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## Photosynthetic performance and resource utilization of two mangrove species coexisting in a hypersaline scrub forest

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**Abstract** In a hypersaline mangrove scrub forest in northern Florida, coexisting trees of *Laguncularia racemosa* and *Avicennia germinans* were either fertilized with nitrogen or phosphorus, or not fertilized (controls). We aimed to test whether nutrient additions differentially altered photosynthetic performance and resource utilization in these two species. In control trees, photosynthetic rates were higher in *L. racemosa* than *A. germinans*. However, leaf nitrogen concentrations were higher in *A. germinans* than *L. racemosa*. *Avicennia germinans* responded to fertilization with nitrogen by increasing leaf nitrogen concentrations and rates of photosynthesis such that they were equivalent to photosynthesis in *L. racemosa*. *Laguncularia racemosa* did not show a response to nitrogen additions. Neither species showed strong responses to phosphorus fertilization. *Avicennia germinans* had high photosynthetic water-use efficiency (photosynthesis/transpiration), but low photosynthetic nitrogen-use efficiency (photosynthesis/leaf nitrogen). In contrast, *L. racemosa* had comparatively low photosynthetic water use efficiency and high photosynthetic nitrogen use efficiency. Leaf level characteristics lead us to hypothesize that coexistence of *A. germinans* and *L. racemosa* should occur where nitrogen levels are low and salinity is moderate, or at least moderate for some period of the year.

**Keywords** Photosynthetic nitrogen use efficiency · Photosynthetic water use efficiency · *Avicennia germinans* · *Laguncularia racemosa* · Florida

### Introduction

Mechanisms leading to species coexistence are those responsible for the maintenance of diversity. One of the most commonly proposed hypotheses for the coexistence of species is that some species are better than others at utilizing resources within an environment (Tilman and Pacala 1993). Here we examine resource use in two mangrove tree species coexisting in a scrub mangrove swamp in Florida. We experimentally manipulated resource levels to test whether changing resource availability is likely to compromise coexistence.

Scrub mangrove forests are an important component of mangrove ecosystems (Cintrón et al. 1978). They are often found at high elevation in the intertidal zone, typically where tidal flushing occurs at low frequency, and evaporation leads to concentration of salt in the soil (although short stature can also be caused by nutrient deficiencies, see Feller 1995). These highly saline scrub mangroves are usually dominated by two tree species: *Avicennia germinans* (L.) L. (Avicenniaceae) and *Laguncularia racemosa* (L.) Gaertn. f. (Combretaceae). These two species often coexist, but in extremely saline areas *A. germinans* is usually dominant (Cintrón et al. 1978). *L. racemosa* can also form monospecific stands (Schaeffer-Novelli et al. 1990; Sherman et al. 1998). The distribution of these species has also been correlated with nutrient availability gradients (Sherman et al. 1998), and laboratory studies have suggested that they differ in their growth rates in response to nutrient enrichment (Pezeshki et al. 1989; McKee 1995). Although many factors could be influential in determining the dominance of a tree species in any given area (Smith 1992), physiological differences among species in their tolerance of environmental conditions are likely to be important (Ball 1988, 1996).

Previous work on the physiology and ecology of mangroves has suggested that mangrove species show more conservative water-use strategies with increasing salt tolerance of the species (Ball 1996). The selective pressure on plants to enhance water-use efficiency in highly saline environments may lead to the evolution of

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traits that result in reductions in the competitive abilities for other resources. For example, there could be trade-offs between photosynthetic water-use efficiency and nitrogen-use efficiency (Field et al. 1983). This could drive changes in forest species composition, structure and function along salinity and resource gradients (Ball 1996). Here, in a hypersaline forest where *A. germinans* and *L. racemosa* coexist, we test whether *A. germinans* has more conservative water-use than *L. racemosa* under moderate to high sediment salinity. By applying fertilizer to pairs of *A. germinans* and *L. racemosa* trees, we also assessed how photosynthetic performance and utilization of water and nitrogen resources for photosynthetic carbon gain were altered by increased nutrient availability. Our aim was to construct predictions of the environmental conditions that would promote coexistence of these species, and also to predict what conditions may lead to dominance of either one.

## Materials and methods

### Site description

The experimental site is in the northern Indian River Lagoon on North Hutchinson Island, St. Lucie County, Fla., USA. Temperature and rainfall are highly seasonal. Conditions are dry and cool from November through to April, and warmer and wetter May through to November. Tidal amplitude has a maximum of 50 cm. Most mangroves areas in this region were impounded for insect control between 1954 and 1970 (Rey and Tain 1991). In this process, a dyke is built around the wetland so water flow and mosquito populations can be manipulated. The experimental site was in the northern end of impoundment no. 23. This impoundment was constructed in 1966 and abandoned because of a breach in the dyke in 1979 when natural tidal flow was reestablished. The sediments are sandy, possibly due to the addition of spoils during dredging of the lagoon. The vegetation has reestablished in a typical zonation pattern observed in many natural mangrove sites. There is a fringing zone of *Rhizophora mangle* approximately 4 m tall, grading into a short (1 m), scrub mangrove adjacent to the terrestrial forest, which is composed of both *A. germinans* and *L. racemosa*, with herbaceous *Batis maritima* and *Salicornia* sp.

### Experimental design

In the scrub forest, *L. racemosa* and *A. germinans* coexist in patches. In May 1997, 18 pairs of similarly sized *A. germinans* and *L. racemosa* trees were randomly chosen from within the impoundment. A third of the pairs of trees were fertilized with nitrogen (N) by coring two 15 cm diameter holes in the sediment between the paired trees, approximately equidistant from each tree, and inserting 200 g urea into each hole and resealing it, a third with phosphorus (P) using 200 g triple super-phosphate, and the final third cored but not fertilized. These were designated as controls (C). All trees were fertilized at approximately 6 monthly intervals for 2 years. Photosynthetic responses of plants to the fertilization treatments were measured in November 1998 during the wet season when leaves of both species were at a similar stage of development. Three leaves from each tree were sampled. At the same time pore water under each species pair was collected using the methods of McKee (1993). Salinity over the paired trees varied from 33 to 55 ppt and mean eH for the scrub mangrove was -166 mV (SD=121,  $n=20$ ).

### Photosynthetic gas exchange

Rates of photosynthetic gas exchange were measured with a Li-Cor 6400 photosynthesis measuring system (Li-Cor, Lincoln, Neb., USA). Photosynthesis was measured on sunny mornings with little or no cloud cover, using natural light. Light levels were generally saturating for photosynthesis (greater than  $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and thus photosynthetic rates were assumed to be close to maximal. Measurements were made on the youngest, fully expanded leaves (usually the penultimate leaf on a twig) that were exposed to full sunlight at the time of measurement. After each measurement was completed (usually in approximately 1 min), the leaf was harvested. Leaf area was measured using a Li-Cor leaf area meter (Li-Cor). Leaves were then dried in an oven at  $60^\circ\text{C}$  and later weighed. Dried leaf material was ground to a fine powder in a small mill. Nitrogen concentration within the leaves was analyzed in a CHN analyzer (Perkin Elmer, Norwalk, Conn., USA) using a small subsample of the ground leaf tissue. Photosynthetic nutrient use efficiency (PNUE) and photosynthetic water use efficiency (PWUE) were calculated as photosynthetic  $\text{CO}_2$  assimilation ( $A$ ) divided by the leaf N concentration ( $A/N$ ), and  $A$  divided by evapotranspiration ( $A/E$ ), respectively (Field et al. 1983).

Chlorophyll fluorescence was measured with a Diving PAM (H.Walz, Effeltrich, Germany) at midday and 2 h after sunset in March 1998. Dark-adapted minimum ( $F_0$ ) and maximum fluorescence ( $F_m$ ) were obtained at midday after placing excised leaves in darkness for 20 min before the measurement. Nighttime values were measured in situ. The variable fluorescence,  $F_v/F_m$ , was calculated as  $(F_m - F_0)/F_m$ .

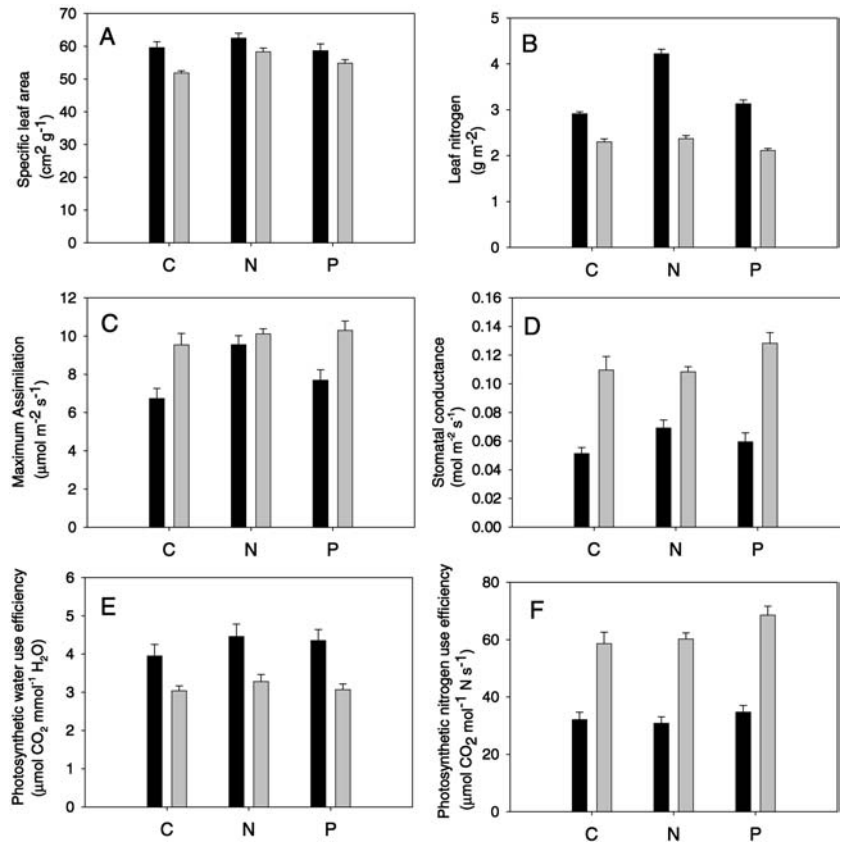
Stomatal densities were measured using impressions made with clear nail polish. Because of the hammer hairs that cover the abaxial surface of *A. germinans* leaves, stomatal impressions were made by peeling away the upper layers of leaf tissue to reveal the internal surface of the abaxial epidermis. *Laguncularia racemosa* has stomata on both sides of the leaf, and thus stomata were counted on both the abaxial and adaxial surfaces. Total stomatal density for this species was calculated as density on abaxial surface + adaxial surface. Stomatal densities were counted from five nail polish peels for one leaf per tree within each treatment at  $\times 250$  using a light microscope.

### Data analysis

Rates of photosynthesis, stomatal conductance, specific leaf area (SLA), leaf nitrogen concentrations, PNUE, and PWUE were analyzed by analysis of variance (ANOVA) using the statistical program Data Desk (Data Descriptions, Ithaca, New York, USA). The effects of fertilization treatments on stomatal densities were also analyzed by ANOVA. Species and fertilizer treatment were fixed effects in the model, while pairs of trees were random. The effect of fertilizer additions on chlorophyll fluorescence parameter  $F_v/F_m$  was analyzed by ANOVA for each species separately as data were not available at both times for both species. For *L. racemosa* fertilizer treatment was a fixed effect in the ANOVA, while for *A. germinans* both fertilizer treatment and time (either midday or nighttime) were considered fixed effects. The suitability of all ANOVA models was determined by inspecting residual plots.

Spearman's Rank correlation, a non-parametric measure of correlation that does not assume a linearity, was used to describe the correlation of substrate salinity under each tree pair with maximum rates of photosynthesis, PNUE, and PWUE for each species.

**Fig. 1** Specific leaf area (A), leaf nitrogen concentration (B), maximum rates of photosynthesis (C), stomatal conductance (D), photosynthetic water use efficiency (E) and photosynthetic nitrogen use efficiency (F) of leaves of *Avicennia germinans* (filled bars) and *Laguncularia racemosa* (shaded bars). Trees were either fertilized with nitrogen (N), or with phosphorus (P), or were unfertilized controls (C). Values are means of 1518 measurements obtained from 56 trees,  $\pm$ SE



## Results

### SLA and leaf nitrogen concentrations and photosynthesis

SLA was similar in both species, but slightly higher in *A. germinans* than in *L. racemosa* (Fig. 1A). Fertilizer application had no significant effect on SLA in either species. In control trees, leaf nitrogen concentrations per leaf area were higher in *A. germinans* than in *L. racemosa* (Fig. 1B). In *A. germinans*, leaf N concentrations were higher in N fertilized trees compared to P fertilized and control plants. Expressed on a dry weight basis, N concentrations for fertilized *A. germinans* were 1.5 times greater than controls and over 2 times the N concentration within *L. racemosa* leaves (26.8 mg N  $\text{g}^{-1}$  in N fertilized *A. germinans*, 17.5 mg  $\text{g}^{-1}$  in *A. germinans* controls and 11.9 mg  $\text{g}^{-1}$  in *L. racemosa* controls).

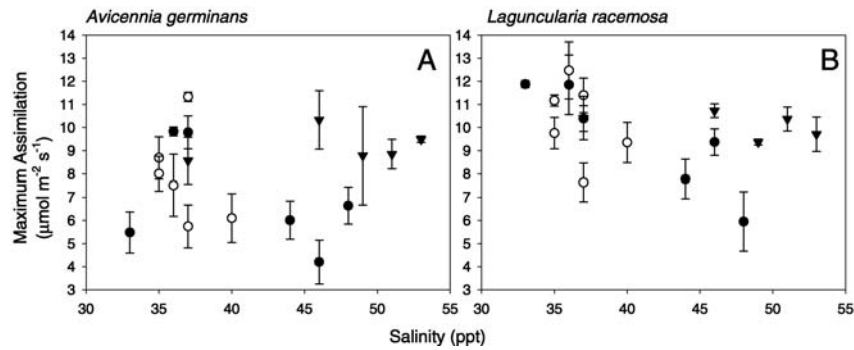
Maximum rates of photosynthesis varied between species and over treatments (Fig. 1C). In control plants, *L. racemosa* had higher rates of photosynthesis than *A. germinans*. Fertilization with N or P had no effect on the

average maximum photosynthetic rates of *L. racemosa*. Fertilization with N enhanced photosynthesis of *A. germinans* leaves relative to controls, while fertilization with P did not. Nitrogen fertilized trees of *A. germinans* had photosynthetic rates that were equivalent to *L. racemosa*. Photosynthetic rates did not correlate with leaf nitrogen concentrations in *L. racemosa*, but did, if weakly, for *A. germinans* ( $R^2=0.13$ ,  $P=0.0041$ , data not shown). Stomatal conductance was greater in *L. racemosa* compared to *A. germinans* (Fig. 1D). Stomatal conductance was slightly higher in N fertilized *A. germinans* than in controls, but this effect was not significant.

To support our measurements of photosynthetic gas exchange, the chlorophyll fluorescence parameter  $F_v/F_m$  was used to provide a measure of photosynthetic efficiency.  $F_v/F_m$  declines as plants are exposed to photooxidative stress. In *A. germinans*, midday  $F_v/F_m$  was lower in control and P fertilized trees than in N fertilized trees, but all leaves recovered to a similar level after dark (Table 1). In *L. racemosa*, fertilization had no significant effects on midday  $F_v/F_m$ .

**Table 1** Midday and nighttime values of chlorophyll fluorescence parameter,  $F_v/F_m$ . Values are means of 1526 measurements on 59 trees  $\pm$ SE

	<i>Laguncularia racemosa</i>		<i>Avicennia germinans</i>	
	Midday $F_v/F_m$	Nighttime $F_v/F_m$	Midday $F_v/F_m$	Nighttime $F_v/F_m$
Control	0.738 $\pm$ 0.009	–	0.688 $\pm$ 0.007	0.770 $\pm$ 0.004
Nitrogen	0.761 $\pm$ 0.009	–	0.736 $\pm$ 0.005	0.788 $\pm$ 0.005
Phosphorus	0.731 $\pm$ 0.012	–	0.705 $\pm$ 0.006	0.776 $\pm$ 0.003



**Fig. 2** Response of maximum rates of photosynthesis of *A. germinans* (A) and *L. racemosa* (B) to variation in salinity over the experimental site. Trees were either fertilized with nitrogen (solid triangles), or with phosphorus (open circles), or were unfertilized controls (filled circles). Values are means of 3 leaves per tree  $\pm$ SE

**Table 2** Stomatal density of abaxial and adaxial leaf surfaces of *Laguncularia racemosa* and abaxial surface of *Avicennia germinans*. Values are means of 30 measurements from 5 leaves for each of the 6 trees within each treatment  $\pm$ SE

	<i>Laguncularia racemosa</i>		Abaxial+adaxial	<i>Avicennia germinans</i>	
	Abaxial	Adaxial		Abaxial	Adaxial
Control	11.3 $\pm$ 1.9	17.9 $\pm$ 0.3	29.2 $\pm$ 2.7	20.0 $\pm$ 2.8	–
Nitrogen	10.5 $\pm$ 1.7	16.7 $\pm$ 0.4	27.2 $\pm$ 3.4	19.1 $\pm$ 2.6	–
Phosphorus	11.0 $\pm$ 2.3	17.7 $\pm$ 0.5	28.7 $\pm$ 4.8	20.6 $\pm$ 2.9	–

Mean photosynthetic rates of *L. racemosa* but not *A. germinans* declined as salinity increased (Spearman Rank Correlation for *A. germinans*=0.148 and for *L. racemosa*=0.583, Fig. 2 A, B). Although pairs of trees were randomly assigned to treatments, in November 1998 sediments under N-fertilized trees were generally more saline, resulting in a non-random distribution of treatments over the salinity gradient and making statistical tests inappropriate. However, visual inspection of the data shows N fertilized trees of both species tended to have high photosynthetic rates than P fertilized trees in the more saline region of the salinity gradient.

Stomata occur on both the abaxial and adaxial surface of *L. racemosa*, and only on the abaxial surface of *A. germinans* (Table 2). In *L. racemosa* greater stomatal density occurred on the abaxial surface compared to the adaxial surface. Measures of total stomatal density (abaxial + adaxial) were lower in *A. germinans* compared to *L. racemosa* ( $F_{1, 15}=72.48$ ,  $P<0.0001$ ). Fertilization did not have a significant effect on stomatal density. There was no reduction in stomatal density with increasing salinity for either species.

#### PNUE and PWUE

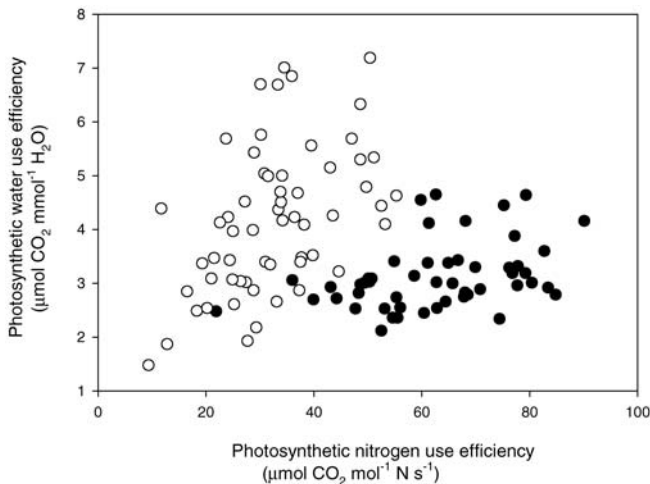
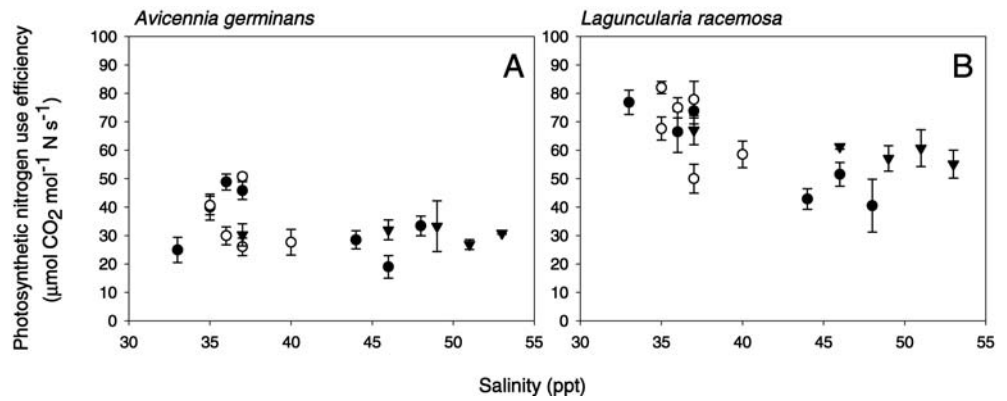
PWUE was higher in *A. germinans* than *L. racemosa* (Fig. 1E). This was largely due to lower stomatal conductance in *A. germinans* compared to *L. racemosa* (Fig. 1D). In both species fertilization with N or P had no effect on PWUE. PNUE was greater in *L. racemosa* than

*A. germinans* (Fig. 1F). Fertilization had no effect on PNUE in *A. germinans*. Fertilization with P slightly increased PNUE of *L. racemosa* compared to controls.

Increases in salinity over the site were correlated with a decline in PNUE in both species, although the effect was stronger in *L. racemosa* than in *A. germinans* (Spearman Rank Correlation for *A. germinans*=-0.193, and for *L. racemosa*=-0.710, Fig. 3A, B). The decline in PNUE in *L. racemosa* with increasing salinity tended to be more apparent in control and P fertilized trees than in N fertilized trees. PWUE did not vary consistently with salinity in either species (Spearman Rank Correlation for *A. germinans*=0.059, and for *L. racemosa*=-0.159).

To assess the relative investment strategies for water and nitrogen for both species, PNUE was plotted against PWUE (after Field et al. 1985, Fig. 4). For *A. germinans*, PWUE was positively correlated with PNUE. Photosynthetic NUE of *A. germinans* was lower than that of *L. racemosa*. PWUE was higher and more variable for *A. germinans* than for *L. racemosa*. In *L. racemosa*, there was no correlation between PNUE and PWUE; instead, *L. racemosa* appears as a cloud of points with high PNUE, but comparatively low PWUE. There is little overlap between the species in this analysis. Fertilization with N or P did not alter the relative positions of the species on this graph.

**Fig. 3** Response of photosynthesis nitrogen use efficiency of *A. germinans* (A) and *L. racemosa* (B) to variation in salinity over the experimental site. Trees were either fertilized with nitrogen (solid triangles), or with phosphorus (open circles), or were unfertilized controls (filled circles). Values are means  $\pm$ SE of 3 measurements per tree



**Fig. 4** Relationship among photosynthetic nitrogen-use efficiency and photosynthetic water-use efficiency of leaves of *A. germinans* (open circles) and *L. racemosa* (filled circles)

## Discussion

### Photosynthetic water-use efficiency

Photosynthetic rates of both *A. germinans* and *L. racemosa* are in the range measured for other mangrove tree species (Ball 1996), but are low compared to herbaceous salt marsh species (Long and Baker 1986; Dai and Wiegert 1997; Lovelock and Ball 2002). Comparable rates of photosynthesis and PWUE have been measured in the Indo-Pacific species *A. marina* growing in highly saline environments, and appear to be typical for this genus (Sobrado 1999; Sobrado and Ball 1999). The decline in photosynthesis, particularly in control and P fertilized trees with increasing salinity in *L. racemosa* confirms the perception that it is less tolerant of highly saline conditions than *A. germinans*.

Our hypothesis that *A. germinans* should have higher PWUE than *L. racemosa* under high salinity to hypersaline sediments was supported by our data (Fig. 1E). The contrasting results presented by Pezeshki et al. (1989) are likely due to the low salinity conditions (50‰ seawater) or some other condition during plant culture. Higher

PWUE in *A. germinans* compared to *L. racemosa* is not due to higher maximum rates of photosynthesis in *A. germinans*, but instead due to relatively lower stomatal conductance at generally lower rates of photosynthesis (Fig. 1C, D). Lower conductance in *A. germinans* compared to *L. racemosa* could be due to morphological differences in leaves between species. *Avicennia germinans* has leaves with trichomes, or 'hammer hairs' (Roth 1992) that cover the stomatal openings on the underside of the leaves. Thus, in addition to lower total stomatal density than *L. racemosa* (Table 2), stomata of *A. germinans* likely have even lower conductance to water vapor due to this additional covering. Declining stomatal density with increasing salinity has been reported for both species (Garcia 1979, cited in Roth 1992), but was not observed in our study, possibly because of the restricted range of salinity occurring at the Fort Pierce site.

PWUE of both species was not greatly affected by variations in salinity over the site. Small increases in PWUE with increasing salinity were reported by Sobrado and Ball (1999) for *Avicennia marina* (PWUE of 4.5  $\mu\text{mol} \mu\text{mol}^{-1}$  and 4.9  $\mu\text{mol} \mu\text{mol}^{-1}$  at 35 and 60 ppt salinity respectively). Increasing PWUE with increasing substrate salinity in mangrove tree species has been observed over a wider range of salinity (1050 ppt) than measured in the current study (Clough and Sim 1989).

### Photosynthesis-nitrogen relationships

Our second hypothesis was that conservative water use would limit plant responses to nutrient additions. Therefore, under hypersaline conditions the less salt tolerant species, *L. racemosa*, should benefit less than the more salt tolerant species, *A. germinans*, with N enrichment. This hypothesis was also supported by our results. Fertilization with N enhanced leaf nitrogen concentrations and the photosynthetic performance, including the mid-day measures of photosynthetic light use efficiency  $F_v/F_m$ , of *A. germinans* but not that of *L. racemosa* (Fig. 1, Table 1). The photosynthetic rate of *A. germinans* fertilized with N was equivalent to *L. racemosa*. These improvements in photosynthetic performance in *A. germinans* were significant despite the higher sediment

salinity observed under N fertilized trees. Higher sediment salinities under N fertilized trees may have arisen over the course of the experiment due to the enhanced photosynthesis and transpiration of *A. germinans*, as theoretically proposed by Passioura et al. (1992).

From the work of Evans (1989), and others (e.g. Seeman and Sharkey 1986; Reich et al. 1989; Poorter and Evans 1998), as well as from the few studies of response of photosynthesis to N additions in higher plants from saline ecosystems (Chalmers et al. 1979; Dai and Wiegert 1997), we expected that increases in photosynthetic rates with N fertilization would be due to a strong relationship often observed among leaf N concentrations, RUBISCO concentrations, and maximum rates of photosynthesis. However, there was no correlation between leaf N concentrations and photosynthesis for *L. racemosa*, and despite increases in leaf N and photosynthesis in *A. germinans* when fertilized with N, photosynthetic rates were not highly correlated with leaf N concentrations. This may indicate that N availability is not the limiting factor for photosynthesis of *L. racemosa* at this site, and is only partially limiting photosynthesis in *A. germinans*.

Other species have also shown low sensitivity to fertilization with N. For example, a weak correlation among photosynthesis and leaf N has been observed in a study of a desert evergreen species (Lajtha and Whitford 1989), and in arctic dwarf species (Baddeley et al. 1994). Weak relationships among maximum rates of photosynthesis and leaf N concentrations are proposed to occur where species have evolved under conditions where investing high concentrations of N in the photosynthetic apparatus is constrained by some other more important environmental pressure (Chapin 1991). The weak relationship among leaf N concentrations and photosynthesis at our hypersaline site suggests N is partitioned into non-photosynthetic tissues, and that in *A. germinans* this somehow, possibly indirectly, leads to increases in rates of photosynthesis. Additionally, in *L. racemosa* fertilization with N appeared to alleviate salinity-related reductions in photosynthesis (Fig. 2). One possible mechanism that could account for the positive effect of N on photosynthesis in *A. germinans* is that N is invested in the osmotically compatible solute, glycine betaine (Popp et al. 1996), resulting in improved water status of tissues. In either species, N could be invested in a greater number of growing apices (roots, shoots or reproductive structures), which in turn may enhance photosynthesis through increased sink strength (Cheeseman 1988; Farrar 1996).

#### Photosynthetic nitrogen-use efficiency

PNUE reflects investment of N in photosynthetic tissue compared to other compartments within leaves. In C3 herbaceous species, PNUE was found to be a major determinant of both plant and leaf N productivity (Garnier et al. 1995). However, whole plant NUE may not only be determined by instantaneous PNUE, but can also depend on patterns of allocation of N and the residence time of N

within plant organs, all factors that can vary among species (Berendse and Aerts 1987). For example, DeLucia and Schlesinger (1995) found that PNUE of swamp species from Florida did not correlate with another measure of NUE, the retranslocation of nutrients out of leaves. *L. racemosa* had levels of PNUE that are similar to what has been observed in many other species (Poorter and Evans 1998). In contrast, *A. germinans* had low PNUE's, approximately half of that observed for *L. racemosa*, and were similar to values reported for Californian desert shrubs (Field et al. 1983). Low PNUE in *A. germinans* is likely due to allocation of N to non-photosynthetic pools (e.g. glycine betaine), although direct measurements of N partitioning have not yet been made. The PNUE of *A. germinans* was insensitive to fertilization and salinity. In contrast, PNUE of *L. racemosa* declined with salinity, suggesting that high salinity compromised this species' utilization of N resources.

#### Trade-offs among PNUE and PWUE and implications for coexistence

After studying photosynthesis in five species of evergreens, Field et al. (1983) first hypothesized there was a tradeoff between PNUE and PWUE in C3 plants. Species with both higher PWUE and PNUE were simply not possible because opening stomata to allow high rates of photosynthesis per unit of nitrogen resulted in catastrophic water loss in plants inhabiting water limited environments. Our data support this hypothesis (Fig. 4), as do other studies (Reich et al. 1989; Mulkey et al. 1991; Wang et al. 1998). *L. racemosa* has relatively high PNUE, but low PWUE, making it a "nutrient conservation specialist". In contrast, *A. germinans* has very low PNUE, and high PWUE making it a "water conservation specialist".

The commonly observed dominance of *A. germinans* in highly saline and hypersaline soils is likely to be at least partially due to its high PWUE. Additionally, if highly saline sites are enriched in N then *A. germinans* may be even more likely to dominate over *L. racemosa*. A recent study has detailed the distribution of mangrove species with respect to soil resource levels. Sherman et al. (1998) found the distribution of *A. germinans* was highly correlated to sediment N concentrations (measured at 50 cm depth), while the distribution of *L. racemosa* was correlated with surface water P concentrations. At their site, *A. germinans* became the dominant species at low salinity, but at high N concentrations. All three common mangrove species (*L. racemosa*, *R. mangle* and *A. germinans*) coexisted in the intertidal zone at a region where salinity was intermediate, N concentrations were low, and P was high or variable. *R. mangle* dominated low in the intertidal. Building on the arguments of McKee (1995), Sherman et al. (1998) hypothesize that *L. racemosa* is the most responsive to high nutrient levels and may out-compete other species where nutrient resources are high. From the results presented here, an

alternative hypothesis is that *L. racemosa* occupies a realized niche constrained by competition with *A. germinans* where nitrogen concentrations are high, and possibly constrained by competition from *R. mangle* lower in the intertidal, or by abiotic stress imposed by flooding (McKee 1996).

We also hypothesize that coexistence of *L. racemosa* and *A. germinans* is facilitated at high salinity by low soil N levels, allowing competitive rates of carbon gain in *L. racemosa*. Additionally, species differences in phenology (M.L. Ewe, unpublished data) and photosynthetic rates over seasons (C.E. Lovelock and I.C. Feller, unpublished data) may indicate that resource use is temporally partitioned by these species, which could also facilitate coexistence (Chesson 1986). For example, each species may experience a period of time that is more favorable for photosynthesis and growth than it is for the other species. Seasonal variation in salinity due to annual patterns in rainfall and evaporation could be responsible, and has been proposed to explain the distribution of other sympatric mangrove species (Ball and Pidsley 1995).

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