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Linking water use and nutrient accumulation in tree island upland hammock plant communities in the Everglades National Park, USA

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Abstract The tree island hammock communities in the Florida Everglades provide one of many examples of self-organized wetland landscape. However, little is understood about why these elevated tree island communities have higher nutrient concentration than the surrounding freshwater marshes. Here we used stable isotopes and elemental analysis to compare dry season water limitation and soil and foliar nutrient status in upland hammock communities of 18 different tree islands located in the Shark River Slough and adjacent prairie landscapes. We observed that prairie tree islands, having a shorter hydroperiod, suffer greater water deficits during the dry season than slough tree islands by examining shifts in foliar δ^{13}C values. We also found that prairie tree islands have lower soil total phosphorus concentration and higher foliar N/P ratio than slough tree islands. Foliar δ^{15}N values, which often increase with greater P availability, was also found to be lower in prairie tree islands than in slough tree islands. Both the elemental N and P and foliar δ^{15}N results indicate that the upland hammock plant communities in slough tree islands have higher amount of P available than those in prairie tree islands. Our findings are consistent with the transpiration driven nutrient harvesting chemo-hydrodynamic model. The water limited prairie tree islands hypothetically transpire less and harvest less P from the surrounding marshes than slough tree islands during the dry season. These findings suggest that hydroperiod is important to nutrient accumulation of tree island habitats.

Keywords Everglades tree islands · Hydroperiod · Nutrient harvesting · Phosphorus · Stable isotope · Water limitation

Introduction

Similar to most terrestrial mosaic landscapes such as savannas, many large wetland ecosystems have patterned landscapes, with a heterogeneous vegetation composition and nutrient concentration that are non-randomly distributed (Rietkerk et al. 2002, 2004). These non-random patterns are proposed to be self-organized by positive feedback loops (van der Valk and Warner 2009). The feedback mechanism usually involves vegetation affecting redistribution of materials and therefore leading to alteration of the environmental conditions such as local and regional

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hydrology, which in turn impacts on vegetation functioning (Eppinga et al. 2009; Rietkerk et al. 2004). One example of these self-organizing patterned landscapes are wetlands with tree islands. Wetzel (2002a) defines tree islands as patches of woody vegetation within a freshwater wetland matrix dominated by non-woody species. Tree islands are relatively young habitats in the wetlands, and are developed as a result of landscape processes and feedback between hydrological and climatic factors after wetland formation (Foster et al. 1983; Glaser 1987; Gumbricht et al. 2004; Wetzel 2002a). Tree islands may be initiated at a range of nucleation sites: on slightly elevated bedrock, floating peat mass, submerged tree branches, or aggregation of floating aquatic plants (Glaser 1987; Huffman and Lonard 1983; Olmsted 1993). In wetlands that accumulate peat, tree islands are often in the form of elevated peat mounds resulting from organic matter accumulation on top of a preexisting base. These tree islands are able to grow in size and nutrient concentration by accumulating litter or root material deposited by woody plants. They generally have a higher nutrient concentration and higher species richness than the surrounding wetland matrix (Slack et al. 1980; Wetzel 2002a).

In this study, we focused on tree islands of the South Florida Everglades. They are the focus of a wide range of nutrient inputs from potential sources such as precipitation, surface water surrounding the tree island, groundwater, plant litter and bird guano deposition, and bedrock mineralization by tree exudates (Wetzel et al. 2005). Therefore tree islands generally have relatively high phosphorus concentration compared to the fresh water marshes. There are two major hypotheses on how tree islands generate and maintain their high P levels. Givnish et al. (2008) suggest that guano deposition is the major P input for the tree islands. The other hypothesis is the chemohydrodynamic model (Ross et al. 2006; Wetzel et al. 2005), which suggests that tree islands accumulate and maintain their high P level by harvesting nutrients from surrounding water and groundwater. This hypothesis suggests that the high transpiration rates of tree island hammock communities cause them to take up water and nutrients from the surrounding marsh and groundwater, especially during the dry season and that nutrients gradually accumulate through this process (Wetzel et al. 2005). These two hypotheses are not mutually exclusive to each other, but this study will be focusing on ramifications of the chemohydrodynamic hypothesis. This hypothesis has been supported by previous studies that have shown that tree island plants can use marsh water during the dry season (Ross et al. 2006; Saha et al. 2010). One of the predictions of the chemohydrodynamic model is that since nutrient harvesting is transpiration driven, tree islands with low dry season transpiration will have lower nutrient accumulation rates than tree islands with high dry season transpiration.

In this study we tested two hypotheses related to the chemohydrodynamic model of transpiration-driven nutrient harvesting. First, we hypothesized that tree islands located in areas where the surrounding marshes dry out during the dry season will experience greater stomatal limitation to photosynthesis and transpiration than those located in areas which are flooded continuously throughout the year. We used shifts of foliar carbon isotope ratios from wet season to dry season to assess dry season stomatal limitation, as drought stress will cause an increase in foliar carbon isotope ratio due to stomatal limitation of photosynthesis (Farquhar et al. 1988). According to the chemohydrodynamic model, tree islands located in areas with longer hydroperiods will harvest relatively more nutrients from the surrounding marshes. We, therefore, tested as a second hypothesis that tree islands surrounded by continuously flooded marsh will exhibit higher total soil P and more P available to plants compared to those located in areas with shorter hydroperiods. We assessed this by measuring total soil P, foliar nitrogen isotope ratios, foliar P concentration and foliar N/P ratios, where total soil P, foliar nitrogen isotope ratio and foliar P concentration are related to P availability (Eppinga et al. 2008; Inglett and Reddy 2006; Inglett et al. 2007; Ross et al. 2006) and foliar N/P ratio are indicator of N or P limitation (Koerselman and Meuleman 1996).

Methods

Study area

The Everglades ecosystem has an annual rainfall averaging 1,300 mm, approximately 70–90% of which falls during the wet season, from June to

November (Renken et al. 2006). The region has a gentle elevation gradient of <4.5 cm per km with a 48 km-wide sheetflow of surface water concentrated in the Shark River Slough (Fling et al. 2004). As a coastal wetland ecosystem, the Everglades consists of a variety of terrestrial and marine habitats including upland pinelands and hammocks, sawgrass marshes, tree islands, mangroves, and coral reefs (Lodge 2004). Covering about 70% of the Everglades area, the freshwater marsh consists of two distinct types of landscape: the mixed ridge-slough matrix and the marl prairies (Bernhardt and Willard 2009). The ridge-slough habitat is characterized by deep organic soils, flooding throughout the year, and maximum water depths of ~1 m. The marl prairies are characterized by marl soils, shallow water (<0.5 m) and short (<180 day) hydroperiods. The Shark River Slough, with water flowing southwestwards into the Gulf of Mexico, serves as the primary flow path in the Everglades ecosystem. The fresh water ridge and slough in the Shark River Slough are dominated by sawgrass (*Cladium jamaicensis*) in the ridges and water lilies (*Nymphaea odorata*) in the slough, while those of the adjacent prairies are dominated by muhly grass (*Muhlenbergia filipes*), which is adapted to a shorter hydroperiod than sawgrass (Fig. 1). Both sloughs and prairies feature scattered, elevated tree islands.

Tree islands are common features in both ridge-and-slough and marl prairie landscapes. In both cases, the best developed islands are characterized by an elevated, mesic head with flood-intolerant hardwood hammock tree communities, and an encircling swamp forest comprised of flood tolerant trees and shrubs (Sklar and van der Valk 2002; Wetzel 2002b). In the ridge-and-slough environment, the surrounding swamp forest forms an elongated tail, while the tails of marl prairie tree islands are often inconspicuous or absent. The heads of such bi-phased tree islands typically remain unflooded in both landscapes, even during the wet season. Decomposition rates in the moist, well-drained environments of the tree island heads in both landscapes are apparently quite rapid, based on litter turnover rates of 0.6–1.2 times per year (Ross unpublished data). However, soil characteristics vary markedly in the two settings. Soils in the highest portions of marl prairie tree islands are shallow (<30 cm), primarily organic (mean of 51.1% organic matter, determined by loss on ignition, in the surface 10 cm at 6 sites), with relatively low mineral content, circumneutral pH. (Ross et al., unpublished manuscript). These Histosols are commonly mapped as Dania or Matcumbe mucks (USDA-NRCS 1996), and resemble the Folists that develop directly on limestone bedrock in the Florida Keys (Ross et al. 2003). In contrast, most ridge-and-slough tree island soils studied so far feature organic (mean of 21.2% organic matter for 62 sites) surface layers above mineral subsoils, with alkaline reaction (Ross et al., unpublished manuscript). Coultas et al. (2008) recently described two profiles from large islands in northeastern Shark Slough. Organic matter decreased downward, and the soils were therefore classified as Mollisols. Most notably, a petrocalcic layer of ~20 cm thickness was present mid-profile, beginning ~60 cm below the surface. The mechanism of development of the petrocalcic layer is uncertain, but has been hypothesized to involve the precipitation of calcite from calcium-rich capillary waters originating in the shallow water table (Coultas et al. 2008; Graf et al. 2008).

Eighteen tree islands were selected along the Shark River Slough and in the adjacent marl prairies. GPS coordinates were recorded for each tree island during field sampling. Ten of the 18 tree islands were located in the Shark River Slough (henceforth called slough tree islands) and 8 of them were located in the adjacent prairies east and west of the slough (henceforth called prairie tree islands). The selection of specific tree islands within each habitat was based on accessibility and permission by the National Park Service (Fig. 1).

Species and sampling

The hardwood hammock community on the head of each tree island is dominated by about 5–10 evergreen or deciduous subtropical tree species. Species common to both slough and prairie tree islands include *Myrsine floridana*, *Bursera simaruba*, *Coccoloba diversifolia*, *Eugenia axillaris*, and *Sideroxylon foetidissimum*. *Celtis laevigata* and *Chrysophyllum oliviforme* are typically restricted to the slough islands, while *Ardisia escallonioides*, *Lysiloma latisiliqua*, *Nectandra coriacea*, *Quercus virginiana*, and *Sideroxylon salicifolium* are more common on the prairie islands. All of these species are intolerant of prolonged flooding (Saha et al. 2010). The deciduous species (*Bursera simaruba* and

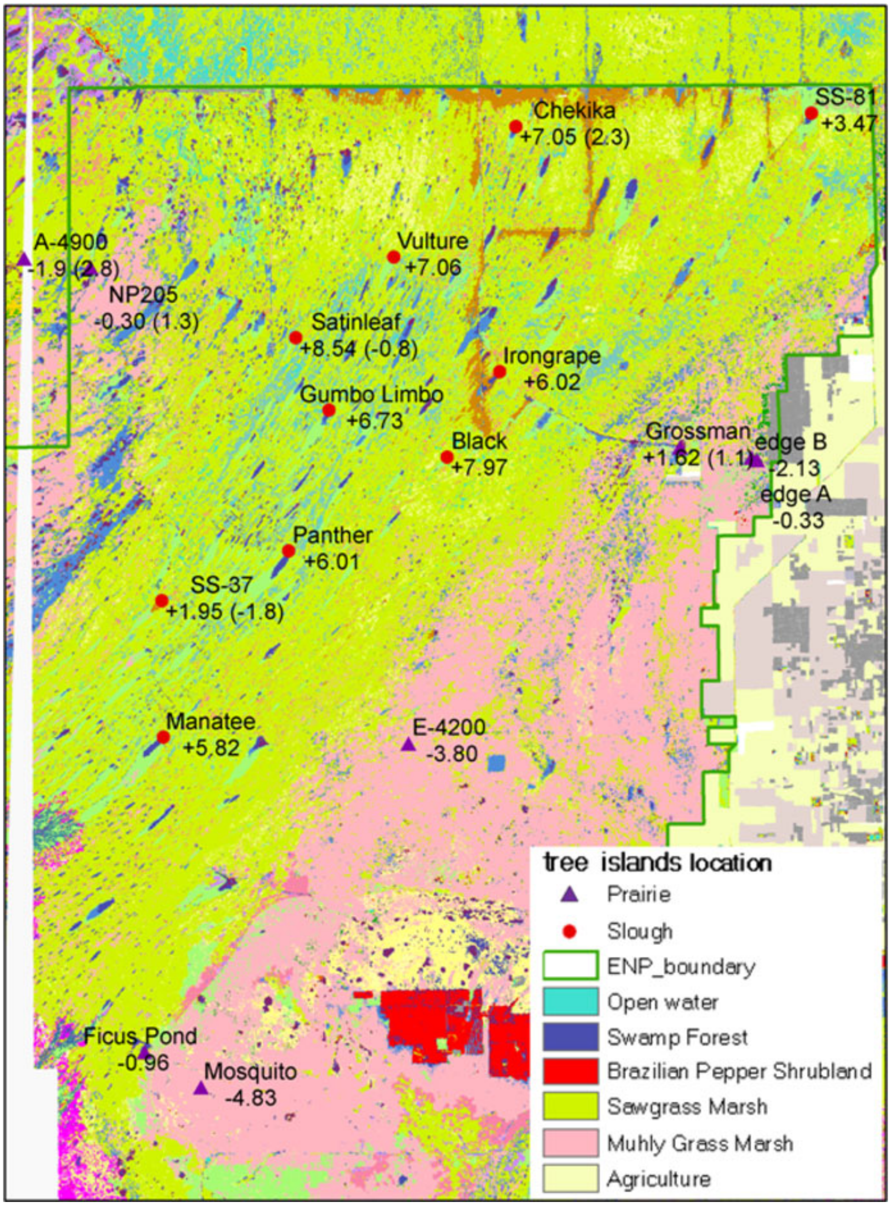


Fig. 1 Geographic map of slough (*filled circle*) and prairie (*filled triangle*) tree islands sampled along the Shark River area. The values following each tree island indicate the average foliar δ^{15}N values (‰) of the upland hammock community, and values in parenthesis indicate the average foliar δ^{15}N values (‰) of sawgrass sampled near the particular tree island. *Background map* of land cover by vegetation class obtained from the FL Gap Project final report. Slough tree islands are surrounded by sawgrass (*Cladium jamaicensis*) mixed marsh, and prairie tree islands are surrounded by muhly (*Muhlenbergia filipes*) mixed marsh

Celtis laevigata) lose their leaves during the January to May dry season, with a leafless period of about 1 month long. There were only a few species common to both slough and prairie tree islands, and species overlap was slight among the prairie tree islands we sampled. For each tree island, species were ranked with Importance Values based on relative density and basal area (Shamblin et al. 2008), and the four species with highest Importance Values in each tree island were selected for isotopic and nutrient analysis (1–3 in cases where the island had low woody plant diversity and five when Importance Values of the fourth and fifth most abundant species were indistinguishable) (Table 1).

Foliar samples were collected during the wet season (September) and dry season (May) between 2006 and 2008 (Table 1). Samples collected from all tree islands during the wet season were used for elemental (N and P) and isotopic (C and N) foliar analysis. The youngest fully expanded 4–5 leaves per tree were sampled from 10 individual trees of the four

Table 1 Type of island, geographical locations, list of sampled species, and time of sampling of each selected tree island

Tree island	Type	Latitude	Longitude	Sampled Species	Time of Sampling
Satin Leaf	Slough	25.6115	−80.6883	CL, **EA**, **CD**, CO, **BS**	Sep 06, May 07
Chekika	Slough	25.7452	−80.6572	CL, **EA**, **MF**, **SF**	Sep 06, May 07
Vulture	Slough	25.5735	−80.7592	**BS**, CL, **EA**, **SF**	Sep 07, May 08
Irongrape	Slough	25.6152	−80.5842	**BS**, CL, **EA**, **SF**	Sep 07
Gumbo Limbo	Slough	25.6306	−80.7410	**BS**, CL, **EA**, **SF**	Sep 07
Black	Slough	25.6460	−80.6648	**BS**, CL, **EA**, **SF**	Sep 07
Panther	Slough	25.4982	−80.8154	**BS**, CL, **EA**	Sep 07
Manatee	Slough	25.6925	−80.7120	**BS**, CL, **EA**, **SF**	Sep 07
SS37	Slough	25.3565	−80.7987	**BS**, **CD**, CL, **EA**, **SF**	Sep 07
SS81	Slough	25.6599	−80.7558	CL	Sep 07
Grossman	Prairie	25.4956	−80.7058	AE, **BS**, **CD**, NC	Sep 06, May 07
A4900	Prairie	25.6887	−80.8477	**BS**, **CD**, LL, **SF**	Sep 07, May 08
E4200	Prairie	25.5534	−80.8160	**CD**, QV, SS	Sep 07, May 08
NP205	Prairie	25.6923	−80.8774	**BS**, **CD**, EA, **SF**	Sep 07, May 08
Ficus Pond	Prairie	25.3708	−80.8240	**CD**, **EA**, SS	Sep 07
Mosquito	Prairie	25.7503	−80.5250	**BS**, **MF**, QV, SS	Sep 07
Edge A	Prairie	25.6100	−80.5498	**MF**, SS	Sep 07
Edge B	Prairie	25.6108	−80.5524	**MF**, SS	Sep 07

Bold tree island names indicate tree islands that were sampled during both wet season and dry season. Species name abbreviations stand for: *Ardisia escallonioides* (AE), *Lysiloma latisiliqua* (LL), *Myrsine floridana* (MF), *Nectandra coriacea* (NC), *Quercus virginiana* (QV), *Sideroxylon salicifolium* (SS), *Bursera simaruba* (BS), *Coccoloba diversifolia* (CD), *Eugenia axillaris* (EA), *Sideroxylon foetidissimum* (SF), *Celtis laevigata* (CL) and *Chrysophyllum oliviforme* (CO). Bold species abbreviations indicate species that were sampled in both slough and prairie tree islands

most dominant species from each tree island. Out of the 18 tree islands studied, a subset of seven tree islands (four slough tree islands and three prairie tree islands) were selected to be sampled during both wet season and dry season for a seasonal comparison (Table 1). We compared seasonal shifts between wet season 2006 and dry season 2007 for three tree islands (two slough and one prairie), and between wet season 2007 and dry season 2008 in four tree islands (one slough and three prairie). A paired *T*-test was used to compare the precipitation of each month between July 2006 to June 2007 and July 2007 to June 2008, and showed no difference between these 2 years. In these tree islands, leaf samples were collected during the dry season in the same manner and from the same species as wet season samples. Leaf samples were collected from five individual trees of each species for isotopic C and N analysis. A subset of six tree islands (three slough and three prairie) were also selected for collecting sawgrass samples near the tree island for N isotope analysis to ensure there is no inherit difference in N isotope ratios of the surrounding marsh water of slough and prairie tree islands. Five replicates of newly grown sawgrass blade samples were collected during the wet season from about 10 to 15 m off the north end (upstream) of each tree islands in order to minimize the influence from tree island runoffs.

Foliar C and N analysis

Leaf samples were dried in an oven at 50°C for at least 2 days. Dried leaf samples were then ground and loaded (5 mg) into individual tin cups. The samples were then analyzed by an automated elemental analyzer (Euro-EA-Elemental Analyzer, Eurovector, Milan, Italy) connected to a continuous flow isotope ratio mass spectrometer (Isoprime, Elementar, Hanau, Germany) for leaf N concentration and C and N isotopic composition. Leaf N concentration is measured as a weight percentage of total foliar N relative to total leaf dry mass, and C and N isotopic compositions are reported as δ^{13}C and δ^{15}N values, respectively. δ^{13}C and δ^{15}N values are expressed as:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = \left[\left(R_{\mathrm{sample}}/R_{\mathrm{std}}\right) - 1\right] * 1000$$

where R_{sample} and R_{std} represent the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ isotopic concentration ratios in the sample and in the standard respectively. The internal lab standards were calibrated for C isotope to the Vienna PeeDee belemnite formation of South Carolina, and for N isotope to air. The precision of the N concentration analysis was ±1 ppm ($\pm 1\sigma$) and the precision of the C and N isotopic analysis was ±0.1‰ ($\pm 1\sigma$). The analyses were done at the Laboratory of Stable Isotope Ecology in Tropical Ecosystems at the University of Miami.

Foliar P analysis

Approximately 0.3 g of ground leaf samples were weighed out in porcelain crucibles and oxidized in a furnace at 600°C for 6 h. The ashes were then digested in 5 ml of 4% sulfuric acid, filtered through glass fiber filter paper (Whatman, UK), and diluted with double distilled water to 25 ml solution. The filtered sample was analyzed by an Alkem 3000 Phosphorus analyzer (Alpkem, OI Analytical, TX, USA) using the USEPA method 365.1 (USEPA, 1984) by the molybdate blue colorimetric approach (Fiske and Subbarow 1925). As in N concentration, the P concentration is measured as a weight percentage of total foliar P relative to total leaf dry mass with an analytical precision of ±0.1 ppm ($\pm 1\sigma$).

Total soil P analysis

Soil was collected from 15 tree islands, nine in slough and six in prairie, by driving a 5.25 cm diameter acrylic core into the soil to a depth of 10 cm, or to the underlying bedrock surface at a few points where soils were shallower than 10 cm. Cores from three locations near the center of the tree island were bulked to obtain a representative substrate. The samples were subsequently stored in plastic bags in the refrigerator until analysis. TP was determined by a modification of sample preparation methods described by Solorzano and Sharp (1980). Samples were oxidized by dry combustion and all phosphorus-containing compounds were hydrolyzed to SRP using $MgSO_4/H_2SO_4$ and HCl, followed by colorimetric analysis according to the standard method for orthophosphate P (EPA method 365.1).

Data analysis

Foliar $\delta^{13}C$ value: Since foliar $\delta^{13}C$ values showed non-homogeneity, we used non-parametric statistical tests. A series of Wilcoxon signed-rank tests were performed to test for the significance of seasonal foliar $\delta^{13}C$ shift on each individual tree island. The significance level of the Wilcoxon signed-rank tests was adjusted by a Bonferroni correction (Sokal and Rohlf 1995).

Foliar N/P ratio and absolute foliar P concentration: A Mann–Whitney U test was performed to examine the differences of foliar N/P ratios between slough and prairie tree islands at the community level (i.e. pooling all species together). In addition, a series of Mann–Whitney U tests were performed on each of the common species found in both slough and prairie tree islands to examine the N/P differences between both island types. The significance level of the Mann–Whitney U tests was adjusted by a Bonferroni correction (Sokal and Rohlf 1995). The same statistical tests were performed to examine the differences of absolute foliar P concentration between slough and prairie tree islands at the community level and at the species level for the five common species.

Foliar $\delta^{15}N$ value: A two-way ANOVA was performed to examine the effects of season and tree island type (slough vs. prairie) on foliar $\delta^{15}N$ values from the 7 tree islands that were sampled in both wet season and dry season. This analysis was done at the community level and species was not considered as a separate factor. Another two-way ANOVA was performed to examine and compare the effects of species and tree island types (slough vs. prairie) on foliar $\delta^{15}N$ values of species found in both slough and prairie tree islands. Only the wet season samples were used in the latter analysis. In addition, a nested one-way ANOVA was performed to examine the main effect of tree island types (slough vs. prairie) and the nested effect of individual tree islands on foliar $\delta^{15}N$ values of sawgrass growing near different tree islands. Before each ANOVA, Q–Q plots for normal distribution were performed to confirm normality and Fligner–Killeen tests were performed to confirm homogeneity of variances. Finally, average foliar $\delta^{15}N$ values of the upland hammock in the wet season and those of the nearby sawgrass where samples were taken were mapped as geographical points onto a land cover map of the ENP area obtained from the Florida Gap Project using software ArcGIS (ESRI, USA).

Many of the above data analyses were done at the community level without considering different species as a separate factor for two reasons. First, these tree islands are isolated habitats, and species composition is quite different among all the tree islands selected. There were only five species common to both slough and prairie tree islands due to their differential hydrological characteristics. These facts make it difficult to test the effect of species in most analyses comparing slough and prairie tree islands. Second, the species selected in these sampling and analyses were the most dominant species on each tree island. As most tree island hammocks are only occupied by 5–10 hardwood species (Shamblin et al. 2008), it is safe for us to assume that the four most dominant species are representative of the hardwood hammock community, and that community level comparisons are reliable indicators of most species behavior.

Results

Foliar δ^{13}C value

The Wilcoxon signed-rank test showed no significant difference in foliar δ^{13}C between wet and dry season for the three slough tree islands, while three out of four prairie tree islands showed significant increase in foliar δ^{13}C from wet season to dry season (Fig. 2).

Soil P concentration

Soil P concentration showed a sharp contrast between slough and prairie tree islands. Total soil P concentration for slough tree islands had much higher values averaging 52,987 ± 17,142 μg/gdw ($\pm\sigma$, $n = 9$) than those for prairie tree islands averaging 2,123 ± 2,419 μg/gdw ($\pm\sigma$, $n = 6$) (Fig. 3).

Foliar N/P ratio and foliar P concentration

Significant differences in foliar N/P ratios and foliar P concentration were found between slough and prairie tree islands at the community level by the Mann–Whitney *U* test, where slough tree islands had lower foliar N/P ratios (Fig. 4) and higher absolute P concentration than prairie tree islands (Fig. 4). This pattern was confirmed at the species level, where four out of the five species common to slough and prairie tree islands showed significantly lower foliar N/P and higher absolute P concentration in slough tree islands than in prairie tree islands (Fig. 4).

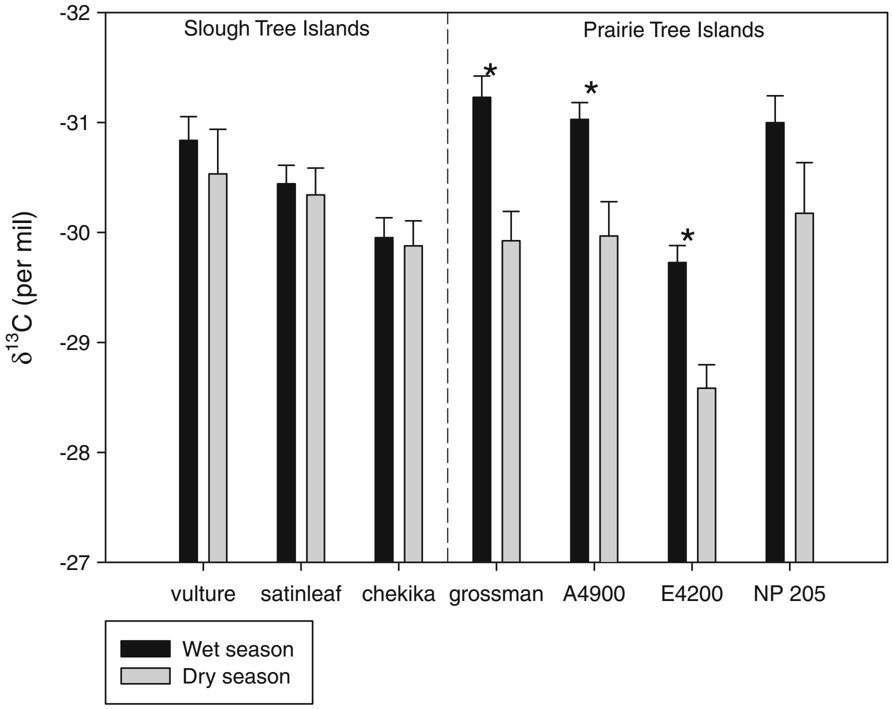
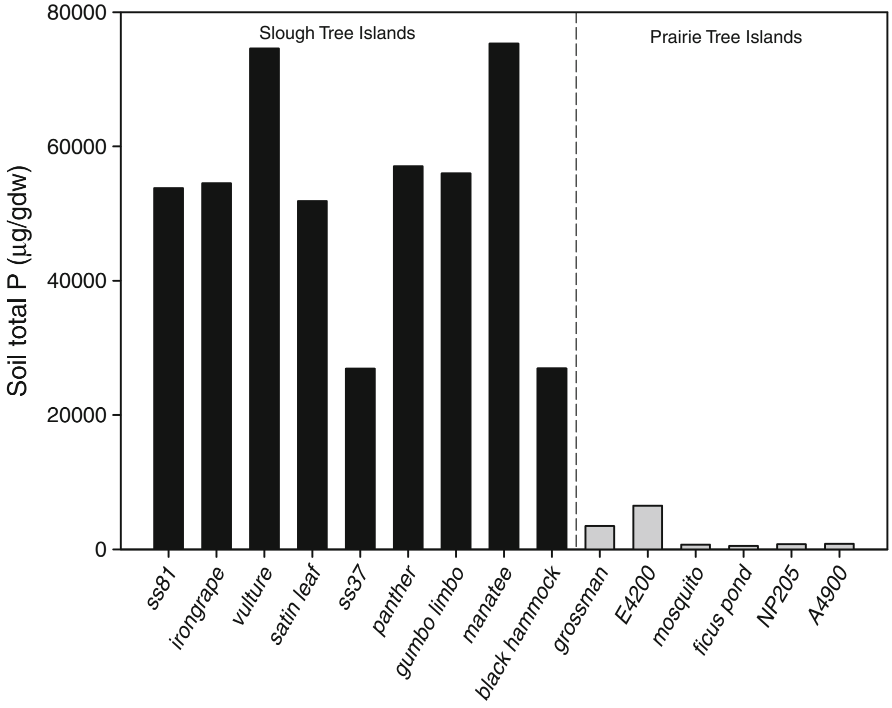


Fig. 2 Average foliar δ^{13}C (‰) of wet (*black*) and dry (*grey*) seasons for three slough tree islands and four prairie tree islands. *Error bars* represent standard error of the mean (SEM). *Stars* indicate significant differences between wet and dry season at $\alpha = 0.007$ (experimental wise error rate after Bonferroni correction)

Fig. 3 Soil total P concentration (µg/gdw) in the surface 10 cm of slough (*black*) and prairie (*grey*) tree islands



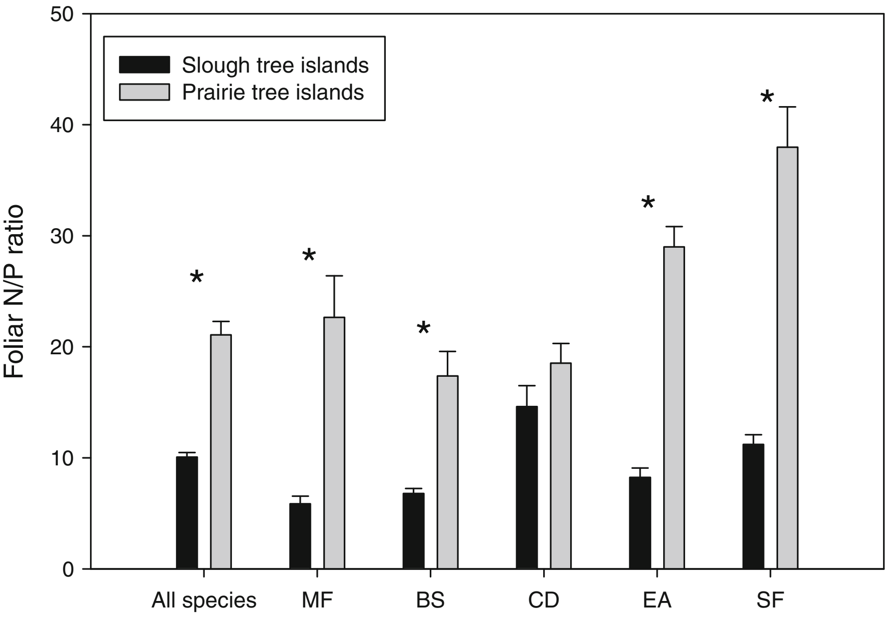


Fig. 4 Average foliar N/P ratios of all species and the common species within each tree island type. *Error bars* represent SEM. *Stars* indicate significant differences of P concentration between slough and prairie tree islands at $\alpha = 0.05$ for the community level analysis and $\alpha = 0.01$ (experimental wise error rate after Bonferroni correction) for the species level analysis. Common species between slough (*black*) and prairie (*grey*) tree islands include *Myrsine floridana* (MF), *Bursera simaruba* (BS), *Coccoloba diversifolia* (CD), *Eugenia axillaris* (EA), and *Sideroxylon foetidissimum* (SF)

Foliar $\delta^{15}N$ value

The average foliar $\delta^{15}N$ of each tree island showed a distinct geographical pattern: slough tree islands had foliar $\delta^{15}N$ values averaging $+6.06 \pm 1.89‰$ ($\pm\sigma$, $n = 10$), which were higher than those for prairie tree islands averaging $-1.58 \pm 1.53‰$ ($\pm\sigma$, $n = 8$) (Fig. 1). The foliar $\delta^{15}N$ differences between slough and prairie tree islands were confirmed by the two-way ANOVA (Table 2a, b). However, no significant seasonal effects on foliar $\delta^{15}N$ were found among the seven tree islands sampled during dry and wet seasons (Table 2a; Fig. 5). Analysis of species common to both types of tree islands showed that species effects, although significant ($P < 0.001$, $F = 22.70$, df = 4), were less distinct in comparison to differences attributed to tree island types ($P < 0.001$, $F = 1228.28$, df = 1) (Table 2b; Fig. 6). Foliar $\delta^{15}N$ values of sawgrass collected near the islands, although significantly different between individual tree islands, were significantly lower near slough tree islands than near prairie tree islands ($P < 0.001$, $F = 17.55$, df = 1) (Fig. 1, Table 2c), with foliar $\delta^{15}N$ values of sawgrass near slough tree islands averaging -0.1 ± 0.5 ($\pm\sigma$, $n = 15$) and those near prairie tree islands averaging $+1.7 \pm 0.4$ ($\pm\sigma$, $n = 15$).

Table 2 Results of univariate two-way ANOVA examining: seasonal and tree island type effects on foliar $\delta^{15}N$ of 7 tree islands (a), species and tree island type effects on foliar $\delta^{15}N$ of the common species (b), and nested univariate one-way ANOVA examining effects of individual tree islands nested in different tree island types on foliar $\delta^{15}N$ of sawgrass growing near 6 tree islands (c)

Source	df	*F*	Sig.
(a) Dependent variable: $\delta^{15}N$			
Season	1	2.962	0.086
Type	1	1471.019	1.04E−137
Season * type	1	1.538	0.216
(b) Dependent variable: $\delta^{15}N$			
Type	1	1338.283	2.03E−106
Species	4	22.702	3.58E−16
Type * Species	4	8.887	9.38E−7
(c) Dependent variable: $\delta^{15}N$			
Type	1	17.546	3.266E−4
Island (type)	4	9.763	7.802E−5

Discussion

These results support both our hypotheses related to the chemohydrodynamic feedback model. Hammock trees in prairie tree islands show a greater stomatal limitation during the dry season compared to those in slough tree islands based on C isotope ratios, which supports the hypothesis that prairie tree island plants suffer from water deficits during the dry season. And the N, P, and isotopic analyses show that slough tree islands have higher soil P concentration as well as less P limitation to the hardwood hammock plants compared to prairie tree islands.

Previous studies have shown that foliar $\delta^{13}C$ is related to plant water use efficiency (Farquhar et al. 1988). In C_3 plants, the principal carboxylation enzyme Ribulose Bis-Phosphate Carboxylase (RuBisCo) discriminates against the heavier isotope ^{13}C during CO_2 assimilation. Stomatal closure, such as that caused by water stress, limits CO_2 supply for photosynthesis and thus lowers the leaf internal CO_2 concentration and the RuBisCo discrimination against ^{13}C (Farquhar et al. 1982). It has been shown by several investigations that plants under water stress increase their foliar $\delta^{13}C$ relative to those without water stress (Farquhar et al. 1988; Farquhar et al. 1982; Farquhar and Richards 1984; Hubick et al. 1986). We show here a significant increase in foliar $\delta^{13}C$ values from wet to dry season in the prairie tree islands (Fig. 2), which indicates that prairie tree island plants have stomatal limitation in their carbon uptake during the dry season. This stomatal limitation would also lower transpiration during the dry season in prairie tree islands. On the other hand, plants in slough tree islands have the same foliar $\delta^{13}C$ values during both wet and dry season (Fig. 2). We, therefore, conclude that prairie tree islands suffer greater dry season water deficits than slough tree islands. These results are consistent with the differences in the average water levels and hydroperiod of the marshes surrounding the slough and prairie tree islands. In a previous study using stable isotope ratios as a tracer of water uptake in tree islands, Saha et al. (2010) showed that Everglades tree island plants use soil trapped rain water during the wet season and marsh water during the dry season. Our foliar $\delta^{13}C$ results suggest that slough tree island avoid water stress by accessing marsh water supply during the dry season, while prairie tree

Fig. 5 Average foliar δ^{15}N (‰) in wet (*black*) and dry (*grey*) seasons for three slough tree islands and four prairie tree islands. *Error bars* represent SEM. $n = 20$–40 per tree island. No significant differences were found between wet and dry seasons

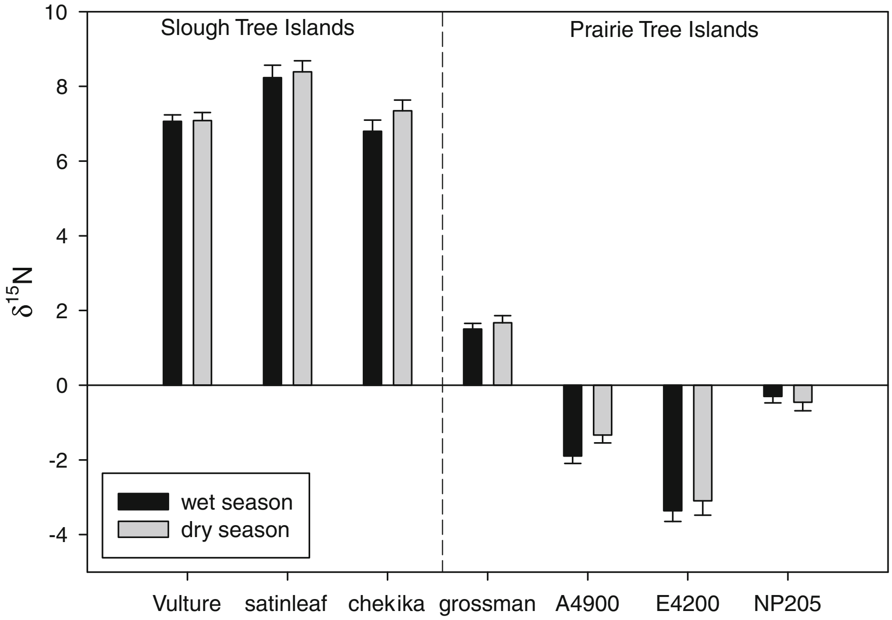
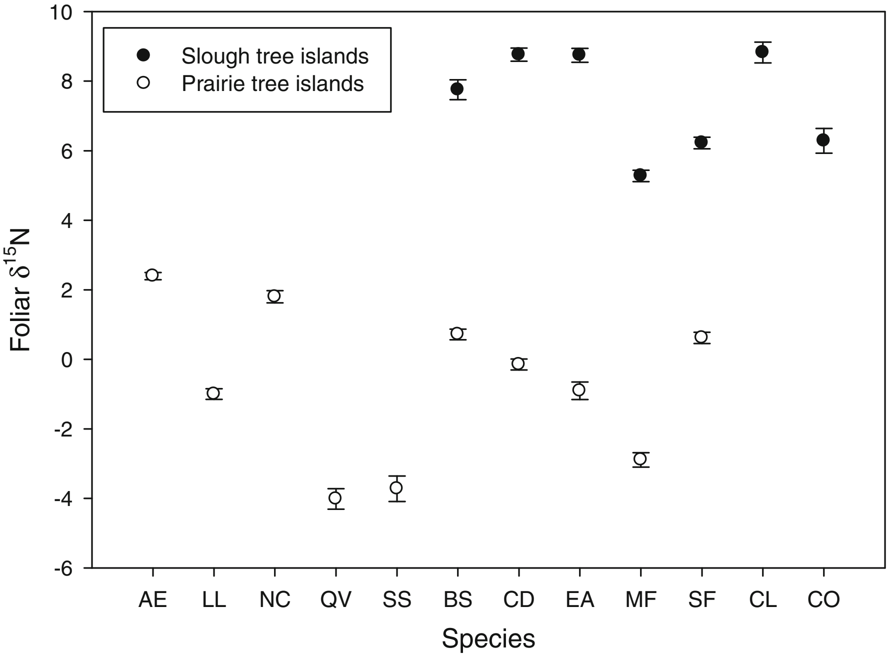


Fig. 6 Foliar δ^{15}N (‰) of different species within each island type. *Data* represent species averages throughout the year and across all slough (*filled circle*) and prairie (*open circle*) tree islands. *Error bars* represent SEM. Species include *Ardisia escallonioides* (AE), *Lysiloma latisiliqua* (LL), *Myrsine floridana* (MF), *Nectandra coriacea* (NC), *Quercus virginiana* (QV), *Sideroxylon salicifolium* (SS), *Bursera simaruba* (BS), *Coccoloba diversifolia* (CD), *Eugenia axillaris* (EA), *Sideroxylon foetidissimum* (SF), *Celtis laevigata* (CL) and *Chrysophyllum oliviforme* (CO)



island plants experience water stress as the surrounding marshes dry out.

Our results, along with those of Saha et al. (2010) are consistent with a temporal component to the chemohydrodynamic model. In this scheme, tree island hammock plants take up water and nutrients from the surrounding marshes during the dry season when there is little or no rain water available. Because the heads of tree islands are rarely flooded, the nutrients taken up by hammock trees remain in the tree island soil and accumulate over time. As suggested by the chemohydrodynamic model, high transpiration and the consequential movement of marsh water is the driving force of nutrient (including

P) accumulation in tree islands (Wetzel et al. 2005). According to Saha et al. (2010), this would occur mainly during the dry season, which is therefore designated as the nutrient harvesting phase. Our results suggest that during the dry season, unlike slough tree islands, prairie tree island plants are under water limitation due to the lack of available water in the surrounding marshes. These islands are expected to have a lower dry season transpiration rate. Therefore we hypothesize that they should also have a lower nutrient accumulation rate than those of slough tree islands. Conversely, slough tree island plants can maintain high water and nutrient uptake rates using surrounding marsh water during the dry season. We thus expect that slough tree islands will have higher P accumulation rates than prairie tree islands and this will be reflected in their P nutrient status.

Our results of total soil P concentration and foliar N/P ratio are consistent with the above scenario of tree island P accumulation. Total soil P concentrations in slough tree islands are 10–100 times of those in prairie tree islands (Fig. 3). Most P in tree island soils are found in unavailable forms (Sklar and van der Valk 2002), and may not reflect P accumulation through transpiration, but rather the mineral substrate of the tree islands. However, Ross et al. (2006) has shown that in similar vegetation types, total soil P concentration is reflective of the general pattern of soluble active P that is available for plants uptake. This is evidenced by leaf concentrations, which show that slough tree islands have significantly lower N/P ratio than prairie tree islands (Fig. 4). Foliar N/P ratio is known to be inversely correlated with P availability (Han et al. 2005), and has been proposed as an indicator of the relative availability and limitation of N and P elements to plants (Gusewell 2004). Foliar N/P ratios of plants worldwide range from 3 to 89 for different ecosystems, and are in part related to climate and geographical locations (Reich and Oleksyn 2004; Wright et al. 2005). However, Gusewell et al. (2004) found that in most terrestrial ecosystems, biomass N/P ratios <10 or >20 often indicate N or P limitation to plant growth respectively. Foliar N/P ratios of plants in European freshwater wetlands range from 7 to 30, with ratios higher than 16 indicating P limitation and lower than 13.5 indicating N limitation at the community level (Gusewell and Koerselman 2002). Foliar N/P ratios in prairie tree islands have a mean value of 21.1 ± 12.6 ($\pm\sigma$), ranging from 17.4 to 38.0 depending on the species; while foliar N/P ratios in slough tree islands have a mean value of 10.1 ± 5.4 ($\pm\sigma$), ranging from 5.9 to 14.6 depending on the species (Fig. 4). According to these results, plants in prairie tree islands are P limited. On the other hand, the average foliar N/P ratios in slough tree islands generally show a stoichiometry indicative of an adequate supply of P relative to N.

The comparison of foliar δ^{15}N in slough and prairie tree islands is also consistent with greater P limitation in prairie tree islands. Foliar δ^{15}N is determined by both the isotopic composition of the N source and the isotopic fractionation during N assimilation (Delwiche and Steyn 1970; Handley and Raven 1992; Robinson 2001). If marsh water is the ultimate nutrient source of the tree island soils, foliar δ^{15}N values of sawgrass near the tree islands should be indicative of the isotopic composition of the N sources of the hammock plants. However, we found that the δ^{15}N values of sawgrass showed an opposite pattern than the foliar δ^{15}N of the hammock plant communities, with sawgrass foliar δ^{15}N values in the slough significantly lower than those in the prairie (Fig. 1). Therefore, different N source from the marsh water cannot be the reason for the observed foliar δ^{15}N pattern for tree island plants. Source effects also include N uptake preference of each individual species (Evans et al. 1996; Houlton et al. 2007; Waser et al. 1998), and N fixing effects (Nair 1993; Nguluu et al. 2002). All the species studied here are tropical hammock species intolerant of flooding and not known to be N-fixers (Jones et al. 2006), thus we make the assumption that N uptake preferences is not a significant factor between these species. The fractionation effect, therefore, should be related primarily to N demand relative to the supply in the rhizosphere (Handley and Raven 1992). Plants will naturally discriminate against ^{15}N during nitrogen uptake. However, when the demand of N is high and the supply is limited, this discrimination is diminished or non-existent (Mariotti et al. 1981). In P limited environments, increased N demand due to P fertilization lowers the discrimination against ^{15}N during plant N uptake and thus increases foliar δ^{15}N (Clarkson et al. 2005; McKee et al. 2002; Nadelhoffer et al. 1996). In the generally P limited Everglades, foliar δ^{15}N of plants has been shown to be an indicator of ecosystem P availability (Inglett and Reddy 2006; Inglett et al. 2007). In addition to foliar N/P ratios, absolute foliar P concentration is also an indicator of P availability both at the community level and within individual plant species (Eppinga et al. 2008, 2009). Higher foliar P concentration found in slough tree islands compared to prairie tree islands suggests slough tree island plants have higher P available at the community level as well as at species level for four out of five of the common species between slough and prairie tree islands.

The overall pattern of foliar δ^{15}N is consistent with those of soil P, foliar N/P ratio and foliar P concentration, with slough tree islands having higher foliar δ^{15}N values than prairie tree islands (Figs. 1, 5, 6). Average foliar δ^{15}N values of tree islands vary geographically, where the tree islands within the Shark River Slough tend to have higher foliar δ^{15}N than tree islands located in the prairies (Fig. 1). This general pattern is not affected by seasonal changes (Fig. 5), and although foliar δ^{15}N values differ between species, the differences between slough and prairie tree islands are clear for species that are common to both slough and prairie tree islands (Fig. 6). All four analyses (total soil P, foliar N/P ratio, foliar P concentration and foliar δ^{15}N value) support our hypothesis that slough tree islands have higher P than prairie tree islands, which is consistent with the chemohydrodynamic model. Moreover, although this study does not disprove the bird guano hypothesis suggested by Givnish et al. (2008), bird surveys done in the Everglades revealed no clear preference pattern of bird activities to hydroperiod and water level (Gawlik and Rocque 1998), which makes it difficult to explain the heterogeneous P pattern observed in tree islands located in slough and prairie landscapes. Whether or not the substrate differences between prairie and slough tree islands is responsible for the contrasting nutrient status observed here needs to be further studied. Studies need to focus particularly on whether these substrate differences might also be caused by the hydrological contrast between prairie and slough tree islands.

Because this study is correlational, and manipulative experiments to prove a nutrient accumulation process which might have taken thousands of years are impossible, we cannot conclude that the chemohydrodynamic model has been shown true. In addition to bird guano nutrient deposition, there are other possible sources of nutrient such as groundwater or the original parent material of the tree island. These alternate sources are still in question and need future research. Our study, however, shows consistency between the transpiration regime, nutrient status, and the predictions of the chemohydrodynamic model.

In this study we used foliar δ^{13}C shifts as a diagnostic for plant WUE and foliar δ^{15}N values as a diagnostic for plant P availability at the community level. Foliar δ^{13}C diagnostic uses the shift of δ^{13}C from wet season to dry season to integrate the variation of WUE from wet to dry season. Although it is only a proxy, the foliar δ^{13}C diagnostic is easier to determine than continuously measuring transpiration or water uptake for an entire year and could be applied when the capacity for continuous measurement is not available. The foliar δ^{15}N values as a P availability diagnostic are constant through the entire year and had no seasonal variations, which makes it a more reliable measurement for P availability than any one time soil nutrient measurements because of the frequent fluctuations of soil pore water (Trent 2009). As compared to the foliar N/P ratio, the process of foliar δ^{15}N analysis requires much less of a labor investment. In habitats like Everglades tree islands, where it is difficult to perform continuous or frequent plant and soil analysis due to the difficulties of access, the foliar δ^{13}C and foliar δ^{15}N diagnostics can be reliable and practical tools.

Conclusions

The findings from this study add knowledge to the nutrient accumulation process of tree island habitats. We showed that the hydrological characteristics of the areas surrounding the tree islands (i.e. marsh dry season water level) is connected to the dry season stomatal limitation of tree island hammock community and to differential P accumulation rates of tree islands. Our findings are consistent with the chemohydrodynamic hypothesis. Tree islands located in the prairies have water limitation during the dry season and therefore have a lower capacity of transpiration-driven nutrient accumulation compared to the slough tree islands. This hydrologically induced difference in P accumulation is a long term effect and has a large impact on the P availability of these tree islands.

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