dead.

cantly greater amount of TPr than that of either MC or MS at $p < 0.01$ (Fig. 3). Furthermore, cattail in the H zone released 92% more TPr than the same species in the M zone. However, the concentrations of TPr released from the two different species in the same zone were not significantly different ($p > 0.05$).

The TPr released from cattail in different zones showed the same pattern: the burning-dead tissues had about twice the TPr release than the senesced-dead tissues (Fig. 3). The TPr of the senesced-dead of HC was as much as 406% that of MC. Similarly, the burning-dead released 266% more TPr from HC than from MC. In addition, the senesced-dead in HC released 29% more TPr than the burning-dead of MC. The burning-dead of HC released significantly more TPr than any of the other three types of dead tissues at $p < 0.01$ and $LSD_{2, 0.01} = 71.7 \times 10^3$ µg P kg^{-1}.

The TPr released from the burning-dead of MC was more than twice that of the senesced-dead of MC. However, the senesced-dead from MS released a greater amount of TPr than the burning-dead of MS while the burning-dead of MC and the senesced-dead of MS released similar amounts of TPr. The burning-dead of MS released a greater amount of TPr than the senesced-dead from MC. The difference in TPr released from the senesced-dead and burning-dead tissues was significant at $p < 0.05$ for cattail but not for sawgrass in the M zone (Fig. 3). In the same zone, the TPr release patterns for the two species were in opposite directions.

Percentage Either of Released Total Phosphorus in Total Phosphorus of the Plant Tissues or of Soluble Reactive Phosphorus in Released Total Phosphorus

The TPp of either the ash or dead plants of both species was significantly different (Fig. 4 and Table 2). The TPr released from different sources also differed significantly (Table 2). The percentage of the TPr released from ash was 84, 63, and 88% for HC, MC, and MS, respectively. The corresponding percentage from the senesced-dead and burning-dead tissues was 17, 9, and 28% and 48, 19, and 23%, respectively. The ash and senesced-dead had the same pattern: MS > HC > MC. The burning-dead had a different pattern: HC > MC > MS. Figure 3 shows the contributions of the SRP and PP in the ash, natural-dead, and burning-dead tissues. The percentage of SRP in the TPr released from the ash was 53, 66, and 57%, respectively. Correspondingly, the percentage in the TPr from the natural-dead was 7, 31, and 22%, for HC, MC, and MS. The percentage in the TPr from the burning-dead was 45, 10, and 7%. The SRP released from the ash was always >50% but that released from the dead tissues was always less than one-third except the burning-dead from HC which had a 45% contribution to the TPr (Fig. 3).

Dynamic Changes in Released Total Phosphorus with Time

Table 3 shows that TPr released from each of the ash samples or dead plants increased with time in the first 24 h of incubation ($r =$

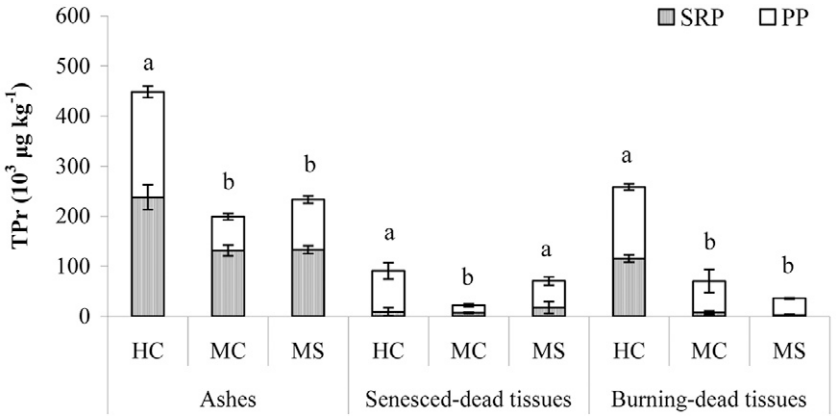

Fig. 3. Total phosphorus (TPr = soluble reactive phosphorus [SRP] + particulate phosphorus [PP]) released (10^3 μg kg^{-1} tissues) from ash or plants either of cattail or sawgrass, the Everglades, Florida. Error bars are SE of SRP or PP. In the same category, the bars sharing the same letter are not significant in TPr at $p < 0.05$. $LSD_{2, 0.05} = 62.9 \times 10^3$ μg P L^{-1} for the ashes, 44.1×10^3 μg P L^{-1} for the senesced-dead, and 50.7×10^3 μg P L^{-1} for the burning-dead, respectively.

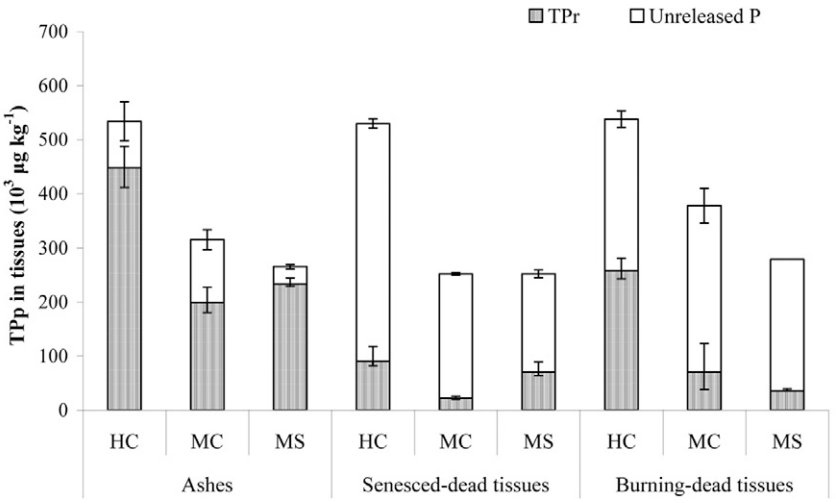

Fig. 4. Total phosphorus (TPp = TPr + nonreleased P) concentrations (10^3 μg L^{-1}) in both cattail and sawgrass plant tissues, the Everglades, Florida. HC, cattail in highly impacted zone; MC, cattail in moderately impacted zone; MS, sawgrass in moderately impacted zone; TPr, total phosphorus released from ash or dead plant tissues. Error bars are SE of TPr or unreleased P.

0.71 to 0.85). The concentrations of TPr for the HC and MS ash were also significantly and positively correlated with time from 24 to 1560 h but those from the senesced-dead and burning-dead in HC, the senesced-dead in MC, and the burning-dead in MS were negatively correlated ($p < 0.01$) or nonsignificant for the same period. The positive correlations within the first 24 h show that the ash continued to release P throughout the incubation period whereas the dead tissues released P generally within the first 24 h. The ash released 52, 97, and 66% TPr for HC, MC, and MS within the first 24 h, respectively. However, TPr released from the dead tissues within the first 24 h was up to five times of what was released during the remaining incubation period (Table 3).

Discussion

One of important findings in the present study was the quick (within a day) release of TPr from ash and dead leaf tissues, which may explain the P surge observed in the surface water immediately following a fire in the marsh (Miao et al., 2010). As expected, differences in P release and P speciation between ash and dead plant tissues were apparent. For example, the TPr released from ash was faster than that of tissues. Most of TPr released from ash was SRP while only a small proportion of that released from the tissues was SRP. A prescribed burning increased P release from the two species significantly. Cattail tissues of both the senesced-dead and burning-dead released threefold TPr in H more than in M. The burning-dead cattail tissues released twofold TPr more than the senesced-dead tissues. However, the senesced-dead sawgrass tissues released onefold TPr more than the burning-dead tissues.

Phosphorus Released from Ash and Plant Tissues

Fire changes the chemistry of an ecosystem. Soluble (e.g., sucrose) and insoluble (e.g., cellulose) carbohydrates from plant tissues are emitted as CO_2 into the atmosphere when limiting carbon sources are burned. However, tricalcium phosphate [$Ca_3(PO_4)_2$], trimagnesium phosphate [$Mg_3(PO_4)_2$], and other salts may be left behind following prescribed fires (Qian et al., 2009). These changes influence P dynamics in the system.

Salts remaining after a prescribed burn can release large quantities of P into surface waters. Tricalcium phosphate can release >3.5 $\times 10^3$ μg P L^{-1} into the water (Liu et al., 2007) and $Mg_3(PO_4)_2$ releases even greater amounts due to its greater solubility product constant (Lide, 1998). Although carbon is lost to the atmosphere, some phosphorus remains for microbial activity such as DNA, RNA, and phospholipid forms that may be released as SRP and PP forms.

Phosphorus release differs depending on the state of the plant (i.e., senesced-dead or burning-dead) after a prescribed burn. The difference may be attributed to the plants' ability to relocate bioavailable P from old to young tissues before death. Accordingly, the senesced-dead tissues had lower TPp than the burning-dead tissues (Fig. 4). However, the senesced-dead and burning-dead tissues in HC had similar amounts of TPp because the H zone is enriched with P and cattail in the H zone does not need to reallocate its P before death (Fig. 4). Nutrient retranslocation in plants is a strategy for themselves to use nutrients efficiently. However, they do not have to do so if there are abundant nutrients in their growth environment. In the M zone, cattail has a higher demand for P than sawgrass because its carbon fixation rate is nearly double that of sawgrass (Richardson et al., 2007, 2008b). This gives cattail a competitive advantage over sawgrass to bioaccumulate P from the environment. Craft et al. (2008) reported that the top 5 cm of soil in the Everglades contains more than twofold P than that at 10- to 15-cm depth. Therefore, system characteristics promote P uptake by cattail more than sawgrass, and thus, burning-dead tissues of cattail had significantly greater TPp concentration than those of sawgrass (Fig. 4). Consequently, the MC burning-dead tissues

had greater TPr release than the MS senesced-dead tissues and the MS burning-dead tissues during the first 1392 h (58 d) of incubation (Fig. 2). In addition, burning significantly accelerated P release from the dead plants because fire breaks down the plant cell architecture by oxidizing carbon and leaving much of the minerals behind with ash. Phosphorus is likely released from ash and dead tissues into the marsh water as P accumulation of 527×10^3 μg P L^{-1} has been reported in their cytoplasm (Mimura, 1999).

Percentage of Soluble Reactive Phosphorus in Released Total Phosphorus

In the Everglades, SRP is the most bioavailable form of P that primary producers can readily absorb (Wetzel, 2001; Richardson et al., 2008a); hence, it is a more instantaneous and influential contributor to plant communities in the Everglades than other forms such as PP. Prescribed burning is highly effective in reducing the number of cattail stems (Nelson and Dietz, 1966; Weller, 1975). The comparison of Fig. 1 and Fig. 2 shows that after burning, the majority of the P in ash was released in a soluble reactive form. This SRP is very mobile. Therefore, slow water movement may reduce the movement of mobile P.

The mean concentration of the instant SRP was generally more than three-fourths of the TPr from ash because most of the TPr was converted into phosphate salts during burning (Table 4). In addition, most of the organic carbon was lost during burning, limiting nutrient availability for microbial activity. However, the PP was up to three-fourths of the TPr released from the senesced-dead tissues. This may have been attributed to the fact that most of the bioavailable P was relocated into the growth center such as new leaves before death (Marschner, 1995). Furthermore, some macromolecules such as nucleic acids may have been partially broken down into soluble molecules of organic phosphorus during the natural senescence of the plants. For the burning-dead from both HC

Table 2. Calcium and magnesium contents in cattail and sawgrass growing in the Everglades, Florida, and comparison of total phosphorus (TPr) released at $p < 0.05$ and $LSD_{2, 0.05} = 8.2\%$.

Identity†	Species	Habitat	Calcium		Magnesium		TPp		TPr				
			% ± SE				10^3 μg ± SE		10^3 μg ± SE		% of TPp ± SE		
Ash													
HC	Cattail	H	5.63	0.00	0.86	0.09	1.60	0.00	1.34	0.10	83.93	6.10	a‡
MC	Cattail	M	6.53	0.44	0.58	0.11	0.95	0.00	0.60	0.05	63.12	5.13	b
MS	Sawgrass	M	0.81	0.10	0.36	0.06	0.80	0.01	0.70	0.02	87.92	2.59	a
Senesced-dead tissues													
HC	Cattail	H	6.89	0.00	0.97	0.10	1.59	0.11	0.27	0.07	16.92	3.63	ef
MC	Cattail	M	7.92	0.00	0.35	0.07	0.76	0.00	0.21	0.04	28.35	5.63	d
MS	Sawgrass	M	0.86	0.00	0.34	0.03	0.76	0.02	0.07	0.01	8.90	1.11	f
Burning-dead tissues													
HC	Cattail	H	4.37	0.01	0.74	0.08	1.62	0.03	0.78	0.07	48.09	3.37	c
MC	Cattail	M	5.13	0.87	0.81	0.14	1.15	0.10	0.22	0.08	19.59	8.32	e
MS	Sawgrass	M	0.76	0.20	0.37	0.08	0.84	0.01	0.11	0.00	12.90	0.05	ef

† H, highly impacted zone; HC, cattail in H; M, moderately impacted zone; MC, cattail in M; MS, sawgrass in M.

‡ Different letters indicate significant differences at $p < 0.05$.

Table 3. Total phosphorus (TPr) released within 24 h and correlation coefficient (*R*) between incubation time and TPr.

Identity†	Species	Habitat	TPr released within 24 h		*R* between TPr and time	
			Concentration	A‡	0–24 h	24–1560 h
			10^3 μg L^{-1}	%	$n = 5$	$n = 13$
Ash						
HC	Cattail	H	1.74	51.72	0.83	0.74**
MC	Sawgrass	M	1.44	96.50	0.82	–0.06
MS	Sawgrass	M	1.15	65.68	0.72	0.74**
Senesced-dead tissues						
HC	Cattail	H	1.71	250.13	0.75	–0.94**
MC	Sawgrass	M	0.61	115.33	0.71	–0.86**
MS	Sawgrass	M	0.82	484.27	0.78	–0.08
Burning-dead tissues						
HC	Cattail	H	3.17	163.40	0.75	–0.38
MC	Sawgrass	M	1.52	281.02	0.85	–0.97**
MS	Sawgrass	M	0.45	167.42	0.76	–0.38
$R_{n-2, 0.05}$					0.88	0.55
$R_{n-2, 0.01}$					0.96	0.68

** Significant at $p < 0.01$.

† H, highly impacted zone; HC, cattail in H; M, moderately impacted zone; MC, cattail in M; MS, sawgrass in M.

‡ A, percentage of TPr released from 0 to 24 h in TPr released from 24 to 1560 h.

and MC, the PP was much less than the SRP but for the burning-dead from MS, the SRP was less than one-third of the PP. The ratio of SRP to PP gives a clearer description: marsh water has an approximately 1-to-1 relationship (Table 4). The ratio for the ash was 3.1 to 4.6 and that for the natural-dead tissues was about 0.4 to 0.7. However, for the burning-dead tissues, the ratios were highly species dependent, that is, those in HC and MC were 1.3 and 1.5 and that in MS was 0.3 (Table 4). As stated above, due to a greater photosynthesis rate, cattail plants grow rapidly and hence the burning-dead cattail had greater bioavailable P concentrations than the burning-dead sawgrass. Furthermore, as aforementioned, cattail has a looser tissue texture than sawgrass. Its loose texture may favor microbial activity, accelerating organic P transformation to SRP when there was readily available carbon source for microbial consumption. On the contrary, sawgrass has a tighter tissue texture than cattail. This textural characteristic makes it relatively harder for microbial activity to occur. Thus, the organic P transformation to SRP in sawgrass might be slower than that in cattail.

Released Total Phosphorus from the Ash or Tissues

The proportion of TPr released from TPp of the ash or tissues of cattail and sawgrass is significantly different. This is closely associated with the extent of impact between the zones and with the plant species. For example, the SRP fraction for the HC ash is significantly greater than that of MC. This is not unexpected, as the cattail plants in the H zone have a much greater P concentration in the tissues and, consequently, HC produces much more P available for biological uptake than MC. The percentage of TPr released from TPp of MS is significantly greater than that from TPp of MC. In the same M zone, the burning-dead tissues of cattail have significantly greater TPp than those of sawgrass (Fig. 4) (Qian et al., 2009). However, the TPr release pattern is opposite for MC and MS. This is attributed to the concentrations of Ca and Mg in the tissues of the two species. In fact, cattail contained about 6 to 9 times more Ca than sawgrass in the same zone. Cattail also had a higher Mg concentration than sawgrass (Table 2), consistent with a previous study (Qian et al., 2009). Therefore, cattail ash has a greater capacity to bind P than sawgrass, but the P release from its ash is low due to the low solubility of $Ca_3(PO_4)_2$ and $Mg_3(PO_4)_2$ (Lide, 1998).

Table 2 shows that the HC ash released 155% more TPr than the mean TPr of the senesced-dead and burning-dead from HC. Similarly, the MC ash or MS ash released >300% more TPr than the mean TPr of the corresponding natural-dead and burning-dead from MC or from MS. This indicates that more TPr was released from cattail and sawgrass with prescribed burning than without burning. Effective management of phosphorus depends on understanding trends in TPr release from either ash or dead plants. The TPr release rate from the ash within 24 h was significantly greater than the mean release rate of the remaining 64 d (Table 3). The dead tissues had mono-peak curves for the TPr within the first 24 h after prescribed fire except the burning-dead from MC. The majority of the TPr from the dead tissues was released within the first day. After that, the actual concentration of TPr decreased generally. This suggests that a considerable portion of the TPr released from the dead tissues in the first 24 h became insoluble thereafter, likely due to microbial uptake of P. The implication is that less P will be mobilized if the water undergoes minimal movement for the first 24 h after the prescribed burn. The quick release of TPr from ash and both dead tissues observed in this experiment may help explain the P surge in the surface water immediately following a fire in the marsh (Miao et al., 2010).

There were large fluctuations in TPr or SRP concentrations in both Fig. 1 and Fig. 2. There may have been a few influencing factors: dynamic, chemical, and microbial. The dynamic cause resulted from the changes in P concentration gradients between the P source (ash or dead plant tissues) and incubation medium (marsh waters from either the H or M zone). At the very beginning, the P concentration gradient was the maximum and hence the rate of P release from the ash or dead plant tissues was the fastest. The rate was slowed down as the P gradient got smaller with time. The chemical factor may have been able to attribute to the precipitation reactions between phosphorus and metal ions such as calcium, magnesium, iron, and/or aluminum. These metal ions may have been released from decomposition of the dead plant tissues. Finally, the microbial factors may

Table 4. Soluble reactive phosphorus (SRP) and particulate phosphorus (PP) fractions in total phosphorus (TPr) released from different sources in the Everglades, Florida.

Identity†	Habitat	Species	TPr ± SE	SRP	PP	SRP/PP
			10^3 μg L^{-1}	%		value ± SE
			Ash			
HC	H	Cattail	3.36 ± 0.24	78.7	21.3	3.69 ± 1.01
MC	M	Cattail	1.50 ± 0.12	82.1	17.9	4.60 ± 0.71
MS	M	Sawgrass	1.75 ± 0.05	75.5	24.5	3.08 ± 0.71
			Senesced-dead tissues			
HC	H	Cattail	0.68 ± 0.18	42.3	57.7	0.73 ± 0.17
MC	M	Cattail	0.17 ± 0.02	33.4	66.6	0.50 ± 0.03
MS	M	Sawgrass	0.53 ± 0.09	26.0	74.0	0.35 ± 0.04
			Burning-dead tissues			
HC	H	Cattail	1.94 ± 0.17	56.3	43.7	1.29 ± 0.06
MC	M	Cattail	0.54 ± 0.20	60.1	39.9	1.51 ± 0.03
MS	M	Sawgrass	0.27 ± 0.00	23.0	77.0	0.30 ± 0.02
			Marsh water			
MW	M	No plants	0.15 ± 0.00	50.2	49.8	1.01 ± 0.14

† H, highly impacted zone; HC, cattail in H; M, moderately impacted zone; MC, cattail in M; MS, sawgrass in M; MW, marsh water from M.

have contributed to biosyntheses of proteins or other biological macro-molecules as the microbial population got larger in the incubation system. These biosyntheses may have interacted with the above metal ions. These interactions may have mobilized the insoluble phosphates formed from the aforementioned precipitations. Bioavailable P concentration may have increased in the marsh waters as a result of these interactions. Additionally, multiplying microbes may have absorbed bioavailable P in the water and reduced P concentration in the marsh water. Thus, the contributions of microbes to the fluctuations of P concentrations were diverse and may have been complicated.

Conclusions

A 65-d incubation at air-conditioned room temperature was conducted with ash produced by burning natural-dead and standing-dead plant tissues of either cattail or sawgrass and with the natural-dead and standing-dead tissues of either of these species. The two species were collected from highly and/or moderately impacted zones in the Everglades. The study concluded that (i) the first 24 h after burning were critical to P pulse; (ii) approximately two-thirds to three-quarters of total P in ash were released to the water; (iii) natural-dead cattail tissues released about 17 to 28% of their total P into the water; (iv) the corresponding sawgrass dead tissues released only 9% of their total P into the water; (v) burning-dead plant tissues released significantly more P than the natural-dead except cattail tissues from the moderately impacted zone; (vi) ash or tissues of cattail always released more P in the highly impacted zone than in the moderately impacted zone. To minimize P transport downstream, it is very important to keep the water motionless in the first 24 h after a prescribed fire.

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