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Nutrient and growth responses of cattail (*Typha domingensis*) to redox intensity and phosphate availability

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• *Background and Aims* In the Florida Everglades, the expansion of cattail (*Typha domingensis*) into areas once dominated by sawgrass (*Cladium jamaicense*) has been attributed to altered hydrology and phosphorus (P) enrichment. The objective of this study was to quantify the interactive effects of P availability and soil redox potential (Eh) on the growth and nutrient responses of *Typha*, which may help to explain its expansion.
• *Methods* The study examined the growth and nutrient responses of *Typha* to the interactive effects of P availability (10, 80 and 500 μg P L^{-1}) and Eh level (−150, +150 and +600 mV). Plants were grown hydroponically in a factorial experiment using titanium (Ti^{3+}) citrate as a redox buffer.
• *Key Results* Relative growth rate, elongation, root-supported tissue/root ratio, leaf length, lateral root length and biomass, as well as tissue nutrient concentrations, were all adversely affected by low Eh conditions. P availability compensated for the negative effect of low Eh for all these variables except that low P stimulated root length and nutrient use efficiency. The most growth-promoting treatment combination was 500 μg P L^{-1}/ + 600 mV.
• *Conclusions* These results, plus previous data on *Cladium* responses to P/Eh combinations, document that high P availability and low Eh should benefit *Typha* more than *Cladium* as the growth and tissue nutrients of the former species responded more to excess P, even under highly reduced conditions. Therefore, the interactive effects of P enrichment and Eh appear to be linked to the expansion of *Typha* in the Everglades Water Conservation Area 2A, where both low Eh and enhanced phosphate availability have co-occurred during recent decades.

Key words: Everglades, growth, nutrient, phosphorus, redox potential, *Typha domingensis*.

INTRODUCTION

The Florida Everglades is one of the world's great wetland ecosystems and the largest subtropical wetland in the United States (Davis and Ogden, 1994). Historically, the freshwater component of the Everglades was dominated by monospecific stands of the sedge sawgrass (*Cladium jamaicense* Crantz; hereafter *Cladium*) and aquatic sloughs. *Cladium* is adapted to the oligotrophic conditions of the Everglades and exhibits low tissue nutrient requirements, slow growth rates, and nutrient conservation through retention and recycling (Davis, 1991; Miao and DeBusk, 1999; Lorenzen *et al.*, 2001; Miao, 2004). In contrast, cattail (*Typha domingensis*; hereafter *Typha*), a fast growing species with high nutrient requirements and low nutrient use efficiency (Miao and Sklar, 1998; Miao and DeBusk, 1999; Lorenzen *et al.*, 2001; Miao, 2004), historically occurred in small and scattered patches throughout the Everglades (Davis *et al.*, 1994). However, the restricted dominance of *Typha* began to change in the mid-1900s (Davis, 1994; Jensen *et al.*, 1995; Rutchey and Vilchek, 1999). For example, in Water Conservation Area 2A (WCA-2A), an impounded area within the northern Everglades, monotypic *Typha* expanded from 442 ha in 1991 to 1979 ha in 2003 (Rutchey *et al.*, 2008).

A number of studies have suggested that phosphorus (P) enrichment (Koch and Reddy, 1992; Urban *et al.*, 1993; Davis, 1994; Craft *et al.*, 1995; Craft and Richardson, 1997; Miao and Sklar, 1998; Newman *et al.*, 1998; Hagerthey *et al.*, 2008) together with altered hydroperiod (Loveless, 1959; Urban *et al.*, 1993; Light and Dineen, 1994; Busch *et al.*, 1998; Newman *et al.*, 1998) are key factors responsible for such community changes. Lengthened hydroperiods and higher water levels frequently occurred in the Everglades, leading to more reduced soil conditions and thus lower redox potential (Eh; Qualls *et al.*, 2001). *Typha* is a highly flood-tolerant species with the capacity for internal pressurized gas flow to rhizomes through a well-developed aerenchyma system that provides oxygen for root growth in anaerobic substrates (Brix *et al.*, 1992). *Cladium*, in contrast, has no convective flow and exhibits root oxygen deficiencies under reduced soil conditions (Chabbi *et al.*, 2000; Sorrell *et al.*, 2000). However, hydroperiod changes alone cannot explain the dominance of *Typha* over *Cladium* in the Everglades (Newman *et al.*, 1996; Richardson *et al.*, 1999). A P-enrichment

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gradient, resulting from a loading of total P (TP) averaging 229 t from 1978 to 1988 and 147 t from 1995 to 2004, extends 5–8 km into the interior of the northern WCAs (South Florida Water Management District, 2006). Nutrient analyses of sediment cores from WCA-2A have shown that soil and pore water TP ranged from 400 mg kg^{-1} and 5–15 μg L^{-1}, respectively, in the unenriched locations to 1500 mg kg^{-1} and 1000 μg L^{-1}, respectively, in areas adjacent to inflows (Vaithiyanathan and Richardson, 1999). Previous research has indicated that *Typha* and *Cladium* respond to P differently, with *Typha* being able to exploit increased P to a much greater extent than *Cladium* (Craft *et al.*, 1995; Newman *et al.*, 1996; Miao and Sklar, 1998). The general consensus has been that in high-P areas in the Everglades, *Cladium* is replaced by dense stands of invasive *Typha* (Jensen *et al.*, 1995; Craft and Richardson, 1997; Rutchey and Vilchek, 1999; Childers *et al.*, 2003). However, field fertilizer experiments could not confirm that adding P alone results in *Typha* invasion (Craft *et al.*, 1995; Chiang *et al.*, 2000; Smith *et al.*, 2008), which suggested that other environmental factors, e.g. hydrology, may have interactive effects with P addition in aiding *Typha* expansion (Richardson *et al.*, 2008*a*).

The effect of altered hydrology on plant communities is often influenced by nutrient availability (White, 1994). However, only limited research has documented the interactive effects of Eh and P availability on the plant growth, nutrient dynamics and species dominance in the Everglades (Lissner *et al.*, 2003*a*; Chen *et al.*, 2005, 2008). Lissner *et al.* (2003*a*) demonstrated that the negative effect of low Eh on the growth response of *Cladium* is ameliorated at enriched P levels. Comparable research on *Typha* has not yet been conducted, although high Eh intensity has previously been shown to reduce the growth and P uptake of the two species (Kludze and DeLaune, 1996; Pezeshki *et al.*, 1996, DeLaune *et al.*, 1999).

Consequently, the present study was designed to document the interactive effects of various redox intensities and P availability on the growth and nutrient acquisition of *Typha*. We hypothesized that any growth reduction in *Typha* that might occur under low Eh levels would be compensated for by high P. Additionally, these responses were compared with those previously demonstrated for *Cladium* (Lissner *et al.*, 2003*a*). Therefore, the present study also aimed to determine if species differences might help to explain the replacement of *Cladium* by *Typha* in the Everglades. Because the mobility of P in a complex soil environment is controlled by both Eh and pH (Faulkner and Richardson, 1989), a hydroponic system was used in this research to control the Eh and P availability precisely (Lissner *et al.*, 2003*b*).

MATERIALS AND METHODS

Plant material

Seeds of *Typha domingensis* Pers. were collected from the oligotrophic area (Site U3) of WCA-2A, Florida, USA. They were germinated in a growth chamber (Environmental Growth Chambers, Model G10, Chagrin Falls, OH, USA) with peat (Jiffy-Mix Plain, Jiffy Products of America, Chicago, IL, USA) as the substrate in a 14 : 10 h, 25 : 10 °C photo- and thermo-period with photosynthetically active radiation (PAR) of 300 μmol m^{-2} s^{-1} on the peat surface. These conditions have previously been found to stimulate their germination (Lorenzen *et al.*, 2000).

Experimental procedures

Six weeks after germination, peat was carefully rinsed from the roots, and plants were transferred to a hydroponic nursery system. Each growth unit of the nursery consisted of a 10-L container with eight plants, within the experimental growth chamber (Environmental Growth Chambers, Model M-75 equipped with Sunbrella fixtures, Chagrin Falls, OH, USA). The chamber was operated with a 12 : 12 h day/night photoperiod and a 28 : 20 °C thermoperiod. The light intensity varied from 2000 μmol m^{-2} s^{-1} PAR at 1 m above shoot base level to 1200 μmol m^{-2} s^{-1} PAR at shoot base level.

A true replicated hydroponic system was designed to cultivate single plants under controlled Eh and to allow accurate and fast control of Eh and P levels (Lissner *et al.*, 2003*a*, *b*). Redox potential was controlled by the automatic addition of a reducing agent, titanium (Ti^{3+}) citrate (DeLaune *et al.*, 1990), or by bubbling compressed air as an oxidizing agent. Each experimental unit consisted of a 4-L bottle that served as a nutrient solution tank. The lid was furnished with a central hole mounted with a *Typha* plant. The lid was also mounted with (1) a calomel electrode, (2) three replicate platinum electrodes of the welded type (Patrick *et al.*, 1996), (3) an inlet pipe terminating in a bubble stone carrying air or nitrogen gas for mixing and purging, and (4) an inlet pipe from an air pump connected to the oxidation–reduction potential controller. A solenoid valve connected to the oxidation–reduction potential controller was used to control Ti^{3+} citrate addition. Flow was generated by gravity using a 125-mL plastic bottle as a Ti^{3+} citrate reservoir.

The hydroponic nursery units contained a nutrient solution (Lissner *et al.*, 2003*a*) that resembles pore water concentrations measured in the unenriched, oligotrophic, central Everglades. An additional solution containing P (as orthophosphate), K, Ca, SO_4 and micronutrients was added daily in 40 μg PO_4-P L^{-1} increments during the establishment phase. Furthermore, a nitrogen addition solution containing NH_4^+ and $FeSO_4$ was prepared fresh daily and added relative to plant uptake. The two addition solutions were designed to compensate for nutrient uptake of *Typha*, thus restoring the ionic composition daily. Available PO_4-P and NH_4^+-N were measured colorimetrically using the ammonium molybdate method (Murphy and Riley, 1962) and the automated phenate method (Method 350·1, EPA-600 4-79-020, US Environmental Protection Agency, 1979), respectively. All solutions were prepared in deionized water. Transpired water was replenished daily with deionized water and pH was adjusted to 6·5. A complete solution renewal was undertaken every week. Phosphorus addition was reduced to 10 μg P L^{-1} d^{-1} for 5 d prior to transferring to the experimental containers with the purpose of depleting any pool of excess P in the plants. The transfer was undertaken 8 weeks after germination when plants were 40–50 cm tall.

The experimental design was a randomized block 3 × 3 factorial replicated four times with a total of 36 experimental

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units (hydroponic cultures). The three P levels were 10 (ambient), 80 (moderately enriched) and 500 μg P L^{-1} (highly enriched) designated P10, P80 and P500, respectively. The three redox levels were −150 (highly reduced), +150 (moderately reduced) and +600 mV (oxic). A detailed description of Eh establishment and maintenance was provided by Lissner *et al.* (2003*b*). The P treatment levels were re-established every 12 h with a deoxygenated P addition solution (Lissner *et al.*, 2003*a*). Addition volumes were calculated every few days based on depletion rates determined from P measurements using the ammonium molybdate method. NH_4^+ and $FeSO_4$ were added daily using a nitrogen addition solution (Lissner *et al.*, 2003*a*). Solution pH was adjusted manually once or twice daily to approx. 6·25 by adding 1 M NaOH or HCl. The nutrient solution was renewed weekly using deoxygenated solutions for the medium and low redox treatments. Reduced Ti^{3+} citrate was used to adjust the redox level of the nutrient solution to treatment level before renewal. Oxidized Ti^{3+} citrate was added to the +150 and +600-mV treatments to achieve the same total concentration of Ti^{3+} citrate as in the −150-mV treatment. Titanium citrate in the reservoirs was renewed twice weekly.

Growth and biomass

Initial fresh weights of 36 plants were determined using a standardized weighing procedure, and the plants were randomly assigned to experimental units. Ten extra plants were sectioned into shoots/leaves, shoot bases (the disc-shaped stem), rhizomes and roots, and initial fresh weights were determined. The average fresh to dry weight of the extra plants and their biomass fractions were calculated after drying to a constant weight in a forced ventilation oven at 65 °C. The biomass data were used to calculate the initial dry weight of each experimental plant and their biomass fractions. After a growth period of 1 month, shoot and root lengths of each plant were measured, and the number of leaves was counted. Plants were then rinsed in deionized water before they were fractionated into shoots/leaves, shoot bases, rhizomes and roots, and dried for dry weight determination. Relative growth rates [RGR (mg d. wt g d. wt^{-1} d^{-1})] were calculated as the difference in the natural logarithm of final and initial dry weights divided by days. Based on the biomass fractions, the ratio of root-supported tissue (shoots/leaves, shoot bases, rhizomes) to the root biomass (RSB/RB ratio) was calculated. In addition, leaf elongation rates (cm d^{-1}) were determined 18 d after onset of treatments by measuring changes in the length of two consecutive, young leaves during a 3-d period.

Tissue nutrients

Nitrogen content (mg N g d. wt^{-1}) was analysed by gas chromatography after combustion of 5-mg samples (Perkin-Elmer, Series II CHNS/O Analyzer 2400, Norwalk, CT, USA) for leaves, shoot bases, rhizomes and roots after being finely ground with a mixer mill (model MM2500, Retsch, Germany). The concentrations of P, K, Ca, Mg (mg g d. wt^{-1}), Mn, Mo, Cu, Zn and Fe (μg g d. wt^{-1}) for plant fractions were determined by inductively coupled argon-plasma spectrometry (Thermo Jarrell Ash ICAP 61, Germany) after digestion of 200-mg samples in HNO_3 and H_2SO_4. Submerged ramets and dead plant material were excluded from the analysis. Initial elemental concentrations in plant fractions were calculated using values averaged from the ten randomly selected plants from the nursery stock. Uptake of N and P were calculated as mg N per plant and mg P per plant, respectively. In addition, nutrient use efficiency of N and P (NUE, g d. wt g N^{-1}, and PUE, g d. wt g P^{-1}, respectively) was recorded as the average inverse N and P concentration using the tissue concentrations of N or P in the plant fractions and the plant fraction biomasses.

Statistical analysis

All variables were analysed using multivariate analysis of variance (MANOVA) with JMP (version 3·1, SAS Institute, Cary, NC, USA). The multivariate model applied for the factorial random block design was Y = f (block, Eh intensity, P level). Logarithmic transformations of most variables were performed to ensure normality of error terms prior to testing. The MANOVA test was significant ($P < 0{\cdot}001$) for the interaction of redox intensity and P. Two-way ANOVAs were subsequently carried out for each independent variable to determine significant differences in responses to redox intensity and P availability. No adjustments of the probability levels were undertaken. Fisher's protected least significant difference procedure was used to separate means at the $\alpha = 0{\cdot}05$ level. The ANOVA tests were carried out using Statgraphics v.3·1 (Statistical Graphics Corp., Rockville, MD, USA).

RESULTS

Growth and biomass

Growth of *Typha* was generally enhanced by increasing P availability and solution Eh (Fig. 1). Significant interactions of Eh and P were detected for RGR, leaf elongation and RSB/RB ratio (Table 1). The negative effect of reducing conditions was most pronounced at P80 for RGR and elongation, and at P500 for RSB/RB ratio (Fig. 1). Meanwhile, all of these parameters were positively correlated with P availability at each Eh level, except for RSB/RB ratio between P10 and P80 (Fig. 1). Furthermore, RGR and leaf elongation were 2–2·5 and 4·5–5·5 times higher when subjected to a 50-fold increase in P availability across all Eh levels (Fig. 1A, B). In general, high P availability compensated for low Eh conditions for RGR, elongation and RSB/RB ratio, all of which peaked in the P500/ + 600 mV combination (Fig. 1).

Redox intensity and P availability also had interactive effects on final leaf and root biomass accumulation (Table 1), both of which were stimulated by high P availability across the three Eh conditions, except that root biomass at +600 mV was maximized at P80 instead of P500 (Fig. 2A, C). As with RGR and leaf elongation, changes in shoot and root biomasses were more dramatic between those under oxic and reduced conditions at P80 than at the other two P levels. The three Eh levels did not significantly affect RGR and root biomass at P500 (Figs 1A and 2C). In addition, there was no interaction between Eh and P on rhizome

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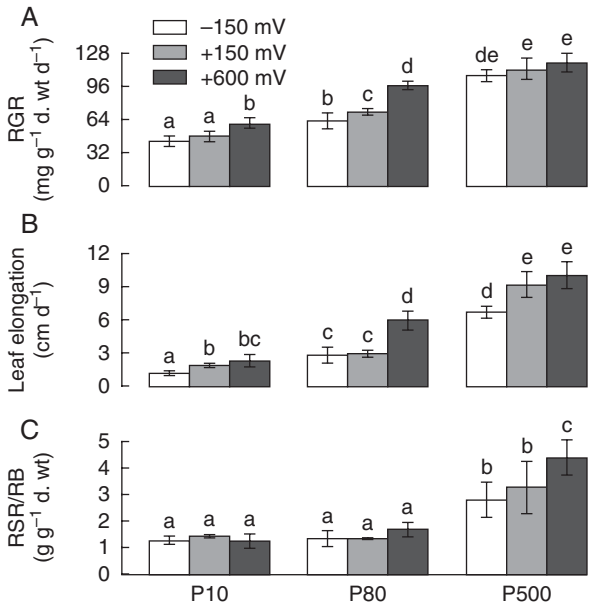

FIG. 1. Relative growth rate (A), leaf elongation rate (B) and ratio of supported biomass (shoots, shoot bases, rhizomes) to root biomass (RSB/RB ratio, C) of *Typha domingensis* plants grown for 1 month at phosphate levels of 10, 80 and 500 μg P L^{-1} and redox intensities of −150, +150 and +600 mV. Values were back-transformed means ±95 % asymmetric confidence limits ($n = 4$). Means with the same letters are not statistically different ($P > 0{\cdot}05$).

biomass and the main effect of Eh was not significant (Table 1). *Typha* accumulated the greatest rhizome biomass under P500 conditions (Fig. 2B). Little rhizome biomass was formed at P10 (Fig. 2B), with some plants producing no rhizomes at all.

Both Eh and P levels significantly affected leaf length and lateral root length of *Typha*, with no interactive effects noted (Table 1). Plants developed longest leaves at P500 (Fig. 3A). In addition, lateral roots in general tended to be longer at P80 than at P10, but did not differ greatly between P80 and P500 (Fig. 3C). The effect of Eh on leaf length or lateral root length was not dramatic (Fig. 3A, C). The effect of P on lengths of primary roots, however, was dependent on the intensity of Eh (Table 1). *Typha* generally produced longer roots at P10 as compared with at P80 and P500 at each Eh level. Solution Eh affected root length differently at different P availabilities. Maximum lengths of primary roots were 65 % longer for P10 plants grown at +600 mV than for plants grown at −150 mV. Eh had a less dramatic effect on lengths of primary roots at P80 or P500, with longest roots at P80 recorded under +150 mV and at P500 under +600 mV (Fig. 3B).

Tissue nutrients

Phosphorus. Interactive effects of P availability and Eh levels were detected for leaf and shoot base P concentrations, but not for root P (Table 1). Overall, highest leaf, shoot base and root P were associated with highest Eh values and highest P availability. Highest P concentrations in these tissues were always found in the P500/+600 mV combination. It was also noted that the differences between −150 and +150 mV, as well as between P10 and P80, were not as dramatic as compared with those between +150 and +600 mV and those between P80 and P500 (Table 2).

TABLE 1. *Analysis of variance for growth, biomass, morphological and nutrient characteristics of* Typha domingensis *grown at phosphate (P) levels of 10, 80 and 500 μg P L^{-1} and redox (Eh) intensities of −150, +150 and +600 mV (n = 4)*

	Block	P	Eh	P × Eh
Growth				
RGR	0·029	**0·001**	**0·001**	**0·004**
Leaf elongation	0·112	**0·001**	**0·001**	**0·004**
RSB/RB ratio	0·073	**0·001**	**0·007**	**0·010**
Leaf biomass	0·115	**0·001**	**0·001**	**0·001**
Rhizome biomass	0·538	**0·001**	0·063	0·587
Root biomass	0·872	**0·001**	**0·001**	**0·001**
Leaf length	0·526	**0·001**	**0·003**	0·465
Root length	0·869	**0·001**	**0·001**	**0·001**
Lateral root length	0·752	**0·001**	**0·001**	0·272
Phosphorus				
Leaves	0·922	**0·001**	**0·001**	**0·002**
Shoot bases	0·102	**0·001**	**0·001**	**0·042**
Roots	0·206	**0·001**	**0·001**	0·996
P uptake	0·666	**0·001**	**0·001**	**0·001**
PUE (g d. wt g P^{-1})	0·600	**0·001**	**0·001**	0·200
Nitrogen				
Leaves	0·712	**0·001**	**0·001**	**0·001**
Shoot bases	0·710	**0·001**	0·079	**0·031**
Roots	0·323	**0·001**	**0·046**	**0·001**
N uptake	0·262	**0·001**	**0·001**	**0·001**
NUE (g d. wt g N^{-1})	0·577	**0·001**	**0·001**	**0·001**
Macronutrients				
Potassium	0·957	**0·001**	**0·005**	0·263
Calcium	0·746	**0·001**	**0·001**	0·139
Magnesium	0·951	**0·002**	**0·001**	0·013
Micronutrients				
Manganese	0·563	**0·001**	**0·009**	0·289
Zinc	0·181	**0·001**	**0·001**	**0·001**
Molybdenum	0·361	**0·003**	**0·001**	0·577
Copper	0·072	**0·001**	**0·001**	**0·007**
Iron	0·378	**0·001**	**0·015**	**0·001**

Values in bold indicate significant effects at $P < 0{\cdot}05$.

Total P uptake showed a similar pattern to tissue P concentrations in response to the three Eh levels and P conditions (Tables 1 and 2). The values of −0·37 and −0·28 mg P per plant for P10/−150 mV and P10/+150 mV represented a net loss (dilution) of P by growth during the experimental period (Table 2). PUE was enhanced by low P. Meanwhile, reduced conditions (−150 and +150 mV Eh) tended to be associated with increased PUE (Tables 1 and 2).

Nitrogen. Interactive effects of P and Eh were found on N content in leaves, shoot bases, roots, N uptake and NUE (Table 1), which generally showed a similar pattern to those of tissue P concentrations, P uptake and PUE (Tables 2 and 3). However, the differences in N content in leaves, shoot bases, rhizomes and roots were less dramatic than for P content (Tables 2 and 3). Total N uptake was 10- to 23-fold greater at P500 than at P10 within each Eh level and was about 1·4- to 5·2-fold greater at +600 mV than at −150 mV within each P level (Table 3). NUE, however, decreased

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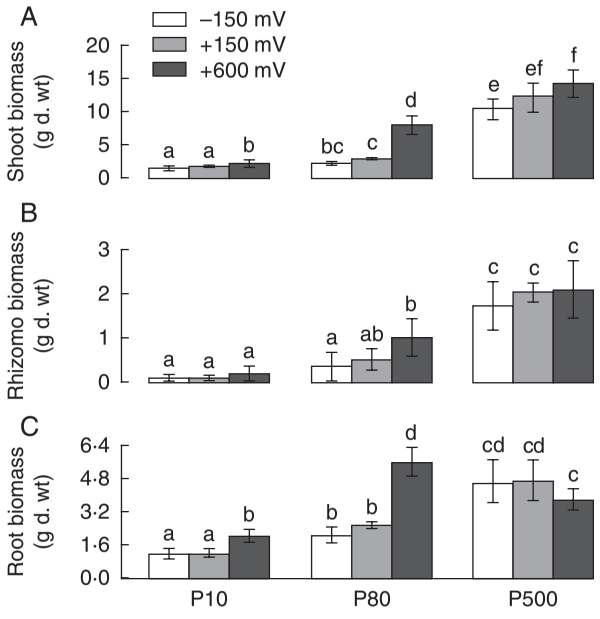

FIG. 2. Final (harvest) biomass of shoots (A), rhizomes (B) and roots (C) of *Typha domingensis* plants grown at phosphate levels of 10, 80 and 500 μg P L^{-1} and redox intensities of −150, +150 and +600 mV. Values were back-transformed means ±95 % asymmetric confidence limits ($n = 4$). Means with the same letters are not statistically different ($P > 0{\cdot}05$).

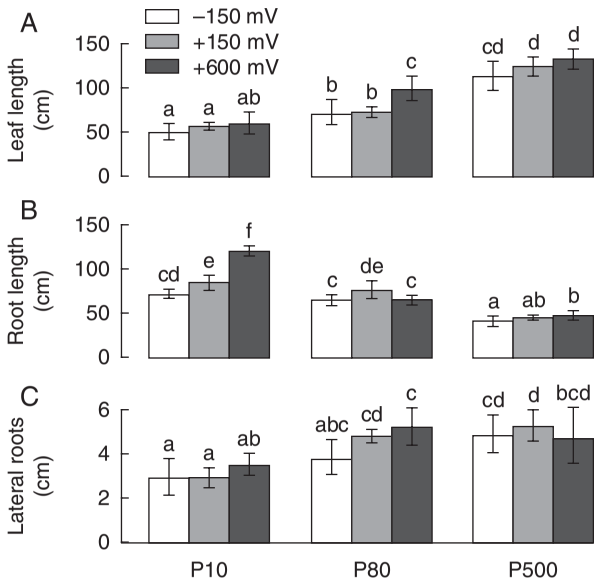

FIG. 3. Shoot length (A), root length (B) and length of lateral roots (C) of *Typha domingensis* plants grown at phosphate levels of 10, 80 and 500 μg P L^{-1} and redox intensities of −150, +150 and +600 mV. Values were back-transformed means ±95 % asymmetric confidence limits ($n = 4$). Means with the same letters are not statistically different ($P > 0{\cdot}05$).

from P10 to P80 to P500 (Table 3). There was a significant P × Eh interaction pointing to a greater effect of Eh level on NUE at low P availability (Tables 1 and 3).

K, Mg, Ca, Mn, Mo, Cu, Zn and Fe. In general, concentrations of leaf K, Mg, Ca, Mn and Mo were positively correlated with P availability and Eh (Tables 1 and 4). Significant interactions

TABLE 2. *Phosphorus concentrations (mg P g d. wt^{-1}), P uptake (mg P per plant) and phosphorus use efficiency (PUE, g d. wt g P^{-1}) in* Typha domingensis *grown at indicated phosphate and redox levels*

		Treatment combinations									
		10 μg L^{-1} P			80 μg L^{-1} P			500 μg L^{-1} P			
		−150 mV	+150 mV	+600 mV	−150 mV	+150 mV	+600 mV	−150 mV	+150 mV	+600 mV	
Leaves	L_1 Mean L_2	(0·27) $0{\cdot}31^{a}$ (0·36)	(0·24) $0{\cdot}28^{a}$ (0·33)	(0·30) $0{\cdot}34^{a}$ (0·39)	(0·27) $0{\cdot}40^{a}$ (0·53)	(0·29) $0{\cdot}40^{a}$ (0·51)	(0·70) $0{\cdot}80^{b}$ (0·90)	(1·43) $1{\cdot}60^{c}$ (1·77)	(1·68) $1{\cdot}86^{d}$ (2·03)	(2·08) $2{\cdot}38^{e}$ (2·69)	
Shoot bases	L_1 Mean L_2	(0·10) $0{\cdot}13^{a}$ (0·17)	(0·12) $0{\cdot}15^{a}$ (0·19)	(0·23) $0{\cdot}24^{b}$ (0·26)	(0·29) $0{\cdot}41^{c}$ (0·59)	(0·26) $0{\cdot}33^{bc}$ (0·43)	(0·85) $0{\cdot}97^{d}$ (1·11)	(2·25) $2{\cdot}48^{e}$ (2·74)	(2·63) $3{\cdot}28^{e}$ (4·08)	(5·13) $5{\cdot}58^{f}$ (6·08)	
Rhizomes	L_1 Mean L_2	(−) 0·17 (−)	(−) 0·33 (−)	(−) 0·07 (−)	(−) 0·35 (−)	(−) 0·38 (−)	(−) 0·81 (−)	(2·23) 2·60 (3·03)	(2·71) 2·97 (3·26)	(3·63) 4·13 (4·70)	
Roots	L_1 Mean L_2	(0·08) $0{\cdot}13^{a}$ (0·19)	(0·09) $0{\cdot}12^{a}$ (0·15)	(0·14) $0{\cdot}22^{b}$ (0·33)	(0·35) $0{\cdot}58^{c}$ (0·97)	(0·38) $0{\cdot}55^{c}$ (0·79)	(0·83) $0{\cdot}99^{d}$ (1·13)	(2·20) $2{\cdot}60^{e}$ (3·07)	(1·83) $2{\cdot}25^{e}$ (2·77)	(3·79) $4{\cdot}35^{f}$ (4·99)	
P-uptake	L_1 Mean L_2	(−0·55) $-0{\cdot}37^{a}$ (−0·18)	(−0·39) $-0{\cdot}28^{ab}$ (−0·16)	(−0·25) $0{\cdot}26^{b}$ (0·86)	(0·53) $1{\cdot}41^{c}$ (2·50)	(1·11) $2{\cdot}05^{c}$ (3·20)	(11·8) $13{\cdot}0^{d}$ (14·4)	(35·4) $40{\cdot}4^{e}$ (46·0)	(43·5) $49{\cdot}4^{e}$ (56·0)	(73·9) $80{\cdot}1^{f}$ (86·9)	
PUE	L_1 Mean L_2	(4200) 4800^{e} (5500)	(4200) 4900^{e} (5700)	(3300) 3800^{e} (4400)	(1600) 2300^{d} (3300)	(1700) 2300^{d} (3200)	(1050) 1150^{c} (1260)	(480) 500^{b} (530)	(430) 470^{b} (520)	(300) 330^{a} (360)	

Values are back-transformed means ($n = 4$) and 95 % confidence limits (L_1 = lower limit, L_2 = upper limit). For each variable, any two values with the same superscript letter do not significantly differ ($P > 0{\cdot}05$).

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TABLE 3. *Nitrogen concentrations (mg N g d. wt^{-1}), N uptake (mg N per plant) and nitrogen use efficiency (NUE, g d. wt g N^{-1}) in* Typha domingensis *grown at indicated phosphate and redox levels*

		Treatment combinations								
		10 μg L^{-1} P			80 μg L^{-1} P			500 μg L^{-1} P		
		−150 mV	+150 mV	+600 mV	−150 mV	+150 mV	+600 mV	−150 mV	+15 mV	+600 mV
Leaves	L_1 Mean L_2	(9·4) 10·5^{ab} (11·7)	(9·5) 9·7^{a} (9·9)	(10·9) 11·3^{bc} (11·7)	(10·7) 11·9^{c} (13·2)	(10·7) 11·9^{c} (13·2)	(19·3) 21·5^{d} (24·0)	(22·0) 24·6^{e} (27·5)	(24·4) 25·5^{ef} (26·7)	(27·2) 28·8^{f} (30·4)
Shoot bases	L_1 Mean L_2	(19·4) 20·3de (21·2)	(17·8) 18·9^{ce} (20·1)	(16·9) 18·3^{bd} (19·9)	(14·7) 17·0^{ac} (19·6)	(12·5) 14·7^{a} (17·3)	(14·0) 16·2^{ab} (18·8)	(19·9) 21·5^{e} (23·2)	(19·9) 21·5^{e} (23·1)	(26·5) 27·0^{f} (27·5)
Rhizomes	L_1 Mean L_2	(12·7) 14·0 (15·3)	(13·7) 14·7 (15·7)	(12·5) 12·7 (12·8)	(12·2) 12·9 (13·6)	(11·8) 12·5 (13·2)	(14·3) 16·1 (18·2)	(23·7) 24·9 (26·3)	(24·2) 25·9 (27·8)	(26·1) 27·0 (28·0)
Roots	L_1 Mean L_2	(14·2) 15·6^{a} (17·1)	(13·8) 15·6^{a} (17·7)	(18·9) 20·0^{cd} (21·1)	(16·8) 18·5^{bc} (20·5)	(19·0) 19·6^{bd} (20·3)	(17·6) 18·0^{b} (18·3)	(20·9) 21·7^{d} (22·4)	(20·5) 21·3^{d} (22·1)	(20·9) 21·4^{d} (21·9)
N-uptake	L_1 Mean L_2	(13) 16^{a} (19)	(13) 19^{a} (29)	(41) 50^{b} (61)	(47) 50^{b} (54)	(66) 71^{c} (77)	(220) 260^{d} (310)	(320) 370^{e} (440)	(370) 430^{ef} (500)	(450) 520^{f} (590)
NUE	L_1 Mean L_2	(51) 53^{e} (54)	(46) 54^{e} (63)	(29) 32^{d} (36)	(31) 33^{d} (36)	(31) 32^{d} (33)	(19) 20^{c} (22)	(17) 18^{b} (20)	(17) 17^{ab} (18)	(15) 16^{a} (17)

Values are back-transformed means ($n = 4$) and 95 % confidence limits (L_1 = lower limit, L_2 = upper limit). For each variable, any two values with the same superscript letter do not significantly differ ($P > 0·05$).

TABLE 4. *Leaf concentrations of potassium, calcium and magnesium (mg g d. wt^{-1}), and manganese, zinc, molybdenum, copper and iron (μg g d. wt^{-1}) for* Typha domingensis *plants grown at the indicated phosphate and redox levels*

		Treatment combinations								
		10 μg L^{-1} P			80 μg L^{-1} P			500 μg L^{-1} P		
		−150 mV	+150 mV	+600 mV	−150 mV	+150 mV	+600 mV	−150 mV	+150 mV	+600 mV
Potassium	L_1 Mean L_2	(20) 23^{a} (25)	(22) 23^{a} (25)	(27) 30^{b} (33)	(24) 32^{b} (42)	(32) 36^{bc} (40)	(39) 40^{c} (41)	(46) 50^{d} (53)	(50) 53^{d} (57)	(48) 52^{d} (57)
Calcium	L_1 Mean L_2	(5·6) 6·6^{a} (7·8)	(5·1) 5·9^{a} (6·9)	(6·9) 8·2^{bc} (9·9)	(5·4) 6·2^{a} (7·1)	(6·1) 6·8^{ab} (7·5)	(8·2) 9·4^{c} (10·9)	(7·8) 8·8^{c} (9·9)	(8·2) 8·7^{c} (9·3)	(8·9) 9·6^{c} (10·3)
Magnesium	L_1 Mean L_2	(1·0) 1·1^{bc} (1·3)	(0·9) 1·0^{a} (1·1)	(1·2) 1·4de (1·6)	(1·0) 1·1^{ab} (1·2)	(1·0) 1·1^{ab} (1·1)	(1·4) 1·6^{e} (1·7)	(1·3) 1·4de (0·5)	(1·2) 1·3^{cd} (1·3)	(1·3) 1·4de (1·5)
Manganese	L_1 Mean L_2	(8) 14^{ab} (25)	(12) 16^{abc} (21)	(14) 18^{bc} (23)	(5) 12^{a} (28)	(15) 26^{cd} (47)	(22) 27^{cde} (32)	(28) 39de (54)	(41) 50^{e} (60)	(40) 45de (50)
Zinc	L_1 Mean L_2	(18) 20^{ab} (21)	(14) 22^{b} (36)	(28) 31^{c} (35)	(12) 14^{a} (16)	(13) 21^{ab} (33)	(47) 53^{d} (59)	(21) 26^{bc} (32)	(63) 68^{d} (74)	(86) 99^{e} (114)
Molybdenum	L_1 Mean L_2	(1·0) 1·4^{ab} (1·8)	(1·6) 1·8^{bc} (1·9)	(2·0) 2·7^{c} (3·5)	(0·7) 1·2^{a} (2·2)	(1·6) 2·0^{bc} (2·4)	(2·1) 2·5^{c} (3·0)	(0·7) 1·0^{a} (1·3)	(0·9) 1·3^{ab} (2·0)	(1·1) 1·3^{ab} (1·6)
Copper	L_1 Mean L_2	(6·9) 8·5^{cde} (10·5)	(6·8) 8·1^{cde} (9·8)	(8·5) 10·6^{f} (13·3)	(6·0) 6·3^{b} (6·7)	(6·3) 7·0^{bc} (7·8)	(8·3) 9·3^{def} (10·5)	(4·2) 4·9^{a} (5·6)	(7·1) 7·7^{bcd} (8·4)	(8·7) 9·7^{ef} (10·9)
Iron	L_1 Mean L_2	(25) 26^{a} (27)	(21) 24^{a} (29)	(24) 30^{a} (39)	(23) 29^{a} (35)	(33) 41^{b} (51)	(41) 47^{b} (53)	(47) 63^{c} (83)	(86) 91^{d} (97)	(41) 45^{b} (50)

Values are back-transformed means ($n = 4$) and 95 % confidence limits (L_1 = lower limit, L_2 = upper limit). For each variable, any two values with the same superscript letter do not significantly differ ($P > 0·05$).

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between P and Eh were found for leaf Zn, Cu and Fe (Table 1). The effects of Eh on Zn and Cu concentrations were greater at P500 than at P10. Iron, by contrast, exhibited a rather erratic response to Eh (Table 4).

DISCUSSION

Growth and biomass

In the present study, an overall increased growth for *Typha* was found in response to P availability, and the best performance was generally observed at P500 among all three P levels. This result was consistent with previous studies that reported an increase in *Typha* growth and dominance with P addition (Craft and Richardson, 1993, 1997; Newman *et al.*, 1996; Miao and Sklar, 1998; Doren *et al.*, 1999; Miao *et al.*, 2000; Lorenzen *et al.*, 2001; Miao, 2004; Macek and Rejmánková, 2007). Elevated P concentrations have also been shown to greatly increase RGR, shoot elongation rate, biomass and photosynthesis of other plant species, including *Cladium* (Lissner *et al.*, 2003*a*; Vymazal *et al.*, 2008), *Rhynchospora tracyi* (Busch *et al.*, 2004; Chen *et al.*, 2008) and *Eleocharis* spp. (Rejmánková, 2001; Busch *et al.*, 2004; Chen *et al.*, 2005; Macek and Rejmánková, 2007). The only growth parameter that was enhanced by low P availability was root length. Increased root length resulting from P stress is considered a strategy that leads to a larger P-absorbing surface area and a greater volume of soil exploited in natural environments (Chapin, 1991; Kirk and Du, 1997).

The present results confirmed that *Typha* has a high capacity for P uptake and therefore supported the general notion that this species is adapted to high P environments and is typical of nutrient-rich habitats (Davis, 1990). In contrast, it was previously shown that *Cladium* growth did not increase much from P80 to P500, indicating that a high level of P availability could not be exploited by this species (Lissner *et al.*, 2003*a*). Furthermore, the growth of this species does not always show a clear response to increasing P availability (Newman *et al.*, 1996; Lorenzen *et al.*, 2001). Craft and Richardson (1997) and Richardson *et al.* (2008*b*) also reported that the frequency of occurrence and above-ground biomass of *Typha* were highly correlated with soil total P, while those of *Cladium* were negatively correlated. Therefore, *Cladium* is a species of low nutrient status (Steward and Ornes, 1983; Lissner *et al.*, 2003*a*) and exhibits traits characteristic of plants adapted to low P conditions (Berendse and Elberse, 1990; Miao and DeBusk, 1999; Lissner *et al.*, 2003*a*).

The data indicated that *Typha* had a reduction in growth under low Eh at each P level. A decrease in growth of both root and root-supported tissue under low Eh conditions is a common response for many plant species (for a review see Pezeshki, 2001). For instance, low soil Eh resulted in significant reductions in root elongation and growth in *Spartina patens*, despite the existence of extensive aerenchyma tissue (Pezeshki *et al.*, 1991). In *Epilobium hirsutum*, after 18 weeks at low Eh due to flooding, total biomass was only 54 % of that in drained conditions (Lenssen *et al.*, 2000). Several mechanisms underlining such responses have been suggested. For example, root growth and function are rapidly affected by low Eh because molecular oxygen is required as an electron acceptor for oxidative phosphorylation (Bertani and Brambilla, 1982; Drew, 1990). Consequently, the adverse effect of low soil Eh on root aerobic respiration and translocation of root-produced metabolites to shoots probably contributed to the reduction in shoot growth (Reid and Bradford, 1984; Kozlowski and Pallardy, 1997). The present study showed that low Eh dramatically impacted growth and performance when P availability was low. In contrast, reduced conditions (especially +150 mV) at high P availability (P500) had no significant effect on the growth of *Typha*. Therefore, the data support the hypothesis that the growth reduction in *Typha* by low Eh can be ameliorated by high P availability. This provides evidence that *Typha* has high tolerance to reducing conditions when P levels are high. This ability, therefore, enables *Typha* to thrive in the Everglades WCA-2A, where reduced soil conditions and P enrichment are common occurrences.

The growth of *Cladium* under solution Eh values of −150, +150 and +600 mV (Lissner *et al.*, 2003*a*) showed a similar pattern to *Typha* under each P level. This is interesting because *Typha* species are known to possess both well-developed internal gas transport systems and efficient convective gas flow, while the former is reduced and the latter is completely absent in shoots of *Cladium* (Sorrell *et al.*, 2000). The radial oxygen loss (ROL) is about twice as high for *Typha* than for *Cladium* at high redox intensity (Kludze and DeLaune, 1996). *Typha* also exhibits higher photosynthetic adaptation than *Cladium* under low soil Eh (Pezeshki *et al.*, 1996). Therefore, *Typha* possesses both morphological and physiological characteristics that give it a competitive advantage over *Cladium* along redox intensity gradients. This may not have been of benefit to *Typha* in the present study, however, as the hydroponic solution had an infinite capacity for reduction and thus impeded the formation of an oxidized rhizosphere. In addition, the results are for relatively immature (<1·5 m tall), single ramets of *Typha*. Larger plants with multiple shoots would probably have performed better under low Eh conditions.

Tissue nutrients

In addition to P concentrations in leaves, shoot bases, rhizomes and roots, whole-plant P uptake in *Typha* was positively correlated with P availability and Eh intensities. Plants grown at P10 and P80, even under +600 mV Eh, contained P that was much less than 1–4 mg P g d. wt^{-1}, the adequate tissue P level for most mature crop plants (Epstein, 1972). As a result, some P deficiency symptoms such as slow growth and die-off of the old leaves would probably have occurred at both P10 and P80, if the experiment had been longer. The P500/ + 600 mV combination represented the most ideal P availability and Eh condition for tissue P concentrations and uptake in *Typha*. Highest P concentrations and uptakes were also found in the P500/ + 600 mV group for *Cladium* (Lissner *et al.*, 2003*a*). However, their differences (percentage increase) between P80 and P500 plants for *Cladium* were not as dramatic as for *Typha*. This indicates that excess P cannot be exploited efficiently by *Cladium* but can by *Typha*, which is in agreement with the pattern in growth for these two species. The different responses of

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tissue P status to P availability between *Typha* and *Cladium* identified in this study and that of Lissner *et al.* (2003*a*) were confirmed by other studies. For instance, Lorenzen *et al.* (2001) found that these two species had similar root-specific P accumulation rates at low P levels, whereas *Typha* had 3- to 13-fold higher P uptake rate at high P levels. Furthermore, a field study in WCA-2A demonstrated that tissue P concentrations of *Typha* responded more to increased P availability than those of *Cladium* (Miao and Sklar, 1998), and a mesocosm experiment showed greater leaf nutrient concentrations in *Typha* than in *Cladium* (Newman *et al.*, 1996). In addition, annual allocation of P to leaves was estimated to be three times greater in *Typha* than in *Cladium* (Davis, 1990). Therefore, *Typha* has a higher capacity for P uptake than *Cladium*. Furthermore, low P and Eh levels both resulted in increased PUE in the present study, which is critical for *Typha* to cope with these stressful conditions (Neumann *et al.*, 1999). Slow-growing, low-nutrient status species generally have higher PUE than faster-growing species to cope with low nutrient levels. In accordance, the maximum growth rates of *Cladium* were associated with PUE as high as 1000 g d. wt g P^{-1} (Lissner *et al.*, 2003*a*) as opposed to 330 g d. wt g P^{-1} for *Typha* found in the present study.

Reduced P availability may also affect the uptake of other essential nutrients (Reinbott and Blevins, 1997), as was shown here. Nitrogen concentrations in all tissue fractions showed similar patterns as P concentrations, with higher concentrations being associated with higher P availability and higher Eh intensity. As with tissue P concentrations and uptake, the most favourable combination of P availability and redox intensity was P500/ + 600 mV for tissue N for *Typha*, while it was P80/ + 600 mV for *Cladium* (Lissner *et al.*, 2003*a*). However, N concentrations in *Typha* and *Cladium* tissues were much less sensitive to P availability than P concentrations, which was consistent with the study on *Eleocharis cellulosa* (Chen *et al.*, 2005). The non-limiting concentration of N for plants is in the range 20–50 mg N g leaf d. wt^{-1} (Marschner, 1995), indicating that in this study, *Typha* had a sufficient N supply only at P500 (Table 3).

In general, concentrations of leaf K, Ca, Mg, Mn, Zn, Mo, Cu and Fe were positively correlated with P availability and Eh (Table 4). Factors responsible for low nutrient concentrations under reduced conditions may include the reduction of the elements. For example, Mo becomes less available under reducing conditions because Mo^{6+} added can be reduced to Mo^{3+}. Low concentrations of the above nutrients at low Eh may also be due to changes in root morphology induced by low Eh, which results in fewer sites for nutrient uptake or reduced metabolically controlled uptake (Lissner *et al.*, 2003*a*). Fe^{2+}, the reduced form of Fe, and Mn^{2+}, the reduced form of Mn, were added in this experiment and should have been able to remain relatively stable under −150 and +150 mV, even though ROL may cause some oxidation of Fe^{2+} to Fe^{3+} and Mn^{2+} to Mn^{4+}. The precipitation of Fe^{3+} and Mn^{4+} could have been very pronounced at + 600 mV, but the high leaf concentrations of Fe and Mn under +600 mV indicated that no significant oxidation of Mn^{2+} and Fe^{2+} took place. All the above nutrient concentrations, except for Fe at P10 and P80, were well within or above the sufficiency range reported for plants (Marschner, 1995; Jones, 1998). Therefore, the growth of *Typha* was probably not limited by these ions.

Typha *versus* Cladium

Typha and *Cladium* have similar growth forms and occupy similar habitats. However, the two exhibit distinct differences in their life-history characteristics, as shown in Table 5. Furthermore, the results from the present study and a companion study by Lissner *et al.* (2003*a*) confirmed that *Typha* has a higher capacity for P utilization and thus it is more competitive than *Cladium* under high P availability. The present

TABLE 5. *Summary of life-history characteristics for* Cladium *and* Typha *from various sources (McNaughton, 1966; Davis, 1989, 1991, 1994; Grace, 1987; Toth, 1987; Chanton* et al.*, 1993; Koch and Rawlik, 1993; Lorenzen* et al.*, 2001), and our personal observations/unpublished data and growth and nutrient responses to P and Eh from the present study and that of Lissner* et al. *(2003*a*)*

	Cladium	*Typha*
Growth		
Relative growth rate	Low	High
Leaf elongation	Low	High
Leaf turnover rate	Low	High
Net production	Low	High
Biomass accumulation	Slow	Fast
Response to excess P*	Small	Large
Response to low Eh (single plants)	Large	Large
Response to low Eh and excess P	Moderate	Large
Nutrients		
Tissue P	High in storage	High in leaves and roots
Leaf P concentrations	Low	High
Nutrient uptake capacity	Low	High
Nutrient use efficiency	High	Low
Response to excess P*	Small	Large
Response to low Eh (single plants)	Large	Large
Response to low Eh and excess P	Moderate	Large
Physiology		
Photosynthetic capacity	Low	High
Stomatal conductance	Low	High
Leaf and root allocation	Not varied	Varied
Tissue lignin	High	Low
Decomposition		
Litter production	Low	High
Nutrient loss from senescing leaves	Low	High
Litter decomposition	Slow	Fast
Demography		
Leaf longevity	28–370 weeks	11–96 weeks
Density and size	Not variable	Variable
Morphology and anatomy		
Leaf	Narrow and tough	Wide and spongy
Leaf cuticle	Well developed	Poorly developed
Air space in leaves	Small	Large
Gas transport	Diffusion	Bulk flow ventilation

An asterisk indicates that the conclusion was based on the percentage increase in growth or nutrient parameters between P80 and P500.

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data also indicated that high P availability could compensate for the negative effect of low redox conditions for both species but could benefit *Typha* more than *Cladium* as the growth and nutrient responses of the latter species were less to excess P (Table 5). Therefore, this study provided additional evidence that the interactive effects of P availability and hydrological regime help to drive changes in vegetative communities in the Everglades. Future research would benefit from experiments that emphasize the interactive effects of plant species with P and Eh levels that simulate specific conditions within the freshwater Everglades where *Typha* expansion is occurring.

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