

Leaf gas exchange characteristics of three neotropical mangrove species in response to varying hydroperiod

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Summary We determined how different hydroperiods affected leaf gas exchange characteristics of greenhouse-grown seedlings (2002) and saplings (2003) of the mangrove species *Avicennia germinans* (L.) Stearn., *Laguncularia racemosa* (L.) Gaertn. f., and *Rhizophora mangle* L. Hydroperiod treatments included no flooding (unflooded), intermittent flooding (intermittent), and permanent flooding (flooded). Plants in the intermittent treatment were measured under both flooded and drained states and compared separately. In the greenhouse study, plants of all species maintained different leaf areas in the contrasting hydroperiods during both years. Assimilation–light response curves indicated that the different hydroperiods had little effect on leaf gas exchange characteristics in either seedlings or saplings. However, short-term intermittent flooding for between 6 and 22 days caused a 20% reduction in maximum leaf-level carbon assimilation rate, a 51% lower light requirement to attain 50% of maximum assimilation, and a 38% higher demand from dark respiration. Although interspecific differences were evident for nearly all measured parameters in both years, there was little consistency in ranking of the interspecific responses. Species by hydroperiod interactions were significant only for sapling leaf area. In a field study, *R. mangle* saplings along the Shark River in the Everglades National Park either demonstrated no significant effect or slight enhancement of carbon assimilation and water-use efficiency while flooded. We obtained little evidence that contrasting hydroperiods affect leaf gas exchange characteristics of mangrove seedlings or saplings over long time intervals; however, intermittent flooding may cause short-term depressions in leaf gas exchange. The resilience of mangrove systems to flooding, as demonstrated in the permanently flooded treatments, will likely promote photosynthetic and morphological adjustment to slight hydroperiod shifts in many settings.

Keywords: *Avicennia germinans*, carbon assimilation, flooding, *Laguncularia racemosa*, photosynthesis, *Rhizophora mangle*, stress physiology, water-use efficiency.

Introduction

Globally, mangrove communities are being subjected to altered flood depths and durations as a result of sea-level rise (Woodroffe 1990, Ellison and Stoddart 1991, Ellison 1993, Parkinson et al. 1994, Woodroffe 1999) and human-induced regional hydrologic changes (Choy and Booth 1994, Twilley et al. 1998, Elster 2000, Mazda et al. 2002). The halophytic nature of true mangroves creates difficulties for scientists attempting to investigate the effects of altered hydroperiod on these coastal systems. On the one hand, inundation with fresh water alone biases assessments of flooding, because optimal growth and physiological activity are likely attained under saline conditions (e.g., Ball 1988, Smith 1992, Ball 1996). On the other hand, salinity at any concentration may confound interpretation of the effects of flooding on mangroves.

Although many studies have investigated the effects of seawater flooding on mangrove seedlings, saplings and trees (see reviews by Popp et al. 1993, Kathiresan and Bingham 2001, Saenger 2002), less is known about the effects that increased flood duration is likely to have on mangrove communities. Studies on the effects of long-term flooding have typically been conducted at optimal salinities. For instance, the growth of *Avicennia marina* (Forsk.) Vierh. and *Aegiceras corniculatum* (L.) Blanco was enhanced by flooding with salinities between 7 and 9 g l⁻¹ (Clarke and Hannon 1970), whereas flooding at similar salinities had no effect on *A. marina* seedlings (Naidoo et al. 1997). Prolonged flooding for up to 80 days with 33% (~12 g l⁻¹) seawater lowered leaf water potential and stomatal conductance in *Bruguiera gymnorrhiza* (L.) Lamk. seedlings, whereas flooding for the same duration with fresh water increased the same parameters (Naidoo 1983). Stomatal conductance was higher in freshwater flood treatments relative to either saline drained or saline flooded treatments for *B. gymnorrhiza*, *A. marina* and *Rhizophora mucronata* Lam. (Naidoo 1985). The study of Naidoo (1985) also indicated that flooding with salt water necessitated greater

osmotic adjustment for seedlings than did flooding with fresh water. Freshwater flooding of *Avicennia germinans* (L.) Stearn. and *Laguncularia racemosa* (L.) Gaertn. f. seedlings for 180 days reduced total leaf area, but it had no effect on net carbon assimilation, stomatal conductance and water-use efficiency, suggesting that increased flood duration may have limited effects on neotropical mangrove communities in the short term (Pezeshki et al. 1990).

Our study was initiated to test how simulated hydroperiods affect leaf gas exchange characteristics of *A. germinans*, *L. racemosa* and *R. mangle* seedlings and saplings over two growing seasons. In addition, we investigated leaf gas exchange responses of *R. mangle* saplings growing at various field sites in flooded and drained conditions. Our interest in determining the relative responses to flooding of neotropical mangrove seedlings and saplings relates to our continued development of unit-level (Chen and Twilley 1998) and landscape-level (Doyle and Girod 1997, Doyle et al. 2003) forest simulation models in support of hydrologic rehabilitation in southern Florida, USA. Our findings link experimental hydroperiods and mangrove susceptibility to different degrees of flooding.

Materials and methods

Greenhouse study

Plant material Fruits or propagules from at least five trees of each of *A. germinans*, *L. racemosa* and *R. mangle* were collected from intertidal environments on Terra Ceia Island near Bradenton, Florida (27° N, 82° W). Fruits or propagules were sown in 180-ml nursery tubes placed on benches under ambient conditions for about 4 months. In December 2001, seedlings were transported to Lafayette, Louisiana (30° N, 92° W) and kept on nursery benches at the National Wetlands Research Center (U.S. Geological Survey); subtropical temperatures were maintained throughout the winter in the greenhouse. Seedlings were then transported to a greenhouse at the Center for Ecology and Environmental Technology (University of Louisiana at Lafayette). After a 1-month acclimation period, each seedling was transplanted to a 27-l white, plastic bucket containing a 5:1 (v/v) mix of peat moss and sand. A 2-cm layer of sand was placed on the surface of each pot to bind peat soils during flood simulations. Initial seedling heights averaged 25.8 ± 0.8 (SE) cm for *A. germinans*, 26.2 ± 0.9 cm for *L. racemosa* and 17.8 ± 0.5 cm for *R. mangle*.

The buckets containing seedlings were placed in 473-l plastic tanks (PT-4822, Polytank Inc., Litchfield, MN) and maintained at a salinity of 7.9 ± 1.1 (SD) g l^{-1} with a commercial seawater mix (Instant Ocean, Aquarium Systems, Mentor, OH). Tank salinity was monitored about every 5 days with a conductivity meter (Model 30, YSI, Yellow Springs, OH) and adjusted to a target value of 8 g l^{-1} . Seedlings were fertilized with a commercial water-soluble 20,20,20 N,P,K fertilizer with micronutrients about every 45 days at a mean rate of 15.6 mg l^{-1} of pot volume. Low background salinity concentrations and adequate soil nutrient concentrations were maintained to promote seedling growth for a better evaluation of

hydroperiod effects among these obligate halophytes (cf. Medina 1999). Water was completely flushed from all tanks and replaced three times over the 424-day experiment to avoid anoxic, stagnant water conditions atypical of the open hydrology of mangrove communities in southern Florida. The hydroperiods maintained similar, though highly variable, soil redox potentials at 10 cm (-4.7 ± 18.2 (SE) mV) during the first year; however, there was a distinct odor of hydrogen sulfide gas during harvest at a depth of about 25 cm in the flooded treatments (Day 424), which was not evident in the unflooded or intermittent flooded treatments.

Beginning in April 2002, seedlings were subjected to the hydroperiod treatments for two growing seasons and harvested as saplings in August 2003. Irradiance in the greenhouse was about 41% of ambient for southern Florida; integrated diurnal light flux, with maximum instantaneous values of $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$, averaged $12.9 \text{ mol day}^{-1}$ during measurements. For comparison, integrated light flux from open sites in southern Florida (Rookery Bay, Naples) averaged 31.8 ± 8.6 (SD) mol day^{-1} for May and June of 2003. Greenhouse temperatures were maintained above 8 °C during winter months but were usually much higher, whereas summer temperatures did not exceed 43 °C and were usually much lower.

Experimental design Three buckets of seedlings of each species were randomly assigned to mixed species arrays in 15 independently maintained tanks. This provided 135 seedlings distributed among five independent experimental replications with all three species having equal representation, but in a different order within each tank.

Hydroperiod treatments included an unflooded hydroperiod (unflooded), an intermittently flooded hydroperiod (intermittent), and a permanently flooded hydroperiod (flooded). For flooded hydroperiods, plants were flooded to about 5–10 cm above the soil surface for the duration of the experiment. Water levels in unflooded hydroperiods were maintained about 15–20 cm below the soil surface to ensure well-saturated soils without flooding. Intermittent hydroperiods included periodic flood and drain cycles in accord with data collected from basin hydrogeomorphic zones (cf. Lugo and Snedaker 1974) in the Rookery Bay National Estuarine Research Reserve (Naples, Florida). While the tanks were flooded, water was maintained at 5–10 cm above the soil surface for periods of 1 to 4 weeks. Flooding was simulated on 11 occasions during the experiment. While the tanks were drained, water was maintained about 15 cm below the soil surface. Water for intermittent hydroperiod simulations was stored in plastic drums, continuously recirculated while stored, and recycled to the experiment. Water was replaced in cycles with the other two hydroperiods. Over the two growing seasons, intermittent hydroperiods were flooded for 189 days, and flooded hydroperiods were flooded for 424 days.

Leaf gas exchange measurements All plants were seedlings (< 1 m tall) during the first growing season (2002), whereas many attained sapling size (> 1 m tall) by the end of the second growing season (2003). The response of leaf gas exchange to

the hydroperiod treatments was measured over 17 days during the 2002 growing season and over 22 days during the 2003 growing season. Measurements were taken in late July and early August of each year.

Individual seedlings or saplings were randomly selected from each treatment tank the day before measurements (after 1500 h) and placed under a green, 75% neutral density shade cloth ($\sim 20\text{--}100 \mu\text{mol m}^{-2} \text{s}^{-1}$) to limit light exposure prior to the light response measurements the following day. From each plant, a single leaf was selected from one of the two highest nodes, with each leaf in an apparent lag phase of growth (i.e., hardened cuticle) on either an apical or strong axillary meristem. On the following day, each selected leaf was placed randomly in the cuvette of an LI-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE) at ambient temperature, a reference CO_2 of $375 \mu\text{mol mol}^{-1}$ and a photosynthetic photon flux (PPF) of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (red/blue light source) for at least 7 min until steady rates of assimilation were observed. The lag between a change in leaf transpirational status and leaf water potential has been recorded as 2–7 min for *A. germinans* (Naidoo and von Willert 1994). After equilibration, the sample CO_2 concentration was adjusted to $375 \mu\text{mol mol}^{-1}$, leaf temperature was set constant to the initial equilibrated cuvette temperature, and humidity was held at ambient. Net CO_2 exchange was measured for each leaf at PPFs of 1500, 1000, 500, 200, 100, 50, 20 and $0 \mu\text{mol m}^{-2} \text{s}^{-1}$, with a 2–5 min re-acclimation interval between measurements.

Field study

Plant material and experimental design Saplings of *R. mangle* were selected from understory locations along the Shark River Slough (SRS) in Everglades National Park, Florida (25°N , 81°W). Sampling sites SRS-4, SRS-5 and SRS-6 were located about 18.2, 9.9 and 4.1 km, respectively, from the mouth of the Shark River, and the sites differed in forest structure, fertility, hydroperiod and salinity regime (Chen and Twilley 1999). The SRS-6 had a distinct tidal hydroperiod, whereas SRS-5 and SRS-4 had progressively dampened aboveground tidal influences and distinct seasonal flooding during wet months (May to October: Krauss 2004).

All saplings were located within 15 m inland of the Shark River and were shaded. During gas exchange measurements, understory irradiance at the leaf plane averaged $54 \mu\text{mol m}^{-2} \text{s}^{-1}$ but ranged from 5 to $650 \mu\text{mol m}^{-2} \text{s}^{-1}$. Height of *R. mangle* saplings in SRS-4 averaged 1.02 ± 0.08 (SE) m, whereas heights in SRS-5 and SRS-6 averaged 0.92 ± 0.06 m and 1.02 ± 0.05 m, respectively. Saplings across all sites had 5–161 leaves and as many as 13 primary branches.

Measurements were taken between 1100 and 1600 h in December 2002, when soils were drained at all sites, and at the same times again in October 2003, when soils were flooded at all sites. Saplings were selected from within a 40-m^2 area. Saplings were haphazardly selected and represented plants that appeared healthy.

Leaf gas exchange measurements Net assimilation (A_n), stomatal conductance (G_w), transpiration (T_r) and instantaneous

water-use efficiency (WUE) were measured on one leaf for each selected *R. mangle* sapling. Individual leaves were selected as described for the greenhouse-grown plants. Each leaf was placed in the cuvette of an LI-6400 Portable Photosynthesis System at ambient temperature, ambient humidity, and a PPF of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (red/blue light source) for at least 10 min, but often longer, until steady rates of assimilation were observed.

Statistical analysis

Greenhouse study All assimilation-light response curves were fit for individual leaves by nonlinear regression (rectangular hyperbola) as $A = (A_{\text{max-g}} \text{PPF}) / (K + \text{PPF}) - R_d$, where $A_{\text{max-g}}$ is gross assimilation rate at light saturation, K is the PPF at 50% of $A_{\text{max-g}}$, and R_d is the dark respiration rate (Givnish 1988). Net assimilation at light saturation (A_{max}) was determined graphically, and apparent quantum yield (ϕ) was determined from the first derivative of the equation for A at a PPF of $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ as $\phi = (A_{\text{max-g}} K) / (K^2 + 2K(\text{PPF}) + \text{PPF}^2)$. Light compensation point (LCP) was determined as $K R_d / (R_d - A_{\text{max-g}})$ (Gardiner and Krauss 2001). Between five and seven leaves were analyzed for each treatment combination (species \times hydroperiod) for both growing seasons as simultaneous and independent replicates, as suggested by Lederman and Tett (1981).

Instantaneous water-use efficiency ($\text{WUE} = A_n / T_r$) was also measured at a PPF of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Total leaf area was determined according to the relationships between leaf length and area for sample seedlings in 2002 (nondestructive) and according to species-specific relationships between fresh mass and area for all leaves of all saplings in 2003 after harvest (destructive). Leaf area was measured with a portable leaf area meter (LI-3000A, Li-Cor).

The experiment was analyzed as a randomized block with one among-subject factor (hydroperiod) and one within-subject factor (species) (Zar 1999). Error terms for both factors were random and included replication ($n = 5$) nested within hydroperiod ($n = 3$) as all or part of the term. Data were analyzed with ANOVA and were square root or natural log transformed where appropriate to satisfy normality and homogeneity of residual variance assumptions. Post-hoc statistical groupings were determined with a Tukey's studentized range test with Bonferroni adjustment at $\alpha = 0.05$ as the rejection criterion. For intermittent hydroperiods, a repeated measures ANOVA was used on pooled data from 2002 and 2003 to determine whether individual gas exchange variables were different when plants were drained versus flooded. All analyses were performed with SAS version 8.02 software (SAS Institute, Cary, NC).

Field study We evaluated effects on A_n , G_w , T_r and WUE by ANOVA using a fully factorial design with a fixed error term (MSE). A priori contrasts compared drained versus flooded conditions in pair-wise comparisons. Data were square root transformed where appropriate to ensure normality and homogeneity of residual variances. Post-hoc statistical groupings were determined with a Tukey's studentized range test at

$\alpha = 0.05$ as the rejection criterion. All analyses were performed with SAS version 8.02 software.

Results

Greenhouse study

Seedling response (2002) With the exception of *R. mangle* in the intermittent hydroperiod, little divergence existed among assimilation–light response curves by species for seedlings subjected to different hydroperiods after only one growing season (Figure 1). Among the six leaf gas exchange variables reported, none differed significantly for seedlings growing in unflooded, intermittent, or flooded hydroperiods (Table 1). For example, A_{\max} varied by only $1.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ among hydroperiods for *A. germinans* (Table 2). Variation in A_{\max} was 3.7 and $4.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *L. racemosa* and *R. mangle* seedlings, respectively. In contrast to the gas exchange variables, leaf area differed among hydroperiods. Non-significant

hydroperiod by species interactions for leaf area (Table 2) and mean separations among treatments indicated that, for all species, seedlings had greater leaf area in unflooded hydroperiods than in flooded hydroperiods over the first growing season. The large relative leaf area response of *L. racemosa* to the hydroperiod treatments dominated this trend.

In contrast to the effects of hydroperiod, species response differed significantly for many gas exchange parameters (Table 1). *Rhizophora mangle* maintained lower ϕ and A_{\max} than *A. germinans*; however, *R. mangle* did not differ significantly from *A. germinans* in total leaf area (Table 2). *Laguncularia racemosa* had the greatest leaf area among species (673 cm^2) but maintained similar leaf-level capacities for R_d , A_{\max} and K as *R. mangle* in all hydroperiod treatments. Among species, WUE ranged from 3.3 to 4.0. *Laguncularia racemosa* seedlings had higher WUE than *A. germinans* seedlings, but neither species differed significantly from *R. mangle* (Table 2).

Rhizophora mangle seedlings did not maintain a steady rate

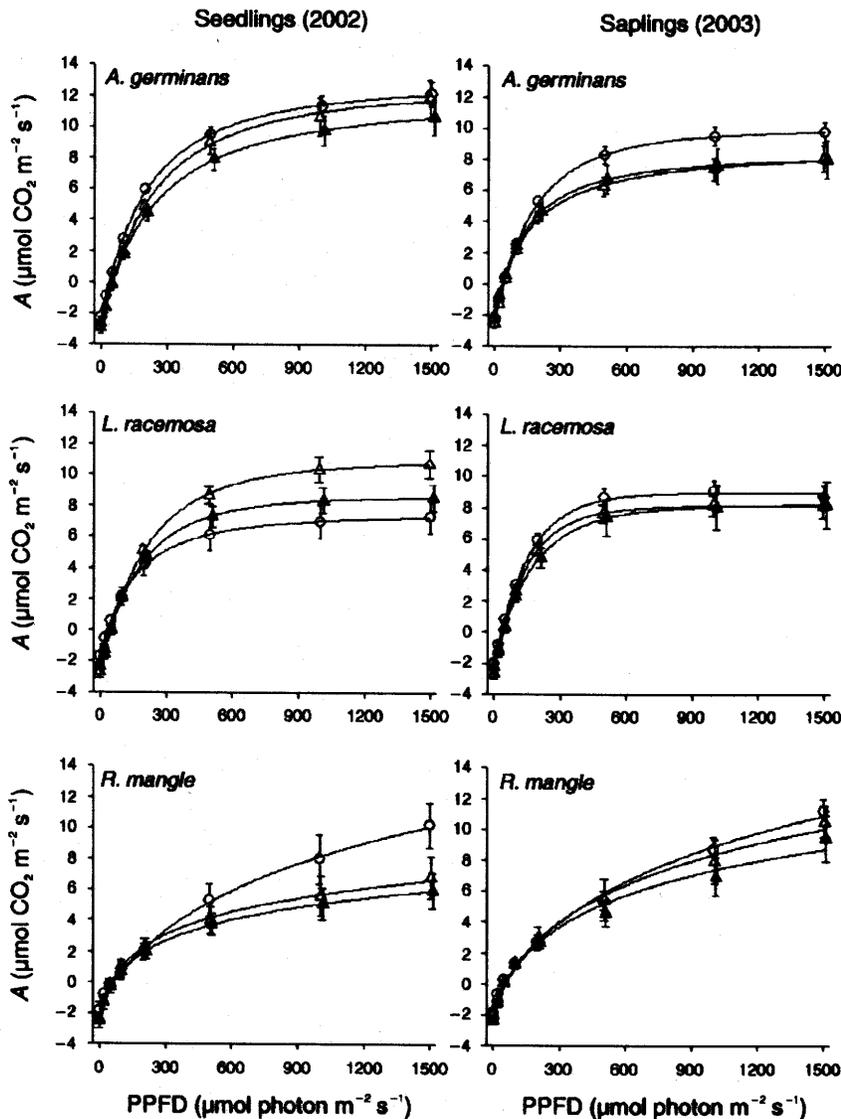


Figure 1. Assimilation–light response (A) for seedlings (2002) and saplings (2003) of *A. germinans*, *L. racemosa* and *R. mangle* subjected to three hydroperiod treatments: \blacktriangle = unflooded; \circ = intermittent; and \triangle = flooded. Carbon assimilation is reported on a per leaf area basis (± 1 SE). Abbreviation: PPFD = photosynthetic photon flux density.

Table 1. Assimilation response curve analysis for seedlings (2002) and saplings (2003) grown under experimental greenhouse conditions. Abbreviations: R_d = daytime dark respiration; ϕ = apparent quantum yield; A_{max} = net photosynthesis rate at light saturation; LCP = light compensation point; K = photosynthetic photon flux (PPF) required to achieve 50% of gross A_{max} ; and WUE = instantaneous leaf-level water use efficiency at a PPF of $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Source of variation	DF, DF _{error}	Leaf gas exchange					
		R_d	ϕ	A_{max}	LCP	K	WUE
<i>Seedlings (2002)</i>							
Hydroperiod	2, 12	n.s. ¹	n.s.	n.s.	n.s.	n.s.	n.s.
Species	2, 20	n.s.	***	*	*	n.s.	**
Hydroperiod × Species	4, 20	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Saplings (2003)</i>							
Hydroperiod	2, 12	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Species	2, 20	n.s.	***	n.s.	***	***	**
Hydroperiod × Species	4, 20	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

¹ Significance level: n.s.: $P > 0.05$; *: $P = 0.01-0.05$; **: $P = 0.01-0.001$; and ***: $P < 0.001$.

of leaf CO_2 gas exchange during the approximately 25-min period it took to make the assimilation–light response curve measurements. Instead, A (as shown in Figure 1), T_r and G_w of these seedlings were all low initially at low irradiances relative to rates maintained at higher irradiances. This response manifested as lower ϕ and higher relative LCP for *R. mangle* (Table 2).

Sapling response (2003) Similar to the seedling responses during 2002, the hydroperiod treatments had little effect on leaf gas exchange of the saplings at the end of the second growing season. The fit of assimilation–light response curves by species and hydroperiod combinations was tighter for saplings than for seedlings (Figure 1). For 2003, A_{max} varied by 1.9, 1.0 and $2.0 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ among hydroperiods for saplings of *A. germinans*, *L. racemosa* and *R. mangle*, respectively (Table 3). Species × hydroperiod interactions were not significant for any gas exchange parameter (Table 1) but were significant for leaf area, prompting leaf area analysis among treatment combinations (Table 3). Leaf area was higher for flooded *L. racemosa* saplings than for unflooded *L. racemosa* saplings and differed from the leaf area of saplings of *A. germinans* and *R. mangle* in all hydroperiod treatments. Leaf area for *L. racemosa* averaged $4,852 \text{ cm}^2$ but was over $11,000 \text{ cm}^2$ for some saplings.

Interspecific differences for saplings were significant for some of the same parameters as found for the seedlings during the first growing season; however, *A. germinans* saplings did not maintain higher A_{max} than *R. mangle* or *L. racemosa* saplings (Table 3). For *R. mangle*, ϕ remained low, whereas LCP and K were significantly higher than in *L. racemosa* and *A. germinans* saplings, reflecting a gradual increase in assimilation rate with increasing irradiance for *R. mangle* (Figure 1). Sapling WUE ranged from 3.8 to $5.2 \mu\text{mol CO}_2 \text{mmol H}_2\text{O}^{-1}$,

with neither *R. mangle* nor *A. germinans* differing from *L. racemosa*, but WUE of *R. mangle* and *A. germinans* differed. Hence, WUE shifted from being higher in *L. racemosa* seedlings than in *A. germinans* seedlings in 2002 to being higher in *R. mangle* saplings than in *A. germinans* saplings in 2003.

Intermittent hydroperiod: short-term flood response All gas exchange measurements previously discussed were taken when the intermittent hydroperiod treatments were drained. Measurements of seedlings and saplings when the intermittent hydroperiod treatments were flooded indicated that R_d , A_{max} and K differed significantly relative to flood state, whereas species × flood state interactions were not significant for any parameter except LCP (Table 4). In all species, plants in drained soils maintained 38% lower R_d than plants in flooded soils (Figure 2), and A_{max} was 20% higher and K was 102% higher for unflooded mangroves than for flooded mangroves.

Field study

Understory *R. mangle* saplings differed significantly depending on location along the Shark River in A_n ($F_{2,99} = 23.12$; $P < 0.001$), G_w ($F_{2,99} = 13.20$; $P < 0.001$) and T_r ($F_{2,99} = 10.48$; $P < 0.001$), but not in WUE ($F_{2,99} = 0.97$; $P = 0.382$). Saplings growing on the two most seaward sites (SRS-6, SRS-5) maintained higher A_n , G_w , and T_r than saplings from the more inland site along the Shark River (SRS-4, Figure 3), which was located near an ecotone boundary to a freshwater marsh. Pairwise contrasts indicated that flooded saplings tended to have higher A_n , G_w and T_r than drained saplings. Significant interactions between site location and flood state for all variables, including WUE, indicated that site conditions, which included different hydroperiods, influenced comparisons. Statistically significant trends included enhanced A_n in drained soils on SRS-5 relative to drained soils on SRS-4 and SRS-6, and reduced WUE in drained soils on SRS-6 relative to flooded soils on the same site (Figure 3).

Discussion

Mangroves have been classified as stress tolerant (cf. Grime 1977, McKee 1995) and, hence, are expected to have a low capacity for resource acquisition or a hormonally mediated growth constraint under many environmental conditions (Chapin 1991). Mangroves are extremely productive wetland ecosystems, however, and some regions support trees with high growth rates that export large amounts of organic carbon (Twilley 1985, Twilley et al. 1986, Saenger 2002). For the mangrove seedlings and saplings developing under different hydroperiods in our study, the significant interspecific differences indicate that the plants were under few, if any, resource constraints and that the effects of the various long-term hydroperiod treatments were negligible.

Initially, *Avicennia germinans* seedlings maintained higher rates of gas exchange for two out of six parameters than *R. mangle* seedlings (Table 2). By the second year, however, A_{max} of *R. mangle* saplings increased relative to that of *A. ger-*

Table 2. Leaf gas exchange variables (\pm SE) for *A. germinans*, *L. racemosa* and *R. mangle* seedlings (2002) subjected to three hydroperiod treatments under greenhouse conditions. Values noted with the same letter for a particular species are not significantly different at $\alpha = 0.05$. Abbreviations: R_d = daytime dark respiration; ϕ = apparent quantum yield; A_{\max} = net photosynthesis rate at light saturation; LCP = light compensation point; K = photosynthetic photon flux (PPF) required to achieve 50% of gross A_{\max} ; and WUE = instantaneous leaf-level water-use efficiency at a PPF of $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$. For all parameters, hydroperiod \times species interactions were not significant (Table 1); treatment and species means followed by the same letter are not different at $\alpha = 0.05$.

Species	Unflooded		Intermittent		Flooded		Species mean	
R_d ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)								
<i>A. germinans</i>	-2.7 \pm 0.4	-	-2.3 \pm 0.2	-	-2.9 \pm 0.4	-	-2.6 \pm 0.2	a
<i>L. racemosa</i>	-2.3 \pm 0.2	-	-1.7 \pm 0.3	-	-2.7 \pm 0.5	-	-2.2 \pm 0.2	a
<i>R. mangle</i>	-2.5 \pm 0.5	-	-1.9 \pm 0.6	-	-2.4 \pm 0.3	-	-2.3 \pm 0.3	a
Treatment mean	-2.5 \pm 0.2	a	-1.9 \pm 0.2	a	-2.7 \pm 0.2	a		
ϕ ($\mu\text{mol CO}_2$ ($\mu\text{mol photon}^{-1}$))								
<i>A. germinans</i>	0.040 \pm 0.003	-	0.048 \pm 0.002	-	0.045 \pm 0.003	-	0.044 \pm 0.002	a
<i>L. racemosa</i>	0.040 \pm 0.003	-	0.036 \pm 0.004	-	0.044 \pm 0.002	-	0.040 \pm 0.002	a
<i>R. mangle</i>	0.027 \pm 0.003	-	0.022 \pm 0.008	-	0.029 \pm 0.005	-	0.027 \pm 0.003	b
Treatment mean	0.037 \pm 0.002	a	0.037 \pm 0.004	a	0.040 \pm 0.002	a		
A_{\max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)								
<i>A. germinans</i>	11.7 \pm 1.2	-	13.4 \pm 0.8	-	13.0 \pm 1.3	-	12.7 \pm 0.7	a
<i>L. racemosa</i>	9.4 \pm 0.9	-	8.1 \pm 1.2	-	11.8 \pm 1.0	-	9.7 \pm 0.7	b
<i>R. mangle</i>	6.6 \pm 1.3	-	11.2 \pm 1.6	-	7.5 \pm 1.5	-	8.1 \pm 0.9	b
Treatment mean	9.4 \pm 0.8	a	10.8 \pm 0.8	a	11.1 \pm 0.9	a		
LCP ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)								
<i>A. germinans</i>	38.6 \pm 7.1	-	27.7 \pm 1.8	-	36.3 \pm 5.2	-	34.5 \pm 3.1	ab
<i>L. racemosa</i>	28.5 \pm 2.4	-	25.5 \pm 6.8	-	32.0 \pm 5.1	-	28.7 \pm 2.7	b
<i>R. mangle</i>	39.3 \pm 5.5	-	83.2 \pm 32.0	-	45.6 \pm 14.8	-	53.1 \pm 10.4	a
Treatment mean	35.3 \pm 3.1	a	40.8 \pm 9.9	a	37.5 \pm 4.7	a		
K ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)								
<i>A. germinans</i>	247.9 \pm 33.9	-	216.0 \pm 11.1	-	241.5 \pm 28.8	-	236.1 \pm 15.4	a
<i>L. racemosa</i>	173.7 \pm 15.3	-	159.4 \pm 18.2	-	214.1 \pm 24.3	-	181.9 \pm 11.7	a
<i>R. mangle</i>	241.4 \pm 101.7	-	938.9 \pm 487.8	-	267.6 \pm 117.8	-	436.1 \pm 150.3	a
Treatment mean	220.0 \pm 28.6	a	375.5 \pm 138.0	a	239.6 \pm 33.2	a		
WUE ₁₀₀₀ ($\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$)								
<i>A. germinans</i>	2.95 \pm 0.24	-	3.61 \pm 0.25	-	3.27 \pm 0.42	-	3.26 \pm 0.19	b
<i>L. racemosa</i>	4.51 \pm 0.54	-	4.40 \pm 0.29	-	3.09 \pm 0.39	-	4.03 \pm 0.28	a
<i>R. mangle</i>	3.21 \pm 0.43	-	4.22 \pm 0.27	-	3.18 \pm 0.41	-	3.47 \pm 0.25	ab
Treatment mean	3.57 \pm 0.28	a	4.06 \pm 0.18	a	3.19 \pm 0.23	a		
Leaf area (cm^2) ¹								
<i>A. germinans</i>	308.0 \pm 27.9	-	217.3 \pm 14.6	-	192.3 \pm 28.6	-	236.8 \pm 18.2	b
<i>L. racemosa</i>	763.7 \pm 129.6	-	890.8 \pm 184.6	-	567.7 \pm 95.3	-	672.9 \pm 77.4	a
<i>R. mangle</i>	227.8 \pm 21.8	-	242.7 \pm 27.4	-	192.7 \pm 13.8	-	227.5 \pm 13.2	b
Treatment mean	443.4 \pm 70.3	a	396.8 \pm 84.0	ab	317.6 \pm 53.4	b		

¹ Leaf area of sample plants only; hydroperiod \times species interactions were not significant ($P = 0.360$); Treatment: $P = 0.019$; Species: $P < 0.001$.

minans saplings (Table 3), possibly because of a loss of maternal hypocotyl reserves in *R. mangle*. Loss of hypocotyl reserves in *R. mangle* also may have led to relative enhancements in ϕ (Table 2) and G_w (data not shown) between 2002 and 2003. Reduced G_w is a characteristic of mangroves (Ball et al. 1988, Pezeshki et al. 1990); this reduction is perhaps related adaptively to the prolonged retention of the hypocotyl. Stomata of *R. mangle*, hence, may close readily in response to tissue water deficits because hypocotyl reserves decrease the demand for photosynthates and hence lessen the need to balance carbon assimilation by leaf water loss.

Instantaneous WUE is usually high in mangroves (Andrews and Muller 1985, Ball 1986). In our study, mean instantaneous WUE ranged from 3.3 to 5.2 $\mu\text{mol mmol}^{-1}$ and was high in both seedlings and saplings of *L. racemosa*, though indistinguishable from that of *R. mangle* (Tables 2 and 3). Various reported rank orders for seedling WUE include *L. racemosa* < *A. germinans* < *R. mangle* (mean range of 4.3–6.5 $\mu\text{mol mmol}^{-1}$; McKee 1996) and *A. germinans* < *R. mangle* < *L. racemosa* (mean range of 4.1–9.0 $\mu\text{mol mmol}^{-1}$; Pezeshki et al. 1990). Higher WUE may reflect a greater competitive potential for the individual species by reducing salt buildup

Table 3. Leaf gas exchange variables (\pm SE) for *A. germinans*, *L. racemosa* and *R. mangle* saplings (2003) subjected to three hydroperiod treatments under experimental greenhouse conditions. Values noted with the same letter for a particular species are not significantly different at $\alpha = 0.05$. Abbreviations: R_d = daytime dark respiration; ϕ = apparent quantum yield; A_{max} = net photosynthesis rate at light saturation; LCP = light compensation point; K = photosynthetic photon flux (PPF) required to achieve 50% of gross A_{max} ; and WUE = instantaneous leaf-level water-use efficiency at a PPF of $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$. For these parameters, hydroperiod \times species interactions were not significant (Table 1); treatment and species means followed by the same letter are not different at $\alpha = 0.05$.

Species	Unflooded		Intermittent		Flooded		Species mean	
R_d ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)								
<i>A. germinans</i>	-2.0 ± 0.2	–	-2.5 ± 0.2	–	-2.5 ± 0.3	–	-2.3 ± 0.1	a
<i>L. racemosa</i>	-2.3 ± 0.5	–	-2.0 ± 0.2	–	-2.7 ± 0.4	–	-2.3 ± 0.2	a
<i>R. mangle</i>	-2.4 ± 0.2	–	-1.9 ± 0.2	–	-2.0 ± 0.2	–	-2.1 ± 0.1	a
Treatment mean	-2.2 ± 0.2	a	-2.1 ± 0.1	a	-2.4 ± 0.2	a		
ϕ ($\mu\text{mol CO}_2$ ($\mu\text{mol photon}$) $^{-1}$)								
<i>A. germinans</i>	0.041 ± 0.003	–	0.046 ± 0.001	–	0.043 ± 0.002	–	0.043 ± 0.001	a
<i>L. racemosa</i>	0.041 ± 0.005	–	0.047 ± 0.001	–	0.047 ± 0.002	–	0.045 ± 0.002	a
<i>R. mangle</i>	0.027 ± 0.003	–	0.023 ± 0.007	–	0.023 ± 0.006	–	0.024 ± 0.003	b
Treatment mean	0.036 ± 0.002	a	0.039 ± 0.003	a	0.038 ± 0.003	a		
A_{max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)								
<i>A. germinans</i>	8.9 ± 1.3	–	10.8 ± 0.7	–	8.9 ± 1.0	–	9.5 ± 0.6	a
<i>L. racemosa</i>	9.1 ± 1.6	–	10.1 ± 0.7	–	9.1 ± 0.8	–	9.4 ± 0.6	a
<i>R. mangle</i>	10.3 ± 1.6	–	12.3 ± 0.9	–	11.6 ± 1.1	–	11.4 ± 0.7	a
Treatment mean	9.4 ± 0.8	a	11.0 ± 0.5	a	9.8 ± 0.6	a		
LCP ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)								
<i>A. germinans</i>	21.8 ± 2.2	–	26.8 ± 2.4	–	25.8 ± 2.9	–	24.8 ± 1.4	b
<i>L. racemosa</i>	23.8 ± 5.0	–	19.7 ± 2.0	–	23.0 ± 3.5	–	22.1 ± 2.0	b
<i>R. mangle</i>	54.0 ± 10.0	–	115.8 ± 48.5	–	145.5 ± 67.7	–	107.2 ± 29.3	a
Treatment mean	32.6 ± 4.8	a	51.0 ± 16.8	a	64.8 ± 25.0	a		
K ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)								
<i>A. germinans</i>	140.5 ± 19.0	–	171.6 ± 13.0	–	146.2 ± 14.6	–	152.8 ± 9.1	b
<i>L. racemosa</i>	145.5 ± 26.0	–	138.0 ± 9.1	–	124.8 ± 12.4	–	135.6 ± 9.1	b
<i>R. mangle</i>	386.6 ± 94.6	–	1195.0 ± 535.6	–	1158.7 ± 500.6	–	926.3 ± 253.4	a
Treatment mean	219.8 ± 40.0	a	466.9 ± 186.1	a	476.6 ± 191.6	a		
WUE ₁₀₀₀ ($\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$)								
<i>A. germinans</i>	4.35 ± 0.66	–	3.21 ± 0.28	–	3.89 ± 0.48	–	3.82 ± 0.29	b
<i>L. racemosa</i>	3.66 ± 0.39	–	4.91 ± 0.46	–	4.79 ± 0.63	–	4.57 ± 0.31	ab
<i>R. mangle</i>	5.71 ± 1.02	–	4.22 ± 0.27	–	4.83 ± 0.83	–	5.15 ± 0.43	a
Treatment mean	4.64 ± 0.46	a	4.33 ± 0.27	a	4.50 ± 0.38	a		
Leaf area (cm^2) ¹								
<i>A. germinans</i>	2106.1 ± 289.6	bc	2172.1 ± 140.4	bc	1739.1 ± 190.1	bc	2005.8 ± 125.1	–
<i>L. racemosa</i>	2648.4 ± 861.8	c	5235.4 ± 728.7	ab	6674.9 ± 525.4	a	4852.9 ± 476.9	–
<i>R. mangle</i>	1934.2 ± 257.0	bc	2549.2 ± 182.2	bc	2058.7 ± 165.5	bc	2180.7 ± 122.6	–
Treatment mean	2229.6 ± 311.1	–	3318.9 ± 322.8	–	3490.9 ± 389.4	–		

¹ Overall leaf area from experiment; hydroperiod \times species interactions were significant ($P < 0.001$); treatment combination means followed by the same letter are not significantly different at $\alpha = 0.05$.

and water deficits at threshold salinities (Pezeshki et al. 1990). Throughout the experiment, *L. racemosa* had among the highest WUEs (Tables 2 and 3) and growth rates (Krauss 2004).

Previous studies have indicated that flooding alone has few potential direct effects on mangroves, but that by-products of flooding can influence mangrove growth, metabolic processes and biochemical activity (Ball 1996). After flooding of experimental mesocosms, for instance, soil oxygen can be depleted by 28% after 6 h and by 72% after 20 h (Skelton and Allaway 1996). Oxygen deprivation is an important consequence of

flooding, yet hypoxia is reported to have little effect on mangrove seedling growth (McKee 1996). The insensitivity of seedlings to hypoxia was attributed by McKee (1996) to morphological adaptations to flooding. The production of prop roots (*R. mangle*) and pneumatophores (*A. germinans*, *L. racemosa*) containing large numbers of lenticels was evident in our study, especially in saplings.

Increased oxygen transport to belowground structures can mitigate effects of phytotoxic by-products associated with flooding, including reduced iron, manganese, methane and hy-

Table 4. Pooled within-subject effects of repeated measures analysis by flood state for seedlings and saplings growing in intermittent hydroperiods in flooded versus drained states. Abbreviations: R_d = daytime dark respiration; ϕ = apparent quantum yield; A_{max} = net photosynthesis rate at light saturation; LCP = light compensation point; K = photosynthetic photon flux (PPF) required to achieve 50% of gross A_{max} ; and WUE = instantaneous leaf-level water-use efficiency at a PPF of $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Source of variation	DF	Leaf gas exchange					
		R_d	ϕ	A_{max}	LCP	K	WUE
Flood state ¹	1, 12	**2	n.s.	*	n.s.	**	n.s.
Species \times Flood state	2, 12	n.s.	n.s.	n.s.	*	n.s.	n.s.

¹ Flood state is the repeated factor (i.e., time).

² Significance level: n.s.: $P > 0.05$; *: $P = 0.01-0.05$; and **: $P < 0.01$.

drogen sulfide (Ball 1996, Youssef and Saenger 1998). Flood tolerance of species coincides with root porosity, which can provide 15 to 46% of free air space in mangrove roots, and with physical barriers to oxygen leakage through roots (Youssef and Saenger 1996). Across all hydroperiod treatments in our study, soil redox potentials tended to be higher for

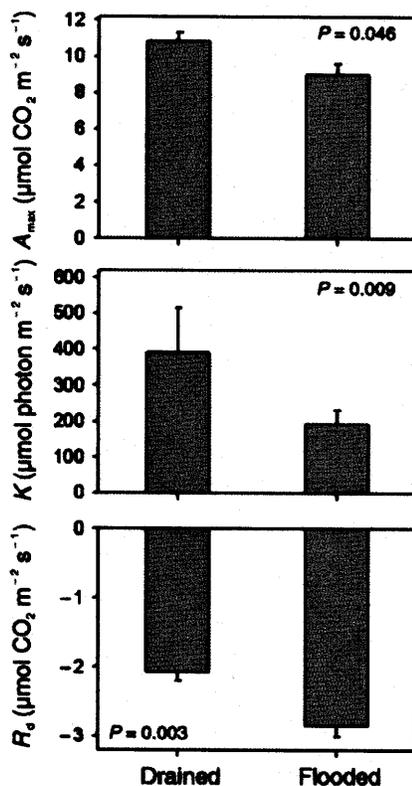


Figure 2. Pooled A_{max} , K and R_d (± 1 SE) of seedlings (2002) and saplings (2003) growing in flooded versus drained states for intermittent hydroperiods. Significance values indicate results of repeated measures analysis with flood state as the repeated factor.

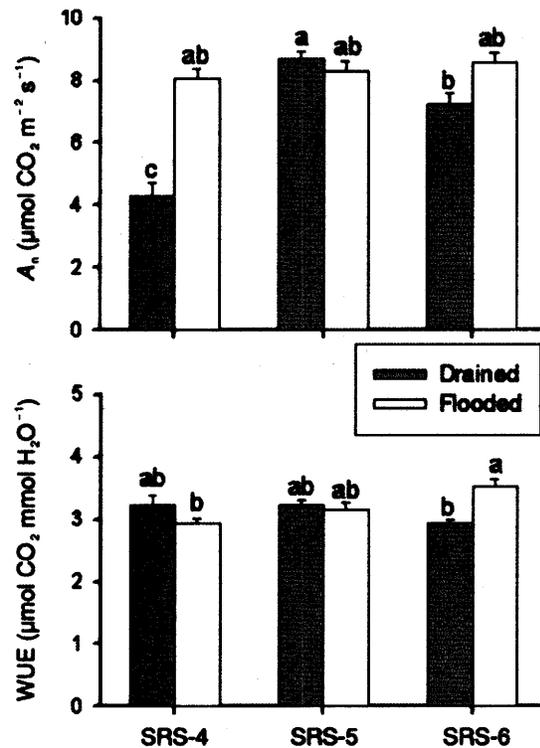


Figure 3. Net assimilation (A_n) and instantaneous water-use efficiency (WUE) of *R. mangle* saplings (± 1 SE) growing along a hydroperiod gradient in the Shark River Slough (SRS), Everglades National Park, Florida. Because interactions between site location and flood state were significant, bars with the same letter are not significantly different among treatment combinations at $\alpha = 0.05$.

L. racemosa and *A. germinans* rhizopheres (13.3 mV) than for *R. mangle* rhizopheres (-42.8 mV), indicating that pneumatophores may be more efficient at oxidizing flooded soils than prop roots, thus partially offsetting the effects of flooding.

Mangrove WUE often increases proportionally to stress (Medina 1999). In our study, no differences in WUE were evident among treatment hydroperiods in seedlings (2002, Table 2), saplings (2003, Table 3) or from different sites along the Shark River (Figure 3). This result provides additional evidence that the hydroperiods tested in our study were not physiologically stressful for mangrove seedlings or saplings. Flooding has been implicated by a past study to have little effect on A_n and T_r and even increase G_w (Naidoo et al 1997), which might explain the insensitivity of the instantaneous WUE (i.e., A_n/T_r) response in our seedlings and saplings. Similarly, saplings along the Shark River from our study maintained greater A_n while flooded than when drained on one site (SRS-4) and maintained greater WUE while flooded than when drained on a different site (SRS-6). Overstory shading or different site physical and chemical conditions may also have affected results along the Shark River.

Short-term flooding for between 6 and 22 days had a greater effect on leaf gas exchange than any of the long-term hydroperiods imposed in this study (Figure 2). Reduced K , for in-

stance, may reflect a greater susceptibility of mangroves to photosystem damage from high irradiance during short-term flood events (Björkman et al. 1988). One potential explanation for the altered characteristics of the light response while seedlings are flooded for short durations may be stomatal adjustments. Stomatal conductance ranged from 0.052 to 0.114 mol m⁻² s⁻¹ among seedlings in 2002 but ranged from 0.104 to 0.141 mol m⁻² s⁻¹ among saplings in 2003, indicating a time-dependent shift. Enhancements in G_w were especially evident for *L. racemosa* and *R. mangle* nearly doubling in both cases. Stomatal closure has been linked to flooding in many studies (Kramer 1969, Kozlowski et al. 1991, Pezeshki 1994), because decreased transpired water replenishment affects guard cell turgor or increases root resistance to water uptake (Naidoo 1983 and references therein). Stomatal adjustments after flooding may, however, proceed slowly. Stomates of *A. marina* seedlings, for example, began closing after 1 day of flooding, while G_w continued to decline for 5 days after the onset of flooding and then remained unchanged for an additional 9 days (Sayed 1995). Longer time periods than those tested here may be required for stomatal recovery after flooding in infrequently flooded neotropical mangrove species.

Among our study species, *R. mangle* exhibited a unique response to the irradiances imposed during the assimilation–light response curve measurements. Some *R. mangle* seedlings and saplings responded initially with a high A_n at the highest irradiance (1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for a short period of time (2–4 min), and then with an uncharacteristically large decrease in A_n of about 2–3 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ at the next lower irradiance (Figure 2). No individual leaves of either *A. germinans* or *L. racemosa* exhibited this response. Perhaps *R. mangle* is sensitive to pressure changes imposed by the leaf cuvette. This response tended to inflate light saturation points and decrease ϕ in *R. mangle*.

In conclusion, our data indicate that the hydroperiod treatments impose few long-term effects on gas exchange in mangrove seedlings and saplings as long as salinity and fertility are held constant. However, short-term flooding in intermittent hydroperiods depressed some gas exchange parameters in the greenhouse. We conclude, therefore, that slightly increased long-term flood durations associated with hydrological rehabilitation may have little effect on neotropical mangrove seedlings or saplings if imposed over long time frames (i.e., measured in months). Leaf gas exchange data for *R. mangle* saplings along the Shark River support results from the greenhouse study and indicate either no effect of flooding or a slight enhancement of A_n and WUE during flooding. Growth responses to flooding, however, may differ from the gas exchange responses, because hydroperiod can interact with nutrient availability to impose shifts in biomass distribution in mangroves. The significant species-level differences across hydroperiods are consistent with the results of previous comparative studies of *A. germinans*, *L. racemosa* and *R. mangle*. The sensitivity of *R. mangle*, and possibly other propagule-bearing mangrove species, to sampling procedures presents difficulties in interpreting the photosynthetic responses to potential environmental stressors.

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