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Differences in morphology, carbon isotope ratios, and photosynthesis between scrub and fringe mangroves in Florida, USA

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ABSTRACT

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All three mangrove species in Florida (USA), *Rhizophora mangle* L., *Laguncularia racemosa* Gaert. and *Avicennia germinans* (L.) L., are found frequently in scrub mangrove forests, in which individuals rarely exceed 1.5 m in height. In the present study, the differences in morphological characteristics, leaf carbon isotope ratios and photosynthetic gas exchange between individuals in scrub and fringe mangrove forests in south Florida were investigated quantitatively. Plants in the scrub forests had much lower canopy height, more main stems per tree and smaller leaves, relative to those in the fringe forests. There was a significant correlation between tree height and leaf $\delta^{13}C$ value, with higher $\delta^{13}C$ values (1-4‰ more positive) for plants in the scrub mangrove forests. Correspondingly, scrub mangroves showed significantly lower intercellular carbon dioxide (CO_2) concentration and higher intrinsic water use efficiency over long-term carbon assimilation, relative to fringe mangroves. Photosynthetic gas exchange measurements on *R. mangle* individuals showed a 15.5% lower CO_2 assimilation rate, 6.1% lower intercellular CO_2 concentration and 11.6% higher intrinsic water use efficiency in scrub mangroves, consistent with those estimated from leaf carbon isotope ratios. A higher slope for the linear correlation between CO_2 assimilation rate and stomatal conductance was observed for the individuals in the scrub mangrove forest, which is in agreement with other measurements indicating higher water use efficiency in scrub mangroves. Possible environmental factors responsible for these morphological and physiological differences between scrub and fringe mangroves are discussed.

INTRODUCTION

Scrub or dwarf mangrove forest is one of six major types of mangrove communities classified by Lugo and Snedaker (1974). Individual plants in scrub mangrove forests rarely exceed 1.5 m in height and many trees (shrubs) are 40 or more years old (Lugo and Snedaker, 1974). In other types of mangrove

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forests (such as fringe forest, overwash forest, riverine forest, basin forest and hammock forest), however, tree height of the same species may range from several meters to over 30 m at maturity (Davis, 1940; Craighead, 1971; Lugo and Snedaker, 1974). The productivity of scrub mangrove forest is also significantly lower than that of any other mangrove forest (Teas, 1974). Many mangrove species may occur in both scrub forest and other types of mangrove communities, especially in the genera *Aegiceras, Avicennia, Ceriops, Laguncularia* and *Rhizophora* (Lugo and Snedaker, 1974; Rao, 1986).

In Florida, all three mangrove species, *Rhizophora mangle* L. (red mangrove), *Laguncularia racemosa* Gaert. (white mangrove) and *Avicennia germinans* (L.) L. (black mangrove), are known to occur frequently in scrub forests. The largest single area of scrub mangrove forest (about 6000 ha) is in southeastern Florida, although smaller areas are scattered throughout mainland south Florida and the Florida Keys (S.C. Snedaker, personal communication, 1990). Many researchers have tried to explain the occurrence of scrub or dwarf mangroves in Florida. Davis (1940) suggested that scrub mangroves result from extreme conditions of salinity and poor aeration of the surface water. Egler (1952) held the same opinion, but placed greater emphasis on waterlogging than on salinity. Craighead (1971), however, believed that scrub mangroves are the result of compacted peat which prevents the deep penetration of roots. Lugo and Snedaker (1974) suggested that scrub mangroves suffer from nutrient limitation because they usually exist in an environment lacking obvious external nutrient sources.

There are few quantitative studies on the morphological and physiological characteristics of individuals in scrub mangrove forests in Florida. Further, reports on the transition from fringe to scrub mangrove communities are of an anecdotal nature. We report here the results of our quantitative comparisons between individuals in the scrub mangrove forests and those in the fringe mangrove forests in south Florida, USA. The following morphological parameters were measured for both scrub and fringe mangrove individuals of all three species: tree canopy height, number of main stems per tree and mean leaf size. We also analyzed leaf carbon isotope ratios for these plants as an indicator of long-term water use efficiency (Farquhar and Richards, 1984; Goldstein et al., 1989). In addition, we compared photosynthetic gas exchange characteristics of *R. mangle* trees in the scrub and fringe forests.

MATERIALS AND METHODS

Study sites

The present study was carried out at Sugarloaf Key, Monroe County (24°41′N, 81°33′W) and Manatee Bay, Dade County (25°15′N, 80°27′W), Florida, USA. Fringe mangrove forest occurs along the northwestern coast of

Sugarloaf Key with the dominant trees of *R. mangle*, and some scattered trees of *L. racemosa* and *A. germinans*, while scrub trees of all three mangrove species as well as buttonwood (*Conocarpus erecta* L.) occur in the area between the fringe forest and hardwood hammock. Soils at this site are formed directly on a limestone bedrock of Pleistocene age. Under the fringe forest canopy, a layer of accumulated peat and plant litter (about 20–30 cm in depth) overlies the soil surface. In the scrub forest, however, the soils are heterogeneously distributed in pockets on the surface of a limestone rocky substrate. At Manatee Bay, only *R. mangle* occurs in both fringe and scrub mangrove forests.

Morphological measurements

At Sugarloaf Key, a 180 m transect across both fringe and scrub mangrove forests was set up, and the tree height of individuals of all three mangrove species as well as *C. erecta* was recorded at 5 m intervals starting from seaward to inland. At the same site, tree height and the number of main stems per tree were recorded on 30 *R. mangle* trees, 20 *L. racemosa* trees and 10 *A. germinans* trees in the scrub and fringe forests, respectively. In addition, 20 mature leaves (second or third paired leaves from the terminal buds) were collected from these trees for all three mangrove species. The maximum length and width, as well as leaf area, were measured on each leaf. For mangroves at Manatee Bay, only tree height and the number of main stems per tree were recorded on 15 *R. mangle* trees in the scrub and fringe forests, respectively.

Leaf carbon isotope analyses

Leaves for carbon isotope analyses were collected from four trees in both scrub and fringe forests for all three species at Sugarloaf Key on 27 June 1990, and for *R. mangle* only at Manatee Bay on 7 April 1990. About five mature leaves were collected from the canopy of each tree and leaf midribs were removed from the leaves. Leaf samples were then dried in an oven at 50°C for at least 48 h and ground in a Wiley mill. Sample tissue (3–5 mg) was combusted for 4–5 h at 800°C in sealed, evacuated Vycor tubes containing copper, cupric oxide and silver. The carbon dioxide (CO_2) produced by combustion was purified cryogenically and then measured on a VG PRISM isotope mass spectrometer. Carbon isotope ratios were reported in δ units relative to the standard PDB (PeeDee Belemnite).

We calculated the average intercellular CO_2 concentration (Ci) over the long-term carbon assimilation from leaf carbon isotope ratio ($\delta^{13}C_{\mathrm{leaf}}$), based on the model of Farquhar et al. (1982a,b)

$$\delta^{13}C_{\mathrm{leaf}}=\delta^{13}C_{\mathrm{air}}-a-(b-a)Ci/Ca \qquad (1)$$

where $\delta^{13}C_{\mathrm{air}}$ is the carbon isotope ratio of the CO_2 in the air (about $-8‰$ at current CO_2 levels), a is the fractionation caused by the slower diffusion of $^{13}CO_2$ relative to $^{12}CO_2$ (4.4‰), b is the fractionation caused by discrimination of ribulose biphosphate (RuBP) carboxylase against $^{13}CO_2$ (27‰) and Ca is the atmospheric CO_2 concentration (at present, 350 $\mu l\ l^{-1}$). In addition, the average intrinsic water use efficiency (WUE) of leaves was calculated as in Andrews and Muller (1985) by using the following equation

$$\mathrm{WUE} = (Ca - Ci)/(Ca - \Gamma) \tag{2}$$

where Γ is the CO_2 compensation point ($\mu l\ l^{-1}$). In this paper, a mean value for Γ of 70 $\mu l\ l^{-1}$ was used in calculating WUE (Clough and Sim, 1989).

Photosynthetic measurements

Photosynthetic gas exchange was measured on intact mature leaves with a LI-6200 portable photosynthesis system equipped with a 1 l leaf chamber (Licor, Lincoln, NE, USA). Measurements were made hourly starting from 10:00 h to 17:00 h on four *R. mangle* trees in the scrub and fringe forests, respectively, on 27 April 1990. Measurements were started only at 10:00 h because dew formation on the leaf surface in the early morning prevented accurate measurements of stomatal conductance. Raw data accumulated by the LI-6200 were used to calculate mean CO_2 assimilation rates, stomatal conductance to water vapor and intercellular CO_2 concentration. The relationship between CO_2 assimilation rate and stomatal conductance was examined by regression analysis of the original data. In addition, the intrinsic WUE was calculated by using eqn. (2) given above.

Statistical analyses

Differences in all measured parameters between the two forests for a given species were compared by Student's *t*-test. The correlation between leaf $\delta^{13}C$ value and tree height, and between assimilation rate and stomatal conductance, was tested by regression analysis. The difference in the slope for the linear regression of assimilation rate versus stomatal conductance between scrub and fringe *R. mangle* trees was tested by ANCOVA.

RESULTS

Morphological characteristics

There was a sharp drop in the tree height distribution at the border between the fringe and scrub forests at Sugarloaf Key (Fig. 1). In the fringe forest, tree height increased gradually from 3 to 7 m, and then declined to 4 m at the border. In the scrub forest, however, tree height was always below 1.5 m and

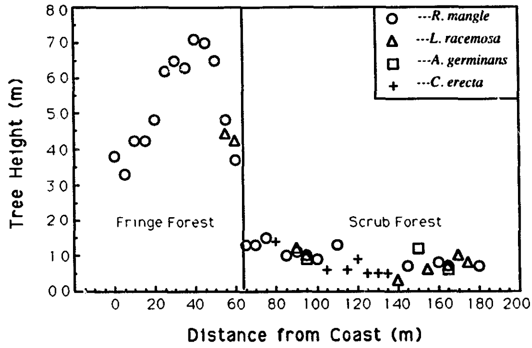

Fig. 1. Tree height distribution along a transect across both fringe and scrub mangrove forests from seaward to inland at Sugarloaf Key.

TABLE 1

Differences in leaf sizes between scrub and fringe mangroves at Sugarloaf Key (mean ± standard error (SE)). An asterisk indicates significant differences between the two forests for a given species ($P<0.05$, Student's *t*-test)

Species	Forest type	Leaf length (cm)	Leaf width (cm)	Leaf area (cm^2)
R. mangle	Scrub	8.7±0.2	3.6±0.1	23.4±1.1
	Fringe	9.3±0.3*	4.2±0.2*	28.5±1.7*
L. racemosa	Scrub	5.5±0.2	2.9±0.1	12.6±0.8
	Fringe	5.9±0.1*	3.0±0.1	14.1±0.6*
A. germinans	Scrub	5.2±0.2	2.4±0.1	9.4±0.7
	Fringe	5.4±0.1	2.3±0.1	8.9±0.4

showed no significant changes over a 120 m transect. For all three mangrove species at Sugarloaf Key, the mean tree height in the scrub forest was 1.0 m, while that in the fringe forest ranged from 3.8 m in *L. racemosa*, to 4.9 m in *R. mangle*, and to 5.9 m in *A. germinans*. At Manatee Bay, *R. mangle* trees in the scrub forest also showed significantly lower canopy height (1.2 m) than those in the fringe forest (8.4 m). The mean number of main stems per tree was 3.0–3.5 for *R. mangle*, 3.0 for *L. racemosa* and 3.1 for *A. germinans* in the scrub forests at both study sites, much higher than that for those in the fringe forest (1.1–1.2 for *R. mangle*, 1.2 for *L. racemosa* and 1.1 for *A. germinans*).

Rhizophora mangle and *L. racemosa* trees in the scrub forest had significantly smaller leaf sizes (maximum leaf length and width, as well as leaf area) than those in the fringe forest, except for maximum leaf width in *L. racemosa* at Sugarloaf Key (Table 1). There was no significant difference, however, in leaf size for *A. germinans* trees in the scrub and fringe forests at the same site (Table 1).

Stable isotope ratios

The leaf carbon isotope ratio was strongly correlated with tree height of the three mangrove species ($r=0.90$, $P<0.01$) (Fig. 2), indicating that there is a relationship between tree height and plant water use efficiency. The $\delta^{13}C$ values of leaves from mangroves in the present study ranged from −25.0 to −29.0‰, well within the range (−24.6 to −32.2‰) reported by Andrews et al. (1984) for Australian mangroves and the range reported for C_3 plants (Smith and Epstein, 1971).

Individuals in the scrub forests showed significantly higher leaf $\delta^{13}C$ (1.0–4.0‰ more positive) than those in the fringe forests for all three mangrove species (Fig. 2), suggesting higher water use efficiency for trees in the scrub mangrove forests. Correspondingly, the average intercellular CO_2 concentration over long-term carbon assimilation in the scrub forest was significantly lower (14.7–62.0 $\mu l\ l^{-1}$ lower) than that in the fringe forest (Fig. 3). As a result, the average intrinsic water use efficiency estimated from leaf $\delta^{13}C$ values was significantly higher for individuals in the scrub mangrove forests (0.53–0.55 for *R. mangle*, 0.49 for *L. racemosa* and 0.46 for *A. germinans*)

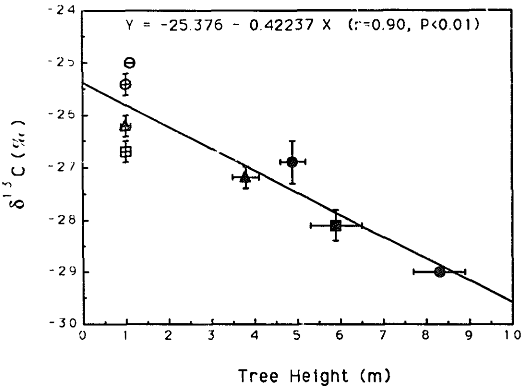

Fig. 2. Correlation between leaf carbon isotope ratio and tree height in mangroves. Error bars are standard errors (four replicates for $\delta^{13}C$ measurements and 10–30 replicates for tree height measurements). Open symbols represent scrub mangroves and solid ones fringe mangroves. At Manatee Bay, four leaf samples were analyzed together for carbon isotope ratios. Symbols: ○ ●, *R. mangle*; △ ▲, *L. racemosa*; □ ■, *A. germinans*.

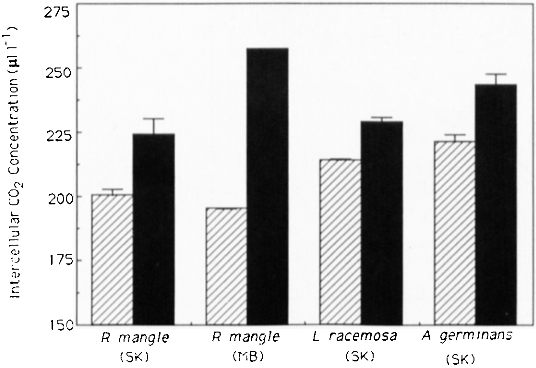

Fig. 3. Differences in the estimated average intercellular CO_2 concentration from leaf $\delta^{13}C$ values between individuals in the scrub mangrove forests (shaded bars) and those in the fringe forests (solid bars). The differences between the two forests at Sugarloaf Key were all significant at the $P < 0.05$ level. Study sites: SK, Sugarloaf Key; MB, Manatee Bay.

than for those in the fringe forests (0.33–0.45 for *R. mangle*, 0.43 for *L. racemosa* and 0.38 for *A. germinans*).

Photosynthetic gas exchange

Rhizophora mangle individuals in the scrub forest showed 15.5% lower CO_2 assimilation rate, 20.5% lower stomatal conductance and 6.1% lower intercellular CO_2 concentration, but 11.6% higher intrinsic water use efficiency relative to those in the fringe forest (Table 2). The differences in intercellular

TABLE 2

Leaf photosynthetic gas exchange of *R. mangle* trees in both scrub and fringe forests at Sugarloaf Key on 27 April 1990 (mean ± SE). An asterisk indicates significant differences between the two forests ($P < 0.05$, Student's *t*-test)

Gas exchange characteristics	*N*	Scrub mangroves	Fringe mangroves
CO_2 assimilation rate ($\mu mol\ m^{-2}\ s^{-1}$)	4	6.32 ± 0.21	7.48 ± 0.53*
Stomatal conductance ($mmol\ m^{-2}\ s^{-1}$)	4	142.7 ± 7.5	179.6 ± 15.8*
Intercellular CO_2 concentration ($\mu l\ l^{-1}$)	4	208.6 ± 1.7	222.2 ± 2.8*
Intrinsic water use efficiency	4	0.48 ± 0.01	0.43 ± 0.01*

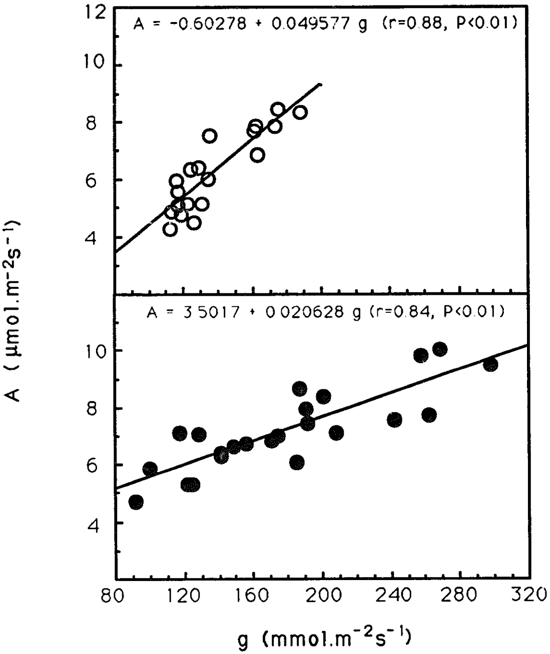

Fig. 4. Correlation between CO_2 assimilation rate (A) and stomatal conductance (g) for leaves of *R. mangle* trees in the scrub forest (open symbols) and fringe forest (solid symbols) at Sugarloaf Key.

CO_2 concentration and intrinsic water use efficiency between the two forests from the gas exchange measurements were consistent with those calculated using leaf carbon isotope ratios (Table 2, Fig. 3). There was a strong correlation between the CO_2 assimilation rate and stomatal conductance for *R. mangle* trees in both scrub and fringe forests (Fig. 4). The slope (or regression coefficient), however, was significantly higher for individuals in the scrub mangrove forest than for those in the fringe mangrove forest (0.021) ($P<0.05$, ANCOVA).

DISCUSSION

Besides tree height, there were two other major morphological differences between individuals in the scrub and fringe forests. First, individuals in the scrub mangrove communities had significantly smaller leaves (Table 1). Second, individuals in the scrub mangrove forests had more main stems per tree, indicating a greater branching in scrub mangroves, which may result from the damage to the terminal bud during the seedling stage. Tomlinson (1986) showed that damage to the terminal buds of *R. mangle*, when at the seedling stage, can result in the formation of a branched tree with a reiterated crown and lower canopy height. The causes for the damage of terminal buds are unknown. It is impossible that more main stems in scrub mangrove trees would be a result of management since the study sites are within the local reserve areas where no former cutting of stems was practiced.

There were significant differences in photosynthetic gas exchange of *R. mangle* trees in the scrub and fringe forests (Table 2). Lower stomatal conductance in scrub mangroves results in slightly lower CO_2 uptake, but prevents water loss through stomata during photosynthesis; thus, scrub mangroves can maintain a higher water use efficiency. It has been demonstrated that stomatal control often represents a compromise between two conflicting demands: the amount of water lost by leaves and the amount of carbon gained (Schulze et al., 1987). This coordination between photosynthesis and water loss is consistent with the strong correlation between CO_2 assimilation rate and stomatal conductance for the mangroves in the present study (Fig. 4). A strong correlation between CO_2 assimilation rate and stomatal conductance in many mangroves indicates extremely conservative water use associated with salinity stress (Ball, 1988), with a higher slope indicating a higher water use efficiency (Ball et al., 1988). The higher slope for the linear regression of CO_2 assimilation rate on stomatal conductance in scrub *R. mangle* (Fig. 4) was consistent with our water use efficiency measurements (Table 2). In addition, leaf $\delta^{13}C$ value, an indicator of integrated long-term water use efficiency in C_3 plants (Guy et al., 1980; Farquhar et al., 1982b; Guy and Reid, 1986), also showed that scrub mangroves have higher water use efficiency than fringe mangroves (Fig. 2).

The discontinuous distribution of tree height at the border between the fringe and scrub mangrove forests suggests that the environmental conditions determining the occurrence of scrub mangrove forests can change rapidly from the fringe mangrove forests to the scrub mangrove forests (Fig. 1). The difference in edaphic conditions between fringe and scrub forests mentioned previously may be one of these factors. We have observed at least two edaphic factors which would account for the differences between the scrub and fringe forests. First, the ground water level in the scrub forest is much lower than that in the fringe forest which, combined with horizontal distribution of scrub mangrove roots, may cause scrub mangroves to depend mostly on surface water for their water resource. Thus, salinity in water available for scrub mangroves may be easily subjected to change due to seasonal differences in precipitation and evaporation. Second, well water in the scrub mangrove forest tends to have a lower concentration of total nitrogen and phosphorus (M. Ross and J. O'Brein, personal communication, 1990), which may also influence the growth of scrub mangroves. More studies are needed to determine the nature of the environmental factors responsible for the occurrence of scrub or dwarf mangroves in Florida and other mangrove areas.

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