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UTILIZATION OF SURFACE WATER BY RED MANGROVE (*RHIZOPHORA MANGLE* L.): AN ISOTOPIC STUDY

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ABSTRACT

Physiological responses of mangroves to salinity changes in the field are difficult to quantify, partly because it is still not clear whether mangroves utilize mostly surface water, as believed by many researchers based on the shallow distribution of mangrove roots in anaerobic soils. To test this axiom, we analyzed oxygen isotope ratios of possible water sources in different soil layers and stem water from red mangroves (*Rhizophora mangle* L.), a dominant mangrove species in Florida, which occurs frequently in two distinct growth forms: dwarf and tall mangroves. $\delta^{18}O$ values of stem water from both dwarf and tall mangroves always matched those of surface water, indicating that they utilize mostly the surface water. Consistently, most fine roots (about 70%) of dwarf mangroves occur in this upper soil layer. $\delta^{18}O$ values of stem water from both dwarf and tall mangroves showed significant changes from the dry season (high values) to the wet season (low values), corresponding to the isotopic and salinity variation in surface water during this period. Fine root biomass also showed a significant increase in the wet season as response to the decrease in salinity of soil surface water. Predawn water potentials decreased with increasing $\delta^{18}O$ values of stem water, while midday water potentials did not show such relationship. The dependence of mangroves on surface water as their sole water source has significant implications for plant water relations, and may explain growth form differentiation in some mangrove species of southern Florida.

The capacity to maintain favorable water relations along gradients of increasing salinity varies among different mangrove species (Ball, 1988). The responses of mangroves to such salinity gradients, however, are notoriously difficulty to quantify, not only because of spatial and temporal variation in soil salinity, but because the sources of water actually used by a plant may not reflect the entire body of water in the soil (Naidoo, 1985, 1989; Ball, 1988). Thus, it is still not clear whether mangroves utilize mainly surface water, as predicted from their shallow root distribution in anaerobic soils (Gill and Tomlinson, 1971, 1977; Hatchings and Saenger, 1987). Previous studies have demonstrated that in certain areas, mangrove species may shift their water sources from typical ocean water to rain-derived freshwater along tidal zones or between the dry season and the wet season (Sternberg and Swart, 1987; Lin and Sternberg, 1992a). The variation in salinity of water available for mangroves, resulting from the shift in water sources, may significantly affect plant water relations, photosynthesis and growth, and thus may control plant distribution along tidal gradients and growth form differentiation in mangroves (Sternberg and Swart, 1987; Lin and Sternberg, 1992a, 1992b).

Analysis of isotopic compositions of xylem sap water or stem water has been used to quantitatively determine the utilization of different water sources by both terrestrial and coastal plants (White et al., 1985; Sternberg and Swart, 1987; Ehleringer et al., 1991; Dawson and Ehleringer, 1991; Sternberg et al., 1991; Lin and Sternberg, 1992a). Such an approach is based on the observation that there are significant differences in isotopic composition between various water sources, and that there is no isotopic fractionation during water uptake (White et al., 1985; Sternberg and Swart, 1987). Isotopic analysis of stem water is the simplest possible technique to determine the utilization of freshwater and ocean water by coastal plants. Comparison of soil water salinity with that of stem water is not useful because some plants may exclude saline water by ceasing transpiration when

salinity rises and resuming transpiration when salinity decreases (Sternberg and Swart, 1987). Further, some plants may exclude salt when exposed to water with high salinity, as has been reported for *Rhizophora mangle* (Scholander et al., 1962; Teas, 1979).

Rhizophora mangle L. (red mangrove) is a dominant mangrove species in southern Florida, occurring frequently in two distinct growth forms, tall and dwarf (or scrub) mangroves (Lugo and Snedaker, 1974; Lin and Sternberg, 1992b). Our previous study demonstrated that the dwarf form of this species had a more pronounced shift in water source from ocean water to freshwater between different seasons than the tall form (Lin and Sternberg, 1992a). In this study, we analyzed oxygen isotope ratios of stem water from red mangroves and possible source waters in different layers of the soil profile, to test whether this mangrove species utilizes mainly surface water. We analyzed only for oxygen isotope ratios of stem water because it was previously shown that mangroves and other coastal halophytes may discriminate against deuterium during water uptake (Lin and Sternberg, 1992c). We also examined the root distribution pattern along the soil profile by measuring root biomass in soil cores. In addition, we measured predawn and midday water potentials as an indicator of the change in plant water status as well as surface water salinity.

Materials and Methods

Location and Description of Study Site.—The study site was located at Biscayne National Park, Monroe County, Florida, USA (25°28'N, 80°20'W). Within the park, one small area (about 1,000 m^2) of mangrove vegetation stand was chosen on the basis of its accessibility. The stand is best characterized as dwarf mangrove forest (Lugo and Snedaker, 1974; Lin and Sternberg, 1992b), which is dominated by small red mangroves (*Rhizophora mangle* L.) about 0.5 m to 1.5 m high, with a few dwarf white mangroves (*Laguncularia racemosa* (L.) Gaertn. f.) and black mangroves (*Avicennia germinans* (L.) Stern) scattered within the stand. The eastern edge of the stand is surrounded by fringe tall red mangrove forest along Biscayne Bay, while the western edge is flanked by the large C-111 canal which carries pure freshwater for irrigation purpose to local farms (Cole, 1989). The northern fringe is edged by a 10 m wide by 1 m deep mosquito-control ditch, probably constructed in the 1930's as part of a widespread mosquito control effort (R. Curry, 1991, pers. comm.), which runs eastward into Biscayne Bay. There are a few tall red mangrove trees growing along the edge of the mosquito control ditch, with the canopy height ranging from 4 m to 16 m. Soil surface water at the dwarf mangrove stand is recharged mostly by saline water from Biscayne Bay during the dry season, and both bay water and rain water during the wet season. The deepers of the soil profile are recharged mostly by freshwater from Canal C-111 through permeation. Thus, a typical salinity/depth profile develops with higher salinity on the surface and lower salinity in deeper layers of the soil profile (Cole, 1989).

Sampling of Source and Stem Waters.—At the study site, a 50 m long transect was set, which ran roughly parallel to the C-111 canal, and was about 50 m from the C-111 canal. On 4 May (the end of dry season), 7 July (the mid wet season) and 9 November (the end of wet season) of 1991, three soil sample cores about 150 cm long were taken at the two end points and the mid point of the transect, respectively, using a standard "push-coring" apparatus with an aluminium tubing of 200 cm in length and 6 cm in diameter. Cores were pushed as deeply as possible into the ground, in this case to about 150 cm. The cores were then sealed, and all of the cores were split and divided into 3 segments (0–50, 50–100, 100–150 cm) within 24 h in the laboratory. Water from a specific section of each core (0–5, 50–55, 100–105, 145–150 cm) was obtained by squeezing (Cole, 1989). Water samples were tested for salinity with a Reichert-Jung optical refractometer (salinometer), and then stored in sealed vials for isotopic analysis.

On the same sampling dates, freshwater from the C-111 canal (canal water), ocean water from Biscayne Bay (bay water) and water from the mosquito control ditch (ditch water) were collected and tested for salinity with five replicates, respectively, and then sealed in sample vials for isotopic analysis. Meanwhile, stem samples were collected from three dwarf red mangrove individuals around each of three soil cores along the transect and four tall red mangrove trees grown along the edge of the mosquito control ditch on each of the three different sampling dates for cryogenic distillation to obtain stem water for isotopic analysis as described previously (Sternberg and Swart, 1987; Lin and Sternberg, 1992a).

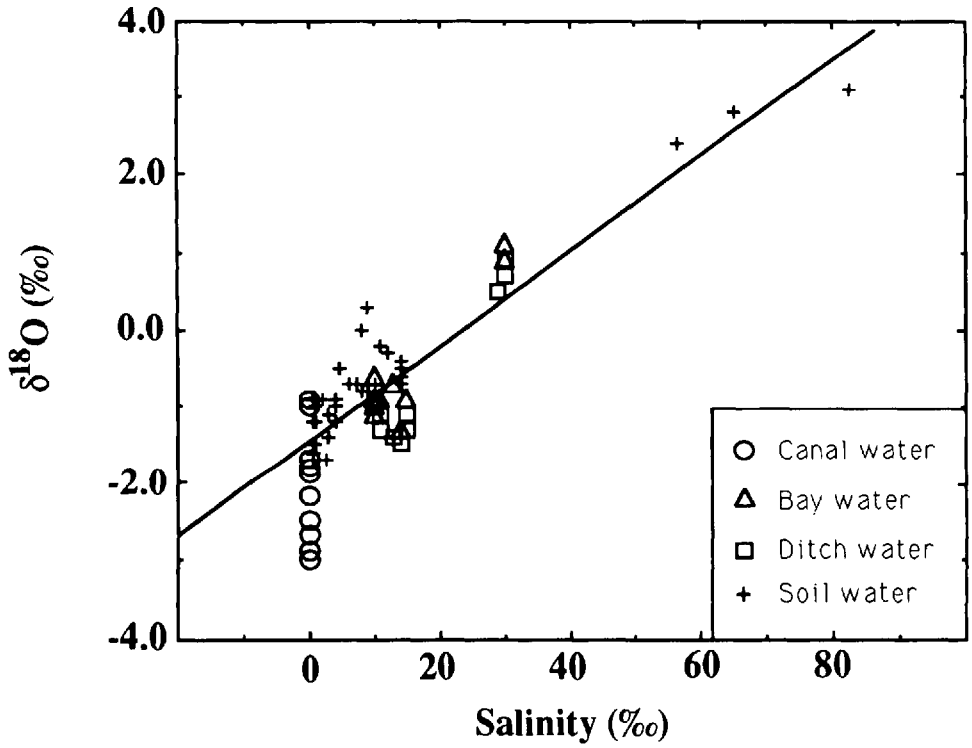

Figure 1. $\delta^{18}O$ values of canal water, bay water, ditch and soil water versus salinity ($\delta^{18}O$ (‰) = $-1.5254 + 0.0068$ Salinity (‰), $r^2 = 0.775$, $P < 0.001$). Symbols: O freshwater from C-111 Canal, △ ocean water from Biscayne Bay, □ ditch water from mosquito control ditch, + soil water in different layers.

Oxygen Isotope Analysis.—Oxygen isotope ratios of water samples were determined by equilibration with carbon dioxide as described by Epstein and Mayeda (1953). Oxygen isotope ratio is expressed in δ unit:

$$\delta^{18}O\ (‰) = (R_{sample}/R_{standard} - 1)\cdot 1{,}000$$

where R refers to the $^{18}O/^{16}O$ ratio of sample and standard, respectively, the standard was SMOW (Standard Mean Ocean Water, Sternberg and Swart, 1987). All isotopic analyses were performed in a VG PRISM isotope mass spectrometer.

Root Biomass Determination.—On two sampling dates (4 May and 7 July), soils from each core segment were washed with tap water, and root material was separated from other components, and divided into three categories, fine roots (<0.1 cm in diameter), small roots (diameter from 0.1 to 1.0 cm) and large roots (>1.0 cm in diameter). These root fractions were then dried in an oven at 105°C over 48 h to determine dry weight. Root biomass in each core segment was expressed as dry weight per unit of volume.

Water Potential Measurements.—On the above three sampling dates, both predawn and midday water potentials were determined on shoots from three individuals of both dwarf and tall *R. mangle*, respectively, with a PMS pressure chamber (Model 600, PMS Instrument Co., Corvallis, Oregon, USA). Predawn water potentials were measured between 4:30 am and 6:00 am, while midday water potentials were measured between 12:30 pm and 2:00 pm local time.

Results

There was a highly significant correlation between salinity and $\delta^{18}O$ value for all water sampled here (Fig. 1). When salinity of water increased from 0 to 80‰, oxygen isotope ratio changed from -3 to $+3$‰. Previous studies have shown

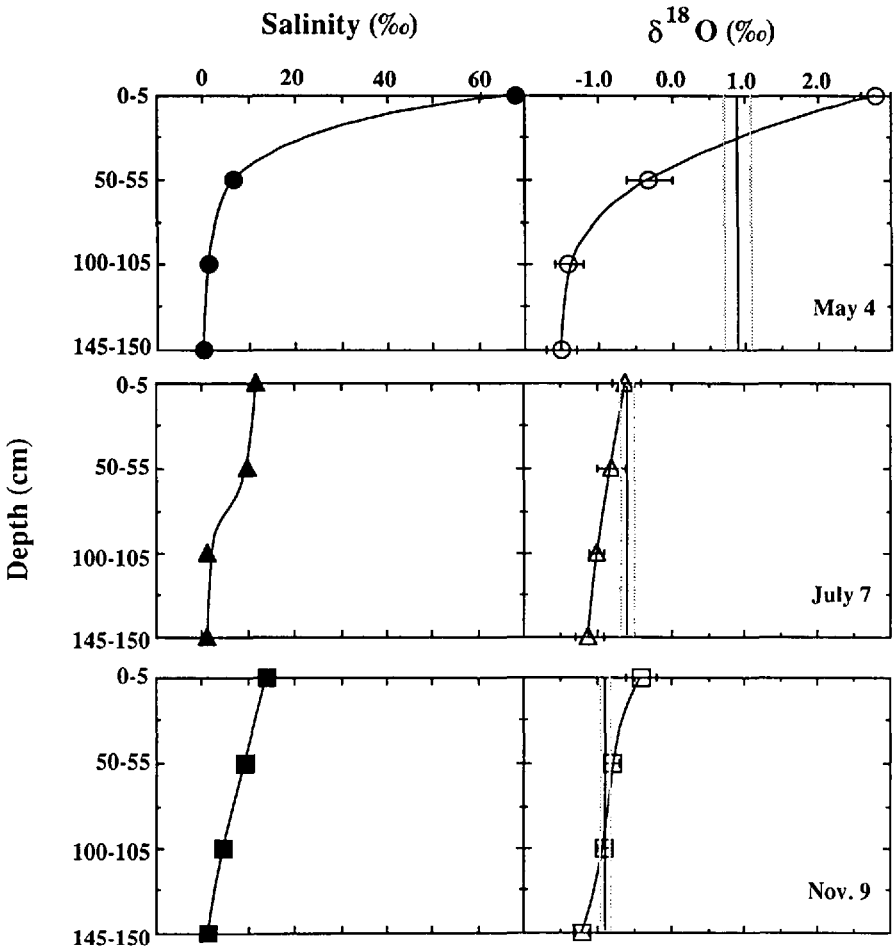

Figure 2. Changes in salinity and $\delta^{18}O$ values of soil water (symbols) with depth in a dwarf red mangrove stand and oxygen isotopic ratios of stem water (solid lines) from dwarf mangroves within the stand on three different sampling dates. Each symbol presents the mean of three measurements and standard errors. Each solid line represents a mean of nine measurements and dashed line represents the standard error.

that $\delta^{18}O$ values of ocean waters in south Florida ranged from +2 to +4‰, whereas freshwater had $\delta^{18}O$ ranging from −1 to −3‰ (Sternberg and Swart, 1987; Sternberg et al., 1991). The correlation between $\delta^{18}O$ value and salinity for the water sampled here is caused by the different proportions of these two water sources having distinct salinity and isotopic compositions.

In the dwarf mangrove forest, both salinity and $\delta^{18}O$ of soil water showed a significant depth profile, with the largest gradients in salinities and oxygen isotope ratios observed on 4 May, at the end of the dry season (Fig. 2). There was a good match between the salinity/depth profile and the $\delta^{18}O$/depth profile, suggesting again that oxygen isotope ratios reflect water salinity. Oxygen isotope ratios of stem water from dwarf red mangroves were between those of water at 0–5 cm and at 50–55 cm deep, especially on 4 May (Fig. 2), suggesting that dwarf mangroves uptake soil water in the upper layer (0–50 cm). $\delta^{18}O$ values of stem water collected on 4 May were much higher than those on the other two sampling dates,

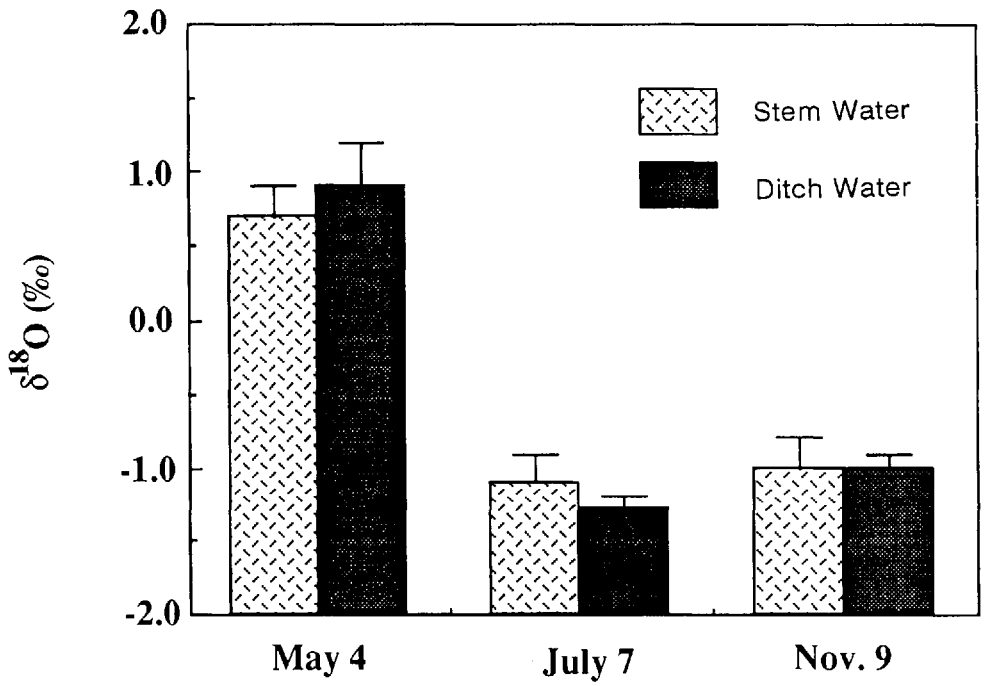

Figure 3. Comparison of oxygen isotope ratios ($\delta^{18}O$) between stem water of tall red mangroves (⊡) and water of mosquito control ditch (□) on three sampling dates. Error bars present standard errors of the measurements with four replicates. There were no significant differences in $\delta^{18}O$ values between stem water and ditch water on each of the three sampling dates ($P > 0.05$).

indicating the shift in uptake of water with a salinity of about 40‰ at the end of dry season to about 5–10‰ in the wet season (Fig. 2).

$\delta^{18}O$ values of stem water from tall *R. mangle* trees were not significantly different from those of ditch water on all three sampling dates (Fig. 3), indicating that tall trees utilize water in the mosquito control ditch. On 4 May, $\delta^{18}O$ values of stem water were higher than those on 7 July and 9 November, indicating a salinity change of water from about 30‰ at the end the dry season to about 15‰ in the wet season for plant water utilization.

Distribution of root biomass in the sample cores along depth showed that most roots of dwarf red mangroves were found in the upper layer of the soil profile from 0 to 50 cm deep (Fig. 4). About 70% of fine roots occurred in this layer in the sample cores collected on both 4 May and 7 July. In the second layer (50–100 cm), there were only 29 and 20% fine roots in the sample cores collected on 4 May and 7 July, respectively. The percentage of fine roots at the deeper soil layer (100–150 cm) was less than 10% for both sampling dates. Small and large root biomass was much less than that of fine roots found in the sample cores, and did not show a typical distribution pattern. Fine root biomass in the sample cores was much higher on 7 July than on 4 May (Fig. 4), indicating increased growth of fine roots when soil salinity decreases during the wet season.

There was a highly significant correlation between predawn water potentials and oxygen isotope ratios of stem water (Fig. 5a). Predawn water potentials decreased with increasing $\delta^{18}O$ values of stem water, corresponding to increase in salinity of water utilized by red mangroves. Midday water potentials, however, showed no such relation with oxygen isotope ratios of stem water (Fig. 5b).

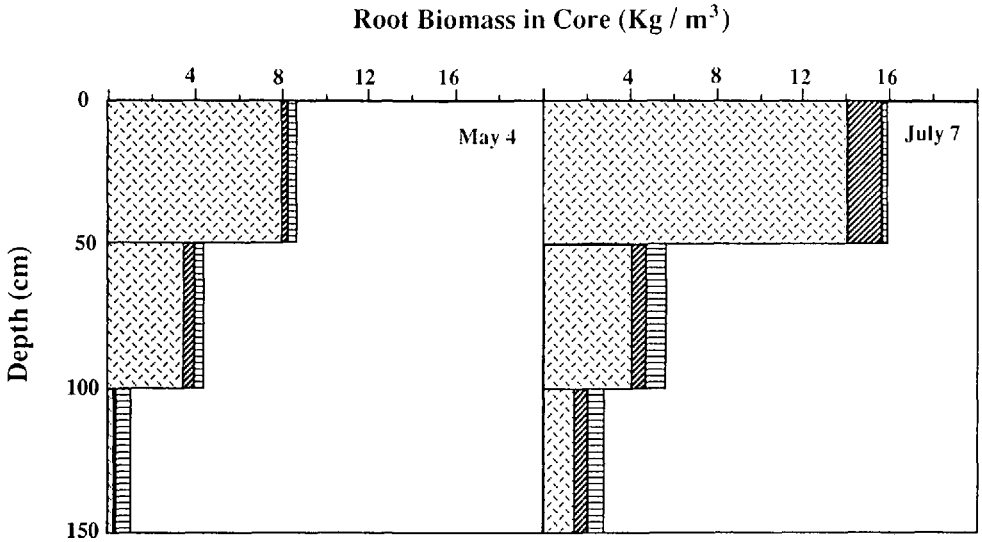

Figure 4. Distribution of root biomass in soil sample cores along depth in a dwarf red mangrove stand on two different sampling dates. Each value is the mean of three cores. Symbols: ☑ fine roots (<0.1 cm in diameter), ▨ small roots (diameter between 0.1 to 1.0 cm), ▤ large roots (>1.0 cm in diameter).

Discussion

Oxygen isotope ratios of stem water indicate that both dwarf and tall red mangroves utilize mostly surface water, even though groundwater may have a much lower salinity as was observed for the dwarf mangrove site (Figs. 2, 3). Consistent with surface water uptake, we observed a shallow distribution of roots

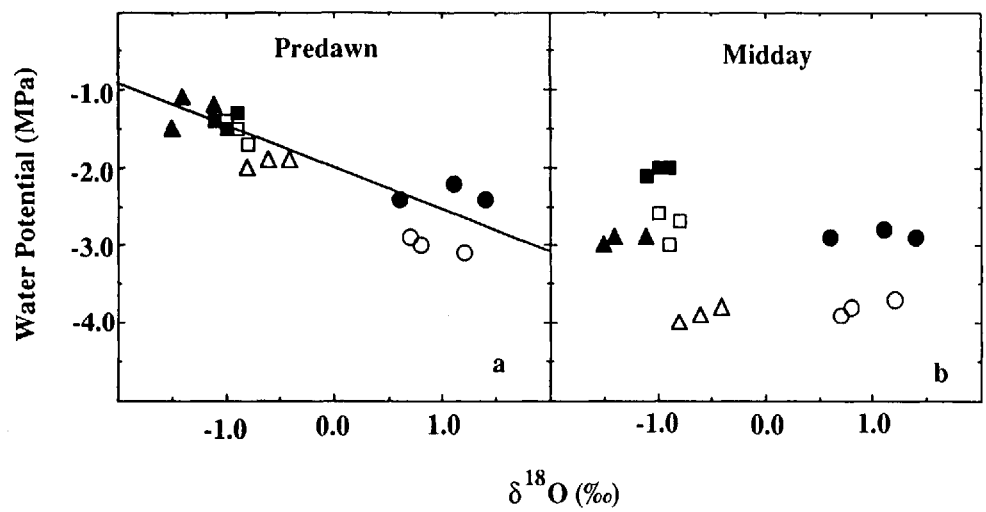

Figure 5. Relation between predawn (a) or midday (b) water potentials and $\delta^{18}O$ values of stem water from dwarf red mangroves (open symbols) and tall mangroves (closed symbols) on three different sampling dates (○●: 4 May; △▲: 7 July; □■ 9 November). Regression for predawn water potentials (WP) of both tall and dwarf mangroves: $WP = -2.08 - 0.56\ \delta^{18}O$; $r = 0.782$, $P < 0.01$.

for this species, as in the case of dwarf trees (Fig. 4). Mangroves usually have a shallow root system and lack a deep taproot (Gill and Tomlinson, 1971, 1977; Tomlinson, 1986). Some species, including the red mangrove studied here, have developed prop roots from the lower parts of the stem and drop roots from branches and upper parts of the stem that extend only a few centimeters into the soil (Odum and McIvor, 1990). For tall red mangroves studied here, newly grown fine roots of prop or drop root system are exposed to ditch water. Thus, their roots take up mostly ditch water, which is typical Biscayne Bay water with salinity of about 30‰ during the dry season (November to April in southern Florida), and about 15‰ during the wet season (May to October).

The dependence of mangroves on surface water at the study site may subject them to the stress resulting from salinity variation of available water, since surface water has higher variation in salinity due to seasonal differences in rainfall, tidal inundation and evaporation (Naidoo, 1989; Lin and Sternberg, 1992a). In southern Florida, about two thirds of the rainfall occurs during the wet season from May to October (Sternberg et al., 1991; Lin and Sternberg, 1992a). Due to the input of rain water, surface water during the wet season will be less saline than that during the dry season. This seasonal variation will be more significant in areas of higher elevation, since evaporation of ocean water on soil surface will cause hypersalinity. As a result, both tall and dwarf individuals of *R. mangle* in this study showed significant changes in oxygen isotope ratios of stem water from samples collected at the end of the dry season to samples collected in the wet season, with significantly higher changes in dwarf trees (Figs. 3, 4).

Such seasonal changes in salinity of water utilized by mangroves will significantly affect their water relations, photosynthesis and thus growth (Ball and Farquhar, 1984a, 1984b; Naidoo, 1985, 1989; Lin and Sternberg, 1992a). Our results indicate that predawn water potentials quickly respond to the changes in salinity of water used by mangroves, as reflected by the strong correlation between predawn water potentials and oxygen isotope ratios of stem water (Fig. 5a). Previous studies, however, demonstrated that plant predawn water potentials were not correlated with soil salinity or soil water potentials in mangroves (Naidoo, 1989) as well as in salt marshes (De Jong and Drake, 1981). This inconsistency between our results and those of previous studies suggests that special attention is needed to determine in which soil layer absorption of water occurs. Midday water potentials, on the other hand, did not correlate with $\delta^{18}O$ values of stem water (Fig. 5b). The reason for this pattern is unknown, but we speculate that mangroves at the study site may always have extremely low water potentials during midday regardless of the soil water salinity, as a result of adaptation to frequent changes in salinity of surface water.

The dependence of mangroves on surface water may be responsible for the growth form differentiation in mangroves at some locations in south Florida (Lin and Sternberg, 1992a, 1992b). Dwarf mangroves in southern Florida often occur in areas with higher elevation where salinity of surface soil water demonstrates considerable variation (as in this study from 82 to 10‰), while individuals of the same species always occur in tall form when grown in habitats with lower elevation such as fringe, riverine or basin locations with more constant salinity (Lugo and Snedaker, 1974; Lin and Sternberg, 1992a, 1992b, as in this study from 30 to 15‰). Although most mangroves are facultative halophytes and are able to grow in both freshwater and saline water, they might not maintain normal growth, and thus occur as a dwarf form, when growing in areas with hypersalinity or/and high variation in salinity. It has been observed that both hypersalinity and frequent changes in salinity can cause stress on plants, and thus reduce photosynthesis and

plant growth (Teas, 1979; Ball and Farquhar, 1984a, 1984b; Hatchings and Saenger, 1987; Lin and Sternberg, 1992d, 1992e).

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