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Water utilization of tropical hardwood hammocks of the Lower Florida Keys

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Summary. Predawn water potential of representative plant species, together with stable isotope composition of stem water and potential water sources were investigated in four low-elevation tropical hardwood hammocks in the Lower Florida Keys, during a one year period. Hammock species had the lowest water potentials when soil water content was low and/or soil salinity was high, but differences in groundwater salinity had no effect on the water potential. Comparison of D/H ratio of plant stem water with soil and ground water corroborates the conclusion that they are primarily utilizing soil water and not groundwater. Thus, tropical hardwood hammocks are buffered from saline groundwater, and are able to thrive in areas where groundwater salinity is as high as 25‰. The effect of sea level rise on these forests may depend more on changes in the frequency of tidal inundation of the soil surface than on changes in groundwater salinity.

Key words: Tropical hardwood hammock – Salinity – Stable isotope ratio – Water relations – Groundwater

Tropical hardwood hammocks are the climax community of some coastal upland areas in South Florida (Craighead 1984; Snyder et al. 1990). Their flora is largely West Indian, and it is closely related to the flora of the Caribbean region of tropical America, namely the islands of Cuba, Hispaniola, Jamaica, Puerto Rico and the Bahamas (Long and Lakela 1969; Long 1974; Alexander and Crook 1984). Tropical hammocks are generally small assemblages dominated by broad-leaf tree species, often associated with palms and upland extensions of the adjacent salt tolerant communities of mangroves and buttonwood. In the Florida Keys several water sources are potentially available for the hardwood hammock plants: fresh to brackish groundwater (these water bodies are floating on salt water, and considered as Ghyben-Hertzberg lenses; Cant and Weech 1986), soil water, and ocean water. Knowledge on the water sources used by coastal hardwood hammocks in South Florida should prove valuable, since the sea level in this area has been rising in the past century (Hicks et al. 1983), causing salt water intrusion, and possible changes in the coastal plant communities (Ross et al. 1991; O'Brien et al. 1991).

Preliminary results (Sternberg et al. 1991) indicated that hardwood hammock plants in Sugarloaf Key (Monroe County, Florida, USA) might be buffered from high-salinity groundwater. It was not known whether this buffering occurs throughout the year, since this was observed for only one sampling date, nor was it known whether this buffering could be generalized for other hammocks. Further, it was hypothesized that soil water having a lower salinity may be responsible for this buffering.

The aim of this study was to answer the above questions. This was done by measuring and comparing plant predawn water potential throughout the year for two low-salinity hammocks (groundwater salinity of up to 5 ppt), and two high-salinity hammocks (groundwater salinity of 15–25 ppt). We tested the hypothesis that soil water is the freshwater source for hammock plants by measuring salinities of soil water and groundwater, as well as the soil water content throughout the year. We also took advantage of previous observations that soil water has a different isotopic composition than that of groundwater (Sternberg et al. 1991). Thus, it was possible to use stable isotope analysis of plant stem water to trace their source of water (Sternberg and Swart 1987; Sternberg et al. 1991; White et al. 1985; Dawson and Ehleringer 1991).

Materials and methods

Sites description

Four study sites were chosen in the Key Deer National Wildlife Refuge, Lower Florida Keys (Monroe County), Florida, U.S.A., two in Sugarloaf Key (24°41′N, 81°33′W) and two in Big Pine Key (24°42′N, 81°25′W). In each site a well was drilled as previously

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described (Sternberg et al. 1991), to allow sampling of groundwater. In each key, one of the sites was a low-salinity hammock, and the other a high-salinity hammock, based on groundwater salinity. No significant differences in the composition of the plant communities were found between the four sites (Ross, personal observations).

The low salinity hammock in Sugarloaf Key (SLLS) is a mature forest at an elevation of approximately 1.1 m above mean sea level, with large trees and a dense understory, indicating conditions favourable to hardwood hammock development. The high salinity hammock in Sugarloaf Key (SLHS) is about 0.7 m above mean sea level, and the forest canopy is lower and less developed. Both the high- and low-salinity hammocks on Sugarloaf Key grade into buttonwood and scrub mangrove associations. Both the high- and low-salinity hammocks on Big Pine Key (BPHS and BPLS, respectively) are located along the west side of the island, surrounded by pinelands, and both are at elevation of about 0.7 m above sea level. BPLS has taller canopy, while BPHS is a lower, more open forest. The shallow water table in all four sites varies in depth and salinity seasonally, and even over a single tidal cycle, but is always within one meter of the soil surface.

Soils of the lower Florida Keys are young limerock-influenced Entisols, originated from the weathering Miami Oolite bedrock (Brown et al. 1990), or carbonated marls of marine origin which were transported inland by hurricanes and tropical storms. Soils of the hammock sites were described as Saddlebunch marls for Sugarloaf Key sites, and Cudjoe marls for Big Pine Key, both lack developed profile (Brown et al. 1990). Burt (1989) reported low organic matter content in those soils (1–5%), but our sites had higher organic matter content: (30.99 ± 13.55%). In all four sites the entisol (called bottom layer in our study) is covered with an organic soil layer (66.17 ± 6.61% organic matter content), called top soil layer.

Water potential measurements

In each site, trees of *Eugenia foetida* Pers. (spanish stopper), *Guapira discolor* (K. Spreng.) Little (blolly) and *Coccoloba diversifolia* Jack. (pigeon plum) were selected and tagged. Predawn (3:00 am–6:00 am) stem water potentials of small branches (2 to 3 mm diameter, 10–15 cm long) of 3–4 trees from each of the selected species in each site were measured eight times, four during the November–April dry season (Dec. 6, 1990; Jan. 22, 1991; Mar. 15, 1991; Apr. 30, 1991), and four during the May–October wet season (Oct. 18, 1990; Jun. 18, 1991; Jul. 30, 1991; Sept. 20, 1991). A Scholander pressure bomb (PMS, model 600) was used for all measurements.

Soil measurements

Soil samples were taken-from the top (0–10 cm depth) and bottom (20–30 cm depth) layers of sites SLHS, BPLS and BKBS. The bottom layer of SLLS was very shallow and discontinuous, and was not sampled. Soil samples were taken at the same eight dates that stem water potential was measured. In each site, five random samples were taken from each soil layer and sealed in metal boxes. Samples were weighted and oven-dried at 85° C for 48 h, and weighted again. Water content was calculated relative to the dry weight of the soil. Salinity measurements of sub-samples of 1 g of oven-dried soil were done, using a Conductivity Meter (Jenway PCM3, Felsted, Gt. Dunmow, Essex, UK). The rest of the sample was oxidized at 360° C over-night, the ash content weighted, and the organic matter content calculated.

Groundwater and rainfall data

Groundwater salinity was determined in all eight dates of the water potential measurements by sampling well water and measuring their salinity with a conductivity meter. Rainfall was measured by daily inspection of precipitation gauges located adjacent to the sites on both Sugarloaf Key and Big Pine Key.

Stable isotope analysis

Three to four stem samples from each of the selected species were collected four times during the year (Oct. 18, 1990; Jan. 22, 1991; Apr. 30, 1991; Jul. 30, 1991) for isotopic analysis, as previously described (Sternberg and Swart 1987). Water from soil samples was distiled by the same method as plant water. Soil samples and groundwater for isotopic analysis were collected at the same dates as the stem samples. Hydrogen isotopic analysis was done as previously described (Sternberg et al. 1991). Hydrogen isotopic ratios are expressed in δ units using SMOW as the standard. The precision of analysis was ±1‰ (S.D.).

Results

The average monthly rainfall, soil water content, soil salinity, and predawn plant water potential for each site during the dry (Nov.–Apr.) and wet (May.–Oct.) season for the four sites, are shown in Table 1. The two seasons had significantly different average monthly rainfall, as previously reported for Key West (Chen and Gerber 1990). Soil water content did not show a seasonal change, while soil salinity showed a seasonal effect for only some of the study sites (soil salinity of SLLS top soil layer, and SLHS top and bottom layer at the dry season were significantly higher than those of the wet season). High soil water content, as found in the soils for some of the sampling dates, are common in soils with a high organic matter content. Predawn plant water potential showed a strong seasonal effect, with dry-season values significantly lower than those of the wet-season. Between-site differences in predawn water potential were not significant ($p > 0.05$), with the exception of SLHS dry-season values being significant lower than the dry-season values of all the other sites ($p < 0.05$).

Plant predawn water potential and soil water content were negatively correlated with number of dry days (rainfall < 5mm) between the sampling date and the last previous rain (rainfall > 5mm, Fig. 1A and B).

Plant predawn water potential was uncorrelated with the salinity of the groundwater (Fig. 2A), but was significantly correlated with the top soil water content during the time of sampling (Fig. 2B). The relationship between plant predawn water potential and top soil water content is best described by a logarithmic relation, where changes in water content of dry soils will have a greater effect on predawn water potential than equivalent changes in wet soils. There was no correlation between plant predawn water potential and water content of bottom soil layer ($r^2 = 0.138$, $P > 0.1$). This is easily understood, as most of the root system of these plants is known to be in the top soil layer (personal observations).

The average δD values and salinities of the groundwater during the study period, in order from nearly freshwater (SLLS and BPLS) through approximately one third sea water salinity (SLHS) to two third sea water salinity (BPHS) are shown in Table 2. The average δD

Table 1. Seasonal changes in environmental parameters and plant water potentials of tropical hardwood hammocks of the Lower Florida Keys

	Dry Season Nov–Apr	Wet Season May–Oct
Monthly Rainfall (mm)		
Sugarloaf Key	56.0±13.6[b]	168.6±39.3[a]
Big Pine Key	55.3±11.9[b]	169.1±51.9[a]
Well Salinity (ppt)		
SLLS	4.1± 0.9[a]	1.7± 0.6[a]
SLHS	13.4± 0.7[a]	11.9± 1.1[a]
BPLS	3.1± 0.6[a]	1.3± 0.4[a]
BPHS	23.0± 1.2[a]	21.3± 0.5[a]
Soil Salinity (ppt)		
SLLS-Top Soil	2.3± 0.8[a]	0.4± 0.1[b]
SLHS-Top Soil	3.3± 1.0[a]	0.3± 0.1[b]
SLHS-Bot Soil	1.2± 0.1[a]	0.6± 0.2[b]
BPLS-Top Soil	4.1± 2.2[a]	1.5± 1.1[a]
BPLS-Bot Soil	1.9± 0.8[a]	1.1± 0.7[a]
BPHS-Top Soil	4.1± 1.8[a]	1.5± 0.8[a]
BPHS-Bot Soil	2.5± 0.8[a]	1.6± 0.5[a]
Soil Water content (% of dry weight)		
SLLS-Top Soil	87.1±14.4[a]	102.3±17.7[a]
SLHS-Top Soil	112.7±17.7[a]	137.5±21.9[a]
SLHS-Bot Soil	125.5±11.4[a]	121.7±13.3[a]
BPLS-Top Soil	98.1±23.7[a]	113.7±32.8[a]
BPLS-Bot Soil	104.3±22.6[a]	83.4±23.8[a]
BPHS-Top Soil	108.5±22.5[a]	85.6±24.8[a]
BPHS-Bot Soil	72.7± 8.8[a]	63.2±12.7[a]
Plant Water Potential (MPa)		
SLLS	−0.70±0.04[b]	−0.42±0.04[a]
SLHS	−1.00±0.07[b]	−0.36±0.03[a]
BPLS	−0.74±0.14[b]	−0.43±0.07[a]
BPHS	−0.69±0.05[b]	−0.52±0.05[a]

SLLS = Sugarloaf Key low-salinity hammock, SLHS = Sugarloaf Key high-salinity hammock, BPLS = Big Pine Key low-salinity hammock, BPHS = Big Pine Key high-salinity hammock
Monthly rainfall is a mean of the six months of each season; Well salinity is a mean of four sampling dates in each season; Soil salinity is a mean of four sampling dates in the dry season and three sampling dates in the wet season, five replication in each date; Soil water content is a mean of four sampling dates in each season, five replicates in each date, Water potential is a mean of four sampling dates in each season, 9–12 trees in each date
Means of the same parameter in two different seasons with the same letter are not significantely different (T-Test, $p<0.05$)
Means are given with ± SEM

value for the two low-salinity sites was −14.2‰, probably representing the average δD value of rainfall during the period of this study. The concomitant increase in δD values with salinity indicates that the salinity of the groundwater is determined by a mixing between the deuterium depleted freshwater and the deuterium enriched ocean water. δD values of soil water were not correlated with the δD values of groundwater ($r^2=0.00$, $p>0.05$ for top soil layer; $r^2=0.22$, $p>0.05$ for bottom soil layer). Thus, after rain recharges these two water pools, the factors responsible for their change in isotopic composition are probably independent of each other. δD

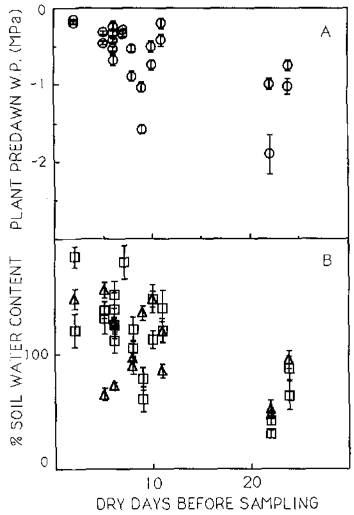

Fig. 1A, B. Plant predawn water potential (Fig. 1A), soil water content (**B**) versus the number of dry days, (< 5 mm of rain), between sampling date and last rain (> 5 mm of rain). Triangles and squares in **B** are for values of bottom soil layer and top soil layer, respectively. Correlations between plant predawn water potential, water content in top and bottom soil layers, versus number of dry days were all highly significant ($r^2=0.378$ for plant predawn water potential; $r^2=0.53$ and 0.30 for soil water content of top and bottom soil layers, respectively; $p<0.01$ for all correlations)

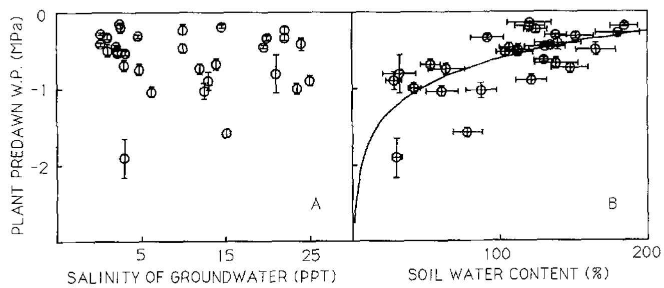

Fig. 2A, B. Average plant predawn water potential versus salinity of groundwater (**A**) and soil water content (**B**). Correlation between plant predawn water potential versus salinity of groundwater was not significant ($r^2=0.01$, $p>0.05$), whereas the correlation between plant predawn water potential and soil water content was highly significant ($r^2=0.46$, $p<0.01$, $y=-2.97+1.76 \log x$)

Table 2. Average δD values and salinity of well waters (±SEM) during the study period

Sites	δD‰	Salinity‰
SLLS and BPLS	−14.2±2.1	2.6±0.6
SLHS	−7.9±2.1	11.6±1.0
BPHS	−4.8±2.0	22.9±0.9

values of water from the top soil layer were highly correlated with those of the bottom soil layer (Fig. 3). δD values of plant stem water were not correlated with those of the groundwaters (Fig. 4A), but were highly correlated with δD values of top soil water at the time of sampling (Fig. 4B), as well as the water from the bottom soil layer (not shown, $r^2=0.63$, $P<0.05$).

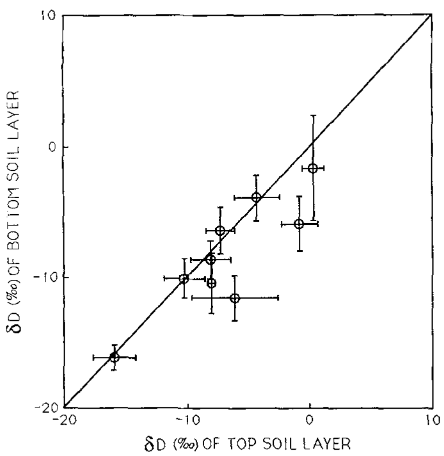

Fig. 3. δD of bottom soil water versus δD of top soil water. Correlation was highly significant and approached that of a one to one relationship ($r^2=0.77$, $p<0.01$)

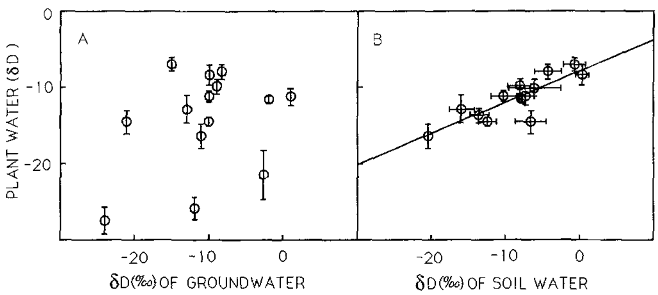

Fig. 4A, B. δD of plant stem water versus δD of groundwater (**A**) and soil water (**B**). Relationship between δD of plant stem water and well water was not significant ($r^2=0.11$, $p>0.05$), but the correlation between δD of plant stem water and δD values of water from top soil layer was highly significant ($r^2=0.71$, $p<0.01$, $y = -7.91+0.41x$)

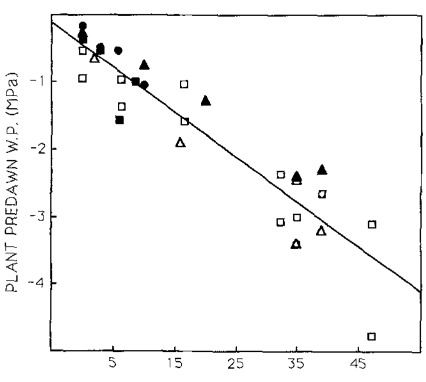

Fig. 5. Predawn water potentials of different plant species exposed to water having different salinities. The relationship was highly significant (W.P. = −0.45–0.07 *Salinity, $r^2=0.86$). □ Avicennia germinans, ▲ *Conocarpus erectus*, △ *Rhizophora mangle*, ● *Coccoloba diversifolia*, ■ *Pinus elliottii*, ○ *Laguncularia recemosa*

Discussion

Soil water content seems to be determined by the number of dry days between sampling date and the previous rain, rather than season (Fig. 1B). Although rainfall during the wet season was greater than that during the dry season, there was no seasonal effect on the soil water content of all sites (Table 1). At Sugarloaf Key sites, the soil salinity values showed a significant seasonal effect that was not observed in Big Pine Key sites (Table 1).

Hydrogen isotopic composition of both top and bottom soil layers was not correlated with that of the groundwater. We propose that after rain recharges soil and groundwater, their waters become isotopically enriched by two different and independent processes. The water in the soil layer will become deuterium enriched because of evaporation, whereas the groundwater will become progressively enriched because of mixing with deuterium enriched ocean water. The lack of correlation between isotopic composition of soil water and groundwater also indicates that these two water pools are independent of each other, and thus soil water of these hammocks does not appear to be recharged by groundwater, but by rain water. No significant differences were observed between δD values of top and bottom soil layers for most sampling dates and the relationship between isotopic composition of water from the top and bottom soil layer approaches a one to one relationship (Fig. 3). Thus δD values of top soil layer are representative of δD values of water throughout the whole soil profile, and will be used hereafter as such. In a few cases the top soil layer was somewhat more deuterium enriched than the bottom soil layer. This was expected, because evaporative processes cause isotopic enrichment of the top soil layer more readily than the bottom soil layer.

Predawn plant water potential showed a seasonal effect in all sites (Table 1), and it is not related to the salinity of the underlying water table (Fig. 2A). Salinities of the groundwater were as high as 25‰, and yet plant predawn water potentials were unaffected. It is unlikely that hardwood hammock species can take up high salinity water without lowering their water potential. Greenhouse experiments revealed a direct and highly significant relationship between plant predawn water potential and salinity of the culture solution (Fig. 5). According to these experiments, plants exposed to groundwater having salinities of 25‰ should have a predawn water potential of about −2.0 MPa. Clearly this is not the case in the field (Fig. 2A). One question that immediately comes to mind is: what determines the predawn water potential for these hammock plants? Fig. 2B shows that the soil water content is an important parameter determining plant water potential. This relationship is best approximated by a logarithmic function. Although the relationship between plant predawn water potential and soil water content is complex and may involve several factors, the concurrent increase in salinity with a decrease in matric potential may be the principal factor for the relationship observed here. For the case of wet soils, an increase in soil water content for plants having a predawn water potential of −0.5 MPa or above, will not have any further effect in increasing plant predawn water potential. This is supported by our observations that −0.5 MPa was the average predawn water potential of plants growing hydroponically in freshwater (Fig. 5). Secondly, for dry soils, in addition to decreasing soil matric potential, soil desiccation will also increase the salinity of the remaining soil solution, which in turn, may cause a further decrease in plant predawn water potential. Thus, the lowest average predawn water potential of −1.9 MPa observed during our study (Fig. 2B), occurred not only when soil water content was at its lowest, but also when the salinity was at its highest.

Our results indicate that the predawn water potential of hammock plants of the Lower Florida Keys is related to the soil water content (Fig. 2B), but not to the salinity of the groundwater (Fig. 2A). Consistent with these findings, our stable isotope measurements of plant and groundwater show that groundwater is only a minor component of the plant water. Fig. 4A shows a nonsignificant correlation between isotopic composition of plant water and groundwater, whereas the correlation between isotopic composition of plant water and that of top soil water was highly significant (Fig. 4B). The slope of the linear regression between δD values of plant water and soil water is 0.41 (Fig. 4), indicating that soil water at the time of sampling on the average contributed 41% to the plant water. The source of the other 59% of plant water can probably be accounted by absorption of rain water through surface roots. During most of this study, rainfall occurred at most 10 days before the sampling dates.

Our isotopic data on plant water corroborates our finding on predawn plant water potential. Plants are utilizing water mostly from soil, whereas groundwater contributes a relatively minor component to the plant water. However, it is possible that during severe drought periods, groundwater may contribute significantly to plant water, and there is a need to determine whether during such droughts uptake of groundwater by hammock plants will continue to be minimized. Our study shows that high rainfall and water storage in the soil layer may buffer hammock species against salinity increase in the groundwater, by providing low-salinity water for plant uptake. The results of this research have important implications in predicting vegetation changes in coastal regions where sea level is rising, not only for the Lower Florida Keys, but for all the Caribbean region that experience a similar sea level rise with possible effects on groundwater and soil water. There is a need to investigate whether other freshwater coastal communities have this buffering capacity as well.

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