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Water-use patterns of woody species in pineland and hammock communities of South Florida

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Abstract

Rockland pine forests of south Florida dominated by *Pinus elliottii* var. *densa* characteristically have poor soil development in relation to neighboring hardwood hammocks. This has led to the hypothesis that Everglades hammock trees are more reliant on soil moisture derived from local precipitation whereas pineland plants must depend more on groundwater linked to broader regional hydrologic patterns. Because soil moisture sources are likely to vary more than groundwater sources, we hypothesized that hammock plants would exhibit correspondingly higher levels of dry season water stress. This was examined by measuring predawn water potentials, and by analyzing water uptake in representative hammock and pineland woody species using stable isotopes of plant water and that of potential sources during wet and dry seasons.

Two species typical of each of the two communities were selected; a fifth species which was found in both communities, *Lysiloma latisiliqua* Benth., was also analyzed. Water content of soils in both communities decreased from wet to dry season. Consistent with our hypothesis, the change in predawn water potentials between the wet and dry season was less in pineland species than that of hammock species. Water potential changes in *L. latisiliqua* in both communities resembled that of hammock species more than pineland plants. Isotopic data showed that pineland species rely proportionately more on groundwater than hammock species. Nevertheless, unlike hammock species in the Florida Keys, mainland hammock species utilized a substantial amount of groundwater during the dry season. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Pine rockland forests and tropical hardwood hammocks are the two principal forested communities typical of southern Florida uplands. Both of these communities exist on limestone outcroppings (Snyder et al., 1990), often just a few cm above the wetter Everglades graminoid prairies and marshes. Based on the data of Olmsted and Loope (1984), pinelands and hammocks comprise ≈4% of the Everglades National Park vegetation cover but are ecologically important in supporting both floral and faunal diversity.

Southern Florida pine forests have an open canopy of slash pine (*Pinus elliottii* Englem. var. *densa* Little & Dorman) with a shrub-palm-herb understory con-

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sisting of species such as wax myrtle (*Myrica cerifera* L.), saw palmetto (*Serenoa repens* (Bartr). Small), tetrazygia (*Tetrazygia bicolor* (Mill.) Cogn.) and wild tamarind (*Lysiloma latisiliqua* Benth.). Soil is poorly developed and tends to accumulate in limestone pockets. Plant composition within the pine forest is maintained by fire. In the absence of fire, the pine forest is replaced by hardwood species typical of hammock communities (Hofstetter, 1974). Hammocks are composed predominantly of flood-intolerant tropical hardwood species similar to those found in the Caribbean (Snyder et al., 1990). Dominant species include gumbo limbo (*Bursera simarouba* (L.) Sarg.), mahogany (*Swietenia mahogani* (L.) Jacq.), and live oak (*Quercus virginiana* L.). The closed canopy within a hammock forms a humid low-light microenvironment (Snyder et al., 1990) with a layer of organic soil overlying the limestone bedrock.

In the Florida Keys, *Pinus elliottii* was shown to utilize deeper groundwater sources while tropical hardwood hammock species utilized shallower soil water (Ish-Shalom et al., 1992; Ross et al., 1993). In our study, we tested to see if similar water utilization patterns characterized mainland pinelands and hammocks. We compared several dominant plant species found in the hammocks and pinelands of Everglades National Park to observe water uptake characteristics of these two communities. We hypothesized that due to poorer soil development, pineland plant species would be dependent on groundwater (a more stable water supply) and thus be exposed to lower water stress resulting from seasonal precipitation. Hammock species were thought to be more dependent on surface soil water (a more dynamic water supply), and would potentially be exposed to greater water stress during the dry season. We used changes in predawn water potential from wet to dry season to assess water stress in plants from the two communities. In addition, we expected that the two potential water sources (soil and groundwater) would have distinct isotopic signatures so that plant water uptake could be determined by isotopic analysis of plant stem water. Differing patterns of water uptake or use in pineland and hammock communities could be important to the fate of these communities in response to management plans involving drainage or rehydration of the Everglades ecosystem.

Stable isotope composition of water has been used to trace plant water uptake patterns in many communities (Ehleringer et al., 1991; Ish-Shalom et al., 1992; Lin and Sternberg, 1992; Sternberg et al., 1991; White et al., 1985). If the hydrogen and oxygen stable isotope ratios of potential water sources are significantly different, then water extracted from plant stems can be used to quantitatively determine the relative contributions of different water sources (Thorburn and Walker, 1993). Surface soil water is generally more enriched in heavier isotopes compared to the deeper groundwater due to evaporation (Sternberg et al., 1991). The uplands of southern Florida have two potential water sources available for plant uptake: rainwater captured locally by shallow surface soils and deeper water which is part of the regional groundwater system. Although both potential water sources ultimately come from precipitation, the groundwater isotopic composition reflects broader, long-term precipitation or water management patterns whereas soil water represents mostly short-term precipitation at a given site. Rainfall at different times of the year or hurricane precipitation (Ehhalt and Ostlund, 1970) may affect the stable isotope signatures of the water sources. However, no hurricanes occurred during our study and it is only the within-season signatures of both water sources that are used in this study.

2. Materials and methods

2.1. Study area

The study area was located on the Miami Rock Ridge (Fig. 1), a mid-Pleistocene marine limestone outcrop that extends from the Atlantic coast southwesterly to end in the southern Everglades (Snyder et al., 1990). The oolitic limestone substrate is <2 m above sea level (a.s.l.) in elevation at Long Pine Key and is pitted with solution holes. A mosaic of pinelands and hammocks are found on these limestone outcroppings.

Three study sites situated at interfaces of pineland and hammock communities were chosen within Everglades National Park (Fig. 1). The sites were located along an east–west rainfall gradient (Snyder et al., 1990). Site 1 (25°23.6′N, 80°37.2′W) is estimated to be ≈1.3 m a.s.l. while site 2 (25°24.2′N, 80°39.3′W), in Long Pine Key, is located at ≈1.5 m a.s.l.; site 3 (25°23.5′N, 80°48.0′W), at ≈1.1 m a.s.l., is the wes-

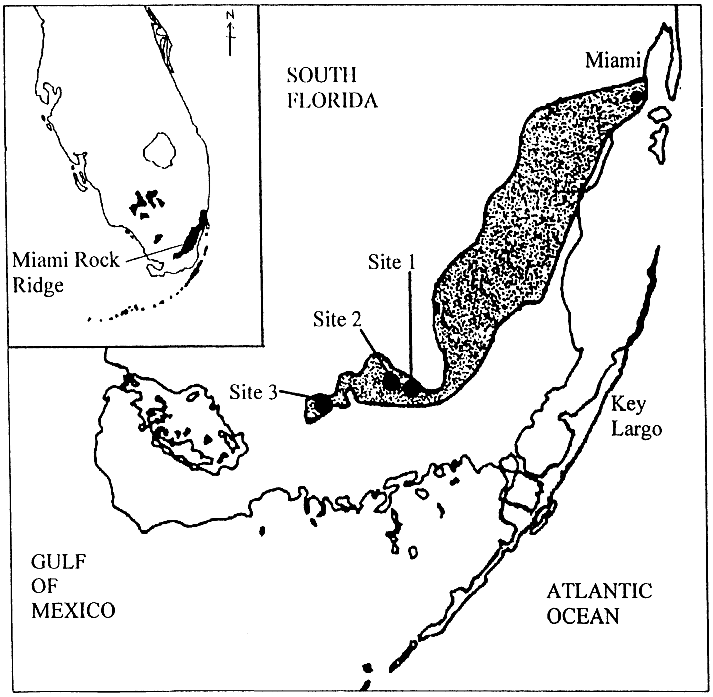

Fig. 1. Map of upland areas in south Florida, indicating the location of the Miami Rock Ridge (inset). The relative locations of the three study sites on this limestone ridge (shaded) are shown.

ternmost and wettest of all three sites. Site 3 is flooded deeper and longer than the other two sites during the wet season. At the end of the dry season, site 2 had the greatest distance to groundwater (≈1.5 m) followed by site 1 (≈1.3 m) and site 3 (≈0.6 m). All these sites are subject to Florida's distinct seasonality; the dry season is typically from November to late May, while the rainy season is from June through October (Chen and Gerber, 1990). Approximately 75% of annual precipitation (1400–1650 mm) falls during the rainy season (Snyder et al., 1990). Both these communities are affected by hurricanes which make landfall in southern Florida on average once every three years (Gentry, 1974). The last major hurricane (Hurricane Andrew, August 1992) minimally impacted our study sites; Armentano et al. (1995) observed that only 11–17% of the trees were severely damaged.

In pinelands, the substrate is predominantly exposed limestone rock. Marl soils and organic litter are found in shallow pockets and solution holes within the limestone bedrock. The plants in this community root into the channels and fissures in the rock (Snyder et al., 1990). In the hammocks, the soil is highly organic but may contain some inorganic matter. This rooting medium is on average 8 to 15 cm deep overlying the limestone bedrock (Olmsted et al., 1980).

2.2. Species sampled

The species sampled were representative of native canopy and understory plants commonly found in each community. In pinelands, we sampled dominant species typical of the canopy (*P. elliottii*) and understory (*M. cerifera*). *Pinus elliottii* grows to ca. 18 m in height while *M. cerifera* is a shrub found in open areas such as pinelands, hammock fringes and also in wetter areas around prairies (Tomlinson, 1980). *Lysiloma latisiliqua* Benth., a tree found in both the pinelands and hammocks, was sampled from both communities. This species is a common semi-deciduous tree within hammocks, but it is also one of the weedy pioneer species in recently-burned pinelands (Tomlinson, 1980).

In the hammocks, we sampled an overstory species (*Q. virginiana*) and an understory species (*Eugenia axillaris* (Sw.) Wild.). *Quercus virginiana* or live oak, is an evergreen oak species; it is often found as a canopy dominant in the hammocks of southern Florida. *Eugenia axillaris* is a small shrub found as an understory species within hammocks. Five individuals of each species were sampled at each site. All sites were sampled twice, once at the end of the wet season (26, 28 and 29 October 1996) and again at the end of the dry season (5, 6 and 7 April 1997).

2.3. Water and soil measurements

To assess between-site variability of groundwater depth, a 5.0 m well was installed at each site. A daily-recording electronic rainfall gauge was also placed at each site. Water table level (i.e. groundwater depth) and rainfall were monitored for approximately six months before initial sampling until the experiment ended. On each sampling date, well water was collected and analyzed for isotopic composition representative of groundwater. Five surface soil samples were collected randomly within each community on each sampling day. The soil samples were weighed before and after water was cryogenically extracted. Water content was determined as in Bannister (1986). The samples were then ashed at 550°C for 24 h to determine organic content of the soil by dividing net loss in weight by dry weight.

2.4. Predawn water potential (PDWP)

Water potential was measured before dawn when water within the plants was at equilibrium with soil conditions (Larcher, 1995). Plant samples were collected for determination of predawn water potential (hereafter PDWP) between 0300 and 0600 h. Stem tips (including leaves) 10–20 cm long and up to 0.5 cm in diameter were used for water potential measurements; in the taller *P. elliottii*, a lightweight aluminum ladder and an extensible pole pruner was used to reach the branches. Samples were immediately stored in plastic bags within a portable cooler until water potential was measured using a pressure chamber (PMS 600, Corvallis, Oregon).

2.5. Stable isotope analysis

At mid-morning, when the plants were transpiring, fully suberized stems sections without leaves 0.5–1.0 cm in diameter and 10–15 cm in length several centimeters from the shoot tip were taken from each plant and stored individually in 50 ml borosilicate tubes sealed with Parafilm. Stem samples were taken several centimeters away from shoot tip and leaves to avoid contamination of stem water with leaf water. The five replicate soil samples from each community and groundwater samples were stored similarly. All samples were returned to the Stable Isotope Laboratory in the Biology Department at the University of Miami and immediately frozen. Water was subsequently cryogenically extracted from the stem and soil samples.

Hydrogen isotopic composition was determined by either the zinc technique (Coleman et al., 1982) or by uranium oxidation method (Bigeleisen et al., 1952) with both methods being calibrated against an internal standard. Stable isotopes of oxygen were obtained by the carbon dioxide equilibration method as described by Epstein and Mayeda (1953). Samples were analyzed on an ion-ratio gas mass spectrometer (VG Isogas, Middlebury, England). The standard used in the ratio for both gases was standard mean ocean water (SMOW) with isotopic abundance expressed in the following manner:

$$\delta\% = [(R_{\text{sample}}/R_{\text{standard}}) - 1]1000$$

where R_{sample} is either the D/H or $^{18}\text{O}/^{16}\text{O}$ ratios of the sample and R_{standard} is either the D/H or $^{18}\text{O}/^{16}\text{O}$ ratios of SMOW.

Stable isotope ratios of stem water were utilized to calculate the percentage groundwater utilization by each species with an end-member mixing model (White et al., 1985). In the absence of other water sources and sinks, when the stable isotope signature of a plant species falls between that of soil and groundwater, the plant is utilizing a mixture of both water sources. The end-member mixing model calculates the fraction of groundwater uptake of the plant with the following equation:

$$\%\,\text{groundwater} = \frac{(\delta_{\text{plant}} - \delta_{\text{soil}})}{\delta_{\text{ground}} - \delta_{\text{soil}}} \times 100\%$$

where δ_{plant} is the isotope signature of the stem water sample, δ_{soil} is the isotope signature of soil water and δ_{ground} is the isotope signature of groundwater.

3. Results

3.1. Soil and water measurements

Water content was positively correlated with the organic content of the soil in both the wet and dry seasons (Fig. 2), i.e. the greater the organic content, the greater the percentage of water. For any particular soil organic content, there was significantly more water within the soils during the wet season than in the dry. The amount of water within soils (% dry weight) ranged from 27.6 to 251.3% during the wet season and between 24.4 to 192.9% during the dry season (Fig. 2).

A three-way analysis-of-variance (ANOVA) of the soil water content showed significant difference between sites and seasons but not between communities (Table 1). For both the wet and dry seasons, site 1 had the least amount of soil water while site 3 had the most (Fig. 2). Organic matter content within individual soil samples ranged from 15.7 to 89.0% (Table 2). There were significant differences in soil organic matter content among sites and communities but not between the wet and dry season (Table 1).

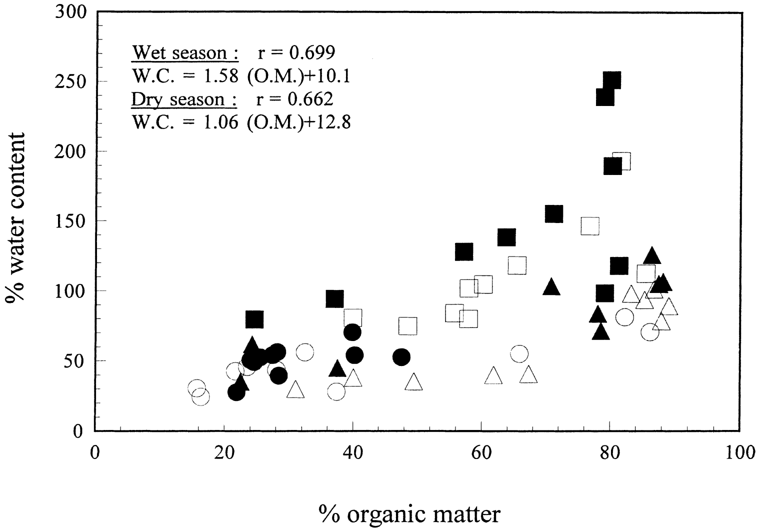

Fig. 2. Relationship between soil water content and soil organic content for the wet and dry seasons. Closed symbols indicate both pineland and hammock during wet season in site 1 (●), site 2 (▲) and site 3 (■). Open symbols indicate dry season in site 1 (○), site 2 (△) and site 3 (□). Analysis of covariance (ANCOVA) indicated that the slopes from the regression of both lines are significantly different ($p \leq 0.05$), with wet season samples having a greater slope.

Table 1
Results of three-way ANOVA showing differences in soil water and organic content over community, site and season

Source	Water content (dry weight %)				Organic content (dry weight %)			
	df	Mean squares	*F* value	PR>*F*	df	Mean squares	*F* value	PR>*F*
Community	1	160.4	0.22	0.640	1	1360.6	4.72	0.035
Site	2	33850.4	46.88	0.000	2	5602.7	19.43	0.000
Season	1	5930.0	8.21	0.006	1	288.2	1.00	0.322
Community×site	2	14255.5	19.74	0.000	2	3745.4	12.99	0.000
Community×season	1	526.1	0.73	0.398	1	11.2	0.04	0.845
Site×season	2	1702.0	2.36	0.106	2	200.9	0.70	0.503
Community×site×season	2	40.4	0.06	0.946	2	230.0	0.80	0.456
Error	48	722.1			48	288.3		

Table 2
Percentage organic content of soil (±SEM) collected in pineland and hammock communities at three sites in Everglades National Park. Samples were collected during the wet season (26, 28 and 29 September 1996) and dry season (5, 6 and 7 April 1997). Superscripts of different letters denote significant differences ($p \leq 0.05$) between season and community within each site

	Organic (%)			
	Wet season		Dry season	
	Pineland	Hammock	Pineland	Hammock
Site 1	30.9 ± 8.7^{a}	30.6 ± 9.6^{a}	32.7 ± 20.6^{a}	49.2 ± 32.2^{a}
Site 2	43.6 ± 23.5^{b}	82.2 ± 7.6^{c}	49.9 ± 15.0^{b}	86.4 ± 2.3^{c}
Site 3	$71.5 \pm 19.3^{d,e}$	$59.1 \pm 21.0^{d,e}$	73.9 ± 10.7^{d}	52.0 ± 7.8^{e}

Overall, the pinelands in site 1 had the lowest amount of organic matter while the hammocks in site 2 had the highest amount of organic matter (Table 2). Within each site, pair-wise comparisons between pinelands and hammocks with the *t*-test indicate (Table 2) that organic content in the two communities was the same for site 1 as well as site 3, but different for site 2.

3.2. Predawn water potentials

The wet season predawn water potentials of pineland and hammock species were similar except for site 1 in which pineland plants had marginally lower water potentials compared to hammock species (p=0.046). The decrease in predawn water potential from wet to dry season was significantly greater for hammock species than for pineland species for all three sites (Table 3, Fig. 3). In both communities, *L. latisiliqua* water potential response to seasonal drying tended to be more like that of a hammock species, although in site 2, *L. latisiliqua* dry season response was intermediate to pineland and hammock species.

Predawn water potential for pineland species in sites 1 and 3 did not vary substantially with season compared to plants in site 2 (Fig. 3). Pineland species (*P. elliottii* and *M. cerifera*) appeared less affected by the dry season whereas in general hammock species experienced decreases in water potential from wet to dry season. For sites 1 and 2 within the hammocks, *E. axillaris* and *L. latisiliqua* tended to have smaller declines in predawn water potential than *Q. virginiana*. Predawn water potential change of *L. latisiliqua* was slightly greater in the pineland than in the hammock for all sites (Fig. 3).

3.3. Stable isotope analysis

Plant water uptake patterns can be determined if stable isotope signatures of groundwater versus soil water are significantly different. Pair-wise comparison of soil water versus groundwater showed significant difference in δ^{18}O and δD values for sites 1 and 2 but not site 3 (Table 4). Specifically, the δ^{18}O value for groundwater was significantly lower than that of hammock soil water during both the wet and dry seasons in site 2 (Fig. 4, Table 4). The δ^{18}O values for groundwater were significantly lower than that of pineland soil during the dry season in sites 1 and 2.

Table 3
Wet season and decrease in plant predawn water potentials (MPa) from wet to dry season (±SEM) within pineland and hammock communities for the three sites sampled. Water potentials of typical pineland (*P. elliottii* and *M. cerifera*) and hammock (*Q. virginiana* and *E. axillaris*) species were considered together, but *Lysiloma latisiliqua* was considered separately to compare its responses in the two communities. Alphabetical superscripts indicate significant differences between samples at each site (*t*-test, $p \leq 0.05$)

Site	Pineland species (n=10)		*L. latisiliqua* (n=5)		Hammock species (n=10)		*L. latisiliqua* (n=5)	
	Wet	Wet–dry	Wet	Wet–dry	Wet	Wet–dry	Wet	Wet–dry
1	-0.59 ± 0.07	0.00 ± 0.05^{a}	-0.37 ± 0.05	0.36 ± 0.10^{b}	-0.39 ± 0.05	0.49 ± 0.12^{b}	$-0.68 \pm 0.05^{+}$	0.33 ± 0.09^{b}
2	-0.52 ± 0.04	0.08 ± 0.06^{d}	-0.70 ± 0.05	$0.16 \pm 0.09^{d,e}$	-0.48 ± 0.05	$0.33 \pm 0.10^{c,e}$	-0.66 ± 0.04	$0.15 \pm 0.05^{d,e}$
3	-0.54 ± 0.06	0.09 ± 0.07^{f}	-0.33 ± 0.04	0.59 ± 0.03^{g}	-0.41 ± 0.03	0.40 ± 0.04^{h}	-0.45 ± 0.03	$0.53 \pm 0.03^{g,h}$

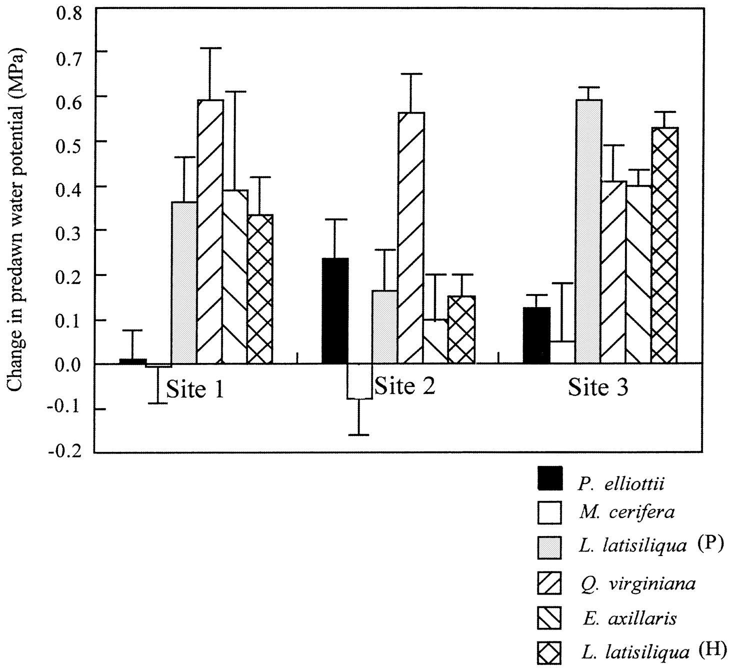

Fig. 3. Average change in PDWP between wet and dry season (±SEM) for individual plant species at all three sites sampled. *Lysiloma latisiliqua* in both communities are indicated as: (P) for pinelands and (H) for hammocks.

Table 4

Average δD and δ^{18}O values (±SEM) of soil and groundwater from each site. Five soil samples were collected from each community but only one groundwater sample was obtained each sample period. The asterisks (*) indicate significance at the 0.05 level using *t*-test pair-wise comparisons of soil water against groundwater

	Wet season		Dry season	
	δD	δ^{18}O	δD	δ^{18}O
Site 1				
Soil water				
Pineland	−15.0±2.6	−1.82±0.39	−9.4±3.2	+1.80±0.52 *
Hammock	−11.3±2.5	−2.74±0.43	−10.6±1.8	+0.50±0.49
Groundwater	−22.5	−2.16	−15.5	−2.10
Site 2				
Soil water				
Pineland	−15.5±2.2	−0.68±0.47	−6.0±0.5 *	+1.74±0.17 *
Hammock	−16.4±4.0	−1.55±0.07 *	−7.3±2.0	+0.95±0.21 *
Groundwater	−18.8	−2.43	−16.3	−2.45
Site 3				
Soil water				
Pineland	−12.6±3.8	−2.15±0.52	−13.6±3.8	−0.85±0.26
Hammock	−7.8±1.8	−1.65±0.24	−4.8±1.8	+0.25±0.38
Groundwater	−17.4	−1.34	−5.0	−0.08

The δD values of site 2 pineland groundwater was also significantly lower than that of soil water values. These isotopic differences between potential water sources provide a basis for determining the source of plant water uptake by analyzing plant stem water.

The δ^{18}O and δD values of plant stem water for pineland and hammock species, excluding *L. latisiliqua*, compared with that of water sources are shown in Figs. 4 and 5. Only sites with a significant difference in isotopic composition between soil water and groundwater for at least one community at a particular season (Table 4) are shown. The average δ^{18}O value of stem water for hammock species in site 2 during the wet season is similar to soil water, whereas pineland species have stem water with δ^{18}O values closer to groundwater (Fig. 4). The δ^{18}O values of stem water for pineland and hammock species for sites 1 and 2 during the dry season are similar to that of groundwater. During the dry season both hammock and

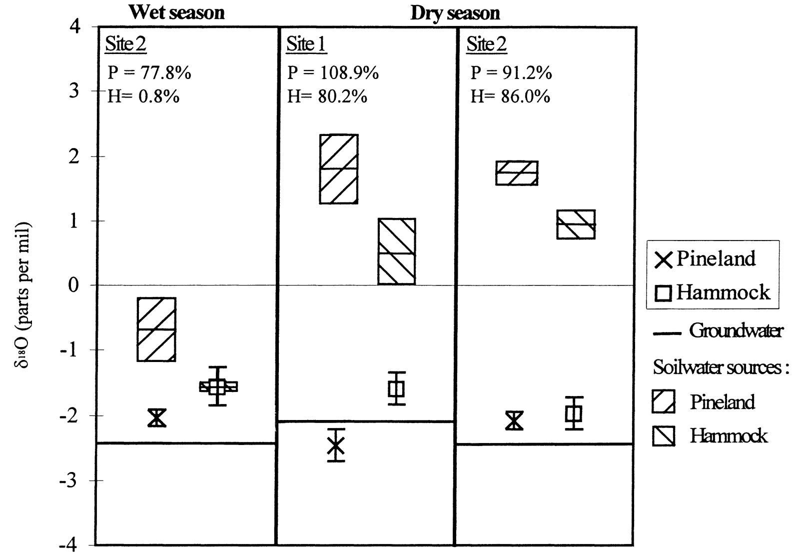

Fig. 4. δ^{18}O values of plant stem water and potential water sources. Also shown are calculated % groundwater utilization by pineland and hammock species.

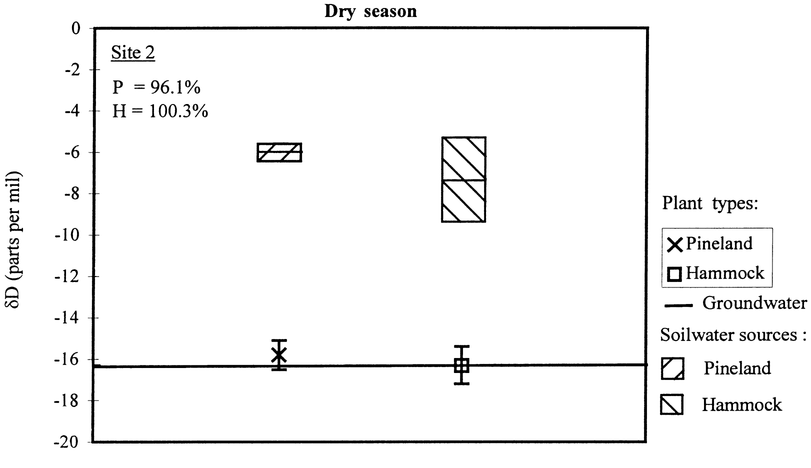

Fig. 5. δD values of plant stem water and potential water sources at site 2 for both wet and dry seasons.

pineland species at site 2 have stem water δD values close to that of groundwater (Fig. 5). Groundwater utilization by pineland species was high in both wet and dry seasons but groundwater comprised only a small proportion of the water used by hammock species in the wet season.

4. Discussion

The greater decrease of predawn water potential during the dry season in hammock plants compared to pineland plants (Fig. 3, Table 3) is consistent with our hypothesis that hammock species may be more dependent on soil water than pineland species. During the dry season hammock plants are likely to be exposed to a greater degree of water stress in response to the drying of the soil water source (Fig. 2). *Lysiloma latisiliqua* which is found in both pinelands and hammocks, showed predawn water potential shifts from wet to dry season that were similar to hammock species (Fig. 3, Table 3). This species is often one of the first hardwood trees to colonize pinelands (Tomlinson, 1980). Its colonizing ability may in part be aided by its capacity to utilize a soil water source that is not exploited by groundwater-dependent pineland species.

Water potential of *L. latisiliqua* and *E. axillaris* during the dry season did not decrease at the site where the water table was deepest (site 2) to the extent observed at sites 1 and 3 where the water table was shallower (Fig. 3). We can think of two explanations for this paradoxical observation. First, a week before our sampling, there was an isolated rainfall event 0.7 cm recorded in site 2; this event could have increased soil moisture within the hammocks. Second, because the water table is deepest at this site, it may allow plants to extend their roots deeper so that the available soil moisture reservoir during the dry season at this site may be greater than the other two sites. We also note that the organic content of soil was significantly greater in the hammock of site 2 compared to the other two sites (Table 1).

The interpretation of isotopic ratios of plant stem water and their potential sources was limited to those isotopes, sites and season where there was a significant difference between isotopic composition of soil water and groundwater (Table 4). In these instances, our results indicate either a higher proportion of groundwater utilization by pineland species or an equally high utilization of groundwater by both pineland and hammock species as shown in Figs. 4 and 5. Unlike the results of Ish-Shalom et al. (1992) for the Florida Keys, mainland hammock plants are able to utilize a substantial amount of groundwater at the end of the dry season. These observations are reflected in our calculation of percentage groundwater utilization by hammock and pineland species shown in Figs. 4 and 5. The $\delta^{18}O$ signatures of pineland species indicate between 78 and 100% groundwater utilization while hammock species vary from 0.8% during the wet season to 86% during the dry season (Fig. 4). Access to deeper groundwater by hammock species during the dry season may, however, not be sufficient to maintain high predawn water potential observed during the wet season. We hypothesize that the lower predawn water potential of the hammock species during the dry season could reflect the balance between obtaining water from deeper groundwater sources and the drying of water sources in the unsaturated soil zone.

5. Conclusion

Taken in conjunction with studies by Ross et al. (1993) and Ish-Shalom et al. (1992), this study demonstrates that woody plants within southern Florida's plant communities can utilize different sources of water. Predawn water potential and stable isotope ratios of plant water indicated that the pineland species shifted their water use source less than hammock species. Plants within hammocks were evidently exposed to greater water stress because of their dependence on more variable soil moisture sources. *Lysiloma latisiliqua* which was found in both communities responded similarly in both the pineland and hammock. The greater dependence on groundwater in pineland species differentiated them from hammock species that shifted water utilization from soil water during the wet season to groundwater during the dry season. The ability of hammock species to access groundwater is not as efficient as pineland species as evidenced by the lowering of predawn water potentials during the dry season.

Drainage and water diversion in the Everglades may indirectly affect the woody species evaluated here.

These influences are likely to be more profound in the groundwater-dependent pinelands due to the potential for regional water table declines. Although seasonal variation in moisture availability is likely to be greater for hammock species, the ability to utilize soil water may buffer hammock trees from anthropogenic hydrological manipulations to some degree. However, the combination of groundwater decline with drought affecting hammock soil moisture could be particularly deleterious for hammock hardwood species.

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