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Linking water sources with foliar nutrient status in upland plant communities in the Everglades National Park, USA

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ABSTRACT

Plant communities within an ecosystem can vary in water source usage and nutrient availabilities, thus permitting community coexistence and diversity. We investigated the differences in water source utilization in two ecologically important upland plant communities: tropical hardwood hammocks and pine rocklands in the predominantly flooded Everglades ecosystem. We then linked these differences with their foliar nutrient levels and photosynthetic performance as measured by δ^{13}C abundance. Based on a comparison of δ^{18}O of plant stem waters with those of potential water sources (nutrient-poor groundwater and nutrient-rich water in organic litter referred to as soilwater), we observed that during the wet season hammock plants relied on soilwater while in the dry season they relied on groundwater. A similar seasonal shift was observed in pineland plants, however, groundwater constituted the major part of water uptake throughout the year except for late wet season. Consistent with the nutrient concentration of different water sources used in the two communities, hammocks had a greater annual mean foliar nitrogen and phosphorus concentration at the community level over pinelands as well as a higher leaf area index. High foliar N concentration in hammock plants was associated with eventual stomatal limitation of photosynthesis. Hammock species being intolerant of flooded soils are restricted to water uptake in the shallow unsaturated soil layer in the wet season, yet access the lowered groundwater table in the dry season. This dependence on a relatively narrow annual range of water table levels should be considered in South Florida water management and Everglades restoration. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS everglades; hardwood hammocks; pine rocklands; stable isotopes; water sources; foliar nutrients; ecohydrology; flood-intolerant vegetation

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INTRODUCTION

Coexisting plant communities in an ecosystem can differ widely in their water sources and nutrient availabilities thereby leading to distinct ecohydrological functioning patterns within the same ecosystem. This is especially evident in hydrologically controlled ecosystems such as the Everglades in South Florida. The Everglades ecosystem is the largest subtropical wetland savanna in North America with a high degree of floral endemism and direct links with the marine ecosystem of Florida Bay. The terrestrial portion of the Everglades National Park (ENP) ranges from sea level to just over 3 m above sea level. Within this elevation span exists a mosaic of plant communities—mangroves, cypress domes, long and short hydroperiod marshes, sawgrass savannas, bayheads, pine rocklands (or pinelands) and tropical hardwood hammocks in ascending order of elevation. Such a diversity of communities is largely a consequence of the wide range of interactions between water flow, hydroperiod, nutrients, fire and faunal effects that change with minor differences in topography, typically less than 1 m (White, 1994; Wetzel *et al*., 2005). Each community is associated with a certain hydroperiod range, and the small elevational differences between communities can result in a high degree of sensitivity to water level fluctuation. This is especially true for upland (emergent) communities which usually do not flood, or do so for very short periods of time. An example of the sensitivity of upland communities is the loss of tree islands in the Everglades over 1950–1970 (Lodge, 2005). This has been attributed to both prolonged flooding by water releases from canals that led to mortality of flood-intolerant hardwood species as well as prolonged dry conditions that led to peat fires lowering tree island elevation rendering them more vulnerable to subsequent flooding (Sklar *et al*., 2004; Wetzel *et al*., 2005). Because of this, knowledge of the sensitivity of upland communities to changing hydroperiods is critical in the management of water resources, which has to address both South Florida urban needs and ecosystem preservation (Lockwood *et al*., 2003; Wilcox *et al*., 2004).

Because of its low elevation and relatively flat topography most of the Everglades are inundated in the wet season and part of the dry season with the exception of the highest parts of limestone outcrops and the Miami Rock Ridge to the east. The Miami Rock Ridge is part

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of the Atlantic coastal ridge, a mid-Pleistocene marine limestone ridge <3 m.a.s.l. running along the SE coast of Florida and ending in the southeastern Everglades (Hoffmeister, 1974) as a series of transverse ridges interspersed with glades. Hammocks occur on the highest parts of this ridge that rarely flood, while pinelands often occur adjacent to the hammocks, and depending on the site, are prone to flooding for 0–3 months (Gunderson, 1994). These two upland plant communities differ in many aspects, key ones including the presence of flood-intolerant species in hardwood hammocks (Carr, 1973) and the paucity of soil with mainly exposed limestone in fire-adapted pinelands. With the exception of a previous study in which comparative measurements were taken once during the dry season and once during the wet season (Ewe *et al*., 1999), not much is known about pineland and hammock ecohydrological functioning throughout the year. Specifically, little is known about their water and nutrient sources and how these may change with water levels over the course of the seasons.

Hardwood hammocks are composed of neotropical evergreen broadleaf trees with a profusion of epiphytes. The closed canopy maintains a humid microclimate inside the hammock that, along with the moist organic soil horizon, is largely responsible for deterring most fires (both lightening-induced and anthropogenic) ranging in from pinelands (Snyder *et al*., 1990). Only large episodic fires can burn down hammocks (Carr, 1973; Craighead, 1974; Robertson and Platt, 2001). Thus, fires maintain a distinct boundary between hammocks and pinelands (Slocum *et al*., 2003; Lodge, 2005). The organic soil layer that has been built up by litter deposition and decomposition directly over the limestone bedrock in hammocks is in general about 5000 years old (Loveless, 1959)and, on average, 10–30 cm thick. In contrast, high fire frequency in open canopy pine rocklands prevents any substantial organic soil formation (Figure 1), except in sinkholes and temporary surface accumulations between successive fires. This relative paucity of soil in pinelands implies that pineland plants depend largely on groundwater (water table at 0–1 m depth) as the main water source (Ewe *et al*., 1999). Hardwood hammock plants, in addition to groundwater may also utilize rainwater trapped in the litter layer (henceforth referred to as soilwater), a potentially significant amount owing to the high water holding capacity of the spatially continuous litter horizon.

From a nutrient availability perspective, the Everglades is an oligotrophic ecosystem (Davis, 1994; Wetzel *et al*., 2005) with extremely low levels of phosphorus. Because plant nutrient uptake mainly occurs in solution (Baldwin, 1975), pineland plants are thought to have access to limited amounts of nutrients owing to their primary reliance on groundwater that has low nutrient concentrations. Hammock plants, on the other hand, may have access to a more concentrated pool of nutrients that is present in soilwater (trapped rainwater) stemming from litter decomposition and faunal sources in the litter layer.

In this study, we characterize soil depth and plant-available nitrogen (N) and phosphorus (P) in water sources of hammock and pineland plants. We then investigate the potential water sources (groundwater and soilwater) used by the hammock and pineland plants over a year using stable isotope techniques that have been widely used for plant source water determination in coastal ecosystems (Sternberg *et al*., 1991; Lin and Sternberg, 1992; Ewe *et al*., 1999; Ewe and Sternberg, 2002; Greaver and Sternberg, 2006). We also test whether the higher levels of exchangeable nutrients in hammock soils compared to groundwater would be reflected in higher foliar nutrient concentrations in hammock communities relative to pineland communities. Foliar nutrient concentrations are widely used as a measure of nutrient status and productive potential (eg. Vitousek *et al*., 1995) ensuring proper sampling that takes into account temporal variations in concentration due to phenology and leaf age. The response of plant communities to increased nutrient availability can be complex: (i) Higher foliar concentrations; (ii) Greater growth, and thus, greater foliar area; and/or (iii) Altered competition within the communities possibly leading to species replacements (eg. Aerts and Berendse, 1988). Numerous studies concerning plants in the wild (involving either a comparison across an existing soil nutrient gradient or experimental fertilization) have shown that higher N and P availability can lead to higher foliar N and P concentrations (Chapin, 1980;

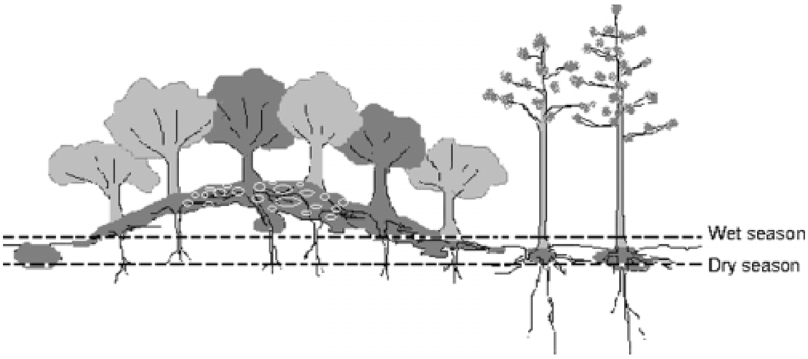

Figure 1. Schematic illustration of a tropical hardwood hammock (left) and a pine rockland (right). Dashed lines indicate relative wet season and dry season water levels. The thin mantle of soil overlying limestone bedrock in the hammock and in sinkholes in the pineland is shaded grey. In the hammock, the wet season soilwater pool is denoted by small ellipses. Understory plants are not shown.

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Vitousek *et al.*, 1995; Aerts and Chapin, 2000; Harrington *et al.*, 2001; Campo and Dirzo, 2003; Lower *et al.*, 2003; Fisher *et al.*, 2006). Periods of high nutrient availability in oligotophic ecosystems can also lead to luxury consumption by plants with attendant increase in foliar concentrations because of storage in vacuoles (Chapin, 1980; Tripler *et al.*, 2002; Bertiller *et al.*, 2006). Studies have also shown that often high soil nutrient concentration areas are populated by communities of species having inherently higher foliar nutrient concentrations (Boerner, 1984; Fensham and Bowman, 1995; Santiago *et al.*, 2005). We refer to this effect as a community-level effect. Since higher soil nutrient availability can also lead to greater growth and leaf biomass, we indirectly compare foliar biomass in hammocks and pinelands using the Leaf Area Index (LAI) as a proxy in each community (Jordan, 1969).

We specifically test the following hypotheses:

Hypothesis 1: Hammocks and pinelands differ in their water utilization throughout the year. In the wet season, hammock plants depend more on soilwater while pineland plants depend more on groundwater. In the dry season, plants in both communities increasingly utilize groundwater.

Hypothesis 2: The foliar nutrient (N and P) content at the community level will reflect the nutrient status of water sources utilized in the respective communities, with hammocks showing higher foliar nutrient levels than pinelands.

Hypothesis 3: The differences in nutrient status will affect photosynthetic properties as measured by the carbon isotope ratios of leaf tissues.

MATERIAL AND METHODS

Study area

The study took place in the ENP from March 2005 to March 2006. The climate is subtropical and humid, with an average annual rainfall of 1450 mm (http://sofia.usgs.gov), more than half of which occurs in the wet season that lasts from June to October. The hammocks on the Miami rock ridge and tree islands in the Shark River Slough constitute the northern boundary of the range of the neotropical tree species that have established owing to winters being free of frost in most years (Lodge, 2005). Periodic hurricanes pass through south Florida every 3–5 years and can cause considerable structural damage in hammocks and pinelands by toppling over shallow-rooted trees (mostly in hammocks) and by breakage of the main trunks known as snap-offs (mostly in pinelands).

Three previously studied sites (Ewe *et al.*, 1999) differing in elevation and hydroperiod were selected on the Miami Rock Ridge within the ENP along an east–west increasing rainfall gradient at Royal Palm (25°23′39″N, 80°37′17″W), Long Pine Key (25°24′10″N, 80°39′05″W) and Sisal pond (25°23′29″N, 80°37′45″W). Long Pine Key had the highest elevation (Ewe *et al.*, 1999) and neither the hammock nor the pineland was flooded during the study period, although the groundwater level in pineland sinkholes was within 10 cm of the mean surface in July 2005. Parts of Royal Palm pineland were briefly flooded, while the pineland at Sisal Pond remained continually flooded (water table above ground surface) from mid-June to the end of September. Each site was located at the interface between a hammock and a pineland. Pinelands in the ENP are subject to a burn cycle of 3–7 years, either lightening-induced or set by the National Park Service. The pineland site on Long Pine Key experienced fire in June 2006 that completely burned the understory to expose bedrock.

Characterization of soil depth to bedrock

A line transect was laid out perpendicular to the border between the hammock and pineland at each site, extending 100 m into each community. Every 2 m, a 1-cm diameter metal rod was pushed down until bedrock or an impenetrable layer was reached, and the depth noted to the nearest cm.

Plant-available nutrient concentration in soil and groundwater

In May 2005, at the onset of the wet season, 5 samples of soil (0–15 cm depth) per site from Royal Palm and Long Pine Key were analysed at the Agricultural Analytical Services Laboratory, University of Pennsylvania, USA, for exchangeable P (Mehlich 3 soil test), nitrate N (NO_3-N) and ammonium N (NH_4-N) (ion electrode method) with the precision of analysis reported as $\pm 0{\cdot}1$ ppm ($\pm 1\sigma$) for P, 0·6 and 1 ppm for nitrate and ammonium N respectively. Soil solution concentrations of the above nutrients were calculated from the above lab measurements (dry soil values) based on a wet season water content of 230% (dry weight of soil), a value chosen within the range 28–250% measured by Ewe *et al.* (1999), and the assumption that all the plant-available nutrients would be in solution. Groundwater was sampled from wells in the same sites at the same time as soils and analysed at the University of Georgia Soil, Plant and Water laboratory, Athens, GA for NH_4-N, NO_3-N and phosphate (PO_4) with precision of analysis reported to be within $\pm 0{\cdot}001$ ppm (1σ).

Collection of sourcewaters and plant stemwater

Groundwater was sampled from wells at Royal Palm and Long Pine Key every two weeks over the study period after pumping out the standing water (that could be evaporatively enriched in ^{18}O and D) and allowing recharge. The Sisal Pond site did not have a well to sample groundwater.

Rainwater collectors (glass bottles with a 1-cm layer of mineral oil to prevent evaporation) were placed in both the hammock and the pineland at each of the three sites and collected at the same time as groundwater. Both rain and groundwater samples were placed in scintillation

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vials, sealed with Parafilm (Pechiney, Chicago, IL, USA) to prevent evaporation and refrigerated in the lab. Five replicates of soils in each community were collected at each site every two months over a range of 0–20 cm depth. These were placed in stoppered glass tubes, sealed with Parafilm and stored in a freezer to avoid fungal/microbial respiration.

Every two months over the year, 25 plants (5 replicates per species for 5 species) were sampled in the hammock as well as in the pineland for each site, to make up a total of 50 plants per site. Individuals were marked with flagging tape for future sampling. Plants were sampled to 50 m inside each community. We sampled species that were the most abundant at each site, keeping in mind that species diversity is higher in the interface of the two communities than inside the hammock (Alexander, 1967). Species sampled in the pineland were: (i) Royal Palm site: *Guettarda scabra, Lysiloma latisiliqua, Myrica cerifera, Quercus pumila, Pinus elliottii var densa*; (ii) Long Pine Key: *G. scabra, L. latisiliqua, Tetrazyga bicolor, M. cerifera, Myrsine guianensis*; and (iii) Sisal Pond site: *Ilex cassine, Crossopetalum ilicifolium, M. guianensis, M. cerifera, Persea borbonia, P. elliottii var densa.* For hammocks, we sampled the following: (i) Royal Palm: *Bursera simarouba, L. latisiliqua, G. scabra, Quercus virginiana, M. cerifera*; (ii) Long Pine Key: *B. simarouba, Chrysobalanus icaco, G. scabra, L. latisiliqua, M. cerifera*; (iii) Sisal Pond: *L. latisiliqua, M. cerifera, Q. virginiana, P. borbonia, Annona glabra.* Despite being flood-tolerant and thus uncharacteristic of hammocks where the majority of species cannot survive on flooded soils, *Annona glabra* was included simply because numerous individuals existed at the Sisal Pond hammock site. For each plant, a well-suberized stem was cut and after removal of the bark and phloem, placed in a sealed glass tube, parafilmed and frozen on return to the lab. Branches high up in the canopy were accessed using a 5 m extensible pole pruner (Corona, CA, USA).

Water extraction and isotopic analysis

Stem and soilwaters were extracted either by the method of West *et al.* (2006) or Vendramini and Sternberg (2007). Extracted water was analysed at the Laboratory of Stable Isotope Ecology in Tropical Ecosystems (LSIETE) 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 δ^{18}O and δD values respectively and calculated as:

$$\delta^{18}\mathrm{O} \text{ or } \delta\mathrm{D} = \{(\mathrm{R}_{\mathrm{sample}}/\mathrm{R}_{\mathrm{SMOW}}) - 1\} \times 1000 \qquad (1)$$

where R_{sample} and R_{SMOW} represents the heavy to light isotope ratio of 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 of $\pm 0{\cdot}1\%$ and $\pm 2{\cdot}0\%$ (1σ) for oxygen and hydrogen isotopes respectively.

Foliar nutrient analysis

Mature leaves numbering 10–15 for each individual sampled for stemwater were collected from the same branch as the stem for water, placed in paper bags and subsequently dried in an oven at 50 °C for 72 h. Dried leaves were then ground and mixed well to homogenize the samples, in preparation for foliar N, P and δ^{13}C analysis at LSIETE. Preparation of samples for P analysis consisted of ashing 700 mg of the dried ground leaves in porcelain cups in a furnace maintained at 600 °C for 6 h followed by digestion in 4% sulfuric acid and filtration through glass fibre 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 analyser (Alpkem, OI Analytical, Texas, USA) and expressed on a weight percentage basis. The precision of analysis was ±0·1 ppm ($\pm 1\sigma$). Foliar N concentration in 5 mg ground leaf samples was obtained using an NC 2100 analyser (Thermoquest CE Instruments, Milan, Italy) and expressed as the percent weight ratio of total N relative to total leaf dry mass, with precision of analysis 1 ppm ($\pm 1\sigma$).

Foliar $\delta^{13}C$ analysis

Ground leaf samples (5 mg) were loaded in individual tin cups (Elemental Micro-analysis, Milan, Italy), rolled into tight balls which were placed in an automated elemental analyser (Euro-EA-Elemental Analyzer, Eurovector, Milan, Italy) connected to a continuous flow isotope ratio mass spectrometer (Elementar, Germany). Carbon-13 abundances are expressed as δ^{13}C values:

$$\delta^{13}\mathrm{C}(‰) = [(\mathrm{R}_{\mathrm{sample}}/\mathrm{R}_{\mathrm{PDB}}) - 1] \times 1000 \qquad (2)$$

in which $\mathrm{R}_{\mathrm{sample}}$ and $\mathrm{R}_{\mathrm{PDB}}$ represent the $^{13}\mathrm{C}/^{12}\mathrm{C}$ ratios of the sample and the universal standard from the PeeDee belemnite formation of South Carolina. The precision of analysis was $\pm 0{\cdot}1\%$ ($\pm 1\sigma$).

Leaf area index analysis

Hemispherical (fisheye) images of the canopy in hammocks and pinelands were obtained at dawn using a Nikon Coolpix 4500 with an 8 mm Nikon LC-ER1 fisheye lens. The camera was positioned at a height of 1 m from the ground surface. LAI estimates were obtained from these images by the software Gap Light Analyzer (Frazer *et al.*, 1999). The emphasis was more on comparing LAI between hammocks and pinelands rather than obtaining the absolute values.

Data analysis

To examine how similar the plant stemwater of pinelands and hammocks are to groundwater, a potential source, we regressed the average $\delta^{18}O$ values of stemwater from each community and site throughout the year against those of groundwater (SPSS, Chicago, USA) using Model II regression, despite having just one groundwater $\delta^{18}O$ value per site due to one well per site. This was carried out only for Royal Palm and Long Pine Key sites where groundwater was collected.

For quantifying the relative contribution of soilwater and groundwater to stemwater, and to see how this contribution may change with season, we computed the proportion of the groundwater fraction in stemwater, x, using an end member mass balance equation of the form

$$\delta_{plant} = x\ \delta_{groundwater} + (1-x)\ \delta_{soilwater} \qquad (3)$$

Here δ signifies $\delta^{18}O$ values of the plant stemwater and the respective sourcewater pools. The fraction x has a value between 0 and 1 that corresponds to 0–100% groundwater fraction in stemwater. When calculations yielded values of $x < 0$ or >1, we considered them as 0 and 100% groundwater usage, respectively.

δD values have not been considered in the above regression and mass balance equation since they exhibit considerably more variation than $\delta^{18}O$. In addition, there is the possibility that certain species of plants discriminate against deuterium during water uptake (Lin and Sternberg, 1993; Ellsworth and Williams, 2007).

To compare foliar nutrient levels between hammock and pineland communities, leaf P averaged over all individuals per species that were sampled in each community and site was plotted against the corresponding leaf N average value. The entire dataset obtained over the study period was considered to minimize the effects of temporal nutrient concentration variation due to species phenology or fire. A Euclidean distance analysis was then carried out on another plot of foliar P versus foliar N, where each point on the plot represents the leaf N and P values averaged over 5 individuals of a species per sampling. The distance, d, of each point, i, from the plot origin (zero values of N and P) was computed using the Cartesian distance formula

$$\delta_i = (N_i^2 + P_i^2)^{0\cdot5} \qquad (4)$$

where N_i and P_i represent the foliar N and P values of the point i as mentioned.

A one-way ANOVA was performed to infer if the Euclidean distances of the pineland points were less than those for hammock datapoints, thus indicating whether the pineland plants had lower combined (N and P) foliar nutrient values relative to hammock plants.

Model II regression and correlation of leaf $\delta^{13}C$ versus leaf N were carried out to examine for differences between hammock and pineland plants in stomatal limitation as a function of foliar nitrogen concentration.

RESULTS

Soil depth and nutrient characterization

Hammocks had a significantly greater depth of soil over bedrock compared to pinelands as confirmed by a 2-way ANOVA with replication ($F = 65$, $P < 0\cdot01$), with a significant site effect ($F = 11$, $P < 0\cdot01$, Table I) This soil, mainly leaf litter in various stages of decomposition mixed with some crushed marl, forms a continuous layer in hammocks. In pinelands, soil is present in scattered sinkholes, and sometimes as a 1–5-cm-deep layer in areas that have not been recently burned. The concentration of plant-available phosphorus, ammonium and nitrate nitrogen in hammock soil at the date of sampling was found to be greater than that in groundwater by 1–2 orders (Table II).

Sourcewater isotopic composition

The isotopic composition of rainfall varied according to the season with wet season precipitation $\delta^{18}O$ and δD values being lower than those of the dry season (Figure 2 showing only $\delta^{18}O$ values). From the end of May 2005, when the wet season commences, rainfall becomes isotopically lighter until July. Isotope ratios of precipitation become higher around the mid-wet season (July–August, Figure 2) coincident with a lull in precipitation as shown in Figure 5(A). Precipitation isotope ratios decrease again towards the end of the wet season (September–October) coincident with resumption of high rainfall. The bimodal peak in rainfall amount over the wet season is typical of South Florida precipitation (Duever *et al*., 1994) and can be observed in rainfall records (1949–2005) at the Royal Palm Ranger Station in the ENP (SERCC, 2008).

Table I. Average soil depth to bedrock (cm) in hammocks and pinelands, ± standard error of the mean (SEM). A 2-way ANOVA with replication confirmed that (i) hammocks have greater soil depth than pinelands ($F = 65$, $P < 0\cdot01$), and (ii) a site effect exists ($F = 11$, $P < 0\cdot01$).

Site	Hammock	Pineland
Royal palm	7·7 ± 0·7 (n = 70)	5·7 ± 0·5 (n = 104)
Long pine key	32·1 ± 3·0 (n = 32)	2·8 ± 0·8 (n = 24)
Sisal pond	15·9 ± 1·5 (n = 51)	5·5 ± 2·1 (n = 51)

Table II. Plant-available phosphorus, ammonium and nitrate concentration ranges (ppm) in hammock soil and groundwater in the ENP (wet season). Soil pore water concentrations are calculated based upon the following assumptions: (1) the entire pool of plant-available nutrients are in solution; and (2) hammock soils contain 230% water by dry soil weight in the wet season (based on Ewe *et al*., 1999).

Nutrient	Hammock		Groundwater
	Soil	Pore water	
Available P	2·1–44·5	0·9–19	0·03–0·05
Nitrate	5·5–126	2·4–54	0·01–0·15
Ammonium	6·52–150	2·8–64	0·09–0·15

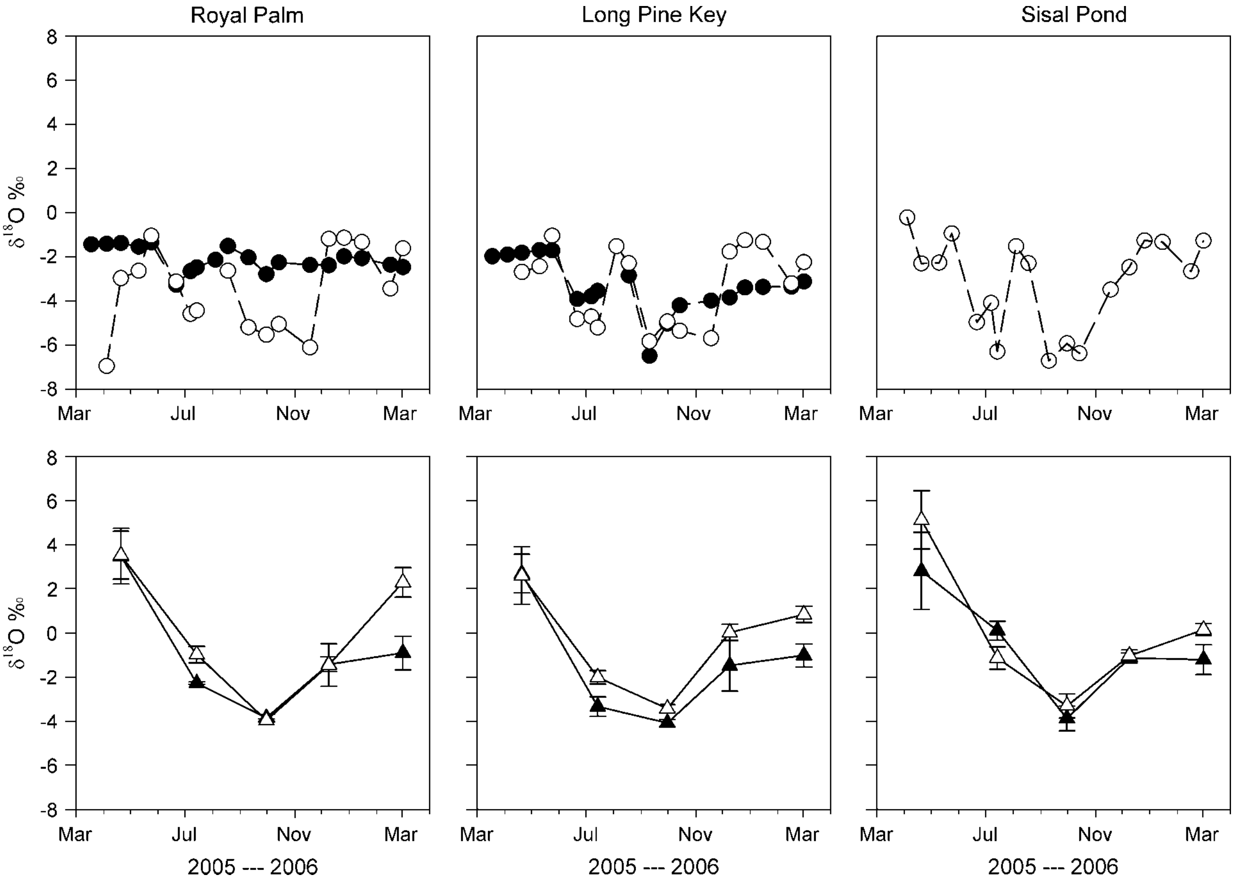

Figure 2. Upper panel: plots of $\delta^{18}O$ values of rain (○) and groundwater (●) for the study sites in the ENP for the period 18 March 2005 to 3 March 2006. Sisal pond did not have a groundwater well. The lower panel depicts soilwater $\delta^{18}O$ values—hammock (▲) and pineland (△) from 22 April 2005 to 18 March 2006. Error bars indicate SEM. Dotted vertical lines denote the wet season (June–November).

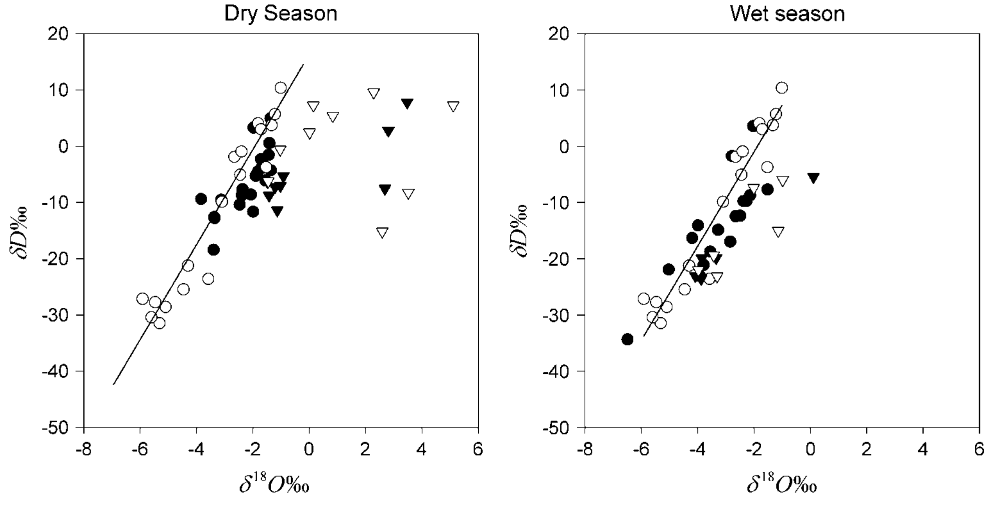

Figure 3. Plot of δD vs. $\delta^{18}O$ for rain (○), groundwater (●) and soilwater (hammock (▼) and pineland (▽) for all 3 sites in the ENP with the ELMWL shown ($\delta D = 8{\cdot}5\ \delta^{18}O + 17\%$, $r^2 = 0{\cdot}93$, $P < 0{\cdot}01$).

Groundwater displays the same temporal and seasonal isotopic pattern as rain in Royal Palm and Long Pine Key, but the amplitude of isotopic variation between successive samplings is dampened, particularly for the Royal Palm site (Figure 2). Soilwater $\delta^{18}O$ values in both hammocks and pinelands follow rainwater $\delta^{18}O$ trends with lighter isotopic composition during the wet season.

Regression of δD against $\delta^{18}O$ values for rain samples collected at all three sites over the entire year forms the Everglades Local Meteoric Water Line (ELMWL-Figure 3) having a slope of 8·5 and deuterium excess of 17 ($r^2 = 0{\cdot}93$). The ELMWL falls within the 95% confidence bounds of the Global Meteoric Water Line (GMWL, slope = 8), and thus, is not significantly different; this has been also seen in Wilcox *et al.* (2004). The larger deuterium excess of the ELMWL, 17 as compared to GMWL's 10 could indicate re-evaporation of shallow Everglades surfacewater. During the dry season,

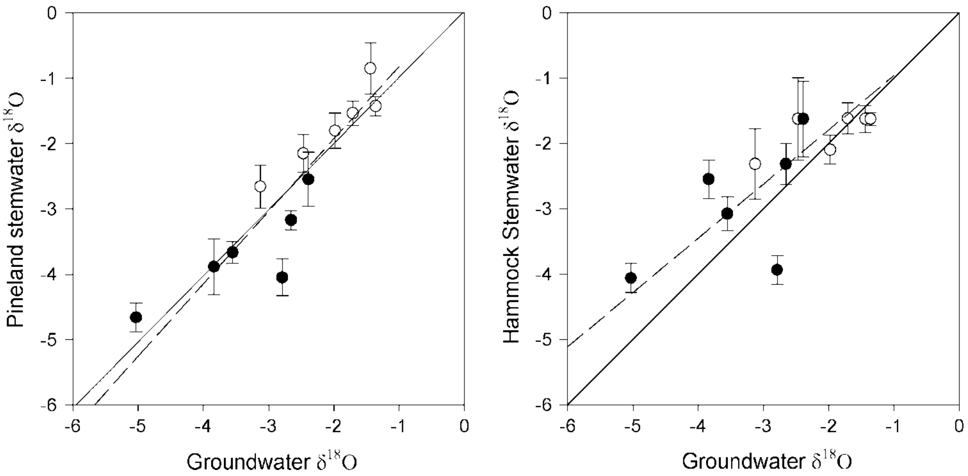

Figure 4. Relationship of average pineland plant $\delta^{18}O$ values (left) and hammock plant $\delta^{18}O$ values (right) with groundwater $\delta^{18}O$ values bimonthly over a year. Filled circles (●) denote wet season data while empty circles (○) dry season values. Each datapoint is the average of all plants in a community (hammock or pineland) at a site. Error bars indicate SEM. There are no error bars for groundwater $\delta^{18}O$ on the x-axis since we had just one sample (one well) per site. The pineland plant stemwater Model II regression equation is $\delta_{plant} = 1{\cdot}10\ \delta_{groundwater} + 0{\cdot}3$, $r^2 = 0{\cdot}82$, $P < 0{\cdot}01$ and this regression line (dashed line) is similar to the 1 : 1 relationship solid line. The hammock plant stemwater Model II regression equation is $\delta_{plant} = 0{\cdot}83\ \delta_{groundwater} - 0{\cdot}13$, $r^2 = 0{\cdot}57$, $P < 0{\cdot}01$.

groundwater values lie to the right of this line, indicative of evaporative enrichment (Friedman *et al.*, 1962). Soilwater values lie further to the right, indicating a greater evaporative enrichment.

Plant stemwater and sourcewater correlation

When considering the dataset of hammock and pineland plant stemwater isotopic values over the year, pineland plant $\delta^{18}O$ values were better correlated with groundwater ($r^2 = 0{\cdot}82$), with a Model II regression slope (1·11) and intercept (0·3) close to 1 and 0 respectively, indicating a 1 : 1 relationship (Figure 4). Hammock plants had a poorer correlation with groundwater ($r^2 = 0{\cdot}57$), with a slope (0·82) and intercept (−0·13). Both pinelands and hammocks exhibit a seasonal variation with increasing groundwater use in the dry season (Figure 5(B)) although pineland plants were utilizing a greater fraction of groundwater on every sampling date except during the late dry season (May 2005). The difference in groundwater utilization between pineland and hammocks was greatest during the wet season.

Foliar nitrogen and phosphorus

Foliar N is related to foliar P by a Model II regression $N = 55\ P - 0{\cdot}43$, $r = 0{\cdot}78$ (Figure 6). The community average foliar N and P is highest for the group of species present only in hammocks (1·70 and 0·056%, respectively) followed by the species group that is present in both hammocks and pinelands (1·59 and 0·032% in hammocks, 1·5 and 0·032% in pinelands) (Table III). The species group restricted to pinelands has the lowest average foliar N and P values (1·22 and 0·037%). There is also considerable interspecific variation in foliar N and P within each community. Foliar N and P values at the community level for pinelands (including all species sampled in pinelands, not just those restricted to pinelands) averaged over the entire year were significantly lower than the same for hammocks (Figure 6), based on the ANOVA of Euclidean distances showing pineland plants being significantly closer to the plot origin (P and N = 0) as compared to hammock plants ($F = 10{\cdot}51$, $P = 0{\cdot}0014$). Average annual N : P ratios of 45 ± 1·15 and 42 ± 1·16 (±SEM) were obtained for hammock and pineland communities respectively, with no significant difference in N : P ratio between the two communities (single factor ANOVA, $F = 3{\cdot}56$, $P = 0{\cdot}059$).

Foliar $\delta^{13}C$

The correlation of $\delta^{13}C$ against foliar N was highly significant for hammock plants ($r^2 = 0{\cdot}41$, $P < 0{\cdot}01$) with a linear regression having a slope of 1·11 (Figure 8). There was no correlation between foliage $\delta^{13}C$ values of pineland plants and their respective nitrogen concentrations ($r^2 = 0{\cdot}15$). At low levels of N (>2%), pineland leaves have higher $\delta^{13}C$ values than hammock plants.

Leaf area index

Hammocks had a higher LAI (2·49 ± 0·27, n = 10) than pinelands (0·35 ± 0·04, n = 5). Values calculated were LAI 4 ring, that is, the effective LAI of the canopy integrated over the zenith angles 0°–60° (Frazer *et al.*, 1999).

DISCUSSION

Sourcewaters are isotopically distinct

The greater depth of soil throughout the hammocks compared to pinelands (Table I) implies a much larger volume of soil in hammocks per unit area as compared to pinelands. In the wet season, rainwater entrapped in this soil ends up bearing nutrients in dissolved form that have been measured and estimated to be 1–2 orders

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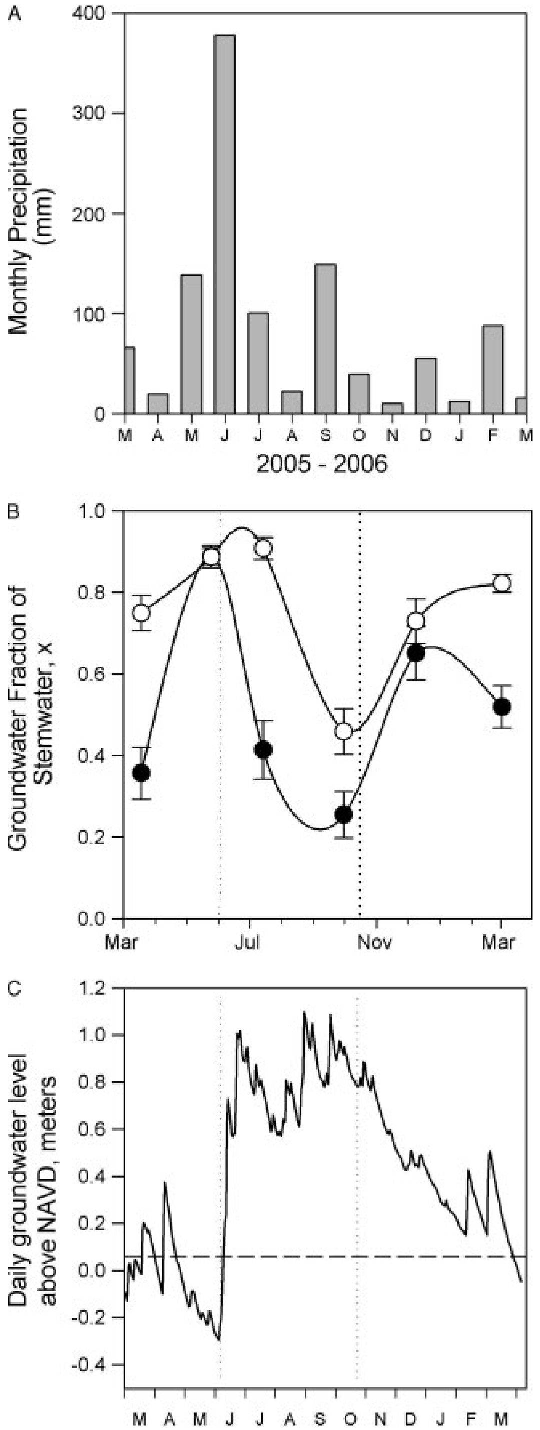

Figure 5. (A) monthly rainfall over the study period (www.usgs.gov). (B) Plot of average groundwater fraction utilized by hammock (●) and pineland (○) communities in Royal Palm and Long Pine Key sites through the year. A value of 1 implies 100% of stemwater is groundwater. Sampling months indicated on the horizontal axis. Vertical dotted lines indicate the wet season, and error bars depict ± SEM. (C) Daily water table values in metres above North American Vertical Datum (NAVD 1988) at well NP72 in Long Pine Key, ENP (latitude 25°23′46″ N, longitude 80°42′11″ W). Dashed horizontal line indicates groundwater level corresponding to approximately 50% groundwater uptake by hammock plants, with lesser groundwater uptake above this line.

of magnitude higher than groundwater (Table II). Thus, hammocks are expected to contain a larger volume of nutrient-rich soilwater than pinelands.

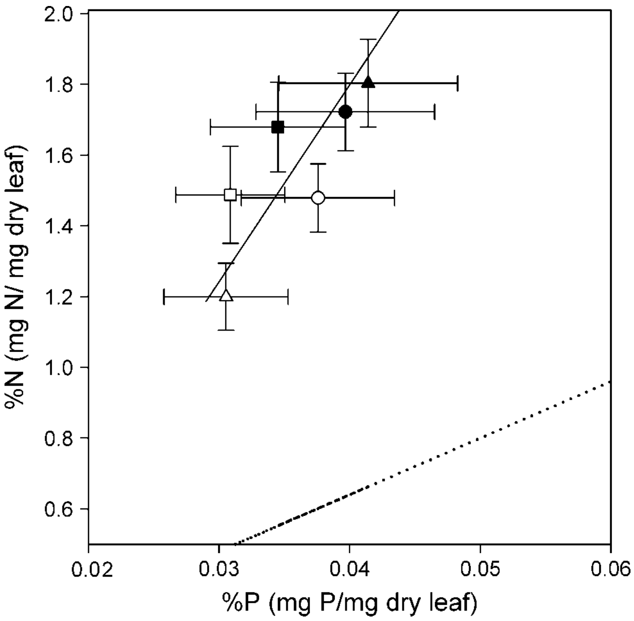

Figure 6. Relationship between average foliar N and P in hammocks (●, ■, ▲) and pinelands (○, □, △) from March 2005 to March 2006 at Royal Palm, Long Pine Key and Sisal Pond, respectively, in the ENP, as shown by a Model II regression line ($N = 55\ P - 0{\cdot}43$, $r^2 = 0{\cdot}61$, $P < 0{\cdot}01$). Each datapoint in the plot represents the average of all plants in a community and site sampled over the year ($n = 150$). Error bars indicate ± SEM. The dashed line in the lower part of the plot represents an N : P ratio of 16, beyond which signifies P limitation for European freshwater wetlands (Koerselman and Meuleman, 1996).

Soilwater was isotopically distinct from groundwater at every instance of sampling, thereby allowing determination of the contribution of each source to plant stemwater by the mass balance approach. Soilwater is essentially rainwater trapped in litter, which is subject to evaporation between successive rain events, and so becomes isotopically enriched relative to rain. At the same time, soilwater was lighter than groundwater in the wet season with correspondingly lower $\delta^{18}O$ values (Figures 2 and 3). While groundwater also receives rain inputs, the extensive volume of the perennial groundwater pool dampens the lighter rain isotopic signal, thus remaining isotopically higher than rain over the wet season (Figure 2). Over the dry season, soilwater (a far smaller pool in comparison with groundwater) undergoes greater evaporative enrichment resulting in higher $\delta^{18}O$ values than groundwater (Figures 2 and 3). Soilwater $\delta^{18}O$ values appear less enriched in March 2006 as compared to March 2005 probably due to differences in precipitation amounts, intervals and evaporative conditions in the months preceding the samplings. For instance there were larger than normal rain events in the 2005–2006 dry season (December 2005 and February of 2006).

Water usage by plant communities

The higher correlation and near 1 : 1 relationship between pineland plant stemwater and groundwater compared to the lower correlation of hammock plant stemwater and groundwater is consistent with groundwater being the major water source for pineland plants (Figure 4)

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Table III. Species level foliar N and P (averaged for all individuals of a species for all sites sampled 6 times over a year) for plants in hammocks and pinelands (n ranges from 30 to 90, depending on the presence of the species in 1 to 3 sites). The SEM was calculated for the entire pool of samples collected over the year.

Species	Foliar N (%) ± SEM		Foliar P (%) ± SEM	
	Hammock	Pineland	Hammock	Pineland
Species found both in hammocks and pinelands				
Lysiloma latisiliqua	2·59 ± 0·16	2·62 ± 0·15	0·047 ± 0·000	0·046 ± 0·002
Guettarda scabra	1·32 ± 0·08	1·07 ± 0·10	0·030 ± 0·004	0·032 ± 0·005
Myrica cerifera	1·45 ± 0·09	1·42 ± 0·11	0·0191 ± 0·0031	0·0182 ± 0·0026
Tetrazyga bicolor	1·34 ± 0·1	1·10 ± 0·16	0·0321 ± 0·0059	0·0284 ± 0·0028
Persea borbonia	1·26 ± 0·15	1·28 ± 0·08	0·0332 ± 0·0038	0·0370 ± 0·0079
Average over species common to hammocks and pinelands	**1·59 ± 0·12**	**1·50 ± 0·12**	**0·0324 ± 0·0046**	**0·0324 ± 0·0051**
Species found only in hammocks				
Annona glabra	2·25 ± 0·12	—	0·0832 ± 0·0177	
Chrysobalanus icaco	1·33 ± 0·12		0·0370 ± 0·0045	
Quercus virginiana	1·44 ± 0·12		0·0378 ± 0·0073	
Bursera simarouba	1·80 ± 0·13		0·0661 ± 0·0137	
Average over species found only in hammocks	**1·70 ± 0·12**		**0·0560 ± 0·0108**	
Species found only in pinelands				
Pinus elliottii var densa		0·79 ± 0·08		0·0289 ± 0·0039
Quercus pumila		1·57 ± 0·12		0·0588 ± 0·0079
Myrsene guianensis		1·06 ± 0·09	—	0·0297 ± 0·0045
Ilex cassine		1·18 ± 0·08		0·0330 ± 0·0039
Crossopetalum ilicifolium		1·51 ± 0·09	—	0·0367 ± 0·0059
Average over species found only in pinelands		**1·22 ± 0·09**		**0·0374 ± 0·0052**

in comparison to hammock plants except for late in the dry season. This conclusion is further corroborated by the relative utilization of groundwater and soilwater by plants in these two communities at different times of the year according to the mass balance equation (Figure 5(B)). We demonstrate the seasonal variation in *both* communities in the proportions of soilwater and groundwater used, noting that pineland plants *also* use soilwater (about 50% on average) in mid to late wet season (Figure 5(B)).

The 2005 wet season commenced with a large pulse in rainfall over June and July (Figure 5(A)), with a slightly delayed increase in the groundwater table level (Figure 5(C)). A concomitant decrease in groundwater fraction of stemwater was observed for hammock plants in July (Figure 5(B)), which can be construed as an increase in soilwater uptake. This could be due to wetting of the soil litter by rain, and/or because the rising water table may restrict hammock plants to water uptake only to the unsaturated surface soil layer, since hammock hardwoods are flood intolerant (Snyder, 1990; Jones *et al.*, 2006). During the early wet season, pineland plants continued to rely upon groundwater, and started to absorb soil water in significant amounts only after July, until almost half their water uptake comprises of soilwater during October (late wet season). This suggests the possibility that pineland plants can tolerate some period of inundation when they almost entirely take up groundwater, after which they gradually increase soilwater uptake. Soilwater in pinelands occurs in litter-filled holes in the limestone bedrock and is probably richer in nutrients than groundwater.

With the advent of the dry season around mid-October, plants in both communities begin to increase groundwater uptake. This is probably a response to decreasing plant-available water in the litter layer because of gradual drying. Another possibility is that the falling water table lowers the anoxic zone thereby permitting regrowth of roots downwards. Water levels rise again after December, possibly in response to rain showers that occurred in December 2005 and February 2006 (Figure 5(A) and (C)) which could once again flood roots and force plants to shift towards newly available soilwater as seen in hammocks (Figure 5(B)).

If there is substantial root mortality in hammock plants because of their intolerance of flooding, then the rate of root regrowth must keep pace with the falling water table over the dry season. If the water levels fall rapidly to levels lower than what is normal in the late dry season, groundwater may become inaccessible to hammock plants, causing water stress. Given that the thin organic soil layer overlies bedrock, and that roots can grow downwards only through existing cracks (at least in the short term), it is possible that roots in many cases may not be able to encounter suitable pathways down to the water table at a rate adequate to meet water demand by the plant. Ewe *et al.* (1999) observed a greater decrease in pre-dawn water potential in hammock trees over pineland trees in the transition from wet to dry season. This indicates a larger seasonal decrease in water availability for hammock trees. Thus, the existence of hammock plant communities appears to be precariously positioned between two critical water levels: too high a water level will lead to flooding stress while too low a level would engender drought stress. Deviation outside this range over time can have irreversible effects culminating in mortality of trees.

Lower than normal water levels caused by droughts or increased water withholdings/diversions from canals can also affect pine rocklands (Oberbauer *et al*., 1997; USFWS, 1999), possibly due to water table access problems similar to hammocks.

Foliar N and P at the community level

As hypothesized, the pooled average foliar nutrient concentration for all plants sampled in the hammock is significantly higher than that in pinelands (Figure 6). This could be a consequence of greater availability and greater uptake of nutrient-rich soilwater in hammocks (Figure 5(B)). The far smaller volume of soil in pinelands, together with the observation that nutrient-poor groundwater is the main water source in pinelands most of the year positions pinelands below hammocks in terms of available nutrient pools (N and P). Other factors can also influence foliar nutrient concentrations, for instance, fire can increase nutrient availability to plants with attendant increase in foliar nutrient concentrations in resprouts. This would be expected mainly in pinelands that experience fires every 3–7 years and is probably applicable to the Long Pine Key site that underwent a fire during the study period.

A preliminary consideration of the foliar nutrient data at the species level suggests a nutrient gradient increasing from pinelands to hammocks (Table III): (i) Pinelands: The dominant species (canopy and biomass) in the pinelands, *Pinus elliottii,* has relatively low values of foliar N and P in comparison to other pineland and hammock species; (ii) Species present in the hammock-pineland interface have mostly intermediate foliar nutrient values; and (iii) Hammocks: At the higher foliar nutrient concentration end is *Bursera simarouba,* one of the few species occurring throughout the range of rockland hammocks (Snyder, 1990) with high abundance (Alexander, 1967). Indeed, the pineland community average would have been even lower than our calculated value had the foliar nutrient concentration of each pineland species been weighted by the relative abundance of foliar biomass of that species.

Despite differing nutrient availabilities between hammocks and pinelands, foliar nutrient concentrations were seen to be similar in individuals of a species common to both communities. Plasticity in foliar N and P ratios is affected by species–specific stoichiometric relationships between foliar N and P that are in turn driven by physiological function and the anatomy of leaves. A plant faced with lower nutrient availability (in comparison to a site with higher nutrient availability) could be restrained by lower growth and have a lower number of leaves, rather than manifest a significant change in the foliar N : P ratio; a study of foliar nutrients in montane rainforest across a chronosequence of Hawaiian soils with a soil nutrient gradient (Vitousek *et al*., 1995) noted no significant change in foliar N : P ratios despite changes in foliar N and P concentrations. Greater nutrient availability (as proposed in hammocks) may also result in greater growth and biomass instead of higher foliar nutrient concentrations. Individuals of the co-occurring species are much larger in the hammocks; however fire is a confounding factor since periodic fires keep burning off these species in pinelands, while hammocks for the most part are spared from these fires. In their review (2000), Aerts and Chapin mention that oligotrophic sites are dominated by slow growing species with low foliar nutrient concentrations, notably evergreens. Sites with higher levels of nutrient availability have species with higher leaf nutrient concentrations (forbs, graminoids and deciduous species). Thus increasing nutrient availability can lead to higher foliar nutrient concentrations at the community level due to both phenotypic responses and species replacements. Species found exclusively in the hammocks at the three study sites in general had higher foliar nutrient concentrations as compared to those found exclusively in the pinelands (Table III).

Foliar N : P ratios can be indicative of the relative availability of N and P to the plant, with N : P ratios being inversely correlated with soil P availability (Gusewell, 2004; Han *et al*., 2005). The literature on N : P ratios in ecosystems in other parts of the world range from 3 to 89 with a mean N : P ratio in the range of 13–16 (Reich and Oleksyn, 2004; Wright *et al*., 2005). Plants in European herbaceous freshwater wetlands were found to have N : P ratios between 7 and 30, with ratios greater than 16 signifying community P limitation in those ecosystems (Koerselman and Meuleman, 1996). Both hammocks and pinelands in the Everglades have high mean N : P values (45 and 42 respectively in this study) indicating a very low level of foliar P, which could result from low soil P availability. Other plant communities in the Everglades have even higher N : P ratios, possibly indicating even lower P availability than upland areas. Wet graminoid prairies are flooded most of the year, cover much of the Everglades and are oligotrophic (Newman *et al*., 1996; Brown *et al*., 2006). They are dominated by sawgrass (*Cladium jamaicense*) which has extremely low levels of P in its tissue, with foliar N : P ratios of 70–84 in areas relatively unaffected by agricultural nutrient enrichment (Richardson *et al*., 1999).

Foliar nutrients and photosynthesis

The correlation between foliar δ^{13}C and foliar nitrogen concentration in hammock plants (Figure 7) can be explained as follows: higher foliar N concentration indicates higher chlorophyll and carboxylation enzyme content in leaves (Duursma and Marshall, 2006) which in turn leads to higher photosynthesis; a positive relationship between photosynthesis and leaf nitrogen content has been widely reported (eg. Field and Mooney, 1986). Higher levels of photosynthesis can increase the proportion of ^{13}C incorporated in leaf biomass, a consequence of the ensuing stomatal limitation on atmospheric carbon

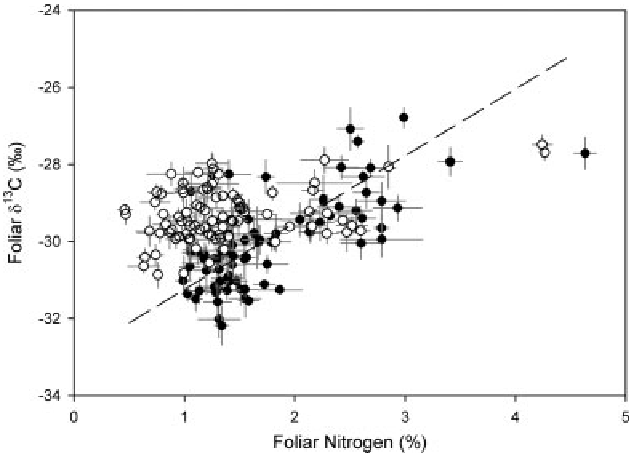

Figure 7. Model II regression of foliar $\delta^{13}C$ (‰) against foliar N for hammock (●) and pineland plants (○). Each datapoint is an average of 5 individuals of a species per sampling event. All 6 bimonthly sampling events over March 2005–March 2006 are included. Correlation was significant in hammocks ($r^2 = 0{\cdot}41$, $P < 0{\cdot}01$) but not in pinelands ($r^2 = 0{\cdot}15$). Error bars indicate ±SEM. The Model II regression equation for hammocks is $\delta^{13}C = 1{\cdot}73\ N - 33$ (dashed line); pineland regression line not shown since correlation is insignificant.

dioxide (CO_2) inflow, thus forcing decreased discrimination by Ribulose Bis-Phosphate Carboxylase against ^{13}C (Farquhar *et al.*, 1982). Stomatal limitation could be caused either by a greater photosynthetic demand of CO_2 over supply, even with stomata fully open, or by some degree of stomatal closure triggered by the need to reduce transpirational water loss in periods when water is limiting.

While positive correlations between foliar $\delta^{13}C$ and foliar nitrogen have been observed in other ecosystems (eg. Li *et al.*, 2007), there also have been negative or absence of correlations reported (eg. Ma *et al.*, 2007). The foliar $\delta^{13}C$—N correlation varies with species, with leaf age and canopy position, and thus, the precise mechanisms underlying the correlation are not well understood (Li *et al.*, 2007). The absence of the above correlation in pineland plants indicates that some other factor could be affecting photosynthesis in pineland plants, such as higher light intensity in pinelands as compared to hammocks. Nevertheless, leaves of pineland plants have higher $\delta^{13}C$ values at low levels of foliar N ($<2\%$) than hammock plants, indicating greater stomatal limitation of photosynthesis at low N.

CONCLUSIONS

The reliance of hammock trees upon nutrient-rich soil-water in the wet season together with their higher levels of foliar N and P supports the idea of the litter layer in hammocks being a nutrient hotspot in the oligotrophic Everglades. The organic soil layer in hammocks thus facilitates establishment and propagation of flood-intolerant neotropical hardwood species by (i) serving as an unsaturated substrate allowing roots to survive in the wet season, and (ii) furnishing a significant water and nutrient source. In addition, the moist nature of this organic layer is partly responsible for preventing ingress of fires that range through pinelands every few years. Thus the organic soil layer in hammocks is an instance of how vegetation can modify the local environment to foster conditions enabling establishment and growth of species that otherwise would not be able to survive as has been observed elsewhere (Scheffer *et al.*, 2005).

Being the only above-water communities along with the emergent areas of tree islands, hammocks and pinelands are critically important to the Everglades ecosystem from both a floral and faunal perspective, but in 1984 they constituted only about 4% of the total ENP area based on data in Olmsted and Loope (1984). In addition, almost all the pine rocklands outside the ENP have been eliminated by logging and urban development (Snyder, 1990; Herndon, 1998; Slocum *et al.*, 2003) with barely 2% remaining as of 2007 (WWF, 2007). Maintenance of these critical upland components of the unique Everglades ecosystem requires that the seasonal water level regime be maintained. The dangers of flooding to hardwood hammocks are well known. This study provides isotopic evidence of the almost exclusive dependence of hardwood hammocks and pinelands on groundwater in the late dry season, thus supporting the contention of Alexander (1967) that droughts due to lowering of the South Florida water table is the most serious deterrent to the continued development and survival of hardwood hammocks. It is thus necessary to manage dry season groundwater levels so that they remain accessible to upland community plants.

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