

Water source utilization and foliar nutrient status differs between upland and flooded plant communities in wetland tree islands

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Abstract Tree islands in the Everglades wetlands are centers of biodiversity and targets of restoration, yet little is known about the pattern of water source utilization by the constituent woody plant communities: upland hammocks and flooded swamp forests. Two potential water sources exist: (1) entrapped rainwater in the vadose zone of the organic soil (referred to as upland soil water), that becomes enriched in phosphorus, and (2) phosphorus-poor groundwater/surface water (referred to as regional water). Using natural stable isotope abundance as a tracer, we observed that hammock plants used upland soil water in the wet season and shifted to regional water uptake in the dry season, while swamp forest plants used regional water throughout the year. Consistent with the previously observed phosphorus concentrations of the two water sources, hammock plants had a greater annual mean foliar phosphorus concentration over swamp forest plants, thereby supporting the idea that tree island hammocks are

islands of high phosphorus concentrations in the oligotrophic Everglades. Foliar nitrogen levels in swamp forest plants were higher than those of hammock plants. Linking water sources with foliar nutrient concentrations can indicate nutrient sources and periods of nutrient uptake, thereby linking hydrology with the nutrient regimes of different plant communities in wetland ecosystems. Our results are consistent with the hypotheses that (1) over long periods, upland tree island communities incrementally increase their nutrient concentration by incorporating marsh nutrients through transpiration seasonally, and (2) small differences in micro-topography in a wetland ecosystem can lead to large differences in water and nutrient cycles.

Keywords Tree islands · Ecohydrology · Everglades · Stable isotopes · Foliar nutrients

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Introduction

Plant species vary widely in their water requirements and tolerance to flooding/drought. Hence the spatial and temporal distribution of water and soil moisture is a major influence on the diversity of plant community types and species in ecosystems throughout the world (e.g., Conner et al. 2002; Furley and Ratter 1988; Rodriguez-Iturbe et al. 2001; Saha et al.

2008). The conjunction of multiple water sources, e.g., precipitation and groundwater, with variable topography, soils, and vegetation, may result in separate pools of water in close proximity. These pools in turn allow different forms of vegetation to coexist in the same ecosystem. For instance, hardwood hammocks on the Florida Keys depend upon a rain-derived freshwater pool while neighboring mangroves utilize sea water (Sternberg and Swart 1987). Pools of water can also differ in their dissolved nutrient concentrations. Since plant nutrient uptake happens in solution (Baldwin 1975), the existence of multiple pools of water can create heterogeneity in nutrient availability to plant species which in turn may increase species diversity (Tilman 1999). Identification of these pools of water is thus a fundamental step in understanding the structure and function of plant communities, how plants adapt to their environment, as well as how these communities may cope with climate change. In this study we look at water source utilization and foliar nutrient status of two adjacent plant communities on wetland tree islands in the Everglades National Park, USA: swamp forests that are flooded through most of the year and upland hammock forests that almost never flood (e.g., Olmsted and Armentano 1997).

Tree islands in wetlands and savanna ecosystems are particularly appropriate for linking different pools of water and nutrients with vegetation pattern, because they exhibit sharp contrasts in plant community types along a relatively mild topographic gradient. Tree islands are patches of woody vegetation in a landscape matrix dominated by non-woody species (Tomlinson 1980) and occur globally, from the tropics to the tundra (Wetzel 2002). Distinct boundaries of vegetation communities on tree islands are aligned along abrupt changes in environmental conditions and biogeochemical processes. In hydrologically-controlled ecosystems such as the Everglades, tree islands are often the only areas above water in an otherwise inundated landscape, with constituent plant communities differing in their flooding tolerances. Tree islands allow colonization by terrestrial, flood-intolerant flora and provide refuge for fauna (Loveless 1959; Heisler et al. 2002). Tree islands also increase landscape ecological complexity by incorporating aerobic biogeochemical processes in a predominantly anaerobic system (McClain et al. 2003; Sklar 2002). This is a

consequence of the accumulation of leaf litter-derived organic matter on the island above the high water level that furnishes an unsaturated soil environment allowing localized terrestrial processes in a wetland matrix. The slight difference in elevation between tree island and surrounding wetland, typically ≤ 1 m in the Everglades (Loveless 1959; Olmsted and Armentano 1997; Willard et al. 2006), makes tree islands extremely sensitive to water level changes (Conner et al. 2002). Hydrologic alterations in the Everglades resulted in a large loss of tree islands from 1950 to 1995 (Alexander and Crook 1974; Craighead 1971; Lodge 2005; Sklar 2002). The prevention of further losses and the restoration of tree islands is an important part of the Comprehensive Everglades Restoration Plan (Sklar et al. 2001), which in turn necessitates identification of the water pools utilized by vegetation and an understanding of the seasonal variability in these water pools.

Tree islands are considered nutrient hotspots in the phosphorus oligotrophic Everglades (Davis 1994; Gann et al. 2005; Wetzel et al. 2005) because soil phosphorus levels (in both bulk soil and in pore water) in the elevated emergent parts of the island (island head) are several orders of magnitude higher than the surrounding swamp and marsh (Ross et al. 2006; Hanan and Ross 2009). Greater nutrient availability to plants in one area over another can be manifested in three ways—(1) increased foliar nutrient concentrations (2) increase in growth and leaf area and/or (3) species replacements. Many studies on wildland plants, involving existing soil nutrient gradients or experimental fertilizations, have shown that higher nitrogen (N) and phosphorus (P) availability in soil can cause species to take on higher foliar N and P concentrations (Chapin 1980; Aerts and Chapin 2000; Harrington et al. 2001; Campo and Dirzo 2003; Lower et al. 2003; Fisher et al. 2006). Furthermore, several studies have shown that the majority of species at sites with high soil nutrient concentrations can have inherently high foliar nutrient concentrations (e.g., Boerner 1984; Fensham and Bowman 1995; Santiago et al. 2005). Such situations can be considered as having high foliar nutrients at the plant community level. Because there is very little species overlap between hammock and swamp forest communities in Everglades tree islands, we propose to investigate whether hammock species collectively have higher foliar P than the swamp forest species.

Thus from a plant community perspective, if phosphorus-rich soil pore water from tree island heads constitutes an important water source for hammock plants, then hammock plants can potentially access a larger pool of phosphorus than can swamp forest plants.

Linking the water sources and nutrient status of the different plant communities on tree islands will therefore enable understanding and prediction of community shifts on tree islands in consequence of hydrological change. The objectives of this study were to test two hypotheses. *Hypothesis 1*: hammock trees have access to rainwater entrapped in soil which is P-rich, in contrast to swamp forest plants that only have access to P-poor regional water. *Hypothesis 2*: foliar P concentrations are related to the water sources utilized by each community within a tree island. For the first hypothesis, we used the natural abundance of stable isotopes of water (^2H , ^{18}O), which have been widely used in coastal ecosystems to identify the proportion of each source water in plant stem water (Ewe et al. 1999; Greaver and Sternberg 2006; Lin and Sternberg 1993; Saha et al. 2009; Sternberg et al. 1991; Sternberg and Swart 1987). For the second hypothesis, foliar nutrient concentrations were measured.

Materials and methods

Study area

The study took place from November 2006 to November 2007 in Shark River Slough, the main hydrological channel in the Everglades National Park (ENP) with a slow moving (0.2–2 cm/s—<http://fcelter.fiu.edu>) surface sheet flow of water. The climate is subtropical and humid, with an average annual rainfall of 1,450 mm (<http://sofia.usgs.gov>), most of which occurs in the wet season that lasts from June to October (Fig. 1). Three tree islands were selected along a west-east direction from slough to adjoining prairie; Satinleaf (80°45'22.21"W, 25°39'35.21"N) and Chekika (80°39'25.58"W, 25°44'40.52"N, Fig. 2) are within the slough while Grossman Hammock (80°35'0.54"W, 25°36'56.95"N) is situated on the eastern edge of the slough. Emergent tree islands present in the Shark River Slough of the southern Everglades are called fixed islands, i.e., they are thought to have originated

on limestone outcrops in the marsh whose tops or heads remain above the wet season high water level (Loveless 1959) (Figs. 2, 3). This is in contrast to another type of tree island that occurs in the northern Everglades, the floating or pop-up tree islands that form on floating chunks of peat or vegetation rafts (Wetzel 2002). The fixed islands have two clearly demarcated plant communities, hammocks and swamp forests with very little species overlap. On the highest part of the island or head, usually on the northern part of the island, are found flood-intolerant hardwoods (also referred to here as upland plants) that are mostly Neotropical in origin. These tropical species are at the northern limit of their global range, because the southernmost parts of Florida are practically frost-free (Craighead 1971; Gunderson 1994; Olmsted et al. 1993; Lodge 2005). Soils on island heads are 10–40 cm deep on average overlying limestone bedrock (Ross et al. 2008) or hard precipitated carbonate layers (Graf et al. 2008) and are composed of a mix of decomposing leaf litter and weathered bedrock limestone that has formed over a span of about 500–6,000 years BP (Willard et al. 2006). The lowland community comprises of swamp forest that includes closed-canopy bayheads and open-canopy bayhead swamp forest and surrounds the upland portion of the tree island, often forming the elongated downstream tail of the tree island. The swamp forest experience a hydroperiod varying from approximately 1 month at the ecotone with the hardwood hammock, to around 6–10 months where it grades into the sawgrass dominated marsh (Olmsted and Armentano 1997). Unlike the hammocks, many swamp forest species are temperate in origin. Soils in lowlands are peat accumulations from 0.5–2 m thick (Craighead 1971).

There are two water inputs to tree islands (Fig. 3)—direct precipitation and the regional surface water/groundwater pool, the bulk of which flows from Lake Okeechobee. Hardwood hammocks can potentially access two distinct water sources—rainwater trapped in the upland soil layer (henceforth termed upland soil water) and groundwater that is part of the regional pool. Swamp forests are probably restricted to uptake groundwater that along with standing surface water from the surrounding marsh constitutes the regional water pool. Upland soil water being in contact with decomposing leaves and animal feces is relatively isolated from the regional water pool and enriched in phosphorus with pore water

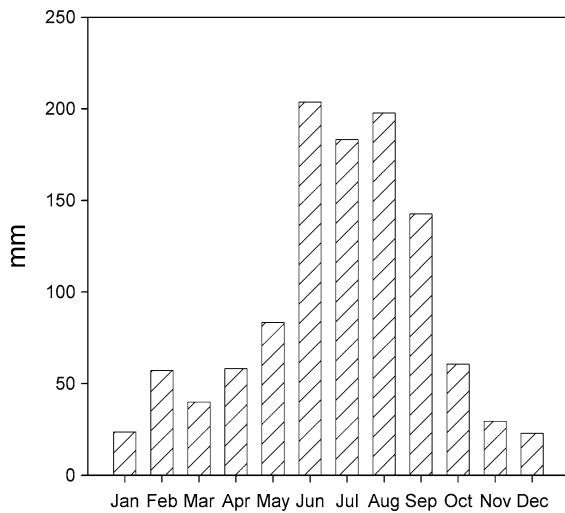


Fig. 1 Monthly precipitation in the Everglades National Park averaged over 30 USGS and ENP stations for the time period 2002–2008. Source: <http://sofia.usgs.gov/eden/nexrad.php>

concentrations several orders of magnitude higher than regional ground/surface water (Ross et al. 2006; Hanan and Ross 2009). Additionally, the head of a tree island typically has greater biomass per unit area than the lowland and surrounding marsh. The regional water, on the other hand, has extremely low concentrations of plant-available nitrogen and phosphorus (e.g. Saha et al. 2009) reflecting the highly oligotrophic Everglades that has multiple causes of P limitation (e.g., Noe et al. 2001).

Collection of soil waters and plant stem water

Upland and lowland soil waters were sampled every two months as follows: In the hammocks, 5 soil cores (composite over 0–15 cm depth) were sampled evenly over each island and placed in stoppered glass tubes, sealed with Parafilm (Pechiney, Chicago, IL, USA) and stored in a freezer to avoid fungal/microbial respiration until distillation of upland soil water. In the swamp forests, 5 soil samples were taken along a transect from the hammock-swamp ecotone to the outer edge of the island, the swamp forest-sawgrass marsh ecotone and similarly processed as hammock soil samples. Water distilled from these samples is termed lowland soil water. In addition, 5 surface water samples were collected from the marsh just outside the tree island, at a depth of 15 cm below the water level. Water samples were placed in scintillation vials, sealed with Parafilm to prevent evaporation and refrigerated in the lab. A rainwater collector (glass bottle with a 1 cm layer of mineral oil to prevent evaporation) was placed in Grossman Hammock, and the isotopic composition of these samples was combined with that of rainfall collected every 2 weeks for a year (March 2005–March 2006) during an earlier study (Saha et al. 2009). This rainfall isotopic data was used to construct the Everglades Meteoric Water Line (EMWL), i.e. the relationship between the oxygen and hydrogen isotopes of precipitation in the

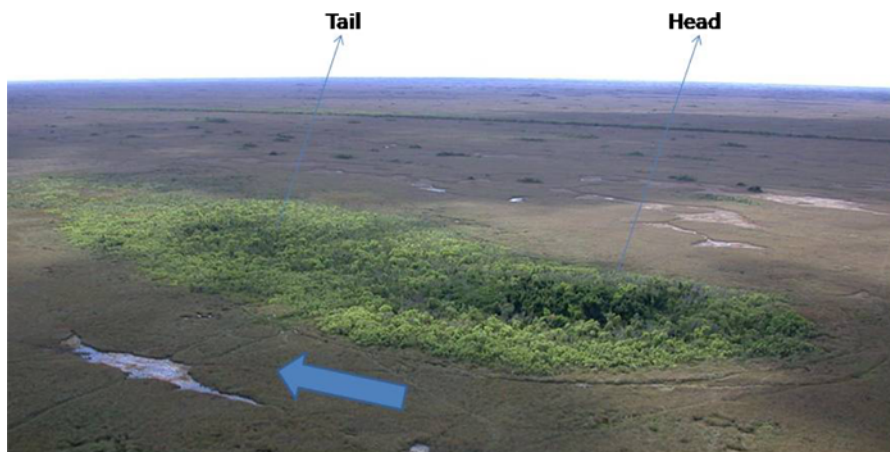


Fig. 2 Aerial view of Chekika tree island showing the head (upland/hammock species) and tail (swamp species). The *block arrow* indicates direction of water flow (southwesterly direction) along which is aligned the longitudinal axis of the tree island

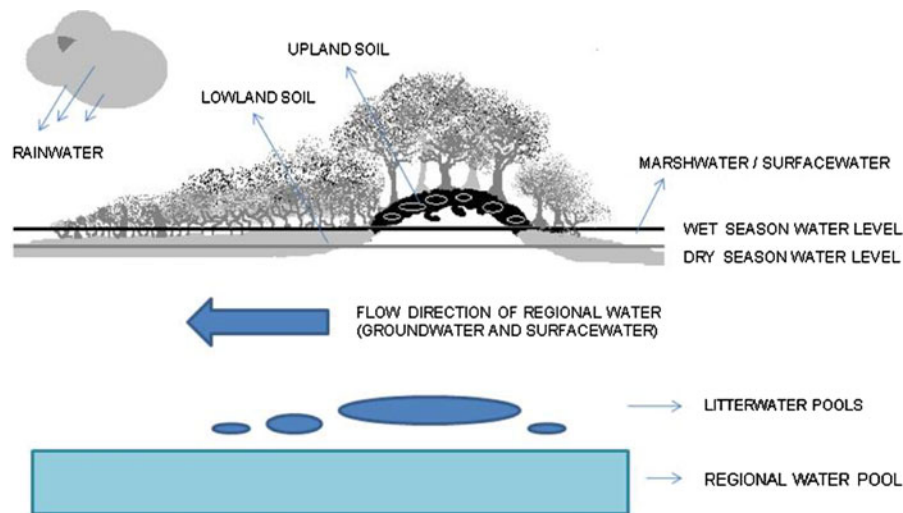


Fig. 3 Exaggerated profile of a fixed tree island in Shark River Slough, ENP showing the two distinct plant communities: the flood intolerant hammock vegetation on the head (above wet season water level) and the flood tolerant swamp forest in the rest of the island submerged in the wet season. The organic soil horizon on the head (upland soil) is shown in *black* while flooded peat sediments (lowland soil) in *gray*. The two water

sources are rainwater trapped in the organic soil layer on the tree island head (shown in *ellipses* within the organic soil layer) and the regional surface/groundwater pool. These two sources are schematically illustrated at the *bottom* of the figure. Water in the upland soil (upland soil water) is mainly entrapped rainwater (wet season) while lowland soil water is primarily regional water with some rainwater

Everglades. The EMWL serves as a reference to identify pools of water in the Everglades that have undergone evaporation. Isotopic plots (δD vs. $\delta^{18}O$ values) of these pools fall to the right of the EMWL, since evaporation results in a disproportionate increase in ^{18}O relative to Deuterium.

Every two months over the year, 20 plants were sampled in the upland (hammock) and 30 plants in the lowland (swamp forest) of each tree island using a 5 m extensible pole pruner (Corona Clipper, CA, USA). Because the topographic gradient in the upland areas appears to influence species composition, plants were sampled at random locations from the highest point of the island to the lowland/upland ecotone. Lowland plants were selected along a transect from the lowland/upland ecotone to the marsh, thus incorporating a range of hydroperiods. The most abundant species were chosen in both communities. Upland hammock species were: (1) Chekika: *Eugenia axillaris* (Sw.) Willd., *Myrsine guianensis* (Aubl.) Kuntze, *Celtis laevigata* Willd., *Sideroxylon foetidissimum* (Jacq.) Cronquist (2) Satinleaf: *E. axillaris*, *Bursera simaruba* (L.) Sarg., *Coccoloba diversifolia* Jacq., *C. laevigata*, *Chrysophyllum oliviforme* L. (3) Grossman Hammock: *Ardisia elliptica*, *C. diversifolia*, *B. simaruba*,

Nectandra coreacea (Sw.) Griseb., *Simarouba glauca* DC. For lowlands, we sampled the following (1) Chekika: *Annona glabra* L., *Salix carolinensis* Michx., *Persea borbonia* (L.) Spreng., *Morella cerifera* L., *Schinus terebinthifolius* Raddi. (2) Satinleaf: *A. glabra*, *S. carolinensis*, *Chrysobalanus icaco* L., *P. borbonia*, *M. cerifera* (3) Grossman Hammock: *A. glabra*, *S. carolinensis*, *M. guianensis*, *M. cerifera*, *S. terebinthifolius*. *A. glabra* and *C. icaco* are the only tropical species in these swamp forests (Olmsted and Armentano 1997). For each plant, a well suberized stem was cut and after removal of the bark and phloem, placed in a sealed glass tube, sealed with Parafilm and frozen on return to the lab. For the tree islands selected, our upland communities were functionally identical as we chose species that were abundant, evergreen, flood intolerant and tropical in origin. Lowland communities shared the same pool of species. Measurements made on same individual over time were treated as repeated measures.

Water extraction and isotopic analysis

Stem and soil waters were extracted by the method of Vendramini and Sternberg (2007). Extracted water was analyzed at the Laboratory of Stable Isotope

Ecology in Tropical Ecosystems at the University of Miami for oxygen and hydrogen isotope ratios by equilibration on an Isoprime[®] Isotope Ratio Mass Spectrometer connected to a Multiflow[®] system (Elementar, Germany) as described by Vendramini and Sternberg (2007). Oxygen and hydrogen isotope ratios are reported here as $\delta^{18}\text{O}$ and δD values respectively and calculated as:

$$\delta^{18}\text{O} \text{ or } \delta\text{D} = \left\{ \left(R_{\text{sample}} / R_{\text{SMOW}} \right) - 1 \right\} \times 1000$$

where R_{sample} and R_{SMOW} represents the ratio of heavy to light isotopes in the sample and the standard respectively. The standard for water isotope ratios used here is Vienna standard mean ocean water (vSMOW) and the precision of analysis $\pm 0.1\text{‰}$ and $\pm 2.0\text{‰}$ for oxygen and hydrogen isotopes, respectively (± 1 standard deviation).

Foliar nutrient analysis

Mature leaves for each individual sampled for stem water were collected from the same branch, placed in paper bags and subsequently dried in an oven at 50°C for 72 h. Dried leaves were then ground and homogenized, in preparation for foliar N and P analysis. Preparation of samples for P analysis consisted of combusting 700 mg of the dried ground leaves to ash in porcelain cups in a furnace kept at 600°C for 6 h, followed by digestion in 4% sulfuric acid and filtration through glass fiber filter paper (Whatman, UK). Analysis was carried out on the filtrate. Foliar P concentration was obtained by the USEPA method 365.1 (USEPA 1984) based upon the molybdate blue colorimetric approach (Fiske and SubbaRao 1925) using an Alpkem 3000 Phosphorus analyzer (Alpkem, OI Analytical, TX, USA), and expressed as the percent ratio of the mass of P in the sample to the mass of the sample (dry leaf). The precision of analysis was ± 0.1 ppm (1 SD). For foliar N analysis, ground leaf samples (5 mg) were loaded in individual tin cups (Elemental Micro-analysis, Milan, Italy), rolled into tight balls and placed in an automated elemental analyzer (Euro-EA-Elemental Analyzer, Eurovector, Milan, Italy) connected to a continuous flow isotope ratio mass spectrometer (Elementar, Hanau, Germany). Foliar N concentration was expressed on a per weight percent basis, similar to foliar P. The precision of analysis was $\pm 0.1\text{‰}$.

Data analysis

To examine whether there were any differences in isotopic ($\delta^{18}\text{O}$) composition in stem water between upland and lowland communities, a repeated measures 2-way analysis of variance (Procedure GLM, SPSS 12.0, Chicago, USA) was performed using $\delta^{18}\text{O}$ as the dependant variable (measured across 5-sampling events through 1 year on the same individual), while community (upland/lowland) and tree island (Chekika/Satinleaf/Grossman) were considered as independent categorical variables. Tree islands and community were both considered as fixed effects because upland and swamp communities are segregated in tree islands along the elevation gradient, while the three tree islands differ in their hydrologic regime (Ross et al. 2008). Between-subject effects were tested first, followed by a univariate test for within-subjects effects that assessed the repeated factor and its interactions with tree island and community with, if necessary, the Greenhouse-Geisser adjustment (Kluth and Bruelheide 2005). Similarly, repeated measures analyses were employed to examine community and tree island level differences in foliar P, N, and N:P over the wet and dry seasons. Census data were first tested for normality (Explore Plots, SPSS 12). Outliers were removed and data transformations were not required.

Results

Source water isotopic composition

$\delta^{18}\text{O}$ values for upland soil water, rain, lowland soil water and surface water (marsh water) averaged for all three islands over a year represented an increasing gradient with rain and upland soil having lower (or less enriched) values than lowland soil water and marsh water (Fig. 4).

Plant stem water isotopic composition in upland and lowland plant communities

The community type showed significantly different stem water isotopic compositions, with lower $\delta^{18}\text{O}$ and δD in upland plants than in lowland plants throughout the year (Table 1, Figs. 4, 5). There was a significant interaction between community and time

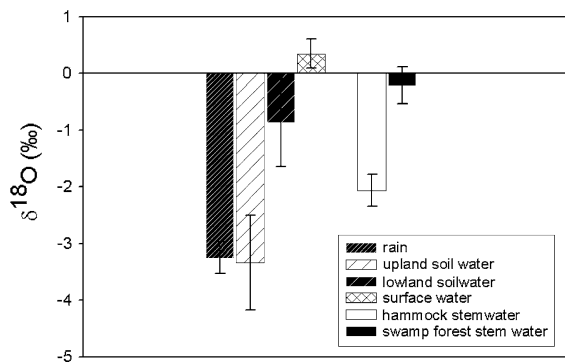


Fig. 4 Average annual isotopic oxygen composition for rain, upland soil water, lowland soil water, surface water, upland plant stem water and lowland plant stem water averaged over 6 bimonthly sampling event at three islands in the Shark River Slough. Error bars indicate the standard error of the mean

with a greater difference between $\delta^{18}\text{O}$ values of stem water from upland and lowland communities during the end of the wet season (November, Fig. 5). As the dry season proceeds, upland plant stem water values tend toward the lowland plant values (January and March, Fig. 5) and almost overlap at the end of the dry season (May, Fig. 5). Then as the wet season follows, upland plant stem water $\delta^{18}\text{O}$ values start to diverge from lowland values (July and Sept, Fig. 5). There was also a tree island effect, whereby tree islands differed significantly in their mean stem water $\delta^{18}\text{O}$ values (Table 1) with Satinleaf island as having the most enriched values followed by Grossman and Chekika ($P < 0.01$). The difference in stem water $\delta^{18}\text{O}$ between upland and lowland communities was similar for Chekika and Satinleaf (2‰ and 1.93‰ respectively) while Grossman had lower difference on average (1.32‰).

Foliar nutrients

The average foliar P concentration in upland communities was found to be significantly higher than in lowland communities (Table 2, Fig. 6). There was also a significant tree island effect upon foliar P concentration (Table 2), with Satinleaf having the highest values followed by Grossman and then Chekika. While in each island uplands had higher foliar P than lowlands, the degree of this difference varied with tree island. Foliar P did not vary significantly with season (time) for either community.

Foliar N concentrations, on the other hand, were significantly lower in uplands at the community level as compared to lowlands (Table 2, Fig. 6). There was no effect of either tree islands or seasons on community level foliar N. The interaction between time and tree island was significant at the 0.05 level indicating that the relative difference in foliar N between lowland and upland differed with tree island.

The N:P ratio was lower in uplands than in lowlands for each island and were between 12 and 20 for upland plants while being greater than 30 for lowland plants. A marginally significant tree island effect was observed (Table 2).

Discussion

Water source usage by upland and lowland plant communities

The two water sources, i.e., upland soil water and regional water have distinct isotopic compositions throughout the year that reflect different exposures to hydrological processes. This consistent difference in source water composition permits determination of the water sources utilized by plants. Surface water has more enriched values (a greater proportion of heavier isotopes ^{18}O and D) than upland soil water (Fig. 4), most probably an outcome of greater exposure leading to higher evaporation rates than upland soil water which is shaded by the tree canopy. Surface water values also vary less with season than upland soil water, because the large volume of this regional pool buffers the isotopic signature of the much smaller rain pool (Saha et al. 2009). Lowland soil water is a mix of rain and regional water, resulting in isotopic values lying between upland soil water and surface water (Fig. 4). Interestingly, as noted in the results, the annual average upland soil water $\delta^{18}\text{O}$ composition is a bit lighter than rain, which might be an artifact of certain sampling events, whereby soil water indicates the composition of water absorbed over the past couple days at the most while the rainwater represents a composite sample over 2 weeks of possible precipitation.

In the $\delta^{18}\text{O}$ - δD plot (Fig. 5), both upland and lowland plant stem water isotopic compositions lie below the EMWL, along the evaporative water line typical for South Florida (Wilcox et al. 2004) thereby

Table 1 Results of a repeated measures analysis of variance carried out on plant stem water $\delta^{18}\text{O}$ as within subject variable sampled over time (5 sampling dates over one year) with community (upland/lowland) and tree island as fixed effects (Chekika/Satinleaf/Grossman)

Dependant variable	Source	df^*	F	Sig.
Stem water $\delta^{18}\text{O}$	Within subject effects			
	Time	3	27.50	<0.0001
	Time \times tree island	5	12.36	<0.0001
	Time \times community (tree island)	3	8.89	<0.001
	Time \times community \times tree island	5	1.38	0.236
	Between subject effects			
	Tree island	2	38.87	<0.001
	Community	1	56.02	<0.001
Tree island \times community	2	20.32	<0.001	

* Estimated df and F values reflect Greenhouse-Geisser corrections

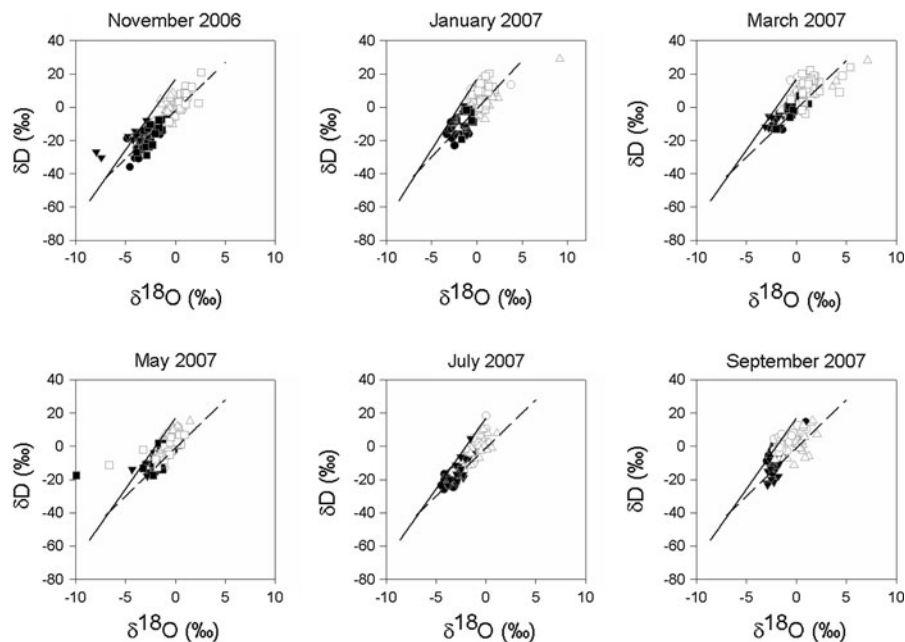


Fig. 5 Plots of δD vs. $\delta^{18}\text{O}$ of plant stem water in upland (shaded/dark symbols) and lowland (open/light symbols) communities for Chekika (circles), Satinleaf (squares) and Grossman Hammock (triangles) sampled every two months from November 2006 to September 2007 in Shark River slough, ENP ($n = 20$ for upland plants and 30 for lowland

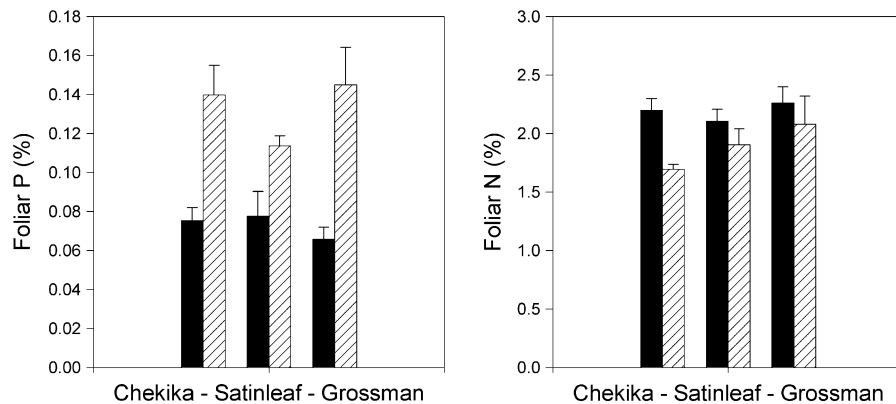
plants per sampling). The solid line is the Everglades local meteoric water line ($\delta\text{D} = 8.5 \delta^{18}\text{O} + 17\text{‰}$, $r^2 = 0.93$, $P < 0.01$) for rainfall collected 2005–2006 ($n = 72$). The dashed line is the evaporative line typical for South Florida ($\delta\text{D} = 5.8 \delta^{18}\text{O} + 1\text{‰}$)

suggesting that the water pools accessed by plants have undergone some degree of evaporation. However, for the Everglades, vertical distance from the EMWL is not a robust indicator of the relative difference in isotopic enrichment in stem water of the two plant communities, since the slope of the evaporative line in humid environments like south

Florida (about 6) is closer to the EMWL or local meteoric water line than evaporative lines in more arid environments (such as 2–3 in Busch et al. 1992). Instead the extent of stem water isotopic enrichment serves as a better indicator. The difference between upland and lowland plant stem water isotopic composition that occurs through most of

Table 2 Results of three repeated measures analyses of variance carried out on foliar P, foliar N and foliar $\delta^{13}\text{C}$ values over seasons as within subject effects, and community (upland/lowland) and tree island (Chekika/Satinleaf/Grossman) as fixed effects

Source	df	Foliar P		Foliar N		Foliar N:P	
		F	Sig.	F	Sig.	F	Sig.
Within subject effects							
Time	1	0.082	0.776	3.09	0.081	4.06	0.047
Time \times tree island	2	0.636	0.531	4.33	0.015	3.93	0.024
Time \times community	1	1.121	0.330	2.32	0.131	0.53	0.468
Time \times community \times tree island	2	1.20	0.275	2.23	0.179	0.578	0.43
Between subject effects							
Tree island	2	4.08	0.019	0.88	0.418	3.23	0.045
Community	1	6.84	0.0001	10.27	0.002	13.26	0.000
Tree island \times community	2	3.11	0.05	2.037	0.197	2.346	0.101

**Fig. 6** Average foliar P (*left*) and average foliar N (*right*) in lowland (*solid*) and upland communities (*hatched*) in all three tree islands at the end of the dry season (May). Values expressed as concentration (e.g., milligrams P/milligrams dry leaf tissue). Upland plant communities have a significantly

higher foliar P concentration and significantly lower foliar N concentration than lowland plant communities. Error bars depict the standard error of the mean. $n = 20$ for uplands and 30 for lowlands respectively

the year (Figs. 4, 5), suggests that different proportions of the two source water pools are utilized by these two plant communities. The upland stemwater isotopic composition is consistently less enriched than lowland stemwater composition throughout the year. During the wet season, upland plants are able to access the rainwater trapped in the organic soil on the tree island head—a conclusion arrived at from the observations that upland plant stem water is isotopically closer to rainwater entrapped in the upland soil for much of the year compared to lowland plant stem water (Fig. 4). As the dry season progresses, we propose that the water in the tree island head soil

begins to dry up, and upland plants start taking up more of the isotopically enriched regional water (groundwater in the rhizosphere). This is suggested by upland stem water $\delta^{18}\text{O}$ composition approaching that of lowland plants (Fig. 5) starting from January with the closest, almost overlapping values in this study being in May near the end of the dry season. Lowland plants use regional water throughout the year as suggested by their stem water $\delta^{18}\text{O}$ values being consistently more enriched than those of upland plant stem water (Fig. 5). This conclusion is further supported by the relatively static nature of lowland plant stem water $\delta^{18}\text{O}$ and δD composition

throughout the year versus that of upland plants (Fig. 5), which reflects surface water composition varying less with season than soil water.

Extended drought can negatively affect upland trees on tree islands

As seen from hurricane blowdowns, most of the rooting zone of hammock trees is confined to the shallow soil layer directly overlying bedrock. Hammock species are known to be intolerant of flooded soils both in the Everglades as well as elsewhere in the Neotropics (e.g. Jones et al. 2006, Armentano et al. 2002), thereby suggesting a lack of root adaptations to flooding. At the same time, our results indicate that hammock trees do use regional water (groundwater) in course of the dry season. It is possible that fine roots re-grow through cracks in the bedrock as the water table drops, and it is these newly extended fine roots that absorb groundwater from the capillary zone near the water table. Lower than usual groundwater tables resulting from extended droughts or water withholdings upstream can make groundwater less accessible for upland hammock species, resulting in water stress or even permanent wilting if roots are unable to find suitable pathways to access the lowered water table. Apart from unavailability of water, lowered water tables can dry up peat-filled sinkholes on tree island heads that can destroy plant roots as has been described for the Long Pine Key hammock fires in 1959 (Craighead 1974).

Plant communities and foliar nutrients

The stable isotope data of stem water indicates that rain-entrapped soil water is an important plant water source for upland plants. Our foliar P concentration data suggests that this nutrient rich water source may be an important nutrient source as well. The canopy in hammocks is typically 3–5 m higher than that of swamp forests indicating a higher biomass per unit area (Olmsted and Armentano 1997); greater P availability in hammocks can result in greater growth and biomass. The link between soil nutrient availability and community level foliar nutrient concentration is also seen for foliar N. The lower community-level foliar N concentrations in upland plants compared to lowland plant species seen in this study agrees with the trend in soil, whereupon soil

pore water nitrogen was found to be lower in tree island heads as compared to lowlands (Ross et al. 2006). Flooded soils can have higher inorganic nitrogen accumulations than well-drained soils because of lower mineralization and immobilization rates arising from slower organic matter breakdown in flooded soils and lower metabolism of anaerobic bacteria respectively (Reddy and DeLaune 2008). The significant interaction between time and tree island on foliar N could perhaps arise from the difference in hydrological processes that each tree island is subject to, on account of their respective spatial locations; such speculation is beyond the scope of this study.

The significantly higher N:P ratio of lowland plants than upland plants (community averages 30–45 for lowlands and 12–20 for uplands) suggests that lowland zones are more phosphorus-limited than upland zones as also found by Ross et al. (2006). Flooding for 3–9 months can result in P transport out of lowland soils, whereas upland soils retain much of their P. Comparing the community N:P ratios of hammock forests on tree islands (12–20) with those from the only other strictly upland plant communities in the Everglades, i.e. hardwood hammocks located further south amidst pine rocklands on the Miami Rock Ridge (N:P around 45—Saha et al. 2009) suggests that hammock communities on tree islands in the slough have higher phosphorus availability than hammock communities on the Miami Rock Ridge. This difference in N:P ratios arises also because of differences in species composition, although both hammock types predominantly have Neotropical hardwoods. Other plant communities and species in the Everglades can have ratios higher than that in tree island hammocks, such as approximately 42 for pine rocklands (Saha et al. 2009) and 27–84 for sawgrass (Miao and Sklar 1998; Richardson et al. 1999; Smith et al. 2009) in the northern Everglades, thus supporting the idea of tree islands as localized phosphorus hotspots in the otherwise extremely oligotrophic Everglades landscape.

Nutrient input into tree islands

Three pathways are thought to exist for nutrient input to tree islands: (1) the transpiration-driven pathway whereby groundwater and marshwater (regional water) is drawn to tree islands; dissolved nutrients

in this regional water get assimilated into foliar biomass which then decomposes to contribute to organic soil over time; (2) atmospheric deposition and (3) animal feces (Wetzel et al. 2005). These inputs can co-occur but how the relative magnitude of each process differs from island to island is not yet known. Our results show that upland plants utilize P-rich upland soil water during the wet season and P-poor regional water during the dry season; this is consistent with the transpiration-driven pathway of P buildup in Everglades tree islands. Our results on water source usage add a temporal dimension to this transpiration-driven nutrient harvesting hypothesis by suggesting a nutrient utilization phase during the wet season (using nutrients already present in organic soil) and a nutrient harvesting phase during the dry season (obtaining nutrients from outside the island). Although the concentration of nutrients, especially P is extremely low in regional water, nutrient buildup on tree islands can happen incrementally over long time periods.

Conclusions

Coupling water sources and foliar nutrient status can be an effective tool to identify nutrient sources and periods of nutrient uptake by plants. This information can enable scientists and restoration ecologists to discern how coexisting plant communities in an ecosystem differ in the partitioning of nutrient pools and how seasonal changes in the sizes of water pools can result in plants altering their water sources. This understanding of water and nutrient pools can also be used to make predictions on the fate of plant communities when subject to modifications of water and nutrient regimes.

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