Effects of inundation on growth and nutrient allocation of six major macrophytes in the Florida Everglades

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ABSTRACT

Understanding the effect of hydrological alterations on the establishment and growth of macrophytes is pivotal for restoring natural wetland plant communities and for managing constructed wetlands. Growth and nutrient storage of six native macrophytes commonly found in the Florida Everglades were studied under two inundation levels (20 and 60 cm) in experimental mesocosms receiving inflow water with a low concentration of phosphorus (P). The six species, which were planted in soils collected from P-enriched areas, included one ridge species (Cladium jamaicense), three wet prairie species (Rhynchospora tracyi, Eleocharis elongata, and Eleocharis cellulosa), one slough species (Nymphaea odorata), and one fast spreading species (Typha domingensis).

Inundation level greatly affected plant survivorship, growth, and nutrient allocation. The macrophytes differed substantially in their abilities to adapt to rising inundation level and in their adaptation strategies. N. odorata exhibited a substantial increase in both biomass and nutrient storage under rising inundation and had the largest accumulation of P and nitrogen among the six species studied. Aboveground biomass (A) and belowground biomass (B) allocation varied with species. Species with a lower A/B ratio under shallow inundation (N. odorata, E. cellulosa, and T. domingensis) adapted better to deeper inundation than those with higher A/B ratios (C. jamaicense, R. tracyi, and E. elongata). Adaptation to deeper inundation was achieved either by an increase in aboveground growth (E. cellulosa and T. domingensis) or by a simultaneous increase in both aboveground and belowground growth (N. odorata). Inability to adjust the A/B ratio in response to deeper inundation was characteristic of species that experienced high mortality (R. tracyi and C. jamaicense). The results of this study, which demonstrate differences in inundation tolerance and differences in mechanisms of inundation tolerance among common and diverse wetland macrophytes, will be useful for wetland restoration and management.

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1. Introduction

Growth and development of a vast majority of vascular macrophytes is impeded by flooding and especially by complete inundation for protracted periods (Jackson and Colmer, 2005). When riverine plants are inundated, their growth and survival rates can be constrained by reduced availability of atmospheric carbon (Blanch et al., 1999; Altor and Mitsch, 2004), oxygen (Yamasaki, 1984; Crawford, 1992), and soil nutrients. To survive inundation, plants either tolerate inundation by developing internal aeration passages (Jackson and Armstrong, 1999), which increase oxygen supply and facilitate the self-repair of oxidative damage (Gibbs and Greenway, 2003; Blokhina, 2003), or physically escape from the inundated environment by increasing shoot growth (Voesenek et al., 2003) and increasing the mass allocated to sexual reproduction (Mony et al., 2010). Developing an emergent canopy to physically escape inundation was reported as a critical element for the survival of many macrophytes (Grace, 1989; Rea and Ganf, 1994; Blanch et al., 1999).

In the historical Everglades, the landscape was comprised of a distinct mosaic of ridges and sloughs that differed in water depth, inundation period, and the rate at which water levels rose and fell (Loveless, 1959; Davis and Ogden, 1994). The higher elevations, with average water depths of less than 1 m and a hydroperiod of about 6 months, were dominated by the emergent sedge Cladium jamaicense (Loveless, 1959). The lower elevations were dominated by floating-leaved vegetation including Nymphaea odorata and Nuphar luteum. In intermediate areas, wet prairie species (Rhynchospora trayci, Eleocharis elongata, Eleocharis cellulosa) dominated.

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In the past several decades, the historic vegetation pattern has been displaced primarily by monospecific cattail stands in a large portion of the nutrient impacted areas of the Everglades. Many research reports have suggested that the replacement of the historic vegetation communities resulted not simply from nutrient enrichment, but also from the interactive effect of nutrient enrichment and altered hydrology (Newman et al., 1996; DeBusk et al., 2001; Busch et al., 2004; Nungesser and Chimney, 2006; Boers et al., 2007). However, it is not clear how species growing in different habitats and species co-dominating the same habitat differ in their growth and nutrient allocation strategies when responding to varied inundation levels (Miao et al., 2009). Such information is critical for restoring natural wetlands, as well as for managing constructed wetlands for the function of nutrient removal (Tanner and Headley, 2011).

One major goal for Everglades' restoration is to restore the vast nutrient-enriched Water Conservation Areas (WCAs) dominated by *Typha domingensis* to wetlands dominated by historical native species (Davis and Ogden, 1994; Nungesser and Chimney, 2006; Miao et al., 2010). To that end, the WCAs have been receiving lower nutrient-concentration water from Stormwater Treatment Areas (STAs) established between 5 and 15 years ago. With the restoration of historical vegetation patterns as either the implicit or explicit goal of many wetland restoration projects, an improved understanding of how macrophytes respond to inundation is critical for restoring the impacted areas of the Everglades and for establishing diverse wetland plant communities in wetlands elsewhere (Dierberg et al., 2002; Kadlec, 2005; Cole et al., 2006; Miao and Zou, 2009). Thus, the objective of this study was to examine the effects of two different inundation levels on survivorship, growth, and nutrient allocation of six major macrophytes grown in soil collected from the WCAs using water from the outflow of STA 1West. We asked two questions: (1) Did the species differ in growth and biomass allocation strategies in response to inundation? and (2) Did the species differ in nutrient accumulation efficacies under different inundation levels?

2. Methods

2.1. Species studied

Six common wetland plant species, adapted to different nutrient and hydrological conditions, were studied: *C. jamaicense*, *E. cellulose*, *E. elongata*, *N. odorata*, *R. tracyi*, and *T. domingensis*. All species, excluding *T. domingensis*, are naturally adapted to soil and water conditions with low phosphorus concentrations and are commonly found in three historical Everglades landscapes: sawgrass ridges, wet prairies, and aquatic sloughs. *R. tracyi*, *E. elongata*, and *E. cellulosa* are considered to be wet prairie species and have clear morphological differences to the ridge or slough species. *R. tracyi* is a slender perennial herb that commonly forms extensive colonies, especially when growing in shallow water (Godfrey and Wooten, 1979). Along with *E. elongata*, *R. tracyi* is a dominant species in the wet prairies of the northern Everglades (Jordan et al., 1997). *E. cellulosa* is a coarse perennial with long and stout rhizomes that forms extensive colonies (Godfrey and Wooten, 1979). *E. elongata* is a slender, rhizomatous perennial, but its stems are narrower than *E. cellulosa*, and it is often weakly erect or partially floating. While both of the *Eleocharis* species are abundant in wet prairie environments, *E. elongata* tends to be dominant in the northern Everglades, while *E. cellulosa* is dominant in the central and southern Everglades (Jordan et al., 1997). *C. jamaicense* is a large, emergent plant that grows naturally in higher elevation sites subject to shallow inundation for 6 months or longer each year (Loveless, 1959); it is a

rhizomatous perennial sedge recognized by its coarse, gray-green, saw-toothed leaves and a large, highly branched inflorescence of brown spikelets (Godfrey and Wooten, 1979; Miao et al., 1997). *N. odorata*, which is very common in the sloughs or lowest elevations of the historical Everglades, is a floating-leaved plant that is widely distributed in the eastern United States and often forms dense mono-specific beds (Gleason and Cronquist, 1991; Richards et al., 2011). Although it is mainly distributed sparsely in low-nutrient reference areas in the Everglades, currently, it also can be found in highly enriched areas where it becomes more dense (McCormick and Laing, 2003). It produces floating leaves and flowers borne on long petioles and peduncles arising from the apices of horizontal, root-bearing rhizomes (Sinden-Hempstead and Killingbeck, 1996). Only one species, *T. domingensis*, a large emergent marsh plant, is commonly dominated in nutrient-enriched areas; it reproduces either by seeds or rhizomes and tends to form dense mono-specific stands (Newman et al., 2004; Miao and Zou, 2009). *T. domingensis* is reported to be able to tolerate a greater water depth and a longer hydroperiod than *C. jamaicense* (Grace, 1987, 1988; Lorenzen et al., 2001). In areas receiving large quantities of phosphorous input in the Everglades, *T. domingensis* has replaced *C. jamaicense* as the dominant marsh species.

2.2. Experimental design

The study was conducted using experimental mesocosms at the STA1W Research Facility of the South Florida Water Management District, Florida. Each mesocosm was a fiberglass tank 6 m long × 1 m wide × 1 m deep. The experiment was a split-plot design with each plot (tank) being divided into two sections to create two water levels (20 and 60 cm) with 9 replicates at the plot level (9 tanks). Within each tank, a total of 18 plants (three plants per species) were randomly placed for each water level. Each of the three plants for a given species was associated with a soil collected from one of the three locations. While the shallow inundation (20 cm) in this experiment was designed to mimic the water level of the wet prairie environment, the deeper inundation level (60 cm) simulated that of the slough habitat.

Each tank was set up as a flow-through system using outflow water from a constructed wetland (STA1 West). The water in the tank was refreshed through a constant inflow equal to 35.3 ml s^{-1} which was controlled by a flow meter. The flow rate was based on our best knowledge of water flow in the natural habitat and on the capability of the experimental tank system. The two inundation levels were achieved by controlling the elevation of pots within the sample tanks: plants subjected to the shallow inundation treatment were placed on a shelf that was 40 cm in height and plants subjected to the deeper inundation treatment were placed on the bottom of the tank. Water level in the tank was increased to 73 cm at the onset of the experiment, so that the inundation level (water depth from the soil surface of the pot to the surface of the water) was exactly 20 cm for shelf pots and 60 cm for bottom pots.

The experiment took place over a period of 15 months, starting in June 2001 and ending in August 2002. To simulate water level fluctuation between the wet and dry season during the study, water depth was fluctuated with the natural seasons. The water depth in each tank was held at 73 cm during the wet season (June 2001–February 2002), but at 0 cm during the draw down of February and March of 2002. At the beginning of February, plants that were being subjected to the deeper inundation treatment were first lifted by 40 cm to the same water depth as plants that were receiving the low inundation treatment for about one month; then, the water table in the tank was dropped by 20 cm so the soil was saturated. At the end of March 2002, all plants were returned gradually (in about three weeks) to their original position (*i.e.* the plants

Table 1

Plant height, number of ramets, shoots or leaves, fresh weight, biomass, and tissue nutrient concentrations for the six major macrophytes in the Florida Everglades (*C. jamaicense*, *T. domingensis*, *E. cellulosa*, *E. elongata*, *R. tracyi*, *N. odorata*) at the onset of experiment (mean ± standard error, n = 27).

Species		R. tracyi	C. jamaicense	E. elongata	T. domingensis	E. cellulosa	N. odorata
Height	(cm)	37.7 ± 2.9	52.7 ± 1.4	29.7 ± 0.7	54.8 ± 1.4	59.9 ± 2.3	–
Ramets	#	1.1 ± 0.2	1	3.5 ± 0.4	1	2.9 ± 0.4	–
Shoots or leaves	#	1.5 ± 0.2	3.7 ± 0.2	24.4 ± 1.3	3.3 ± 0.1	5.9 ± 1.0	3.5 ± 0.5
Fresh wt. (g)		1.85 ± 0.28	19.07 ± 1.06	8.37 ± 0.68	33.60 ± 1.37	10.08 ± 0.97	35.97 ± 4.41
Biomass (g)	Aboveground	0.19 ± 0.04	0.84 ± 0.05	0.73 ± 0.04	1.05 ± 0.05	0.77 ± 0.12	0.56 ± 0.14
	Belowground	0.12 ± 0.02	0.96 ± 0.11	0.79 ± 0.06	1.36 ± 0.07	0.73 ± 0.10	5.80 ± 0.90
	Total	0.31 ± 0.05	1.80 ± 0.15	1.52 ± 0.09	2.41 ± 0.11	1.50 ± 0.19	6.35 ± 0.96
TP Concentration (mg kg^{-1})	Aboveground	1330 ± 20	3749 ± 111	3152 ± 319	1638 ± 114	3375 ± 367	1659 ± 92
	Belowground	3329 ± 151	3696 ± 141	3142 ± 197	2160 ± 30	4313 ± 502	2309 ± 110
TN Concentration (mg kg^{-1})	Aboveground	10153 ± 385	4975 ± 148	7458 ± 999	6366 ± 196	10539 ± 335	20971 ± 474
	Belowground	6529 ± 218	6852 ± 881	9738 ± 1581	6229 ± 274	8264 ± 2060	6469 ± 222
N/P	Aboveground	16.90 ± 0.54	2.94 ± 0.09	5.45 ± 1.12	8.72 ± 0.82	6.97 ± 0.54	28.09 ± 0.96
	Belowground	4.35 ± 0.16	4.08 ± 0.39	6.99 ± 1.40	6.38 ± 0.20	4.49 ± 1.50	6.25 ± 0.47

receiving the deeper inundation treatment were placed on the floor again), and the depth was reset at 73 cm until August 2002.

Prior to the study, soils were collected from the three locations at STA1W (26°35.50″N, 80°26.21″W), STA2 (26°27.064″N 80°27.353″W), and STA3/4 (26°19.550″N, 80°34.110″W) adjacent to WCA1, WCA2, and WCA3, respectively. At each location, the top 30 cm of soil was collected with caution to keep the soil profile undisturbed as much as possible. The soil collected was stored in a walk-in cold room with temperature around 4 °C until the initiation of the study. Soils from each location were laid into flat tanks separately in a staging area and were saturated with STA1W outflow water for about two months to allow seed germination from the soil. Germinated seedlings were removed from the soil to prepare them for propagation of the six species tested in this study.

Seedlings of *C. jamaicense*, *T. domingensis*, *R. tracyi*, and *E. cellulosa* were germinated from seeds, and young plants of *N. odorata* and *E. elongata* were propagated from rhizomes collected from WCA 2A. Because of different rates of seed germination and growth rate, the plant preparation of all species lasted over six months. Individual plants of similar height for a given species were measured for fresh weight, height, and numbers of leaves and ramets, if any, and then planted into 4-L pots (13 cm in height) filled with soil from one of the locations. Potted plants were then transferred to the fiberglass tanks with soil in the pots being saturated for about 2 weeks to avoid transplanting shock before the onset of the experiment. Detailed information on plant size and nutrient concentration for each species is presented in Table 1.

2.3. Water quality and soil measurement

Water samples were collected bi-weekly at the inflow and outflow of each tank for total phosphorus (TP) analysis. These samples were collected in plastic bottles and were then acidified with H_2SO_4 and stored at 4 °C until analysis was performed. In addition, temperature, conductivity, pH, and dissolved oxygen were measured for each sample using a multiprobe sensor (Hydrolab Corp., Austin, TX78727). Weekly light readings were taken at the center of each tank using a Li-Cor light sensor. For each tank, readings were taken at three vertical locations (above the water surface and 20 cm and 60 cm below the surface), with five replicates for each location.

TP and total nitrogen (TN) for soil and plant materials were analyzed using standard methods of the USEPA (1983). Soil nutrient concentrations were converted to concentrations by volume

based on the bulk density of intact wet soil in the pot. The initial soil nutrient concentrations were averaged over six samples for each of the three locations where samples were collected in 2001.

2.4. Final harvest

All tanks were drained at the end of the 15-month experimental period to conduct final harvesting. Dead plants were first identified, recorded, and then discarded without further analysis. Parameters measured on live plants included morphology (plant height, number of leaves, and number of rhizomes), growth (biomass of plant components), biomass allocation (above- and belowground ratio), and nutrient allocation (TN and TP in different parts of plant). Plant height was defined as petiole length for *N. odorata* and as the length of the longest leaf or stem for all other species. The total number of ramets was determined for *C. jamaicense*, *E. elongata*, and *T. domingensis*. The aboveground biomass included leaves and stems, and the belowground biomass consisted of roots, rhizomes, and shoot bases for all species but *N. odorata* of which the belowground biomass consisted of roots and rhizomes only. Different plant components were oven-dried at 60 °C, weighed, analyzed for TP and TN concentrations using ash methods.

2.5. Data analysis

We used the SAS mixed model (SAS Institute Inc., Cary, NC, US) for standard split-plot design with inundation level (water depth) as the whole-plot factor to detect individual and interactive effects of water depth and species on mortality, growth attributes, and nutrient concentrations for each species. *Post hoc* Duncan's multiple range test was used to distinguish differences in mortality, growth attributes, and plant nutrient concentrations between water depths and among species.

Percent mortality for each species at each water level was the average of percentage mortality calculated for each tank (n = 9). Similarly, treatment effect on plant growth metrics and nutrient concentration were analyzed based on the mean value of survived plants in each tank. If all three plants at a given tank were dead, then one replicate was lost. For inundation of 20-cm, the replicates for all species are 9 except for CJ (n = 8). For inundation of 60-cm, the replicates are 1, 4, 5, 7, 9 and 9 for *R. tracyi*, *C. jamaicense*, *E. elongate*, *T. domingensis*, *E. cellulose*, and *N. odorata*, respectively.

Table 2
Summary of statistics (p values) for the effects of water depth, species, and their interactions on plant growth and nutrient parameters based on a SAS mixed model for standard split-plot design with water depth as the whole-plot factor.

	Water depth	Species	Depth × species
Growth attribute			
Mortality rate	<0.0001	<0.0001	0.0001
Height (cm)	<0.0001	<0.0001	0.1383
#Ramet	0.2571	<0.0001	0.7765
#Leaf	0.2113	0.3328	0.4481
#Shoot base	0.0254	<0.0001	0.0485
Leaf biomass (g)	0.3539	<0.0001	0.0151
Root biomass (g)	0.3280	<0.0001	<0.0001
Rhizome biomass (g)	0.8087	<0.0001	0.1413
Total biomass (g)	0.3348	0.0001	0.0004
A/Below ratio (%)	0.0791	<0.0001	0.0500
Nutrient concentration			
Total P (mg kg^{-1})	0.0121	<0.0001	<0.0001
Total N (mg kg^{-1})	0.0023	<0.0001	0.0147

3. Results

3.1. Water and soil conditions

TP concentration in the soils collected from three impacted wetland areas ranged from 0.052 to 0.062 mg cm^{-3}, and TN concentration ranged from 2.61 to 3.51 mg cm^{-3}. TP and TN concentration did not statistically differ among these soil samples.

The TP concentration of the inflow water averaged $25 \pm 0.0\,\mu g\,L^{-1}$ over the course of the experiment. Flow rate during the experiment was $35.3 \pm 0.1\,ml\,s^{-1}$, and the light penetration at the soil surface for the 20-cm and 60-cm treatments was 40 ± 0.4 (%) and 14 ± 0.2 (%), respectively. The mean pH, dissolved O_2, and conductivity were 7.4 ± 0.0, 2.7 ± 0.1 (mg L^{-1}), and 1041 ± 6.0 ($\mu S\,cm^{-1}$) ($n = 110$), respectively, with no significant difference in any of these factors among tanks.

3.2. Plant mortality

Mortality differed significantly among species ($p < 0.0001$) and between water depths ($p < 0.0001$). A significant interaction between species and water depth ($p = 0.0001$) was found as well (Table 2 and Fig. 1), indicating that species differed in their responses to different inundation levels. With shallow inundation (20-cm water depth), the mortality of *R. trayci* and *C. jamaicense* was >40% (40.7% and 48.1%, respectively), while *E. cellulosa*, *E. elongata*, *T. domingensis*, and *N. odorata* showed either no mortality or only minor mortality (<11.2%). With deeper inundation (60-cm water depth), the mortality of all species significantly increased ($p < 0.05$) except that mortality remained at 0% for *N. odorata*. *N. odorata* was the only species that showed no mortality at both inundation levels (Fig. 1).

3.3. Growth of surviving plants

Both water depth and species significantly affected some, but not all plant growth attributes (Table 2). Overall, water depth significantly affected ($p = 0.0001$) plant height but not the number of rhizomes or live leaves for all species (Table 2). For each species, height was generally increased by the deeper inundation level and the increase was statistically significant for *N. odorata*, *E. cellulosa*, *T. domingensis*, and *E. elongata* (Fig. 2). Moreover, interactions between water depth and species were significant for all biomass components except rhizome biomass (Table 2). Deeper inundation significantly increased the total biomass of *N. odorata*, did not change the total biomass of *T. domingensis* or *E. elongata*, and
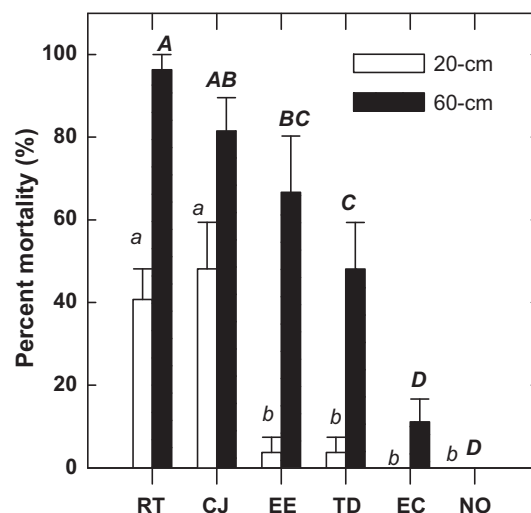

Fig. 1. Percent mortality for six wetland plant species at two water depths (mean ± standard error, $n = 9$). For a given depth, percent mortality among species are not significantly different if their means share the same letter. Species abbreviations: RT, *R. trayci*; CJ, *C. jamaicense*; EE, *E. elongata*; TD, *T. domingensis*; EC, *E. cellulosa*; NO, *N. odorata*.

significantly reduced the total biomass of *C. jamaicense* and *E. cellulosa* (*R. trayci* was not tested due to high mortality) (Fig. 2). Aboveand belowground biomass allocation as indicated by A/B ratios was affected by both water depth and species. Among the six species, the A/B ratio of *N. odorata* was the lowest at $15.2 \pm 3.9\%$ and did not change with water depth. For *T. domingensis* and *E. cellulosa*, however, the deeper water depth significantly increased A/B ratios from $43.4 \pm 4.9\%$ and $82.8 \pm 6.5\%$, respectively, to $69.2 \pm 12.0\%$ and $127.5 \pm 8.8\%$, respectively. Water depth did not affect the A/B ratio for the remaining species. Finally, at the shallow inundation level, *R. tracyi*, *C. jamaicense*, and *E. elongata* allocated most of their biomass aboveground rather than belowground (A/B ratio > 144.1%). In contrast, *T. domingensis*, *E. cellulosa*, and *N. odorata* allocated most of their biomass belowground at the shallow inundation level (A/B ratio < 82.8%).

3.4. Plant nutrient concentration and nutrient storage

TP and TN concentrations (mg kg^{-1}) in plants significantly differed among species ($p < 0.0001$) and inundation levels; the interaction between species and inundation level was also significant for these factors (Table 2). At the whole-plant level (without regard for different plant parts), the TP concentration was highest in *N. odorata* and tended to be lowest in *E. cellulosa* and intermediate among the remaining species (Fig. 3). TN concentration was highest for *N. odorata* and tended to be lowest for *C. jamaicense* and *E. cellulosa* and intermediate for the remaining species (Fig. 3).

Within the same species, differences in nutrient concentrations among different plant parts were highly species-specific and without obvious trend (Fig. 4). The leaves of *N. odorata* and *T. domingensis* contained high TP concentrations compared with the overall mean TP concentration of 513.98 ± 33.45 mg kg^{-1} in the leaves of all the species combined. The nitrogen concentration was high in *N. odorata* leaves compared with the overall mean nitrogen concentration of 8159.32 ± 509.98 mg kg^{-1} in all the leaves of all the species combined. Among the belowground parts, phosphorus and nitrogen concentrations were generally higher in shoot base than in other parts for *R. tracyi*, *C. jamaicense*, and *E. cellulosa* but not for *T. domingensis* (Fig. 4).
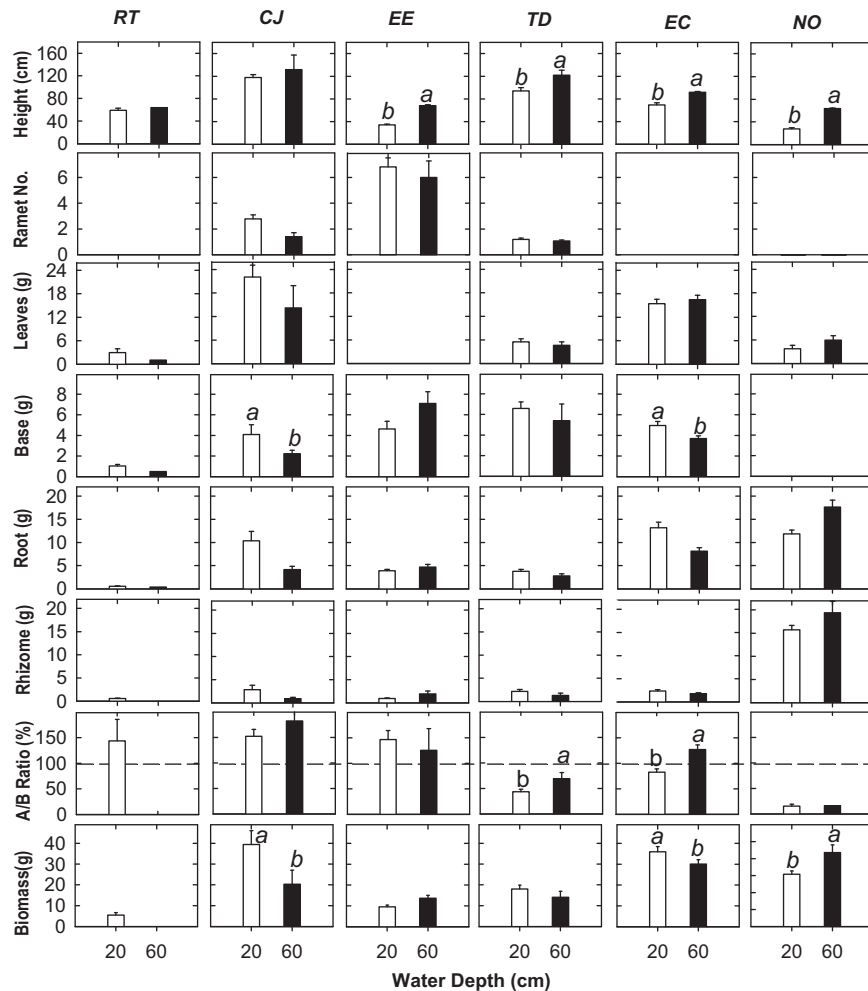
Fig. 2. Plant height, number of ramets, leaf biomass, shoot base biomass, root biomass, rhizome biomass, above- (A) and belowground (B) biomass ratio, and total biomass at two water depths (mean ± standard error). The dashed line represented 1:1 ratio of aboveground and belowground biomasses. For each species and parameter, means with different letters are significantly different according to *post hoc* Duncan's multiple range tests.

Both TP and TN concentrations increased substantially for *R. tracyi* and *C. jamaicense* under deeper inundation (Fig. 4). *Post hoc* tests indicated that the increase was significant only for TP in all parts of *C. jamaicense* and TN for leaves and bases.

4. Discussion and conclusion

Overall, our results demonstrate that under a low P condition the six species studied exhibit different inundation tolerances, with *N. odorata* being the most tolerant, followed by *E. cellulosa*, *T. domingensis*, *E. elongata*, and *C. jamaicense*; and *R. trayci* was the least tolerant. Moreover, the species differed in strategies of growth and of allocation of biomass and nutrients in response to inundation. The most tolerant species, *N. odorata*, is also the most efficient in accumulation of phosphorus and nitrogen in its tissues. Mechanisms of flood tolerance in these macrophytes are likely associated with their species-specific ability to use, redistribute, and store nutrients when water levels change.

Inundation could stimulate the production of plant hormones that in turn enhance shoot elongation (Voesenek et al., 2003) and biomass allocated to sexual reproduction (Mony et al., 2010). However, rapid shoot elongation and increase in aboveground biomass requires increased nutrient uptake and therefore sufficient belowground biomass to provide additional nutrients and to provide

adequate anchorage. It follows that, for an increase in aboveground biomass in response to inundation to improve survival, the plant should have a high belowground biomass before inundation, as indicated by a low A/B ratio. Our results suggest that the A/B ratio could serve as a useful indicator of the ability of a species to adapt to deeper inundation. Changes in the A/B ratio reflect the reallocation of resources among different parts of a plant. Developing an emergent canopy to physically escape inundation requires rapid mobilization of nutrients either among plant parts or from soil uptake. This explains why, in the present study and in other studies (Grace, 1989), plants were taller under high inundation levels than under low inundation levels.

The three species with high mortality rates (*R. trayci*, *C. jamaicense*, and *E. elongata*) all had relatively high A/B ratios (over 140%) at the low inundation level, and this ratio did not significantly change at the high inundation level, indicating a lack of growth plasticity. The two ridge and wet prairie species with low mortality (*T. domingensis* and *E. cellulosa*) had a low A/B ratio (less than 83%) and were able to increase this ratio substantially to increase aboveground growth under increased submersion in order to avoid inundation. *N. odorata* had the lowest A/B ratio among all species and was the only species that showed no mortality at both inundation levels; this species exhibited enhanced growth and nutrient accumulation in deeper water while maintaining a similar A/B
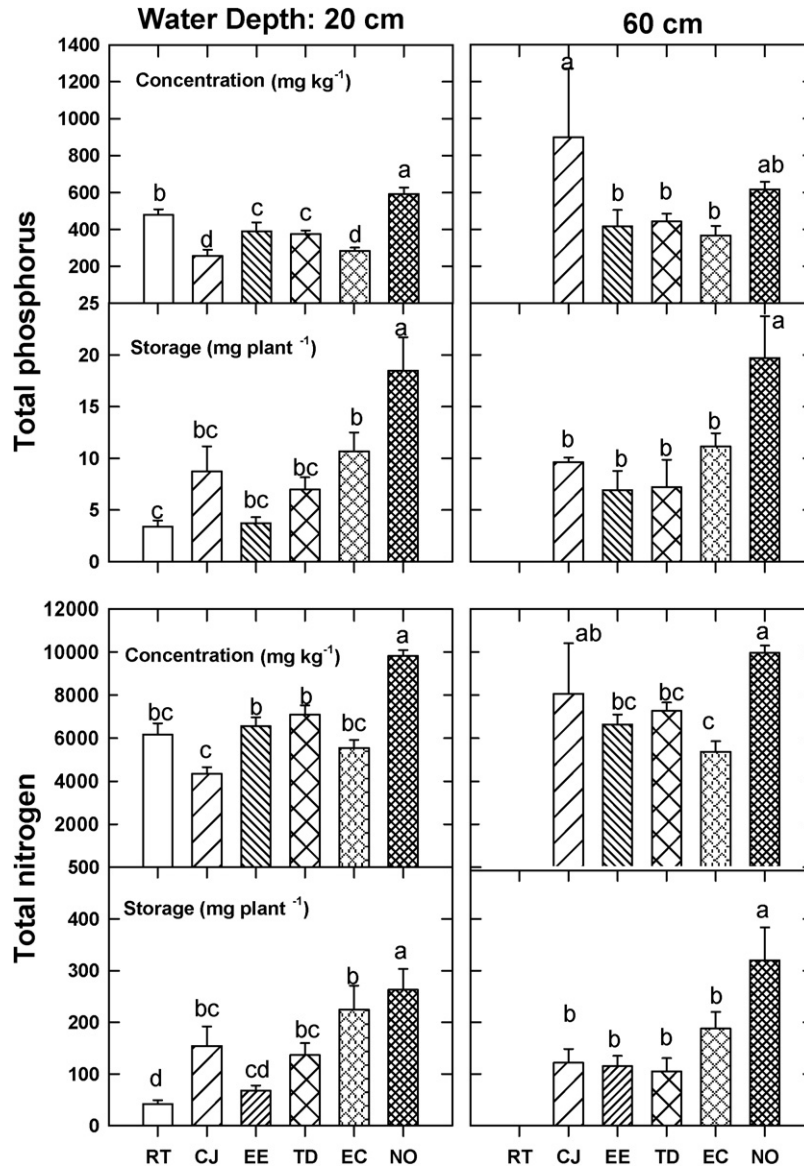
Fig. 3. Phosphorous and nitrogen concentrations and average nutrient storage for the six plant species at harvest at two water depths (mean ± standard error). Within each panel, means with the same letter are not statistically different according to a *post hoc* Duncan's multiple range test.

ratio. We infer that the adaptive strategy for *N. odorata* is to balance above- and belowground growth when the inundation level increases.

Our results suggest that the ability of co-occurring or co-dominant macrophytes to adapt to increasing inundation differs and that these differences cannot simply be inferred from the hydrology of the habitats. At the low inundation level, for example, the wet prairie species, *R. trayci*, had a very high mortality rate while other wet prairie species had almost 100% survivorship. Although mortality of all wet prairie species increased under high inundation, *R. trayci* suffered higher morality than *E. cellulosa*. Our results are consistent with other physiological studies, which demonstrated that the ability of *R. trayci* to extract nutrients was greatly affected by the redox intensity, which is differentially affected by nutrient condition and protracted inundation (Lissner et al., 2003; Chen et al., 2005, 2008; Busch et al., 2006). In contrast, *E. cellulosa* is less affected by low redox potentials (Chen et al., 2005) and has strong growth plasticity, as demonstrated by its ability to shift resources

from belowground to aboveground with rising water level (Busch et al., 2006).

N. odorata is a dominant species of the deeper slough community in southern Florida and plays an important role in peat formation (Gleason and Stone, 1994). It has become less common in many areas of the Everglades because of reduced water depth and hydroperiod (Richards et al., 2011), nutrient enrichment, and associated cattail expansion. In our study, *N. odorata* had the best ability to tolerate and even prevail under inundation. Raising the inundation level from 20 cm to 60 cm resulted in a substantial increase in plant biomass, but did not significantly alter mortality or nutrient concentration; as a consequence, this species had the highest tissue nutrient concentration (phosphorus and nitrogen) and accumulated the most nutrient during the period of the study. The capability of *N. odorata* to accumulate phosphorus was also found in other studies (McCormick and Laing, 2003; Newman et al., 2004; Hagerthey et al., 2008). Considering its inundation tolerance and nutrient accumulation capability, conservation and enhancement
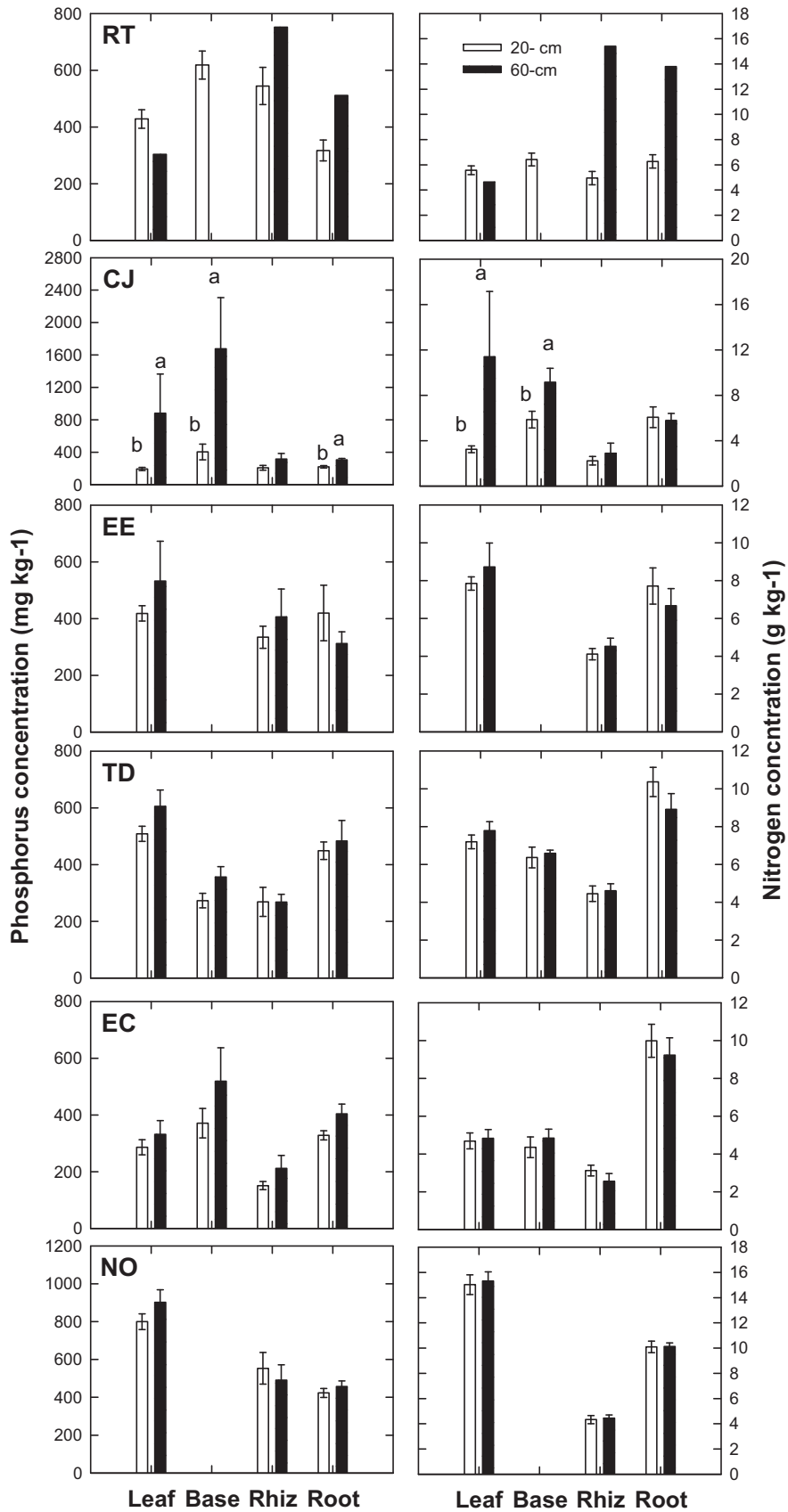
Fig. 4. Effect of water depths on total phosphorus and nitrogen concentrations in components of the six plant species studied. Means with different letters are statistically different according to a *post hoc* Duncan's multiple range tests.

of *N. odorata* in STAs could maximize nutrient-removal efficiency, particularly under a low P condition.

The expansion of *T. domingensis* and the concomitant reduction of *C. jamaicense* in the nutrient-enriched area of the Everglades have been areas of great concern in restoration. Our results show that *T. domingensis* has strong morphological plasticity and effectively adapts to increased inundation; this finding is in agreement with other studies (Grace, 1988, 1989). Success of such an adaptation is supported by morphological and ecophysiological characteristics that enable *T. domingensis* to adapt to low redox intensities associated with rising and protracted inundation (Boers et al., 2007); this gives *T. domingensis* a competitive advantage over *C. jamaicense* along a redox intensity gradient (Kludze and DeLaune, 1996; Li et al., 2010). Likely, a combination of enhanced phosphorus availability and reduced redox in the nutrient-enriched areas in the Florida Everglades benefited *T. domingensis* whilst disadvantaging *C. jamaicense*.

Since plant tissue nutrient concentration $(mg\,kg^{-1})$ is closely related to the amount of nutrients, as well as the weight of tissue mass examined, its change between the inundation level might be associated with either the change in nutrients alone, tissue mass alone, or both. For *C. jamaicense* and *E. cellulosa*, higher TP in the shoot base might be largely a result of decreased biomass in the shoot bases. However, for *T. domingensis*, TP in the shoot base was reallocated and directly contributed to aboveground biomass buildup. This increase in aboveground biomass is closely associated with the ability to survive inundation.

In summary, the current study has provided fundamental information about how a range of common wetland plant species adapt to inundation under a low P condition. The information will be useful for predicting potential trajectories of vegetation re-assembly under altered hydrology and for managing nutrient removal in nutrient-enriched natural and constructed wetlands.

Acknowledgements

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