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Growth and physiological responses of neotropical mangrove seedlings to root zone hypoxia

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Summary Seedlings of *Rhizophora mangle* L., *Avicennia germinans* (L.) Stearn., and *Laguncularia racemosa* (L.) Gaertn. f. were cultured in aerated or N_2-purged solution for 12 weeks to assess their relative responses to low oxygen tensions. All three species responded to low oxygen treatment by modifying physiological and morphological patterns to decrease carbon loss by root respiration. However, the extent to which seedling physiology and morphology were altered by low oxygen treatment differed among species. Maintenance of root oxygen concentrations, root respiration rates and root extension rates by *R. mangle* demonstrated an ability to avoid low oxygen stress with minimal changes in root morphology and physiology. In contrast, oxygen concentrations in *A. germinans* and *L. racemosa* roots declined from 16 to 5% or lower within 6 h of treatment. Root hypoxia led to significant decreases in respiration rates of intact root systems (31 and 53% below controls) and root extension rates (38 and 76% below controls) by *A. germinans* and *L. racemosa*, respectively, indicating a greater vulnerability of these species to low oxygen tensions in the root zone compared with *R. mangle*. I conclude that the relative performance of mangrove seedlings growing in anaerobic soils is influenced by interspecific differences in root aeration and concomitant effects on root morphology and physiology.

Keywords: carbon loss, flood tolerance, forested wetland, oxygen, root respiration, tropical trees.

Introduction

Mangroves are salt- and flood-tolerant trees and shrubs that inhabit the intertidal zone along many tropical and subtropical coastlines (Tomlinson 1986). Three species, *Rhizophora mangle* L. (red mangrove), *Avicennia germinans* (L.) Stearn. (black mangrove), and *Laguncularia racemosa* (L.) Gaertn. f. (white mangrove) are common to Florida and the Caribbean region where their spatial distributions across the intertidal zone suggest differential flood tolerance (McKee 1993*a*, 1993*b*, 1995). Because seedling mortality and growth directly influence spatial distribution and abundance of trees, knowledge of seedling responses to soil aeration is essential to an understanding of regeneration patterns across flooding gradients typical of these intertidal forests. Little information exists, however, on mangrove species' differences in flood tolerance or mechanisms allowing seedlings to survive flooding (McKee 1993*a*, 1993*b*). In contrast, extensive work has been conducted to determine impacts of soil aeration and flooding on tree species in freshwater habitats (Kozlowski et al. 1991).

Field observations of seedling distributions and results of controlled flooding experiments demonstrate that relative survival and growth of neotropical mangrove species vary with depth and duration of flooding (McKee 1993*a*, 1993*b*, 1995). One explanation for differential performance is interspecific differences in ability to avoid oxygen deficiencies when seedlings are periodically flooded. An alternative hypothesis is that flooding does not substantially impact root aeration in seedlings, but instead, generates changes in biomass partitioning patterns or morphology that decrease a species' potential to acquire other limiting resources, e.g., nutrients or light. Previous work has shown that anaerobic solution culture results in decreased internal root aeration and altered root metabolism of *A. germinans* seedlings (McKee and Mendelssohn 1987). However, interspecific differences in morphological and physiological responses of neotropical mangrove seedlings to low oxygen tensions have not been assessed.

The aim of this study was to compare the relative resistance of *R. mangle*, *A. germinans*, and *L. racemosa* to low oxygen tensions and to determine how seedlings avoid or tolerate root hypoxia. These objectives were addressed in a controlled experiment that allowed measurements of root aeration as well as shoot and root growth and physiology. The results, which demonstrated differential responses of species to low oxygen in the root zone, provide insight into mechanisms influencing mangrove seedling performance across flooding gradients.

Materials and methods

Plant material

Random samples of *R. mangle*, *A. germinans*, and *L. racemosa* propagules (200–300 per species) were collected from several sites along the Belize coast, (16°50′ N, 88°06′ W) during the dispersal period (December). A subset of propagules determined to be free of insects was transported to the greenhouse

at Louisiana State University where the propagules were established in individual pots containing sand flooded with 10% (w/v) artificial seawater (Instant Ocean®, Aquarium Systems, Inc., Mentor, OH) and supplemented with a 10% nutrient solution (Hoagland and Arnon 1950). After two months, the seedlings were carefully removed from their containers by slowly flushing the sand from around the roots. Fresh weights were determined, and ten individuals per species were harvested immediately to provide an initial fresh to dry mass relationship. The remainder were transferred to solution culture for experimentation.

Experimental procedures

Relative responses of the three species to low oxygen tensions were examined in solution culture purged with N_2. Although N_2 purging does not generate an oxygen demand as great as flooded soil (Sorrell and Armstrong 1994), it does increase the gradient for oxygen diffusion from the atmosphere to the root zone and causes oxygen deficiencies in the roots of mangroves (McKee and Mendelssohn 1987). In addition, solution culture allows an assessment of the response to oxygen deficiency exclusive of other factors that may vary with flooding intensity (e.g., phytotoxins or nutrient availability).

The two-month-old seedlings were transferred to solution culture in 1 dm^3 plastic containers with threaded lids drilled with openings for the stem and aeration tubing as described previously (McKee and Mendelssohn 1987). The seedlings were positioned in the containers so that a minimum of stem was below the lids, and the solution level was maintained flush with the lid to minimize head space. The culture solution (25% Hoagland solution plus 1 mM MES buffer) was vigorously aerated at 40 $cm^3\ min^{-1}$ and adjusted in steps to 35‰ salinity (w/v with artificial sea salts), which is typical of the intertidal habitat in which these species occur. The seedlings were randomly assigned to two treatments: solution culture purged with either air (control) or N_2 gas at a rate of 40 $cm^3\ min^{-1}$. The shoots remained exposed to the atmosphere, and constant N_2 purging maintained oxygen concentrations in the treatment rooting medium below 0.05 mM. The seedlings were maintained in a growth chamber adjusted to provide day/night temperatures of 27/24 °C, a relative humidity of about 75%, and a 14-h photoperiod. Irradiance at mid-canopy level was 400 $\mu mol\ m^{-2}\ s^{-1}$, which is typical of conditions in small canopy gaps in mangrove forests where regeneration takes place (McKee 1995). Solutions were changed weekly, but disturbance of the root systems was minimized by rapid ($\leq$ 45 s) replacement with pre-aerated or N_2-purged solutions.

An additional set of seedlings was similarly prepared for determination of short-term changes in root oxygen concentrations. Gas samples were extracted for oxygen measurement as described below at intervals over a 24-h period of N_2 purging, followed by re-aeration.

Physiological measurements

Rates of net photosynthesis and transpiration were determined with an open-flow, differential system (Analytical Development Company, LCA-2, Hoddeson, UK). Measurements were conducted between 0900 and 1100 h, with the first fully expanded leaf pair (rinsed with deionized water to remove salt crystals) at ambient quantum flux densities in the growth chamber (400 $\mu mol\ m^{-2}\ s^{-1}$) and ambient CO_2 concentrations (367 $\pm$ 2 ppm). Molar air flow, transpiration rate, leaf conductance and CO_2 uptake were calculated according to von Caemmerer and Farquhar (1981).

Respiration rates of the intact root systems were determined by measuring CO_2 efflux according to Nobel and Palta (1989), with the following modifications. The seedling root systems were surface sterilized (0.5% NaOCl), rinsed with deionized water, and placed in a water bath (25 °C) in a darkened root chamber. The compressed gas stream, which was humidified before entering the root chamber, contained either 0 or 21% O_2 to maintain experimental conditions during respiration measurements. In addition, the gas stream (5 $cm^3\ s^{-1}$) was passed through a soda lime column to absorb CO_2 before entering the root chamber, a precaution that ensured root respiration was not differentially affected by variation in CO_2 concentrations in the gas streams (Reuveni et al. 1993). Both analytical and reference gas streams were passed through columns of magnesium perchlorate to lower and equalize relative humidities before entry into the infrared gas analyzer. The CO_2 differential was recorded 30 min after transfer of each root system to the chamber. The percentage of daily carbon assimilation lost in root respiration (PRR) was calculated as:

$$\mathrm{PRR} = (R_r W_r)/(L_l A_l)100,$$

where R_r = root respiration rate ($\mu mol\ kg^{-1}\ s^{-1}$), W_r = root biomass (kg), L_l = leaf area (m^2), and A_l = net carbon assimilation rate ($\mu mol\ m^{-2}\ s^{-1}$) (after Van der Werf et al. 1990).

Measurements of photosynthesis and root respiration were conducted once near the end of the 12-week experimental period. To avoid unnecessary stress, particularly to the root systems, repeated measurements were not taken.

Root oxygen measurements

Root oxygen concentrations were determined from gas samples extracted directly from lacunal air spaces. Oxygen concentrations were measured with either a gas chromatograph (Carle Instruments, Loveland, CO) (McKee and Mendelssohn 1987) or a flow-through oxygen system (Model DO 166 FT, Lazar Research Laboratories, Los Angeles, CA) (McKee 1993*b*).

Oxygen concentrations in seedling roots maintained under two aeration regimes for 12 weeks were determined at the end of the experiment. Gas samples for the short-term (48 h) aeration experiment were also taken directly, but with an *in situ* assembly to facilitate repetitive sampling. A small gauge (No. 23) needle was inserted into the root cortex and connected by capillary tubing to a larger needle (No. 18 gauge) fitted with a small septum. The capillary tubing was threaded through an opening in the root chamber lid so that the septum was accessible without interruption of the aeration treatment. A small volume of gas was drawn to evacuate the tubing and discarded before each gas sample (0.3 cm^3) was collected for oxygen

measurement. A standard gas mixture ($[O_2]$ = 10.24%) was used to test the system and to calibrate the oxygen electrode. Roots selected for gas sampling were similar in length and diameter, and the gas sample was extracted at a distance of 4 cm from the root base.

Growth measurements

Average relative growth rates over the experimental period were calculated as the difference in the natural logarithm of initial and final seedling biomass divided by time (12 weeks). Root elongation rates were determined once during the eighth week by measuring changes in the length of tagged roots. After 12 weeks, the seedlings were harvested and divided into component parts. The fresh leaves were photocopied, and leaf area was determined gravimetrically (Beerling and Fry 1990). Total number, length, and diameter (mid-root) of main root axes were also determined. Specific root length (SRL) was calculated by dividing length (cm) by biomass (g) of root sections. The total number of lateral roots was counted on two representative root axes per seedling. Root-specific gravity was determined by the pycnometer method (Jensen et al. 1969) and converted to root porosity, based on a predetermined relationship between specific gravity and porosity for each species (McKee 1993*b*). Cross-sectional air space area (CSA) was calculated as the product of the mid-root cross-sectional area and porosity. All tissue was freeze-dried and final dry weights of leaves, stems, and roots were determined.

Statistical analyses

Numbers of replications necessary to detect significant differences for each plant variable were calculated based on preliminary measurements of sample variance and the desired confidence interval (Steele and Torrie 1980). A two-way ANOVA was conducted on data collected from the seedlings grown with or without aeration for 12 weeks. Time course changes in root oxygen concentrations were assessed with a multi-way repeated measures ANOVA, where aeration treatment was the grouping factor and time was the within-factor repeated measure. Measurements of photosynthesis and root respiration were conducted in a randomized block design to account for potential diurnal variation. Analysis showed no block effect, indicating that variation over the measurement period was not significant ($P > 0.05$). Significant differences among means were determined by contrast analysis, and unless otherwise stated, all significant differences were determined at the 0.05 probability level. In a few cases, the data were log-transformed to stabilize the variance before ANOVA, but the untransformed means ± 1 SE are used for presentation of results.

Results

Root oxygen concentrations

Root oxygen concentrations declined from 16 to below 5% within 6 h after *L. racemosa* and *A. germinans* were subjected to N_2 purging (Figure 1). On re-aeration, root oxygen concentrations began to recover to pretreatment values. In contrast, oxygen concentrations inside *R. mangle* roots were independent of external oxygen tensions (Figure 1).

Growth response

In response to aeration, significant differences in root morphology and root extension rates occurred among species

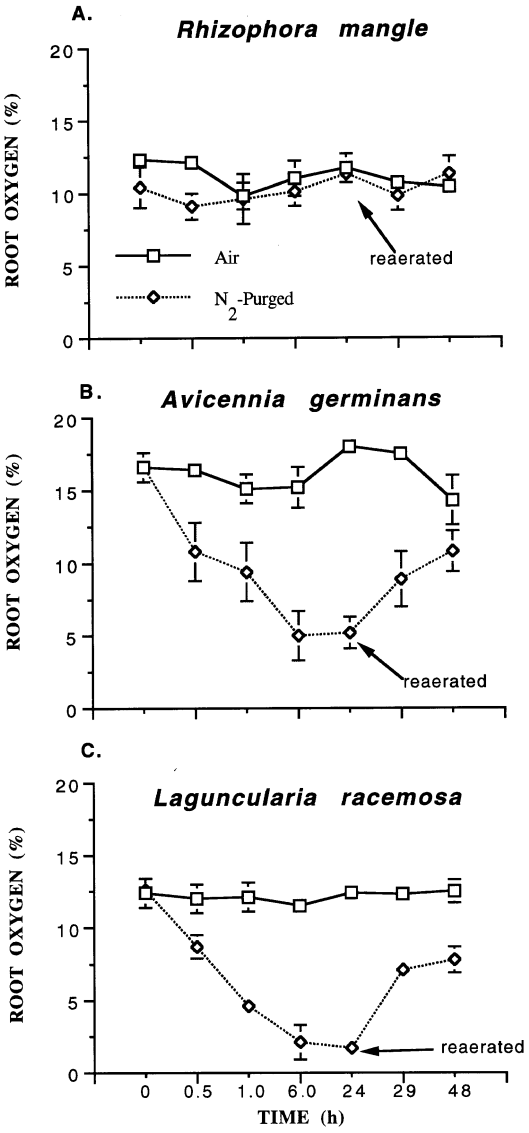

Figure 1. Effect of aeration treatment on internal root oxygen concentrations (%) of *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* seedlings grown in solution culture. Values are means ± SE (n = 3). Arrows indicate when N_2-purging was stopped and root chambers were re-aerated. A repeated measures ANOVA indicated significant effects of treatment ($F_{1,4}$ = 17.7, P = 0.014; $F_{1,4}$ = 37.66, P = 0.0036) and time ($F_{6,24}$ = 11.2, P = 0.0001; $F_{6,24}$ = 52.2, P = 0.0001) and a significant interaction ($F_{6,24}$ = 12.9, P = 0.0001; $F_{6,24}$ = 44.6, P = 0.0001) for *A. germinans* and *L. racemosa*, respectively. There were no significant effects of treatment ($F_{1,4}$ = 0.85, $P > 0.05$) or time ($F_{6,24}$ = 1.60, $P > 0.05$) and no interaction ($F_{6,24}$ = 1.51; $P > 0.05$) for *R. mangle*.

Table 1. Characteristics of *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* root systems after 12 weeks in solution culture subject to two aeration treatments. See text for calculations of specific root length (SRL), porosity, and cross-sectional air space area (CSA). Values are means (± SE) (n = 5). Results of a 2-way ANOVA are indicated at the end of the table; NS = nonsignificant F-value.

Treatment	Number of main root axes	Average root length (cm)	Maximum root length (cm)	Root diameter (mm)	SRL (cm g^{-1})	Laterals per cm	Porosity (%)	CSA (mm^2)
Rhizophora								
Air	7.4 (0.9)	8.9 (1.2)	12.5 (1.1)	3.3 (0.8)	55 (12)	3.7 (1.0)	8 (2)	32 (7)
N_2-purged	6.0 (0.9)	9.2 (1.1)	12.3 (1.5)	3.5 (0.6)	54 (17)	2.8 (1.4)	9 (3)	27 (6)
Avicennia								
Air	4.0 (0.5)	21.8 (1.3)	28.7 (1.4)	2.5 (0.4)	105 (36)	1.8 (0.2)	23 (1)	118 (30)
N_2-purged	6.2 (0.4)	15.3 (2.1)	20.1 (1.5)	2.8 (0.3)	82 (11)	1.3 (0.3)	30 (4)	214 (73)
Laguncularia								
Air	3.0 (0.7)	26.9 (2.0)	30.6 (2.5)	2.1 (0.2)	170 (33)	1.8 (0.2)	15 (1)	49 (11)
N_2-purged	4.8 (0.4)	14.0 (2.5)	19.6 (2.6)	1.5 (0.1)	165 (34)	1.4 (0.4)	19 (1)	36 (7)
Probability of > F								
Treatment	NS	0.0002	0.0001	NS	NS	0.007	NS	NS
Species	NS	0.0001	0.0001	0.001	0.0009	0.0001	0.0001	0.0001
Treatment × Species	0.023	0.006	0.008	NS	NS	NS	NS	NS

(Table 1, Figure 2). Hypoxia caused a significant decrease in root extension rates of *A. germinans* and *L. racemosa* (38 and 76%, respectively, below aerated controls), but not of *R. mangle* (15% below aerated controls) (Figure 2, Table 1). Hypoxia also caused dieback of *L. racemosa*'s root tips. All three species responded to hypoxia with a decrease in number of lateral roots (Table 1). Although no significant effect of aeration treatment on SRL was found, there were substantial differences among species in the following order: *L. racemosa* > *A. germinans* > *R. mangle* (Table 1). Significant species differences in root diameter, porosity, and CSA were found, but treatment effects were not significant (Table 1).

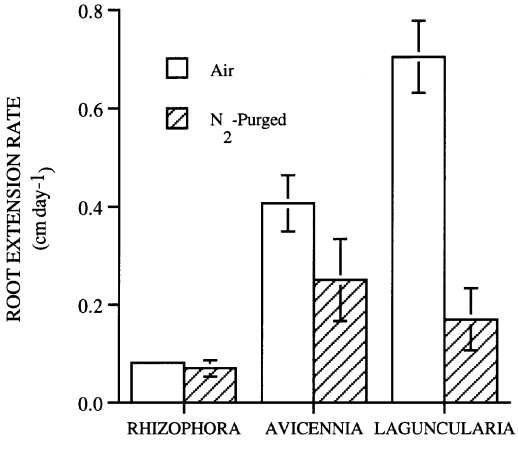

Figure 2. Root extension rates (cm day^{-1}) by *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* seedlings grown for 8 weeks in solution culture subject to two aeration treatments. Values are means ± SE (n = 5). A 2-way ANOVA indicated significant main effects of treatment ($F_{1,24}$ = 24.6, P = 0.0001) and species ($F_{2,24}$ = 21.9, P = 0.0001) and a significant interaction ($F_{2,24}$ = 9.89, P = 0.0007).

Aeration treatment had a significant positive effect on shoot height, but no effects on total leaf area or relative growth rate (Table 2). Root hypoxia caused an increase in height of *R. mangle* and *A. germinans* shoots (34 and 18% above controls, respectively), but only a 3% increase in height of *L. racemosa* shoots (Table 2). Interspecific differences in growth rate, leaf area, and shoot height were significant when averaged over aeration treatments. Relative growth rate and total leaf area of *Rhizophora mangle* were lower than those of the other two species (Table 2). After 12 weeks in solution culture, total biomass of *R. mangle* (9.0 ± 0.7 g) was significantly greater ($F_{2,24}$ = 8.12, P = 0.0024) than that of *A. germinans* (5.9 ± 0.7 g) and *L. racemosa* (4.0 ± 0.7 g), primarily because of its large hypocotyl, which develops while the seedling is still attached to the parent tree.

Physiological response

Root respiration rates increased linearly with temperature (20 to 45 °C) for all three species. Arrhenius plots revealed a disjunction in the respiration curves between 30 and 35 °C (Figure 3). The Q_{10} values for *R. mangle*, *A. germinans*, and *L. racemosa* were significantly different (P < 0.05) over the temperature range of 20–30 °C (1.48, 1.73, and 2.68, respectively), but similar at a range of 30–40 °C (1.32, 1.52, and 1.47, respectively). The activation energy also differed among species in the 20–30 °C range (Figure 3).

Root respiration rates in aerated solution culture were highest for *L. racemosa* and lowest for *R. mangle* (Figure 4). Low oxygen tensions in the N_2-purged solution, however, caused a 31 and 53% decrease in root respiration rates of *A. germinans*

Table 2. Growth and shoot morphology of *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* seedlings grown for 12 weeks in solution culture subject to two aeration treatments. Values are means ± SE (n = 5). Results of a 2-way ANOVA are indicated at the bottom of the table; NS = nonsignificant F-value.

Treatment	Relative growth rate ($g\ g^{-1}\ week^{-1}$)	Shoot height (cm)	Leaf area (cm^2)	Basal stem diameter (cm)
Rhizophora				
Air	0.022 ± 0.003	21.0 ± 1.8	93 ± 17	1.31 ± 0.04
N_2-purged	0.017 ± 0.006	28.1 ± 2.9	82 ± 16	1.23 ± 0.07
Avicennia				
Air	0.078 ± 0.011	22.2 ± 2.5	208 ± 36	0.53 ± 0.03
N_2-purged	0.085 ± 0.007	26.1 ± 0.8	257 ± 47	0.67 ± 0.06
Laguncularia				
Air	0.082 ± 0.012	12.1 ± 1.4	221 ± 33	0.36 ± 0.04
N_2-purged	0.075 ± 0.019	12.4 ± 0.7	215 ± 60	0.51 ± 0.04
Probability of > F				
Treatment	NS	0.0217	NS	NS
Species	0.0001	0.0001	0.0016	0.0001
Treatment × Species	NS	NS	NS	NS

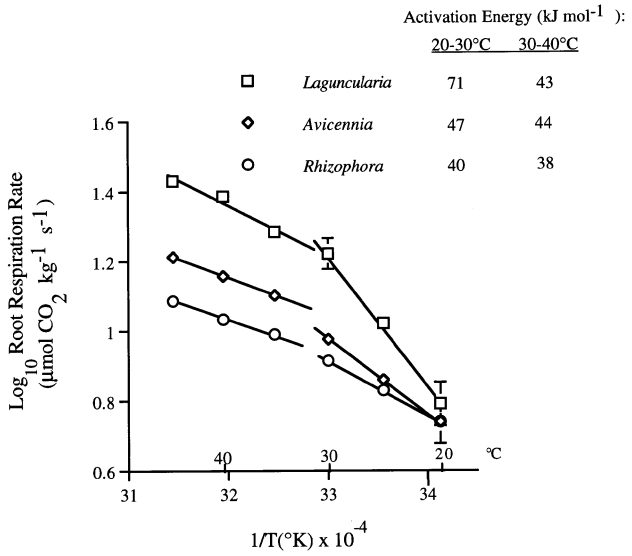

Figure 3. Arrhenius plots ($\log_{10}$ of the respiration rate plotted against the reciprocal of the absolute temperature, $1/T$) for *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* seedlings. Values are means ± SE (n = 2). Standard error bars are smaller than symbols in some cases. Activation energies for root respiration over two temperature ranges were also calculated for each species. Apparent breaks in the Arrhenius plots suggest that the temperature dependence of root respiration rate changes near 30 °C.

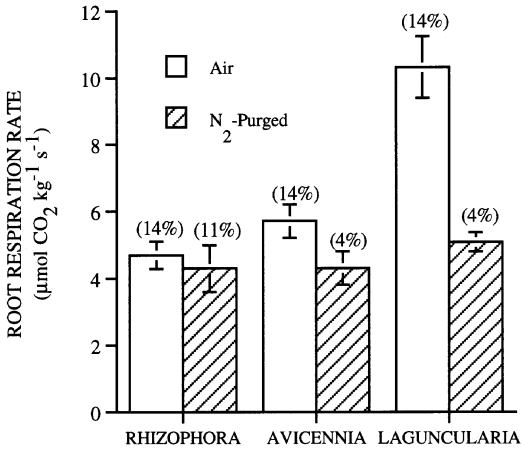

Figure 4. Root respiration rates (μmol $CO_2\ kg^{-1}\ s^{-1}$) of *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* seedlings measured after 12 weeks in solution culture subject to two aeration treatments. Values are means ± SE (n = 5). A 2-way ANOVA indicated significant main effects of treatment ($F_{1,24}$ = 32.7, P = 0.0001) and species ($F_{2,24}$ = 16.8, P = 0.0001) and a significant interaction ($F_{2,24}$ = 11.1, P = 0.0004). Internal root oxygen concentrations are indicated in parentheses above each bar.

and *L. racemosa*, respectively, but no significant change in root respiration rate of *R. mangle*. *Avicennia germinans* and *L. racemosa* seedlings grown for 12 weeks in N_2-purged solutions also had significantly lower root oxygen concentrations compared with aerated controls (Figure 4).

There were no significant differences in net photosynthetic rate or leaf conductance among the three species or between aeration treatments (P > 0.05, data not shown). Water use efficiency (mmol $CO_2\ mol^{-1}\ H_2O$), however, differed among species as follows: *R. mangle* (6.5 ± 0.6) > *A. germinans* (5.7 ± 0.3) > *L. racemosa* (4.3 ± 0.7) (P = 0.0021).

The percentage of daily carbon loss to root respiration (PRR) differed significantly among the three species and decreased in response to hypoxia (Figure 5). The lack of a

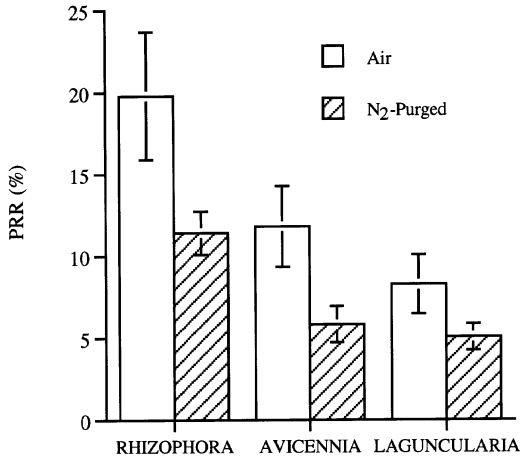

Figure 5. The percent of fixed carbon lost through root respiration (PRR) by *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* seedlings grown for 12 weeks in solution culture subject to two aeration treatments. See text for calculations. Values are means ± SE (n = 5). Results of a 2-way ANOVA indicated significant main effects of treatment ($F_{1,24}$ = 4.3, P = 0.049) and species ($F_{2,24}$ = 11.8, P = 0.0003), but no interaction ($F_{2,24}$ = 1.03, P > 0.05).

significant interaction between treatment and species indicated that the pattern of response to hypoxia was similar across species. There was also a significant negative correlation between PRR and relative growth rate (R = –0.493, P = 0.01), indicating that root respiratory losses of carbon accounted for approximately 24% of the variation in seedling growth rates.

Discussion

Previous work with *A. germinans* seedlings demonstrated that hypoxic treatment caused a decrease in root oxygen concentration, a switch to anaerobic pathways of metabolism, and a decline in root energy status (McKee and Mendelssohn 1987). The results of the current study showed a similar response to low oxygen tension by *A. germinans*, but additionally demonstrated interspecific differences in the ability of mangroves to avoid root oxygen deficiencies (Figure 1). Substantial decreases in root oxygen concentration, respiration rate and extension rate by *A. germinans* and *L. racemosa* roots and dieback of *L. racemosa* root tips indicated that low oxygen tensions interfered with root aeration, which in turn induced changes in physiology and growth patterns. In contrast, *R. mangle* showed minimal morphological and physiological root responses to low oxygen in the culture solution.

Differences in root aeration following exposure to hypoxic conditions may be due to several factors. In the current study, the root systems were not isolated from a supply of oxygen, because the shoots remained exposed to the atmosphere. The effectiveness of oxygen transport in maintaining internal concentrations was, therefore, dependent on: (1) resistance of the diffusional pathway and (2) oxygen losses along the diffusional pathway (Armstrong and Beckett 1987). The diffusional resistance is directly related to pathway length and tortuosity and inversely related to porosity (% air space). The oxygen loss is determined by respiration and leakage to the surrounding medium (Armstrong and Gaynard 1976, Chiu-Yu and Chou 1993, Sorrell and Armstrong 1994).

Significant decreases in root oxygen concentrations demonstrated that a short-term imbalance between oxygen supply and oxygen loss occurred in roots of *A. germinans* and *L. racemosa*, but not of *R. mangle*, when the external oxygen concentrations in solution were lowered (Figure 1). The gradient for oxygen diffusion out of the roots was increased by N_2 purging and probably caused the decline in root oxygen concentrations in *L. racemosa* and *A. germinans* (Sorrell and Armstrong 1994). Possible reasons for the maintenance of root oxygen concentrations in *R. mangle* include: (1) a relatively higher diffusive conductance of oxygen through the shoot to the root system; (2) lower root respiration rates; and (3) a relatively lower root permeability to oxygen leakage. A greater oxygen diffusion gradient (e.g., in a flooded soil) would induce greater leakage from plant roots (Sorrell and Armstrong 1994), and possibly generate lower oxygen concentrations in *R. mangle* roots than reported here, but the relative effect on the other two mangrove species would likely be greater (Figure 1). Differences in porosity or CSA (Table 1) cannot explain the pattern of response to root aeration. Measurements of field-grown mangroves indicate that porosity is somewhat variable depending on age and soil conditions, but the patterns generally do not show a positive relationship between root porosity and relative flood tolerance (e.g., seedling/adult root porosity: *R. mangle* = 30 ± 5%/58 ± 2%, *A. germinans* = 43 ± 4%/60 ± 1%, *L. racemosa* = 20 ± 5%/33 ± 1%; K. L. McKee, unpublished data).

The three mangrove species showed little change in net carbon assimilation or conductance per unit leaf area in response to low oxygen tensions as reported elsewhere for plants grown in flooded soil culture (Pezeshki et al. 1990). However, measurements of aboveground gas exchange do not incorporate root respiration, and consequently may not accurately assess physiological response to root hypoxia. Up to 30% of carbon fixed in photosynthesis is respired in roots, and variation in PRR can be a major factor determining plant growth responses (Van der Werf et al. 1990). For the three mangrove species, a negative correlation between PRR and relative growth rate suggested that decreases in the proportion of fixed carbon lost through root respiration would have a positive influence on growth. The decrease in mangrove seedling PRR may explain why relative growth rates were not significantly decreased under low oxygen treatment.

Ecological implications

Flood-tolerant trees exhibit various morphological and physiological adaptations to waterlogged soils that allow avoidance or tolerance of low oxygen conditions, depending on the species and environmental conditions (Kozlowski et al. 1991). This study has shown that mangrove seedlings modify physiological and morphological patterns so that the balance between carbon acquisition and carbon loss through root respiration is maintained during low oxygen conditions in the

root zone. As a consequence, hypoxia *per se* did not affect overall growth rates of mangrove seedlings under the experimental conditions.

Field and greenhouse experiments, however, have shown that these species differ in their sensitivity to flooding stress: *R. mangle* < *A. germinans* < *L. racemosa* (McKee 1993*a*, 1993*b*, 1995). The current study has further shown that these mangrove species differ in their ability to maintain root aeration when external oxygen concentrations are low, and that root aeration in turn affects root morphology and physiology. Changes in root growth and morphology would affect seedling ability to acquire nutrients, a process strongly influenced by root morphology (Boot 1990), root extension rates (Christie and Moorby 1975), and root energy status (Koch et al. 1990). In addition, tidal fluctuation causes periodic submergence of mangrove seedlings and, depending on seedling height growth, may interact with edaphic factors to inhibit root aeration differentially.

Other environmental factors may interact with flooding to influence seedling performance in the field. Soil temperature in mangrove forests, for example, is influenced by irradiance and varies with canopy structure and occurrence of light gaps (McKee 1993*b*, McKee 1995). Interspecific differences in Arrhenius plots and activation energies (Figure 3) indicate that seedling growth responses will vary spatially and temporally as a result of temperature effects on root respiration rates.

Species distribution in mangrove forests has often been attributed to specialized adaptation of species to factors that vary across the intertidal zone. Considerable work has focused on salinity responses (Ball 1988*a*, 1988*b*, Lin and Sternberg 1993), but much less is known about effects of other stresses associated with the mangrove habitat. The pattern of seedling response to low oxygen in the root zone indicates that differential flood tolerance during early growth is also an important factor contributing to mangrove regeneration patterns.

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