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# Comparative study of water uptake and photosynthetic gas exchange between scrub and fringe red mangroves, *Rhizophora mangle* L.

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**Summary.** The red mangrove (*Rhizophora mangle* L.) occurs frequently in both scrub and fringe mangrove forests. Our previous study demonstrated that individuals of this mangrove species growing in scrub and fringe forests differ significantly in both morphological and physiological characteristics. To further characterize physiological differences between scrub and fringe mangroves, we compared their differences in water uptake and photosynthetic gas exchange during different seasons. In the wet season (June–October, 1990), scrub mangroves showed lower δD and $\delta^{18}O$ values of stem water than fringe mangroves, indicating more usage of rain-derived freshwater. In the dry season (Jan–April, 1991), however, scrub mangroves utilized the same water source as fringe mangroves, reflected by their similar δD and $\delta^{18}O$ values of stem water. Consistently, there were significant differences in predawn water potentials between scrub and fringe mangroves in the wet season (October 1990) with higher values for scrub mangroves, but no significant differences in the dry season (January 1991). Higher elevation in the scrub forest seems to be the major factor responsible for the shift of water sources in scrub mangroves. On Apr. 27 and Aug. 8, 1990, scrub mangroves showed lower $CO_2$ assimilation rate, stomatal conductance, and intercellular $CO_2$ concentration than fringe mangroves. There were no differences in these gas exchange characteristics on the other two measuring dates: Oct. 17, 1990 and Jan. 11, 1991. Instantaneous water use efficiency was significantly higher for scrub mangroves than for fringe mangroves on three of the four sampling dates. Similarly, leaf carbon isotope discrimination of scrub mangroves was always significantly lower than that of fringe mangroves, indicating higher long-term water use efficiency. Higher water use efficiency in scrub mangroves is a result of stomatal limitation on photosynthesis, which may entail considerable carbon cost to the plants.

**Key words:** Water uptake – Photosynthetic gas exchange – Stable isotope ratios – Water use efficiency – Scrub mangroves

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The red mangrove (*Rhizophora mangle* L.), a dominant species in mangrove swamps of Florida, occurs frequently in scrub or dwarf mangrove forests, in which individuals rarely exceed 1.5 meters in height (Lugo and Snedaker 1974; Lin and Sternberg 1992). Individuals of *R. mangle* in other mangrove forests (such as fringe forest, overwash forest, riverine forest, hammock forest and basin forest), however, can grow to trees with canopy height from several to over 30 meters at maturity (Lugo and Snedaker 1974). Our previous study showed that, based on a single date measurement (April 1990), *R. mangle* trees in the scrub forests had significantly lower $CO_2$ assimilation rate, stomatal conductance to water vapor, and intercellular $CO_2$ concentration, but higher water use efficiency (WUE) and leaf $\delta^{13}C$ values than those in the fringe forests (Lin and Sternberg 1992). In the present study, we further characterized physiological differences between scrub and fringe red mangroves by comparing their water uptake and photosynthetic gas exchange during different seasons.

Scrub mangroves frequently occur in the areas with higher elevation than fringe mangroves, we thus hypothesized that water uptake by scrub mangroves may shift from typical ocean water, during occasional high tides, to freshwater after heavy rainfall, while fringe mangroves utilize only ocean water. In this study, we took advantage of the fact that rain-derived freshwater and ocean water have different isotopic compositions to determine whether red mangroves in the scrub forest utilize rainfall water to a different extent than those in the fringe forest. Previous studies have shown that freshwater and ocean water in South Florida have different isotopic composition, with freshwater showing less deuterium and oxygen-18 enrichment than ocean water (Sternberg and Swart 1987; Swart et al. 1989; Sternberg et al. 1991). Isotopic composition of plant stem water can reflect stable isotope ratios of water available for plant uptake (White et al. 1985; Sternberg and Swart 1987). Thus, by analyzing the isotopic composition of stem water in different seasons, we can determine the relative uptake of freshwater and ocean water by mangroves. We also measured predawn water potentials of shoots as an indicator of changes of water salinity in the soil (Naidoo 1989; Sternberg et al. 1991). No direct measurements on soil salinity were made since soils were only heterogeneously distributed on the sediment surface in the scrub forest.

Because of seasonal variation in irradiance, temperature, rainfall as well as soil salinities, mangroves should demonstrate seasonal changes not only in their water relations (Naidoo 1989) but also in their photosynthetic gas exchange (Moore et al. 1973; Duke et al. 1984). Our previous study compared the difference in photosynthetic gas exchange on a single date between scrub and fringe mangroves. In this study, we compared the differences in photosynthetic gas exchange of red mangroves between the scrub and the fringe forests in different seasons. In addition, carbon isotope discrimination of newly grown leaves of *R. mangle* trees was also compared between the scrub and the fringe forests throughout the year to indicate the differences in their long-term water use efficiency (Farquhar et al. 1982; Hubick et al. 1986; Goldstein et al. 1989).

## Study site

Measurements were made at Sugarloaf Key, Monroe County, Florida, USA (24° 41′ N, 81° 33′ W). *R. mangle* trees in the fringe forest form a dense forest belt along the northwestern coast of the key, while scrub *R. mangle* trees occur in the area between the tall mangrove forest and inland hammock forest (Lin and Sternberg 1991). The soils at the study site are spatially heterogeneous, extremely shallow (rarely exceeding 15 cm in depth), predominantly organic by volume, and without significant profile development. Soils are formed directly on a limestone bedrock of Pleistocene age (Sternberg et al. 1991).

For the Florida Keys, annual rainfall over the period 1951–1980 averaged 1052 mm; mean yearly temperature was 25.3° C. Approximately two-thirds of the rainfall occurs during the wet season (May to October). Rainfall during the study period (January 1990 to March 1991) at the study site is shown in Fig. 1 (Ross and O'Brein, personal communication).

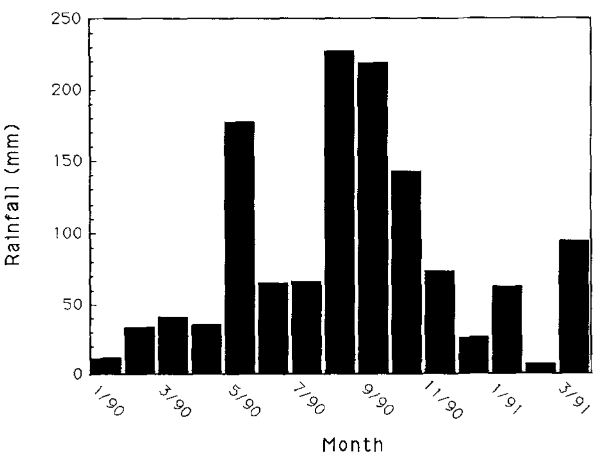


**Fig. 1.** Monthly changes in rainfall during the study period (from January 1990 to March 1991) at the study site. Rainfall pattern in this year is similar to the 30 year average (1951–1980) for the Florida Keys, with a wet season from May to October and a dry season from November to April, except that there was relatively lower rainfall in June and July 1990 at the study site

## Methods

### *Stem water isotope analyses*

Stem samples were collected from *R. mangle* trees in both the scrub and the fringe forests in the wet season (June to October, 1990) and the dry season (January to April, 1991). Plant water was extracted from stem samples as in Sternberg and Swart (1987). Hydrogen isotope ratio of stem water was determined by passing 2 to 4 μl of water through a hot uranium furnace (750° C) as described by Bigeleisen et al. (1952). Hydrogen released from this reaction was collected with a Toepler pump and used for isotopic analysis. Oxygen isotope ratios were determined by equilibration with carbon dioxide as described by Epstein and Mayeda (1953). Hydrogen and oxygen isotope ratios were reported in $\delta$ units relative to SMOW (Standard Mean Ocean Water).

### *Water potential measurements*

Predawn water potentials of shoots were measured for *R. mangle* trees in the scrub and fringe forests respectively on Oct. 17 1990 and Jan. 11 1991 with a pressure chamber (Model 600, PMS Instrument CO., Corvallis, Oregon, USA). All water potentials were measured between 4:30 am and 6:30 am, and reported in MPa units (Naidoo 1989).

### *Gas exchange measurements*

Photosynthetic gas exchange was measured with a LI–6200 portable photosynthesis system equipped with a one-liter leaf chamber (Licor, Lincoln, Nebraska, U.S.A.). Measurements were made hourly on intact mature leaves (the 2nd or 3rd pair of leaves from the terminal bud of each shoot) of both scrub and fringe *R. mangle* trees from 10:00 am to 5:00 pm on the following dates: Apr. 27, 1990 (the end of the dry season), Aug. 8, 1990 (mid wet season), Oct. 17, 1990 (the end of wet season) and Jan. 11, 1991 (mid dry season). The measurements were started only at 10:00 am since dew formation on leaf surfaces in the early morning prevented accurate measurements of stomatal conductance. The raw data accumulated by the LI–6200 were used to calculate $CO_2$ assimilation rate (A), stomatal conductance to water vapor (g), intercellular $CO_2$ concentration (Ci) and water use efficiency (Geber 1990). The results from the measurements on Apr. 27, 1990 have been reported previously (Lin and Sternberg 1991), but were used in the interpretation of the results presented here.

### *Carbon isotope analyses*

For carbon isotope analyses, newly grown leaves were collected from *R. mangle* trees in both the scrub and the fringe forests on the same dates when photosynthetic measurements were made. Leaf samples were dried in an oven at 50° C for at least 48 h and ground in a Wiley mill. 3–5 mg of sample tissue was combusted for 4–5 h at 800° C in sealed, evacuated Vycor tubes containing copper, cupric oxide and silver. The carbon dioxide produced by combustion was purified cryogenically, and then measured for $\delta^{13}C$ value on a VG PRISM isotope mass spectrometer relative to the standard PDB (PeeDee belemnite). Carbon isotope discrimination ($\Delta$) was calculated as

$$\Delta = (\delta_a - \delta_p)/(1+\delta_p)$$

where $\delta_a$ and $\delta_p$ are the isotopic compositions of atmospheric $CO_2$ and plant material respectively (Farquhar et al. 1989). A mean $\delta^{13}C$ value of −8.0‰ for $\delta_a$ was used in this study (Ehleringer 1990). $\delta^{13}C$ values of leaves collected on Apr. 27, 1990 at the same study site have been reported previously (Lin and Sternberg, 1991), but were also used to calculate Δ and reported here for comparisons.

### *Statistical analyses*

On each measuring date, the differences in predawn water potentials, photosynthetic gas exchange and instantaneous water use efficiency of red mangroves between the scrub and the fringe forests were tested by Student's *t*-test. Seasonal changes in gas exchange and carbon isotope discrimination were tested by one-way ANOVA.

## Results

Stem water from scrub red mangroves showed lower δD and $\delta^{18}O$ values than that from fringe mangroves in the wet season (June–October, 1990), but similar values in the dry season (January–April 1991) (Fig. 2). Compared with the ranges of δD and $\delta^{18}O$ values for ocean water and fresh water, δD and $\delta^{18}O$ values of stem water indicate that isotope ratios of water available for scrub mangroves shifted from values typical of ocean water in the dry season to values closer to freshwater in the wet season, while isotope ratios of water available for fringe mangroves is similar to values typical of ocean water in both the wet and the dry seasons (Fig. 2). Thus, in general, scrub mangroves showed more seasonal variation in isotopic composition of their stem water, indicating more seasonal changes in their relative utilization of freshwater and ocean water. Consistently, predawn water potentials showed significant differences between scrub and fringe mangroves in the wet season, but not in the dry season (Fig. 3). In the wet season, scrub mangroves had significantly higher predawn water potentials than fringe mangroves suggesting significantly lower salinity of water available for scrub mangroves.

There were no significant differences in $CO_2$ assimilation rate (A) and stomatal conductance (g) between scrub and fringe mangroves on all sampling dates except Apr. 27, 1990 when scrub *R. mangle* trees showed 15.5% lower A and 20.5% lower g respectively (Fig. 4a, b). On Aug. 8, 1990, both A and g were also lower for scrub mangroves than fringe mangroves, but statistical tests showed only slight significance ($P = 0.10$ for A, 0.08 for g) because of variability in light intensity during this sampling date. Both scrub and fringe mangroves demonstrated significant seasonal changes in A during the study period ($P < 0.01$), while only scrub mangroves showed significantly seasonal changes in g ($P < 0.01$ for scrub mangroves, and $P = 0.910$ for fringe mangroves). *R. mangle* trees in the scrub forest maintained significantly lower intercellular $CO_2$ concentration (Ci) than in the fringe forest on both Apr. 27 and Aug. 8,

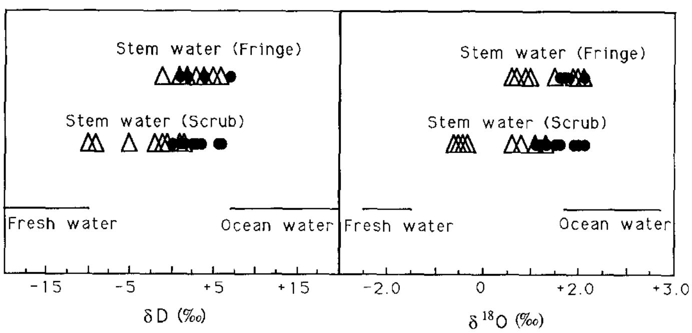


**Fig. 2.** δD and $\delta^{18}O$ values of stem water from scrub and fringe red mangroves in the wet season, June–October 1990 *(open triangles)* and the dry season, January–April 1991 *(Closed circles)* compared with the range of isotopic ratios of freshwater and ocean water in south Florida (Solid bars, from Sternberg and Swart 1987)

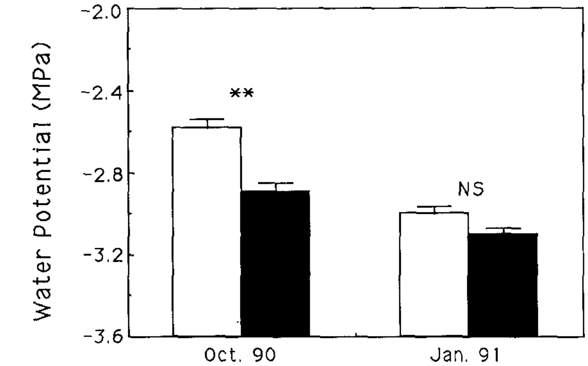


**Fig. 3.** Differences in predawn water potentials of shoots (mean ± se, $n = 4$) between scrub *(open bars)* and fringe red mangroves (solid bars) in the wet season (October 1990) and the dry season (January 1991). Two asterisks indicate a highly significant difference ($P < 0.01$)between scrub and fringe mangroves, while NS means no significant difference ($P > 0.05$)

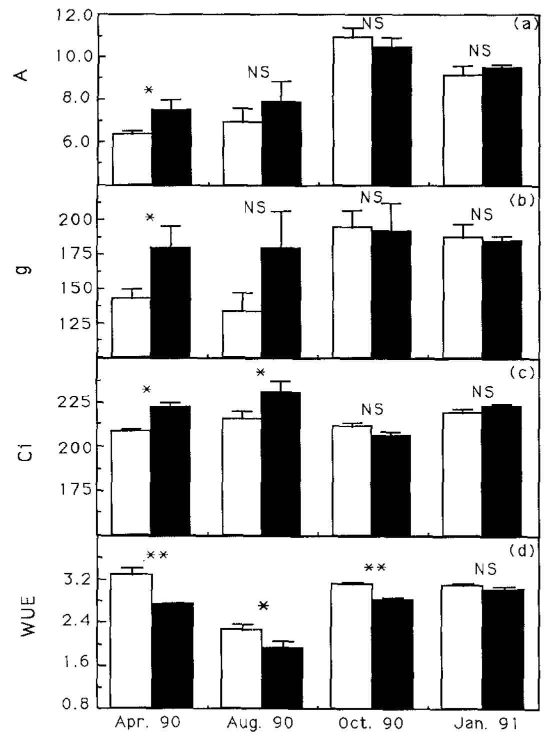


**Fig. 4.** Differences in $CO_2$ assimilation rate (A, mmol · $m^{-2}$ $s^{-1}$), stomatal conductance to water (g, mmol · $m^{-2}s^{-1}$), intercellular $CO_2$ concentration (Ci, μl · $l^{-1}$) and instantaneous water use efficiency (WUE, mmol · $CO_2$/mol · $H_2O$) between scrub *(open bars)* and fringe red mangroves *(solid bars)* on four different measuring dates. Error bars are the standard errors of measurement with 4 replicates. Single asterisk indicates a significant difference at $P < 0.05$ level, and two asterisks indicate a highly significant difference at $P < 0.01$ level, while NS means no significant difference ($P > 0.05$)

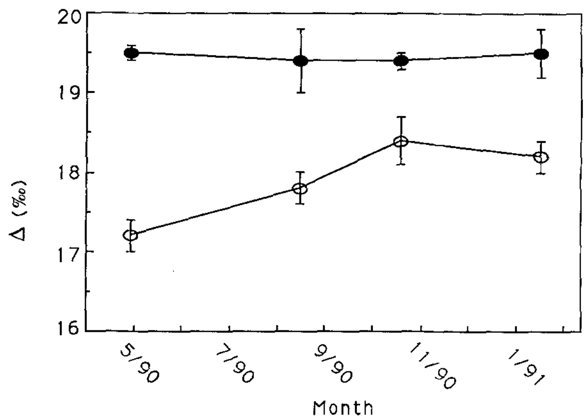


**Fig. 5.** Seasonal changes in carbon isotope discrimination (Δ‰) of leaves from scrub *(open circles)* and fringe red mangroves *(closed circles)*. Error bars are the standard errors of 4 measurements. The differences in Δ between scrub and fringe mangroves were highly significant at $P<0.01$ level for all four measuring dates

1990, but no significant differences on the other two sampling dates (Fig. 4c). In addition, scrub mangroves had significantly higher instantaneous water use efficiency (WUE) than fringe mangroves on all sampling dates except Jan. 11, 1991 (Fig. 4d).

Carbon isotope discrimination (Δ) of newly gown leaves from *R. mangle* trees in the scrub forest was always significantly lower than in the fringe forest (Fig. 5), indicating higher long-term water use efficiency (Hubick et al. 1986; Farquhar et al. 1989). Scrub mangroves showed significant seasonal changes in Δ ($P<0.01$), while fringe mangroves did not show any seasonal changes in Δ during the same period ($P=0.977$).

## Discussion

Scrub red mangroves at the study site utilized a greater proportion of freshwater than fringe mangroves in the wet season, although they utilized a similar water source in the dry season as reflected in the isotopic compositions of their stem water (Fig. 2). This difference is due to the higher elevation of the scrub forest, where tidal water inundates sediment surface only during occasional high tides. The mean elevation for the scrub forest at the study site is 59.9 cm above sea level, while that for the fringe forest is only 23.7 cm above sea level (Ross, personal communication). Thus, during the wet season (May to October), freshwater from heavy rainfall (Fig. 1) accumulates on the sediment surface in the scrub forest and is subsequently utilized by scrub mangroves. In the fringe forest, however, most mangrove roots are always inundated by tidal water, so rainfall has little effect on salinity of water source because of the buffering ability of ocean water. Higher predawn water potentials in the wet season for scrub mangroves (Fig. 3) also indicated lower salinity of water available to the plants (Naidoo 1989). In the dry season (November to April), on the other hand, much lower precipitation (Fig. 1) prevents the accumulation of freshwater on the sediment surface of the scrub forest. Water available for scrub mangroves comes mostly from tidal water, which reaches the scrub forest during occasional high tides. Thus, scrub mangroves showed similar predawn water potentials as fringe mangroves during the dry season (Fig. 3).

Instantaneous water use efficiency was usually significantly higher for scrub mangroves than for fringe mangroves (Fig. 4d). Consistently, carbon isotope discrimination of scrub mangrove leaves also indicated higher long-term water use efficiency (Fig. 5). Higher water use efficiency in scrub mangroves probably results from stomatal limitation on photosynthesis since $CO_2$ assimilation rates of scrub mangroves covaried with stomatal conductance throughout 4 seasons (Fig. 4a, b). Only scrub mangroves demonstrated significant seasonal changes in stomatal conductance, although both scrub and fringe mangroves showed similar seasonal changes in $CO_2$ assimilation rates (Fig. 4a, b). This feature of scrub mangroves may entail considerable carbon cost to the plants. Higher water use efficiency, or more conservative water use is a consequence of the stressful conditions (eg. high salinity, water deficiency, etc.), and also contributes to the maintenance of favorable carbon/salt/water balance (Ball 1988b). However, restriction of the rates of water efflux by decreasing stomatal conductance also restricts the rates of $CO_2$ influx, and thus the growth rates (Cowan 1977).

Frequent changes of salinity resulting from shifts in water sources from ocean to freshwater, or vice versa, may have significant effects on growth and distribution of scrub mangroves. Red mangroves are facultative halophytes with several mechanisms (such as salt exclusion, osmoregulation and ion compartmentation), which allow them to grow well in saline conditions (Ball 1988a: Werner and Stelzer 1990), but they are also capable of growing well in fresh water (Teas 1979). In the areas where salinities change quickly, however, mangroves may not adapt well to salinity. Rapid salinity changes may present the additional burden of acclimation to salinity, and thus plants may not maintain normal growth in these kinds of habitats. Since scrub red mangroves in south Florida occur frequently in slightly higher areas as at the present study site (Teas 1979), we propose that salinity fluctuation is an important environmental factor responsible for the occurrence of scrub mangroves in this area. Presently, we are conducting greenhouse and field studies to test this hypothesis.

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