

Vegetation and soil response to hydrology in a re-created Everglades

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Abstract Water depth and flow effects on growth and nutrient content of three marsh plants (*Cladium jamaicense* Crantz, *Eleocharis cellulosa* Torr., and *Nymphaea odorata* Aiton) and on soil-building were estimated in the Loxahatchee Impoundment Landscape Assessment where macrocosms contain habitats distinguished by relative water depth (deep slough, shallow slough, and mid-ridge) but that differ in flow. We hypothesized that optimal growth would vary with water depth and species, paralleling distributions in the natural environment, and that growth and tissue nutrients would be positively affected by flow. In addition, we hypothesized that plant morphology would influence sediment deposition with the dense

growth of *C. jamaicense* supporting greatest accretion. Our hypotheses were partly supported. *Cladium jamaicense* unexpectedly grew best in deep sloughs at depths greater than previously reported. *Eleocharis cellulosa* had a wide depth tolerance and grew best in flowing conditions. *Nymphaea odorata* grew best in slough habitats. Nutrient contents differed among species and plant parts but were not affected by flow. Soil accretion did not vary with biomass but partially varied with depth and flow, both key factors in conceptual models of vegetation and soil dynamics in wetlands, especially in the Everglades ridge-and-slough topography.

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Introduction

The ridge-and-slough landscape of the Everglades is characterized by elevated ridges, typically dominated by the emergent macrophyte *Cladium jamaicense* (sawgrass), and deeper water sloughs, characterized by the floating-leaved *Nymphaea odorata* (white water lily) (Larsen et al., 2009; McVoy et al., 2011; LoGalbo et al., 2013) and emergent *Eleocharis cellulosa* (Gulf Coast spikerush). *Eleocharis cellulosa* is also found in

wet prairies, which have hydrology intermediate between ridges and sloughs (Givnish et al., 2008; McCormick et al., 2009). Historically, the Everglades ridge-and-slough landscape was elongated parallel to the direction of flow. Approximately 50% of the original Everglades have been drained for agricultural and residential uses (Davis et al., 1994). Disruption of the slow, natural sheet-flow of water south from Lake Okeechobee through the Everglades to Florida Bay has caused the loss of north–south ridge-and-slough landscape patterning across much of the remaining Everglades (Davis et al., 1994; McVoy et al., 2011). Alteration of the pattern has been accompanied by expansion of sawgrass ridges into areas that are drier than in the past, and expansion of deep water sloughs into areas that are now wetter (McVoy et al., 2011).

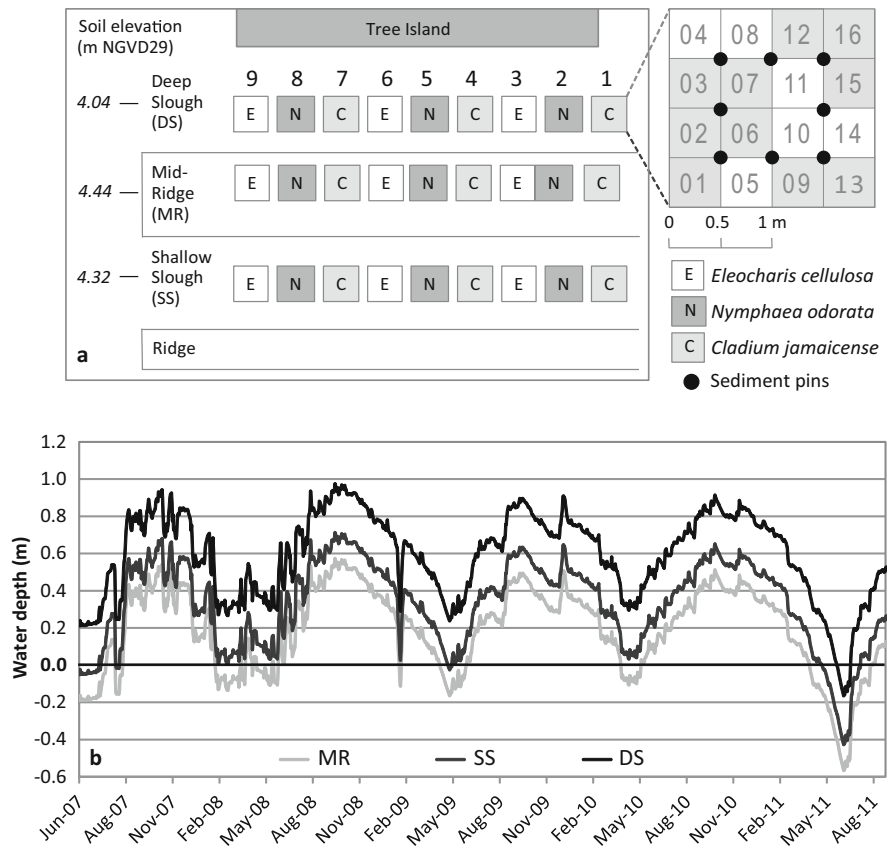
Conceptual models suggest that the spatiotemporal patterning of the ridge-and-slough landscape can be explained by the integration of surface water flow, sediment transport, and vegetation and soil dynamic processes (Lago et al., 2010; Larsen et al., 2011). In the Everglades ecosystem, changes in soil elevation, which influences hydrology, result from feedbacks among vegetation production, respiration, and hydrologic conditions (Givnish et al., 2008; Watts et al., 2010). The most common Everglades soils are peats (histosols) derived primarily from either sawgrass (Everglades peat) or water lily (Loxahatchee peat) (Davis, 1946; McVoy et al., 2011). Differences in the rates of peat accretion relative to decomposition lead to variation in the ridge-and-slough topography; an equilibrium exists with respect to the water surface when rates of organic matter decomposition and production are equal (Larsen et al., 2011). Serna et al. (2013) showed that leaf or stem litter decomposition in a re-created wetland was similar among flow treatments and habitats but differed by species, confirming the importance of litter nutrient content. Therefore, we examined the effect of water depth and flow (nutrient and sediment transport) on the growth and survival of three dominant ridge-and-slough species, *C. jamaicensis*, *E. cellulosa*, and *N. odorata*, and determined whether these species influenced soil elevation by increasing peat accretion after ≈ 4 year of growth. Although much data exist on sawgrass, other prominent Everglades species, such as water lilies, have little published research on their growth in response to hydrology, especially under field conditions. Our objectives were to compare the three

species under varying water depth and flow conditions for the differences in (1) growth and survival; (2) biomass allocation and standing stocks; (3) nutrient allocation; and (4) soil building. Based on previous studies that have demonstrated the influence of water levels and periods of inundation on Everglades marsh vegetation in mesocosm experiments or through field-based correlation analyses (Newman et al., 1996; Edwards et al., 2003; Childers et al., 2006; Noe & Childers, 2007; Richards et al., 2011), we hypothesized that (1) flow and greater water depth would result in increased plant growth and survival, plant biomass, plant nutrient contents, and soil sedimentation rates for the two slough species *N. odorata* and *E. cellulosa* but decreased effects for *C. jamaicensis*; and (2) plant physical structure (i.e., different forms and densities of plant parts in the water column) would influence sediment deposition patterns, with *C. jamaicensis* causing greater peat accretion than the other two species.

Materials and methods

This research was conducted at the Loxahatchee Impoundment Landscape Assessment (LILA) site located in the Arthur R. Marshall Loxahatchee National Wildlife Refuge (LNWR) in Boynton Beach Florida, USA. LILA consists of four replicate wetland macrocosms (M1 through M4) that mimic features of the Everglades marsh while maintaining relative control over water depth and flow (Aich et al., 2011). Our experiments were conducted between June 2007 and July 2011 in the western side of the ‘no-flow’ macrocosm (NFM) M1 and the ‘flowing’ macrocosm M2 (FM, $\approx 0.5 \text{ cm s}^{-1}$ mean water velocity in deep sloughs). Both macrocosms contained three marsh habitats. The deep slough (DS) had the lowest elevation, followed by the shallow slough (SS), then the mid-ridge (MR; Fig. 1a). These differences in elevation produced differences in water level and period of inundation with the MR going dry each year of the ≈ 4 -year study, while the SS and DS remained wet except during an extreme drought event towards the end of the study (Fig. 1b). The DS, SS, and MR had mean annual water depths of 0.59 ± 0.23 , 0.33 ± 0.23 and 0.19 ± 0.23 m, respectively, with average annual low and high water depths of 0.18 and 0.94, -0.08 and 0.67, and -0.22 and 0.53 m,

Fig. 1 a Diagrammatic representation of a LILA macrocosm (not to scale) showing experimental plots planted with three Everglades marsh species. Inset: eight sediment pins and the planted subplots in each of the nine plots from the three habitats at different elevations (DS, SS, and MR). Plant presence/absence was determined in all 16 subplots, while plant density and size was determined in the six white subplots. **b** Mean water depth of NFM and FM (combined) in each of the three habitats



respectively. LILA water level highs and lows differ from the Everglades seasonality of precipitation. As in the greater Everglades, the LILA stage and water level (inundation and depth) lag behind south Florida rainfall with the deepest water levels occurring from September to January (wet conditions), and the lowest levels occurring from April to June (dry conditions) (Fig. 1b). In general, water levels were maintained within an operational hydrograph (Aich et al., 2011); however, an exceptional drawdown occurred in summer 2011 across South Florida, including at LILA (NOAA, 2011; Fig. 1b). Additional details of the study site and experimental design are given in Serna et al. (2013) and Aich et al. (2011).

Between June 2007 and spring 2008, *C. jamaicense*, *E. cellulosa*, and *N. odorata* were planted in 2 × 2 m plots that were located approximately 3 m apart along transects (Fig. 1a, not to scale) in the NFM and FM. Three plots of each species were established in each habitat (DS, SS, and MR; Fig. 1a), with species alternating along the east–west transects, for a total of

n = 54 locations. For each species, a single plant was transplanted into 16 0.25 m² subplots in each 2 × 2 m plot (Fig. 1a, inset). It became apparent within 4–8 weeks after planting that transplanted *C. jamaicense* did not establish. *Cladium jamaicense* was therefore grown from seed by a commercial supplier (Aquatic Plants of Florida, Sarasota FL) and planted mid-February to mid-March 2008, giving the *C. jamaicense* plots at least 8 weeks to become established before data collection began in May 2008.

Plant measurements over time, biomass allocation and standing stocks

Plant measurements were designed to estimate survival, density, and size for each species. For all species, survival was estimated by recording the presence of the target species in 16 0.25 m² subplots in each 2 × 2 m plot (Fig. 1a, inset). Plant density was estimated by counting number of stems (*C. jamaicense* and *E. cellulosa*) or laminae (*N. odorata*)

in six randomly selected subplots (Fig. 1a, inset). Subplot selection was stratified so that four were located along the plot edge and 2 were located in the plot interior. Plant size was assessed by measuring leaf length (*C. jamaicense*), photosynthetic stem length (*E. cellulosa*) or lamina width (*N. odorata*) on a plant from each of the same six subplots. Plants were measured at 3 month intervals for the first 18 months, and then at 6 month and 1 year intervals, starting in May 2008.

In June 2011, approximately three years after plant measurements began, plant material was harvested from one subplot in each 2 x 2 m plot from each habitat in each macrocosm. Subplots were randomly selected from one of the six subplots measured over time. The entire subplot was excavated to a nominal soil depth of 15 cm. Nine depth measurements of the void were averaged to estimate the soil volume sampled, which was then used to normalize root biomass to a unit volume. All plant material was thoroughly washed to remove soil. To determine biomass allocation and recognizing all plants consist of leaves, stems, and roots but that the morphologies of these parts differ in our three species, plant material was separated into live and dead leaves, live and dead stems, and roots for *C. jamaicense* and *N. odorata*. *Eleocharis cellulosa* does not form photosynthetic leaves, rather produces vertical, emergent, photosynthetic stems and horizontal, below-ground, non-photosynthetic stems (Baksh & Richards, 2006). Thus, *E. cellulosa* plants were separated into live and dead vertical stems, live and dead horizontal stems, and roots. For all three species, roots biomass consisted of both live and dead material at harvest (Cairns et al., 1997). Plant material was dried at 70°C to constant mass and weighed. Weights were normalized to a 1-m² area. A subsample of tissue from each plant part was analyzed for total carbon (TC), total nitrogen (TN) and total phosphorus (TP) following the methods described in Serna et al. (2013) and based on EPA method 365.1 (USEPA, 1983), Nelson & Sommers (1996), and Solórzano and Sharp (1980). Measurements of TC, TN and TP were used to compute C/N, C/P, and N/P molar ratios. Using nutrient concentrations and biomass of the different plant parts, we calculated C, N and P standing stocks (Noe & Childers, 2007) for each species.

Soil elevation changes

Soil elevation changes were measured annually from summer 2008 to spring 2011, using eight sediment accretion pins installed in each plot in early June 2008 (Fig. 1a, inset). Measurements were made from the surface of the soil to the top of the sediment pin; a decrease in height from the soil surface to the top of the sediment pin indicated soil building and an increase in height indicated soil loss. Differences between mean soil elevation (8 pins) at the same plot over time provided rates of elevation change (Boumans & Day, 1993).

Statistical analyses

Analyses were performed using SPSS 18.0 (SPSS Inc., Chicago, Illinois, USA) or JMP 8.0 (SAS Institute Inc., Cary, NC, USA), with significant effects at $p < 0.05$. Shapiro–Wilk’s tests were used to evaluate data normality. Nonparametric analyses were conducted where normality could not be attained. Kruskal–Wallis (KW) tests and ANOVAs were used to analyze effects of flow treatment and habitat on plant presence at the final sampling (June 2011). To analyze effects of flow treatment and habitat on plant size in the final sample, a two-way ANOVA was performed, followed by a one-way ANOVA when no effect of flow was found.

Comparisons of mean biomass per area of each plant part (i.e., live/dead leaves, live/dead stems, and roots per m² for *C. jamaicense* and *N. odorata*; live/dead photosynthetic stems, live/dead horizontal stems, and roots per m² for *E. cellulosa*) were made by two-way ANOVAs to test the effects of flow treatment, habitat and their interaction. All interactions were not significant except for live horizontal stems for *E. cellulosa* ($p = 0.024$, details given in Appendix 1—Supplementary Material). Data of biomass per area were log transformed to achieve normality before performing ANOVAs. Multiple comparisons for treatment means were evaluated with Tukey’s HSD tests.

The effects of flow, habitat, plant part, and all interactions on plant nutrient concentrations and ratios were tested using a three-way ANOVA separately for each species. Outliers, falling outside the 90th percentile (SPSS Inc., Chicago, Illinois, USA), were removed from the nutrient data (4 from the TC data, 2 from the TN data, 4 from the TP data, 3 from the C/N,

and 2 from the C/P). Data for TP and nutrient ratios were log transformed to achieve normality before performing ANOVAs. Because these results indicated an effect of plant part, a second one-way ANOVA compared nutrient concentrations and nutrient ratios between the five main live/dead plant parts of each species in the DS, SS, MR, and for the three habitats combined. Although there was an effect of habitat on nutrient concentrations and ratios, data of all three habitats were combined to compare them with samples collected in March 2011, when surface water was still present in all habitats (Serna et al., 2013); this comparison examined tissue nutrients from plants, when all sites were inundated, versus the final sampling in June 2011, when a drought caused all sites to dry. Total standing stocks of C, N and P were compared by non-parametric KW tests, followed by a Mann–Whitney test averaging the data of all habitats to examine for differences between species. Total standing stocks by species were compared using one-way ANOVAs after data were log transformed to achieve normality (*C. jamaicense* and *E. cellulosa*) and KW tests (*N. odorata*, including samples that had no plant, i.e., zero values included) to test the effect of habitat.

Comparisons of mean values of soil elevation changes were made by three-way ANOVA after averaging the data of the eight sediment accretion pins by plot to test the effects of flow, habitat, species, and all interactions, for a total of $n = 54$ locations. Pearson's correlation was used to examine the relation of change in soil height to total biomass, to belowground biomass (live stems, dead stems and roots for *C. jamaicense*; live horizontal stems, dead horizontal stems and roots for *E. cellulosa*, and live stems, dead stems and roots for *N. odorata*), to root biomass, to live belowground biomass, and to dead belowground biomass.

Results

Marsh vegetation growth and survival over time in relation to flow and habitat

There was no significant effect of water flow at an average velocity in the sloughs of 0.5 cm s^{-1} on the number of plants present and plant size at the final sampling, except for *C. jamaicense*, while there was a significant difference among habitats for *C. jamaicense* and *N. odorata* (Fig. 2).

A significantly greater number of *C. jamaicense* plants survived in flowing conditions and the DS habitat ($p = 0.001$, one-way ANOVA) than in the SS or MR, which did not differ in plant presence (Fig. 2a, left). Although not statistically compared, *C. jamaicense* plants also produced more stems per plant in the DS habitat (Fig. 2b, left). The number of stems per plant varied between wet and dry conditions and declined over time in all habitats (Fig. 2b, left). Flowing conditions and deep slough plants also produced longer leaves than plants in the SS or on the MR, which showed similar leaf lengths (Fig. 2c, left; $p = 0.003$, one-way ANOVA for final data collection).

Eleocharis cellulosa had high survival and/or re-colonization in the DS and SS habitats (Fig. 2a, center). Plants on the MR died off early in the experiment, with reduced numbers present through the first year, but showed some recovery with the onset of wet conditions in May 2009 (Fig. 2a, center) resulting in final plant number that did not differ significantly between habitats ($p = 0.291$, KW test). *Eleocharis cellulosa* had a greater number of stems per subplot in the two slough habitats than on the MR (not statistically compared), with increasing density between May and October and decreasing density between November and April during the first two years of the experiment (Fig. 2b, center). *Eleocharis cellulosa* plants in the deep sloughs had significantly longer stems than in the shallow sloughs and the ridges (Fig. 2c, center; $p = 0.002$, one-way ANOVA for final data collection). Stem length varied with water depth in all habitats, being longer during wet conditions and shorter during dry conditions. These patterns were only observable during the first 18 months due to the relatively higher frequency of sampling (Fig. 2c, center).

Nymphaea odorata survived best in the DS, with second best survival in the SS (Fig. 2a, right). Plants on the MR had reduced survivorship at the first data collection (May 2008) and did not recover or re-colonize over the course of the experiment, but a few plants persisted in these drier habitats. Although *N. odorata* was present in the shallow sloughs throughout much of the study, there was a dramatic decrease in their presence during the last year (Fig. 2a, right). The final numbers of plants differed significantly among habitats ($p = 0.001$, KW test), with more plants present in the DS habitat compared to the SS and MR, which did not significantly differ. Although not statistically compared, the number of floating laminae

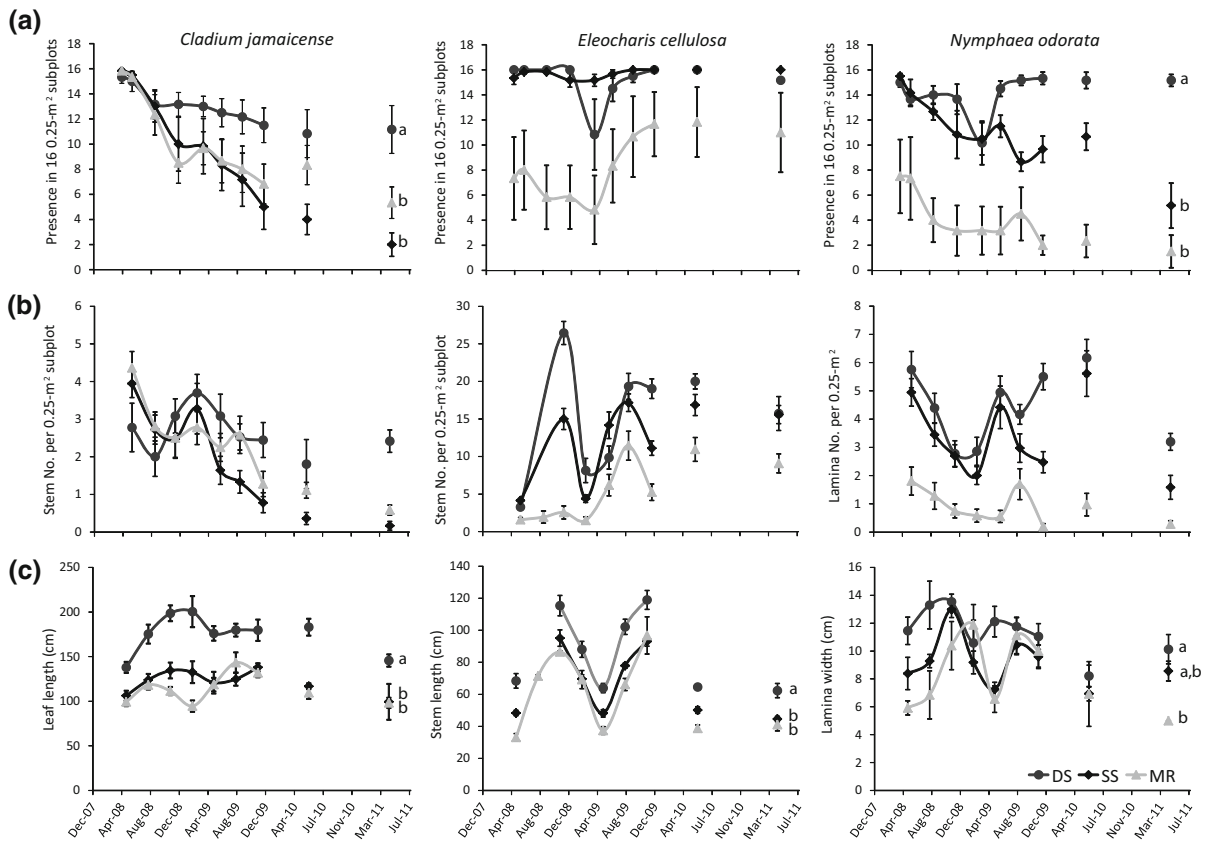


Fig. 2 Survival, density, and size of three Everglades plant species over time in the deep slough (DS, circle), shallow slough (SS, diamond) and mid-ridge (MR, triangle) of both no-flow (NFM) and flowing (FM) macrocosms combined. Values are mean \pm SE. **a** Presence of plant ($n = 6$); **b** Stem (culm) number (*C. jamaicense* and *E. cellulosa*) or number of lamina (*N. odorata*) per 0.25-m² subplot ($n = 36$); **c** Leaf length (*C. jamaicense*), stem length (*E. cellulosa*) or lamina width (*N.*

odorata) ($n = 36$). Different letters in presence (**a**) and size (**c**) in the final sample indicate significant differences among habitats as determined by KW tests and one-way ANOVAs. Absence of designation denotes no significant difference in presence (**a**) and size (**c**). LILA deeper water levels occur from September to January (wet conditions), and lower levels occur from April to June (dry conditions; Fig. 1b)

per subplot was much greater for the DS and SS habitats than for the MR and was greatest during wet conditions (Fig. 2b, right). *Nymphaea odorata* plants in the DS had wider leaves than plants in the MR, while lamina width of plants in the SS was intermediate between and marginally significantly different from the DS and the MR (Fig. 2c, right; $p = 0.043$, one-way ANOVA for final data collection). Lamina width was greater during wet conditions and decreased during dry conditions.

Biomass allocation in relation to flow and habitat

Live leaf, root, and total biomass of *C. jamaicense* were significantly greater in flowing conditions, while

live stem and dead biomass (leaves and stems) did not significantly differ by flow regime (Table 1). In the DS habitat, the *C. jamaicense* live biomass was generally about three to six times greater than and significantly different from plants in the other habitats (Table 1). The mass allocation in live leaf biomass compared to live stem allocation was the greatest for the DS, about equal in SS, and lower in the MR (Table 1). The mass of dead leaves (the greatest percent of total biomass for all samples) was significantly higher in the DS than in the SS or and MR (Table 1), but the percent of total biomass in dead leaves ($55 \pm 8\%$, $61 \pm 4\%$, and $58 \pm 11\%$ for DS, SS, and MR, respectively) was similar in the three habitats (prob. $> X^2 = 0.35$, Kruskal–Wallis test). Root biomass showed the same

Table 1 Mean biomass per area ± SD of three Everglades plant species in the no-flow (NFM) and flowing (FM) macrocosms, the three habitats (DS, deep slough, SS, shallow slough, and MR, mid-ridge), and overall (flow regimes and habitats combined)

Species	Treatment	n	Live biomass (g m ⁻²)		Dead biomass (g m ⁻²)		Root biomass (g m ⁻²)		Total biomass (g m ⁻²)
			Leaves	Stems	Leaves	Stems	Leaves	Roots	
<i>Cladium jamaicense</i>	NFM	9	52.3 ± 65.8	41.9 ± 33.5	236.4 ± 199.7	35.3 ± 28.5	25.0 ± 22.0	390.9 ± 308.2	
	FM	9	153.0 ± 166.6	80.0 ± 66.9	418.4 ± 330.0	42.6 ± 15.7	59.4 ± 65.2	753.4 ± 614.6	
	DS	6	248.1 ± 144.7 ^a	108.5 ± 65.1 ^a	603.5 ± 296.3 ^a	49.2 ± 28.6	87.3 ± 68.3 ^a	1096.5 ± 540.3 ^a	
	SS	6	29.3 ± 33.0 ^b	25.3 ± 28.6 ^b	199.7 ± 181.2 ^b	40.0 ± 21.0	25.5 ± 14.3 ^b	319.9 ± 261.2 ^b	
	MR	6	30.5 ± 19.6 ^b	49.1 ± 28.3 ^{ab}	179.4 ± 98.8 ^b	27.6 ± 14.1	13.9 ± 5.9 ^b	300.2 ± 139.4 ^b	
Overall		18	102.7 ± 133.4	61.0 ± 54.9	327.4 ± 280.7	38.9 ± 22.6	42.2 ± 50.4	572.2 ± 507.2	
<i>Eleocharis cellulosa</i>	NFM	9	37.3 ± 23.1	2.4 ± 2.4	49.2 ± 39.0	2.7 ± 2.7	18.4 ± 14.5	109.9 ± 69.2	
	FM	9	75.6 ± 41.1	9.6 ± 8.8	79.0 ± 57.7	12.0 ± 7.1	31.9 ± 21.7	208.1 ± 132.0	
	DS	6	83.6 ± 52.6 ^a	9.9 ± 11.3	109.1 ± 61.2	11.0 ± 10.8	42.8 ± 22.5 ^a	256.4 ± 153.0 ^a	
	SS	6	54.0 ± 10.5 ^a	4.2 ± 2.9	37.5 ± 13.1	4.8 ± 2.7	21.3 ± 8.8 ^b	121.8 ± 23.5 ^{ab}	
	MR	6	31.8 ± 19.4 ^b	3.9 ± 3.8	45.7 ± 30.8	6.3 ± 4.5	11.4 ± 6.9 ^c	98.9 ± 53.7 ^b	
Overall		18	56.5 ± 37.9	6.0 ± 7.3	64.1 ± 50.1	7.3 ± 7.1	25.1 ± 19.2	159.0 ± 114.1	
<i>Nymphaea odorata</i> ^a	NFM	9	1.0 ± 2.0	193.0 ± 249.0	2.4 ± 4.3	8.8 ± 17.6	20.4 ± 29.3	225.7 ± 290.7	
	FM	9	0.2 ± 0.2	108.8 ± 130.2	2.4 ± 3.0	9.0 ± 11.0	9.5 ± 12.5	129.8 ± 142.5	
	DS	6	1.1 ± 2.4	172.0 ± 249.1	3.5 ± 4.6	6.3 ± 10.4	21.4 ± 28.8	204.2 ± 282.1	
	SS	6	0.5 ± 0.8	205.6 ± 194.1	1.7 ± 2.2	20.4 ± 17.9	19.6 ± 25.4	247.8 ± 229.3	
	MR	6	0.1 ± 0.2	75.2 ± 148.2	2.0 ± 3.9	0.0 ± 0.0 ^b	3.9 ± 8.8	81.1 ± 160.8	
Overall		18	0.6 ± 1.4	150.9 ± 197.6	2.4 ± 3.6	8.9 ± 14.2	15.0 ± 22.6	177.7 ± 227.5	

Significant differences at $p < 0.05$ from two-way ANOVAs between NFM and FM samples are in italics, and differences among habitats are designated by dissimilar uppercase letters. Absence of designation denotes no significant difference

Photo. stems photosynthetic stems, *Hor. stems* horizontal stems

^a *N. odorata* data include samples that had no plants (i.e., zero values included)

^b In one of 6 plots a small dead stem was found but its mass was not determined

pattern of variation among habitats as live and dead leaves and live stems (Table 1).

Total biomass and biomass of all plant parts of *E. cellulosa* were significantly greater in the FM than in NFM except for the dead photosynthetic stems (which comprised $40 \pm 11\%$ of the total biomass) (Table 1). Although *E. cellulosa* had greater biomass in all plant parts in the DS, dead photosynthetic stems, and live and dead horizontal stems, were not significantly different between habitats, while live photosynthetic stems and root biomass were significantly lower in the MR habitat than in the DS (Table 1).

There were no significant differences in the biomass of *N. odorata* between flow regimes or habitats. Biomass sampling at the study conclusion occurred during a drought when all habitats were dry (Fig. 1, June 2011) and there was very little leaf biomass in any habitat (Table 1). Over 90% of live biomass was allocated to stems in all habitats (Table 1). The MR habitat had less live and dead stem biomass compared to the sloughs, but because of high variability in the data, these differences were not significant. Unlike *C. jamaicense* and *E. cellulosa*, the *N. odorata* plots contained little dead biomass except in one SS site that had a single large dead stem.

Cladium jamaicense had a final total biomass 3.6 times that of *E. cellulosa* and 3.2 times that of *N. odorata* (Table 1). For all three species, final total biomass was the lowest on the MR (Table 1). For *E. cellulosa* and *N. odorata*, this reduced biomass was seen early in the experiment both in survival and in the number of stems or leaves per area, with approximately 50% survival on the MR at the first data collection (May 2008; Fig. 2). Growth of *C. jamaicense* differed from both of these species, as it had high survival in all habitats during the first year but then declined in the MR and SS while surviving best in the DS (Fig. 2).

Marsh vegetation tissue nutrient allocations in relation to flow and habitat

We present results that describe relations between hydrologic parameters and plant nutrient contents. More details of nutrient concentrations and nutrient molar ratios for plant parts of the three species are given in the supplemental material (Appendices 2–4—Supplementary Material). Overall, tissue nutrients and nutrient ratios were not significantly different between flow regimes, except for TN, C/N, and N/P of *C.*

jamaicense and TP of *E. cellulosa*. The C/N of *C. jamaicense* was slightly higher in the FM ($p = 0.005$), and TN ($p = 0.009$) and N/P ($p = 0.006$, three-way ANOVA) were higher in the NFM than in the FM. Total P of *E. cellulosa* was slightly but significantly higher in the NFM than in the FM ($p = 0.041$). Tissue nutrients and nutrient ratios of *C. jamaicense* were not significantly different among habitats, except for N/P ($p < 0.001$). In contrast, tissue nutrients and ratios of *E. cellulosa* and *N. odorata* differed significantly among habitats, except for TC of *E. cellulosa* ($p = 0.083$), and TC ($p = 0.731$) and TN ($p = 0.167$, three-way ANOVA) of *N. odorata*. A significant interaction was found between flow, habitat, and plant part for *C. jamaicense* and between flow and habitat for *E. cellulosa* (Appendix 5—Supplementary Material). High mortality of *N. odorata* plants in the MR (Fig. 2a, right), as well as high mortality during the 2011 drought, resulted in unbalanced tissue nutrient samples and significant differences in nutrient concentrations and ratios.

Tissue nutrients and nutrient ratios differed significantly among plant parts and live versus dead tissues (Table 2). Dead material was depleted in TN and TP for all species. In all three species, live photosynthetic tissue had more TP than roots and thus lower values of the associated C/P and N/P ratios. In *N. odorata*, these ratios were less in live stems than in roots. Total N of *C. jamaicense* live leaves was lower than in samples collected in March 2011, when water depths were decreasing, but surface water was still present in all habitats (Table 2, Serna et al., 2013).

Nutrient standing stocks

Nutrient standing stocks reflected biomass allocation patterns in all three species and their growth patterns in the different habitats (Fig. 3; Table 1). Total standing stocks of C, N, and P were significantly different between species (all $p < 0.05$, KW test of C, N and P), regardless of habitat. *Cladium jamaicense* had greater total standing stocks of C and N than either *E. cellulosa* or *N. odorata* (Fig. 3; note differences among species in y-axis scales for C and N). *Cladium jamaicense* had greater total standing stocks of P than *E. cellulosa*, while *N. odorata* was intermediate between *C. jamaicense* and *E. cellulosa* (Fig. 3). Total nutrient standing stocks differed among habitats, being significantly greater in the DS for C

Table 2 Nutrient concentrations and nutrient molar ratios of plant parts of three Everglades plant species

Species	Plant Part	n	TC (mg g ⁻¹)	TN (mg g ⁻¹)	TP (mg g ⁻¹)	C/N	C/P	N/P
<i>Cladium jamaicense</i>	Spring live leaves ^a	14	471 ± 113	9.7 ± 1.4	0.34 ± 0.06	57 ± 9	3698 ± 669	65 ± 9
	Live leaves	17–18	435 ± 20 ^{ab}	5.5 ± 1.8 ^a	0.34 ± 0.11 ^a	107 ± 57 ^a	3363 ± 845 ^a	37 ± 7 ^a
	Dead leaves	15–18	455 ± 19 ^a	3.1 ± 1.0 ^b	0.11 ± 0.04 ^b	185 ± 62 ^b	12,333 ± 4051 ^b	64 ± 17 ^b
	Live stems	17	424 ± 23 ^b	4.7 ± 1.6 ^{ac}	0.27 ± 0.15 ^{ac}	123 ± 63 ^{ac}	5232 ± 2740 ^c	45 ± 20 ^{ac}
	Dead stems	17–18	446 ± 31 ^{ab}	4.0 ± 1.3 ^{bc}	0.16 ± 0.06 ^d	149 ± 63 ^{bc}	7913 ± 2332 ^d	57 ± 21 ^{bc}
	Roots	18	454 ± 30 ^a	5.4 ± 1.3 ^a	0.21 ± 0.04 ^{cd}	102 ± 23 ^{ac}	6031 ± 1482 ^{cd}	60 ± 15 ^b
<i>Eleocharis cellulosa</i>	Spring live stems ^a	17	436 ± 8	14.9 ± 2.6	0.74 ± 0.15	35 ± 6	1578 ± 294	45 ± 4
	Live photo. stems	17–18	419 ± 28 ^a	6.5 ± 1.5 ^a	0.40 ± 0.08 ^a	80 ± 24 ^a	2739 ± 802 ^a	36 ± 12 ^a
	Dead photo. stems	16–17	427 ± 13 ^{ab}	3.8 ± 1.2 ^b	0.14 ± 0.07 ^b	144 ± 54 ^b	9325 ± 4470 ^b	70 ± 28 ^b
	Live horiz. stems	16–17	434 ± 17 ^{ab}	3.1 ± 1.4 ^b	0.20 ± 0.11 ^{bc}	186 ± 96 ^b	6799 ± 2934 ^{bc}	39 ± 25 ^a
	Dead horiz. stems	14–18	436 ± 27 ^b	4.2 ± 1.2 ^b	0.15 ± 0.06 ^{bc}	124 ± 47 ^{ab}	7932 ± 2242 ^b	73 ± 45 ^b
	Roots	17–18	419 ± 22 ^a	5.8 ± 1.3 ^a	0.23 ± 0.10 ^c	93 ± 40 ^a	5320 ± 2424 ^c	60 ± 28 ^{ab}
<i>Nymphaea odorata</i>	Spring live lamina ^a	16	440 ± 15	22.0 ± 3.1	0.99 ± 0.15	24 ± 4	1178 ± 184	50 ± 8
	Live leaves	2	423 ± 5 ^{ab}	13.5 ± 4.9 ^a	1.00 ± 0.00 ^a	38 ± 13 ^{ab}	1522 ± 442 ^{ab}	41 ± 2 ^{ab}
	Dead leaves	8	422 ± 23 ^a	12.4 ± 2.3 ^{ab}	0.03 ± 0.08 ^{bc}	42 ± 7 ^a	5911 ± 1206 ^{ac}	143 ± 24 ^c
	Live stems	9–12	379 ± 33 ^b	4.7 ± 2.3 ^c	0.39 ± 0.49 ^{ac}	111 ± 56 ^c	3337 ± 2291 ^b	30 ± 23 ^a
	Dead stems	6–7	426 ± 34 ^a	2.0 ± 1.5 ^c	0.02 ± 0.05 ^b	269 ± 130 ^d	13,834 ± 4625 ^c	59 ± 24 ^b
	Roots	11	434 ± 17 ^a	6.4 ± 2.1 ^{bc}	0.12 ± 0.32 ^{ac}	89 ± 44 ^{bc}	4815 ± 2505 ^{ab}	52 ± 17 ^b

Data (mean ± 1SD) are from flow regimes (no-flow, NFM and flowing, FM macrocosms) and habitats combined (DS, deep slough; SS, shallow slough, and MR, mid-ridge) to compare them with samples collected in March 2011 (Spring live), when surface water was still present in all habitats (Serna et al., 2013). Within each column, values followed by different superscripts are significantly different among plant parts at *p* < 0.05

^a Values correspond to the center 15–20 cm of *C. jamaicense* live leaves, *E. cellulosa* emergent photosynthetic stems and *N. odorata* lamina of floating leaf blades collected in March 2011 (Serna et al., 2013)

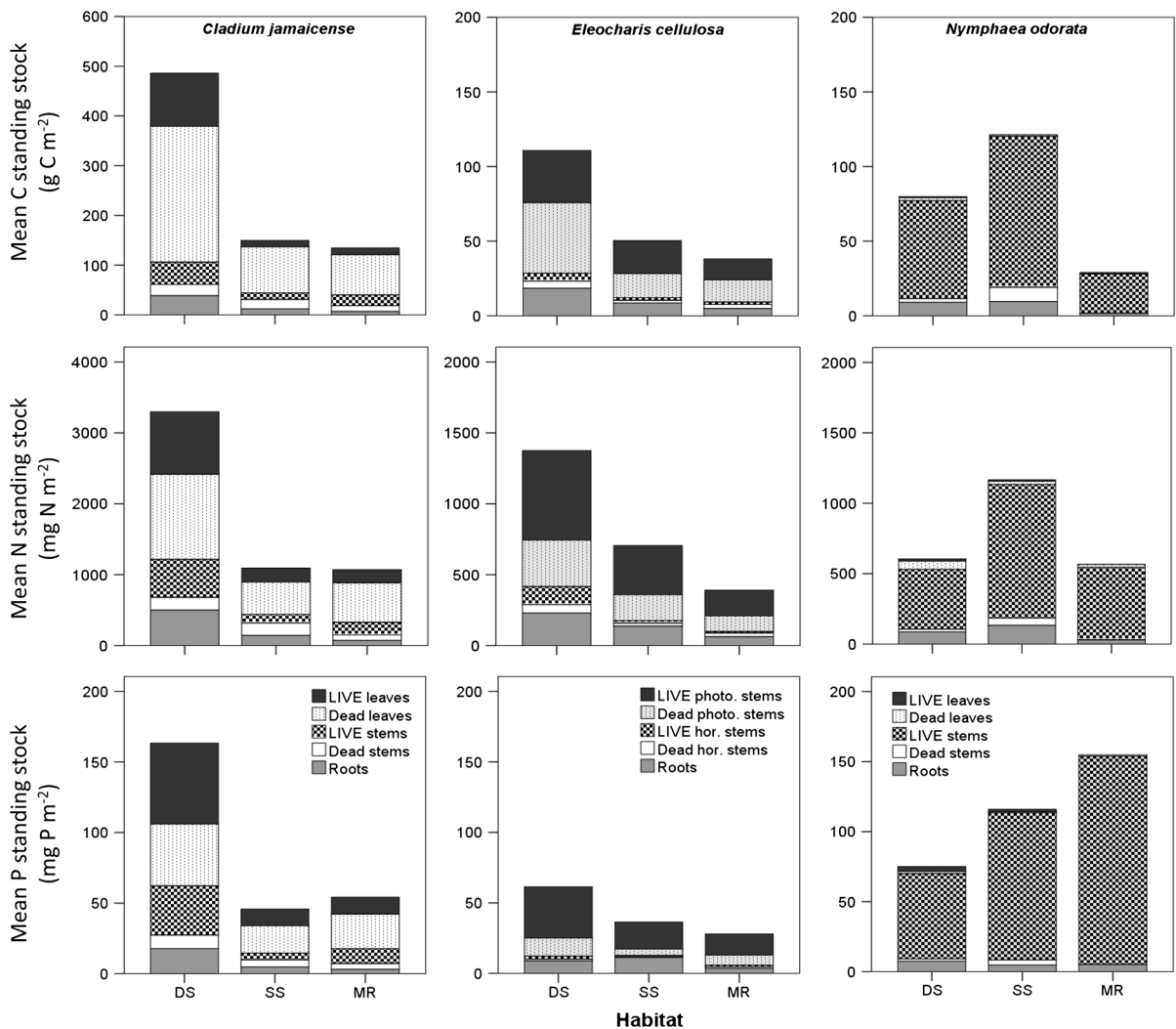


Fig. 3 Calculated C, N, and P standing stocks separated by plant parts ($n = 6$) of three Everglades plant species in the deep slough (DS), shallow slough (SS), and mid-ridge (MR) in both no-flow (NFM) and flowing (FM) macrocosms combined. Note

different y-axis scales for *C. jamaicense* C and N versus the other species. Abbreviations: Photo. stems = photosynthetic stems; Hor. stems = horizontal stems

($p = 0.03$, one-way ANOVA), N ($p = 0.001$, one-way ANOVA), and P ($p = 0.001$, one-way ANOVA) in *C. jamaicense*. Total standing stocks of C ($p = 0.04$, one-way ANOVA) and N ($p = 0.013$, one-way ANOVA) were significantly greater in the DS than in the MR in *E. cellulosa*, but intermediate in the SS. Total standing stocks of P were not significantly different among habitats in *E. cellulosa* ($p = 0.123$, one-way ANOVA). Total nutrients stocks in *N. odorata* were greater in the SS than in the other habitats, although differences were not significant (all $p > 0.05$, KW test). Patterns of nutrient allocation

also differed among the plant parts of the three species (not statistically compared). The C and N stocks of *C. jamaicense* were greatest in dead leaves in all three habitats. The P stocks were greatest in the dead leaves of the SS and MR habitats, while in the DS, the greatest P stocks were in the live leaves (Fig. 3). For *E. cellulosa*, the greatest standing stocks of C, N, and P were in the live photosynthetic stems for all habitats except for the C in the DS where most of the C was in dead photosynthetic stems. *Nymphaea odorata* had the greatest amount of all three nutrients in all habitats (Fig. 3).

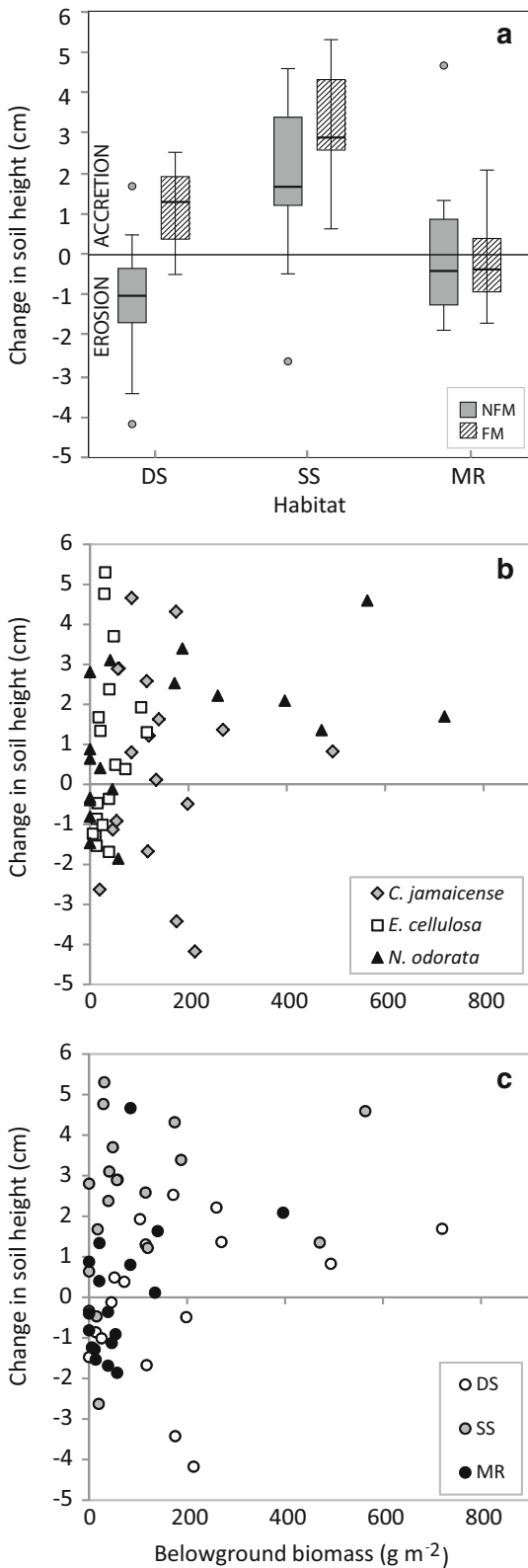


Fig. 4 Level of soil accretion or erosion in the deep slough (DS), shallow slough (SS), and mid-ridge (MR) in both no-flow (NFM) and flowing (FM) macrocosms. **a** Change in soil elevation in the NFM and FM after ~4 year of plant growth (data from all habitats and species plots combined, $n = 9$). **b** Change in soil elevation in relation to belowground biomass by species *Cladium jamaicense* (live and dead stems, roots), *Eleocharis cellulosa* (live and dead horizontal stems, roots) and *Nymphaea odorata* (live and dead stems, roots) (data from all habitats in NFM and FM combined, $n = 54$). **c** Change in soil elevation in relation to belowground biomass by habitat (data from all species plots in NFM and FM combined, $n = 54$)

Soil accretion/sedimentation

Significant differences in soil height were found between flow regimes ($p = 0.012$) and among habitats ($p < 0.001$), but not between species ($p = 0.476$) or for any interactions (all $p > 0.05$, three-way ANOVA). Soil accretion was significantly higher ($p = 0.012$) in the FM (1.4 ± 1.9 cm) than in the NFM (0.3 ± 2.3 cm). Sedimentation pin data show that after ≈ 3 –4 years of plant growth, there was a noticeable accretion of soil only in the SS (Fig. 4a) with soil height changes varying around zero in the DS and MR. Despite substantial variability between flow regimes and habitats, the mean change in soil height, given all these factors, was 0.8 ± 2.2 cm ($n = 54$), corresponding to an accretion rate of 2.7 mm year^{-1} over the period from 2008 to 2011. Soil building was observed in 61% of the planted plots (Fig. 4b, c).

One objective of this study was to determine whether plant species influenced soil accretion. The number of plants present in *C. jamaicense* plots decreased over time, with SS having the poorest survival but noticeable soil deposition, while DS had the greatest number of plants surviving, significantly higher total biomass than SS and MR (Table 1), but little soil deposition (Figs. 2a, 4a). *Eleocharis cellulosa* and *N. odorata* plants were more consistently present in the sloughs, where soil accretion was also observed; these species had reduced numbers of plants present on the MR (Fig. 4a) and low total biomass (Table 1), coinciding with a lack of soil formation (Fig. 4a). Plant biomass did not affect soil elevation (Pearson’s correlations for change in soil height x total biomass, belowground biomass, root biomass, live belowground biomass, and dead belowground biomass, all $p \geq 0.055$).

Discussion

Vegetation patterns in the Everglades are thought to be largely determined by hydrologic conditions with variations in mean annual water depth (MAWD) and inundation duration being among the most influential forcing functions (Ogden, 2005). Hydrologic manipulations in South Florida that have adversely affected the Greater Everglades Ecosystem (GEE) include compartmentalization that has disrupted sheet flow and has caused alterations in the spatial, seasonal, and inter-annual variations in water depths (Ogden, 2005). Evaluation of the effectiveness of the Comprehensive Everglades Restoration Plan (CERP; USACE & SFWMD, 1999) relies heavily on the responses of the “best living indicators” (Ogden, 2005). Critical pathways leading to ecological responses in the Everglades, and therefore targets of the restoration efforts, include those focused on the effects of water levels and flow on important members of the plant communities in Everglades ridge-and-slough habitats. In the LILA experimental wetlands, hydrologic variation results from topographical habitat differences (based on relative soil elevations) and semi-controlled water stage manipulation (Fig. 1; Aich et al., 2011).

We hypothesized that variations in MAWD and flow (no-flow to approximately 0.5 cm s^{-1} average sustained flow in sloughs) would differentially influence the survival and growth of marsh vegetation with the three species proliferating in each of their “hypothetically-optimal” habitats; that is, *C. jamaicense*, *E. cellulosa*, and *N. odorata* growing best in the MR, SS, and DS, respectively. Generally all three species grew better (biomass) and had the highest survivability in deeper water habitats (i.e., DS), although *N. odorata* generally did best in the SS at intermediate depths and period of inundation. Similarly, in peatlands of Poland, Wassen et al. (2003) found increased plant abundance and biomass of several species in deeper water.

Surprisingly, the survival and growth of *C. jamaicense* was the best in the deepest habitat. *Cladium jamaicense* is the “signature” species of ridges in the Everglades ridge-and-slough landscape (McVoy et al., 2011) and is generally thought to occupy shallower, shorter hydroperiod habitats (David, 1996; Ross et al., 2003, 2006; Givnish et al., 2008). Experimental field and mesocosm data support this

idea (Newman et al., 1996; Childers et al., 2006). McVoy et al. (2011) provided estimated pre-drainage (pre-1880s), long-term, average annual low, and high water depths of -15 and 46 cm, respectively, as optimal for *C. jamaicense* growth. The SS and MR habitats were within this range, while the DS habitat exceeded it. However, review of the literature on *C. jamaicense* water depth optima and tolerances reveals MAWD that vary from 0 to 49 cm (Richards & Gann, 2008) with mid-wet season average depths of 58 ± 3 cm and 19 ± 2 cm mid-dry season water depths across Everglades marshes (Richards et al., 2008). Gann & Richards (2015) found the median was 64 cm (Water Conservation Area 1) and 74 cm (Water Conservation Area 2) for maximum wet season water depth of sawgrass communities spread throughout 982 km^2 in northern Everglades regions. During the ≈ 4 years of hydrologic data in this study, our median maximum water depth in the DS was 94 cm, about 20% deeper. Although *C. jamaicense* is characteristic of ridges, modern sawgrass ridges formed on sites that were originally occupied by marshes (Bernhardt & Willard, 2009). Thus, *C. jamaicense* has broad inundation and water depth tolerances, and optimal wet-season water levels can be relatively deep.

Eleocharis cellulosa also grew and survived best in the DS, and although it remained present on the ridge (MR), it produced fewer stems and had reduced biomass in the MR habitat. This is in contrast to results following individual plants in mesocosms, where plants in 7 cm water produced greater biomass than plants in 52 cm water (Edwards et al., 2003). Childers et al. (2006) found no relationship between *Eleocharis* spp. stem density and three hydrologic variables that included water depth. In our study, *E. cellulosa* plants were more consistently present in the two slough habitats over time, confirming previous studies of *E. cellulosa* growing in emergent sloughs (Ross et al., 2003, 2006; McCormick et al., 2009) and indicating that *E. cellulosa* has a wide water depth range, especially under conditions similar to this study.

The observed effect of habitat (i.e., water depth) on survivorship and density of *N. odorata* agrees with the results of outdoor mesocosm experiments in southern Florida showing that water depth affects leaf morphology and plant biomass allocation in *N. odorata* (Richards et al., 2011). The MAWD of the DS in our experiments was less than 60 cm with a

maximum of <100 cm. Richards et al. (2011) proposed water levels of ≥ 75 cm as optimal growth conditions for *N. odorata*. Sinden-Hempstead and Killingbeck (1996) suggested a significant effect of water depth on *N. odorata* growth and a water depth maximum of 220 cm. Studies of the vegetation composition of the LILA ridge-and-slough landscape suggest that *N. odorata* has failed to become established in abundance in any of the LILA habitats, including the deeper sloughs, although it is present in deep feeder canals of the LILA system (Scinto et al., 2013). *Nymphaea odorata* maintained its presence in the DS but was virtually eliminated from the SS and MR by the end of this study. The greatest decrease in its presence occurred when sampling was conducted during a drought, suggesting *N. odorata* is susceptible to marsh dryouts. Dryouts in the Everglades are thought to have increased in frequency and duration compared to the historic past due to hydrologic manipulations (Ogden, 2005).

The three species studied had very different total biomass and different strategies of biomass and nutrient allocation with *C. jamaicense* having greater than three times the final biomass of the other species. The nutrient contents of varying plant parts were generally similar across species and varied more between plant parts within a species than for comparable parts between species. There were generally higher nutrient concentrations (TN and TP) in the living tissues of the leaves and stems than in the corresponding dead parts for all species, as might be expected. There was generally little difference in TC concentration between species for corresponding plant parts, in contrast to what we originally expected, considering the different morphologies displayed by these species, e.g., emergent sawgrass versus floating leaved water lily. Thus, the spatial distributions of TC, TN, and TP were due more to biomass allocation and condition (i.e., live versus dead) than to differences in tissue concentration between species. The data suggest a loss of nutrients during senescence, which is supported by differences between two closely spaced sampling events, March 2011 and June 2011, which occurred during a period of inundation and drought, respectively. The photosynthetic tissue sampled in this study in June 2011 had generally lower nutrient concentrations than photosynthetic tissue sampled in the same plots in March 2011 (inundated; Serna et al.,

2013). For example, the June live leaves of *N. odorata* had 38% of the TN and 24% of the TP compared to the March leaves. Previous experiments at LILA for these three species showed greatest loss in TP during decomposition, especially in the leaves of *N. odorata* (Serna et al. 2013). Although biomass differences greatly influenced the mass of nutrients per unit area between species (Fig. 3), a larger relative fraction of the biomass and nutrient allocation was generally contained in the standing dead material in *C. jamaicense* in all habitats, whereas the live material contained the greatest biomass and nutrients in *E. cellulosa*, and *N. odorata*.

Nutrient allocations, concentrations, and standing stocks assist in developing datasets on which to build biogeochemical and ecological budgets (e.g. Noe and Childers, 2007) and provide information to monitor environmental change in response to restoration and/or increased degradation. We therefore compiled nutrient data from the literature for three dominant Everglades marsh vegetation species to compare to our results; we furnish them as supplementary data (Appendix 6—Supplementary Material).

The TP contents of leaves, rhizomes, and roots of *C. jamaicense* have been shown to vary with soil or nutrient media TP levels (Appendix 6—Supplementary Material). Total P levels in *C. jamaicense* live/dead leaves from LILA were comparable to those reported for leaves from the reference or the unenriched field sites or in low P in experimental conditions (Appendix 6—Supplementary Material). Data for *C. jamaicense* roots and rhizomes presented here resemble those from unenriched to moderately enriched soils or nutrient media (Appendix 6—Supplementary Material). Nutrient data reported for *E. cellulosa* consist primarily of data for the photosynthetic stems (Appendix 6—Supplementary Material), although Chen et al. (2005) and Miao and Zou (2012) also provide data for roots and rhizomes. As in the case of *C. jamaicense*, our data for *E. cellulosa* are consistent with data for samples from unenriched to moderately enriched soils or media. There have been very little tissue nutrient data published for *N. odorata* from the Everglades, and most of these data were only for live leaves. Our nutrient values for LILA *N. odorata* leaves are very similar to those for live *N. odorata* leaves collected throughout the year in Water Conservation Area (WCA) 3A and in unenriched sites in WCA 2A. Total P in *N. odorata* shoots from central

Everglades National Park had a slightly lower value (0.73 mg g^{-1} ; Noe et al., 2002). *Nymphaea odorata* plants grow across a range of soil TP concentrations (Vaithiyathan & Richardson, 1999; Hagerthey et al., 2008), and similar to *C. jamaicense* and *E. cellulosa*, *N. odorata* leaf TP varies with TP availability (Newman et al., 2004; Hagerthey et al., 2008). Live *N. odorata* leaves and stems had significantly more N- and P-rich tissues than the other two species at LILA (this study, Appendix 6—Supplementary Material, and Serna et al., 2013).

Conceptual models that seek to explain the formation and distribution of the higher-elevation vegetated sawgrass ridges and lower-elevation, open water slough topography have to account both for the elevation differences between these habitats and for the landscape morphology (e.g., size, shape, and orientation parallel to flow). A recent synthesis hypothesized that feedbacks in peat accretion and thus habitat elevation differences relied on vegetation processes, including biomass production and decomposition, while feedbacks on vegetation colonization through sediment transport and nutrients explained patterning (Larsen et al., 2011).

Everglades peats are believed to arise from “roots and rhizomes and, to a lesser extent, the stems and leaves of the Everglades plant communities” (Gleason & Stone, 1994). The three species studied here had very different total biomass and different strategies for biomass and nutrient allocation. When belowground parts such as live and dead stems (rhizomes) plus roots of the species were compared, *N. odorata* had a greater total subterranean biomass (approximately 1.2 times that of *C. jamaicense* and 4.6 times that of *E. cellulosa*). These belowground parts contribute directly and immediately to soil building. The TP and TN contents of these parts were similar in the three species (Table 2), so differences in their contributions to soil accretion would primarily be based on biomass production and, ultimately, degradability (Table 1).

The belowground biomass of *E. cellulosa* was much lower than that of the other species, suggesting a reduced input to soil building from this species. Although the belowground biomasses of *C. jamaicense* and *N. odorata* were roughly similar at harvest, *C. jamaicense* had more root biomass than *N. odorata*. Because roots are dispersed throughout the soil and, compared with stems, they have a higher surface-to-volume ratio, they provide more surface in

immediate contact with the environment, and therefore may be degraded faster than stems. In addition, for a given length, *C. jamaicense* stems have a much narrower diameter than *N. odorata* stems, giving them a higher surface to volume ratio and, potentially, greater degradability. Most of the *N. odorata* biomass was in relatively unbranched, massive, living rhizomes that are not directly processed into soil during decomposition (Table 1). For all three species, the dead material, which was depleted in nutrients, especially P, is the material that contributes directly to soil building. In *C. jamaicense* and *E. cellulosa*, this dead material was retained in the aboveground portion of the plants, representing a significant nutrient storage. *Nymphaea odorata* did not retain significant amounts of dead material, and for *N. odorata* the major nutrient storage was in the rhizome.

By the end of the experiment, *C. jamaicense* had more than three times the final biomass (approximately 75% was in aboveground live and dead leaves), compared to the other species. Although the large amount of standing dead leaves in *C. jamaicense* could contribute to soil building, these leaves are known to decompose slowly (Newman et al., 2001; Serna et al., 2013) and to act as a fire fuel (Herndon et al., 1991; McVoy et al., 2011). These aboveground parts may be more important for nutrient cycling in the water column and for increased productivity after fires; thus the contribution of this biomass to soil building may occur more indirectly than the contribution from belowground parts.

Allocation of biomass to roots was lower on the deeper organic MR soils (Table 1). Theory predicts and experimental studies confirm that plants allocate more resources to roots on sites deficient in N and/or P in order to optimize nutrient uptake (Bloom et al., 1985). Due to site grading involved in the construction of LILA, soils in the DS and SS have lower nutrient concentrations (TC, TN, and TP) and higher bulk density than soils in the MR (Serna et al., 2013). Moreover, plots in the MR with lower water depth had a smaller total load of aqueous nutrients due to shorter flood durations and depth. Plant growth declined with decreased flooding levels, consistent with the idea that the response of plants to water depth involves both responses to water per se and responses to nutrient load (Newman et al., 1996). The nutrient data presented in this study, combined with the biomass data, suggest that the aboveground biomass of

photosynthetic tissue, which is more nutrient rich than the belowground parts, is not necessarily a good indicator of the nutrients that are available to soil microbes for decomposition.

We hypothesized that (1) flow and greater water depth would result in increased plant growth and survival, greater plant biomass, and nutrient content, and higher soil sedimentation rates for the two slough species *N. odorata* and *E. cellulosa* but decreased effects for *C. jamaicense*; and (2) plant physical structure (i.e., different forms and densities of plant parts in the water column (Bouma et al., 2005) would influence sediment deposition patterns (Tooth & Nanson, 2000) with *C. jamaicense* causing greater soil building due to the trapping of suspended sediments. For all the hydrologic conditions studied, soils accreted at an average rate of 2.7 mm year⁻¹, a value similar to estimations reported by Craft & Richardson (1993) from nutrient-unenriched sites of WCA 2A (2.3 mm year⁻¹) but higher than those reported by Craft & Richardson (1998) from the northern LNWR (0.8–1.2 mm year⁻¹). However, most of the accretion in this study came from that in the SS habitat, whereas little was seen in the other habitats (Fig. 4). The absence of significant soil accretion in the ridges might be related to reductions in overall biomass in this habitat compared with the other two, especially regarding differences between *C. jamaicense* growth between the MR and the DS.

Greater soil deposition occurred in the flowing macrocosm but most significantly in the SS. As mentioned, sediment redistribution via transport from slough to ridges has been postulated as a mechanism to create ridge-and-slough topography (Larsen et al., 2007). Although flow encouraged greater biomasses in *C. jamaicense* and *E. cellulosa* across all habitats and possibly increased soil accretion in the SS, differences in water velocities from no-flow to an average slough velocity of approximately 0.5 cm s⁻¹ over several years (≈ 4 in this study) did not have a great influence on soil building. Similarly, in Everglades field studies, Noe et al. (2010) concluded that entrainment velocities capable of redistribution of sediment and the associated nutrients do not, or rarely occur. Moreover, in a study to characterize the effects of altered hydroperiod on Everglades soils, Craft & Richardson (1993) found higher accretion rates in areas of extended hydroperiod, again suggesting that depth has a greater effect than flow.

Conclusion

Plant biomass allocation and tissue nutrient concentration responded to distinct water depth and flow generated in the LILA facility, with water depth having a much greater effect. *Cladium jamaicense* was found to have greater optimal water depth range than commonly reported—a potentially important result for defining depth targets for restoration of Florida's Everglades. The effects of depth and flow on the growth of the three common ridge-and-slough species, *C. jamaicense*, *E. cellulosa*, and *N. odorata*, can help to establish realistic hydrologic targets. The average water velocities in flowing macrocosms maintained in this study (0.5 cm s⁻¹) were shown to encourage plant productivity and can be used as baseline for further studies aiming to predict ecosystem responses to natural and/or anthropogenic variations in wetland water regime. Plant tissue nutrients and nutrient ratios differed among plant parts and between live and dead tissues; these data are critical to developing realistic nutrient budgets for Everglades marsh, especially as conditions may change under hydrologic restoration. Soil building partially responded to water depth and flow and was not significantly affected by species (biomass or morphology) after ≈ 4 year of plant growth but may be related to nutrients and OM content in LILA soils. *Cladium jamaicense* and *N. odorata* had relatively greater belowground biomasses than *E. cellulosa*, reinforcing the importance of *C. jamaicense* to peat building in ridges and *N. odorata* in sloughs. All three species grew in relatively deep water, suggesting that restoration efforts aimed at increasing the volume of water moving into the Everglades should be beneficial to marsh plant productivity. Our findings support others that did not find significant effects of low-velocity flow on particle transport and sediment accretion.

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