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Influences of salinity and shade on seedling photosynthesis and growth of two mangrove species, *Rhizophora mangle* and *Bruguiera sexangula*, introduced to Hawaii

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Abstract

Rhizophora mangle was first introduced to Hawaii in 1902 to promote shoreline stabilization. Intertidal competition with native and introduced salt marsh species was low, and beyond the early 1920s, mangrove forests expanded rapidly. An additional mangrove species, *Bruguiera sexangula*, was introduced in 1922 and currently co-occurs with *R. mangle* in only a few stands on the north shore and windward sides of Oahu. Where the two species overlap, *R. mangle*, having colonized intertidal zones first, forms nearly monospecific forest stands. To determine why *R. mangle* remains the dominant mangrove, we initiated a greenhouse study to compare seedling growth and photosynthetic light response of both species growing at two light levels and contrasting salinity regimes (2, 10, 32 PSU). The asymptotic nature of *B. sexangula*'s assimilation response is indicative of stomatal regulation, whereas only light level appears to regulate photosynthesis in *R. mangle*. Shifts in patterns of biomass allocation and physiological response indicate two contrasting strategies relative to sunlight and salinity. *B. sexangula*'s strategy is characterized by slow growth with little variation under favorable conditions and morphological plasticity under stressful conditions, which allows for adjustments in carbon gain efficiency (morphological strategy). On the other hand, *R. mangle*'s strategy involves faster growth under a wide range of environmental conditions with physiological enhancement of carbon assimilation (physiological strategy). Low salinity combined with reduced light, or simply low sunlight alone, appears to favor *R. mangle* and *B. sexangula* equally. High

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salinity places greater, but not overwhelming, stress on *B. sexangula* seedlings, but tends to favor *R. mangle* at higher light levels.

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1. Introduction

In Hawaii, where mangroves are not native, several species were introduced in the early 1900s. Of those species, *Rhizophora mangle* L. and *Bruguiera sexangula* (Loir.) Poir. are known to have become naturalized, the former being far more common and widespread (Wester, 1981; Allen, 1998; Allen et al., 2000). Where the two species co-occur in Hawaii, *R. mangle* completely dominates the seaward edge of the stands, while mature *B. sexangula* trees are everywhere less common and are generally restricted to upstream locations. Under the forest canopy of these stands, *B. sexangula* saplings may be relatively common. In these same forests, *R. mangle* overstory trees and seedlings are common throughout, but saplings appear to be common only in gaps.

Based upon inferences made from intertidal distributions, these two species appear to differ in their sensitivity to sunlight and salinity (Clough, 1992; Smith, 1992). The patterns of species and size class distributions we have observed in Hawaii may well be due to the interaction of these two stressors across the intertidal gradient. This study was initiated in order to characterize the relative invasiveness of the two introduced mangrove species to Hawaii and to identify general ecophysiological strategies that may be applicable to other ecological systems. With these considerations in mind, we hypothesized that *B. sexangula* should perform better in shade under moderate salinity than *R. mangle* through differential patterns of photosynthetic carbon acquisition and growth allocation. *R. mangle*, on the other hand, should perform better at high salinity, regardless of light level. Inherent in this study design was the search for “tradeoffs” that might help to explain not only the patterns of mangrove distribution in Hawaii, but also to frame strategies relative to ecophysiological hypotheses proposed by Ball (1998) in describing the maintenance of species diversity along a natural intertidal gradient.

2. Materials and methods

2.1. Collection and greenhouse protocols

Mature *R. mangle* and *B. sexangula* propagules were collected on Oahu in October 1999 either directly from trees or from the ground if they were freshly fallen (i.e., judged as propagules that were firm with barely emerged plumules). Propagules from *R. mangle* were collected from approximately 30 parent trees located within two source stands (Kahaluu and Heeia Swamp, Oahu, HI, USA), and *B. sexangula* propagules were collected from at least eight parent trees in one source stand (Haliewa, Oahu, HI, USA). Propagules were

transported to the University of Hawaii's Agricultural Research Station in Waimanalo, Hawaii, USA. The greenhouse has sides constructed of fiberglass screening and a roof of translucent corrugated fiberglass. Maximum photosynthetic photon flux densities (PPFD) measured over a 15-month period from September 1998 to March 1999 and again from August 1999 to March 2000 were $750\text{--}850\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ while maximum PPFD exterior of the greenhouse was around $2500\ \mu\text{mol m}^{-2}\text{ s}^{-1}$. Air temperature ranged from 18 to $34\ ^\circ\text{C}$, water temperature in treatment mesocosms averaged $25\ ^\circ\text{C}$, and relative humidity averaged 75% over the sampling period.

Propagules that were still floating after several hours in fresh water were selected, and their lengths were measured to the nearest 0.1 cm. They were then placed vertically in 25 cm deep, 656 ml plastic pots filled with a commercial potting medium (Sunshine[®] 1 Mix, SunGro Horticulture, Bellevue, WA, USA). Pots were then assigned randomly to one of six treatment combinations of light and salinity: (1) unshaded, 2 PSU; (2) unshaded, 10 PSU; (3) unshaded, 32 PSU; (4) 80% shade, 2 PSU; (5) 80% shade, 10 PSU; and (6) 80% shade, 32 PSU. The salinity level of 32 PSU (i.e., $32\ \text{PSU} = 32\ \text{g l}^{-1}$) was chosen to approximate the maximum salinity in which *B. sexangula* has been reportedly found, while it remained well within the range of distribution for *R. mangle* (Smith, 1992; Lin and Sternberg, 1993).

Salinity treatments were created with tap water and a commercial seawater mix that closely approximates the true ionic composition of seawater (CoralLife[®], Energy Savers Unlimited Inc., Carson, CA, USA). Pots were flooded to approximately 2 cm below the soil surface, which, because of the capillary movement of water, ensured that all of the soil volume was saturated. Shading was created artificially by using 80% neutral density, black knitted shade cloths (DeWitt Company Inc. Sikeston, MO, USA), which created an average maximum PPFD of $125\ \mu\text{mol m}^{-2}\text{ s}^{-1}$. Each individual treatment combination (i.e., light \times salinity) was assigned randomly to a separate 378 l tank, with a small submersible pump on the bottom to keep water well mixed but not aerated (18 tanks total). All six treatment combinations were replicated three times, with 10 seedlings of each species per salinity/shade combination (360 seedlings in the entire study): 6 treatments \times 3 replicates \times 2 species \times 10 seedlings.

Approximately half way through the 9-month experiment, all tanks were drained, cleaned, and refilled at appropriate treatment salinities; seedlings were watered with tap water to flush out excess salts. Seedlings were fertilized approximately every 28 days with a water-soluble 20–20–20 NPK fertilizer with micronutrients (Scotts Miracle-Gro Products Inc., Port Washington, NY, USA) at an average rate of $0.15\ \mu\text{l ml}^{-1}$ pot volume. Fertilizer was applied to ensure that nutrient limitations did not confound experimental results. Seedlings remained nearly insect-free throughout the experiment, with the exception of minor leaf damage to a few *B. sexangula* seedlings and signs of scale colonization on the tops of *R. mangle* propagules; seedlings were treated twice with a diluted Malathion solution.

2.2. Leaf gas exchange measurements

The effects of light and salinity on leaf gas exchange were evaluated over a period of 21 days, beginning after seedlings had been exposed to their treatments for 6 months. In the mid- to late afternoon, a randomly selected set of seedlings was placed in a low light ($\sim 4\text{--}20\ \mu\text{mol m}^{-2}\text{ s}^{-1}$), well-ventilated environment until measurement the following day.

Seedlings were placed in buckets at approximately the same treatment salinity they were exposed to in the experiment and maintained under these conditions.

For each seedling, a single leaf from the youngest pair of fully expanded leaves was selected, placed in the leaf cuvette of a Li-6400 Portable Photosynthesis System (Li-Cor Inc., Lincoln, NE, USA), and allowed to equilibrate for at least 10 min at ambient air temperature and a PPFD of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (red light source generated with a silicon photodiode). The cuvette environment was then adjusted for all measurements to actual leaf temperature and molar fraction (mmol) of H_2O present in the leaf and a CO_2 concentration of $375 \mu\text{mol CO}_2 \text{mol}^{-1}$ air. For each leaf, assimilation (A) was measured at a PPFD of 2000, 1500, 1000, 500, 200, 100, 50, 20, and $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ of artificial light, with a 2–5 min interval between each measurement.

A rectangular hyperbola was used to model individual leaf assimilation (A) versus light (PPFD) using the formula $A = (A_{\text{max-g}} \times \text{PPFD}) / (K + \text{PPFD}) - R_{\text{day}}$, where $A_{\text{max-g}}$ is the gross assimilation rate at light saturation, K is the PPFD required to achieve 1/2 of $A_{\text{max-g}}$, and R_{day} is the dark respiration rate (Givnish, 1988). Quantum yield (Φ) was calculated from the first derivative of the equation for A as $\Phi = (A_{\text{max-g}} \times K) / [K^2 + 2K(\text{PPFD}) + \text{PPFD}^2]$, while light compensation point (LCP) was calculated as $K \times R_{\text{day}} / (R_{\text{day}} - A_{\text{max-g}})$ (Gardiner and Krauss, 2001). All calculations were performed simultaneously and as independent replicates (Lederman and Tett, 1981); between five and seven seedlings per species were evaluated per treatment combination.

2.3. Growth measurements

Relationships between propagule length and dry weight biomass were developed through linear regression for *R. mangle* ($y = 0.089x - 9.016$; $r^2 = 0.77$; $F(1, 28) = 93.91$; $P \leq 0.001$) and *B. sexangula* ($y = 0.075x - 1.447$; $r^2 = 0.69$; $F(1, 28) = 63.72$; $P \leq 0.001$); equations were used to calculate initial dry weight biomass of all propagules in the experiment. Heights of individual shoots (cotyledonary ring to apical bud) were measured initially but were small at the beginning of the experiment; no propagules initiated shoot elongation by the onset of treatments. Heights were remeasured at approximately trimonthly intervals. After a treatment period of 284 days (~9 months), all seedlings were harvested and separated into roots, stems, and leaves. Relative growth rates (RGR) were determined using total biomass [i.e., root + stem (including propagule) + leaf] at the end of the experiment and calculated propagule biomass at the beginning of the experiment as $\text{RGR} = [\ln(\text{total biomass}) - \ln(\text{initial propagule biomass}) / \text{time in treatment (weeks)}]$ (from Pattison et al., 1998). Leaves were counted and total leaf area (LA: cm^2) was measured for each seedling using a Li-3100 Leaf Area Meter (Li-Cor Inc., Lincoln, NE, USA). All components were then dried at 70°C to a constant mass and weighed on an analytical balance. Root mass (RM: g dry wt), stem mass (SM: g dry wt), and leaf mass (LM: g dry wt) were recorded, and one commonly used derived variable, specific leaf area (SLA: $\text{cm}^2 \text{g}^{-1}$), was also determined.

After biomass measurements, all leaves from one randomly selected seedling in each treatment combination and replication ($N = 18$) were retained for foliar analysis of Na and K ions. Shifts in relative proportions of these foliar ions indicate cellular strategies, in particular, the selective uptake of Na from seawater in lieu of K at ratios exceeding 1.0, which can indicate ion stress in some salt sensitive species (Greenway and Munns,

1980). These elemental concentrations (%) were determined by the University of Hawaii's Agricultural Diagnostic Service Center (Honolulu, HI, USA).

2.4. Statistical analysis

This split-plot experiment had one main-plot effect (light), two subplot effects (salinity, species), and three true replicates of the entire experimental design. All data were analyzed with the general linear model option of SAS software (SAS Institute, Cary, NC). Growth data were analyzed with an analysis of covariance (ANCOVA), with a hybrid factorial and nested error structure appropriate for testing differences for split-plot designs. Initial propagule biomass was used as the covariate since it is becoming widely accepted that differences in propagule size among mangrove species can affect the outcome of experimental growth studies (Smith and Snedaker, 2000). Na:K ratios and physiological data were analyzed with an ANOVA under a similar framework but without specifying a covariate.

For the growth and physiological responses of each species to shade and salinity, comparisons were made with an analysis of variance (ANOVA) under an identical model specified for the ANCOVA but with the species effect excluded. All data were square-root transformed where appropriate to improve the homogeneity of variance and normality, with adjustments being added to avoid negative values. Means and standard errors are presented in figures and tables throughout.

3. Results

3.1. Gas exchange

Fitted assimilation curves for seedlings of *R. mangle* and *B. sexangula* differed significantly for A_{\max} and LCP across all possible treatment combinations (Tables 1 and 2). A_{\max} values for *B. sexangula* were on average 56% the level of *R. mangle*. *B. sexangula* also had a reduced leaf-level LCP of $6.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ compared with $29.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *R. mangle*. Leaf-level light saturation points for *R. mangle*, as estimated by K ($R. mangle = 611.0 \pm 217.8 \text{ S.E.}$; $B. sexangula = 62.4 \pm 7.3 \text{ (S.E.) } \mu\text{mol PPFD m}^{-2} \text{s}^{-1}$; $F(1, 4) = 18.19$; $P = 0.013$), also appeared to be higher, although extrapolations were avoided in this study since several leaves of *R. mangle* did not saturate at the maximum evaluated light level of $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$. *B. sexangula*, which saturated in every case, may be better adapted to low light physiologically. Also, *R. mangle* maintained greater physiological potential under high light regardless of developmental light level. Although mean values for Φ did not differ significantly between the two mangroves, quantum yield of *B. sexangula* was more variable under different combinations of sunlight and salinity (Fig. 1). *B. sexangula* responded favorably to short bursts of sunlight at light levels below $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ under both light treatments at 32 PSU and in unshaded light treatments at 2 PSU (Fig. 1).

R_{day} was low and did not differ significantly between the two species ($R. mangle = -0.82 \pm 0.07 \text{ S.E.}$; $B. sexangula = -0.79 \pm 0.11 \text{ (S.E.) } \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$; $F(1, 4) = 0.03$; $P = 0.875$). Carbon assimilation of *B. sexangula* leaves was typically maintained at steady, low levels regardless of developmental salinity level. Assimilation rates for *B.*

Table 1

Significance values of assimilation response curve and growth parameters for species comparisons (*R. mangle* vs. *B. sexangula*) and for light and salinity comparisons by individual species^a

Treatment type	Source of variation	DF	Leaf gas exchange			Growth parameters						
			Φ	A_{\max}	LCP	Ht	RM	SM	LM	RGR	LA	SLA
<i>R. mangle</i> vs. <i>B. sexangula</i>	Species	1, 4	NS	*	**	NS	NS	**	*	NS	***	**
	Species \times light	1, 8	NS	NS	NS	*	*	*	NS	*	NS	*
	Species \times salinity	2, 8	NS	*	**	***	***	***	**	***	**	**
	Species \times light \times salinity	2, 8	NS	NS	NS	NS	**	*	NS	NS	NS	**
	Propagule weight (covariate)	1	—	—	—	***	***	***	***	***	***	*
<i>R. mangle</i>	Light	1, 4	NS	NS	NS	*	**	**	NS	*	*	*
	Salinity	2, 8	NS	NS	NS	NS	NS	NS	NS	NS	NS	*
<i>B. sexangula</i>	Light	1, 4	NS	NS	NS	NS	**	*	**	**	NS	*
	Salinity	2, 8	NS	NS	NS	*	*	NS	NS	*	NS	*

Φ : apparent quantum yield; A_{\max} : light saturated assimilation rate; LCP: light compensation point; Ht: seedling height; RM: root mass; SM, stem mass; LM, leaf mass; LA, leaf area; RGR, relative growth rate; SLA, specific leaf area.

^a NS: not significant at the 0.05 level.

* Significant at 0.01–0.05 level.

** Significant at 0.01–0.001 level.

*** Significant at 0.001 level.

sexangula reached a maximum between 3 and 5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and remained uniform from a PPFD of approximately 250 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ to the highest light level targeted (Fig. 1). *Rhizophora mangle* light response curves, on the other hand, did not develop the characteristic asymptote of *B. sexangula*, ultimately resulting in significant interactions between species and salinity responses for A_{\max} and LCP (Table 1). No differences were detected for physiological variables by light or salinity treatment for either *R. mangle* or *B. sexangula* when analyzed by individual species (Table 1).

The relationship between stomatal conductance and assimilation followed similar curvilinear patterns for the two species up to a stomatal conductance of about 0.17 $\text{mol m}^{-2} \text{ s}^{-1}$ (Fig. 2); stomatal conductance ranged to almost 0.40 $\text{mol m}^{-2} \text{ s}^{-1}$ for *R. mangle*. Where stomatal conductance rates did overlap, the response of *R. mangle* was more variable than that of *B. sexangula*. Lower rates of stomatal conductance for *B. sexangula* probably limited A_{\max} (Fig. 1).

3.2. Growth responses

In general, growth responses differed more within species than between, indicating intraspecific morphological plasticity for the two species among the treatment combinations investigated (Tables 1 and 3). Increases in root biomass and relative growth rates in unshaded environments for both species contrasted to slight relative increases in height, leaf area, and specific leaf area in more shaded environments. Seedlings developing under shade allocated

Table 2

Means of assimilation response curve parameters (\pm S.E.) measured for *R. mangle* and *B. sexangula* seedlings growing in unshaded and shaded environments and at 2, 10, and 32 PSU

Variable	<i>R. mangle</i> (salinity pooled)		<i>R. mangle</i> (light levels pooled)			<i>B. sexangula</i> (salinity pooled)		<i>B. sexangula</i> (light levels pooled)		
	Unshaded	Shade	32 ppt	10 ppt	2 ppt	Unshaded	Shade	32 ppt	10 ppt	2 ppt
Φ ($\mu\text{mol CO}_2/\mu\text{mol photon}$)	0.02 \pm 0.01	0.03 \pm 0.01	0.02 \pm 0.01	0.03 \pm 0.01	0.03 \pm 0.01	0.03 \pm 0.01	0.03 \pm 0.01	0.02 \pm 0.01	0.03 \pm 0.01	0.03 \pm 0.01
A_{max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	9.4 \pm 1.2	9.2 \pm 1.0	10.5 \pm 1.9	9.3 \pm 1.2	8.3 \pm 0.9	5.3 \pm 0.4	5.0 \pm 0.5	4.1 \pm 0.4	5.1 \pm 0.5	6.1 \pm 0.5
LCP ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)	40.6 \pm 16.2	19.7 \pm 10.1	69.0 \pm 27.7	14.8 \pm 5.0	10.4 \pm 2.6	9.9 \pm 1.4	3.2 \pm 0.4	7.0 \pm 2.4	5.9 \pm 1.1	6.6 \pm 1.4

Measurement replication was five to seven for each treatment combination.

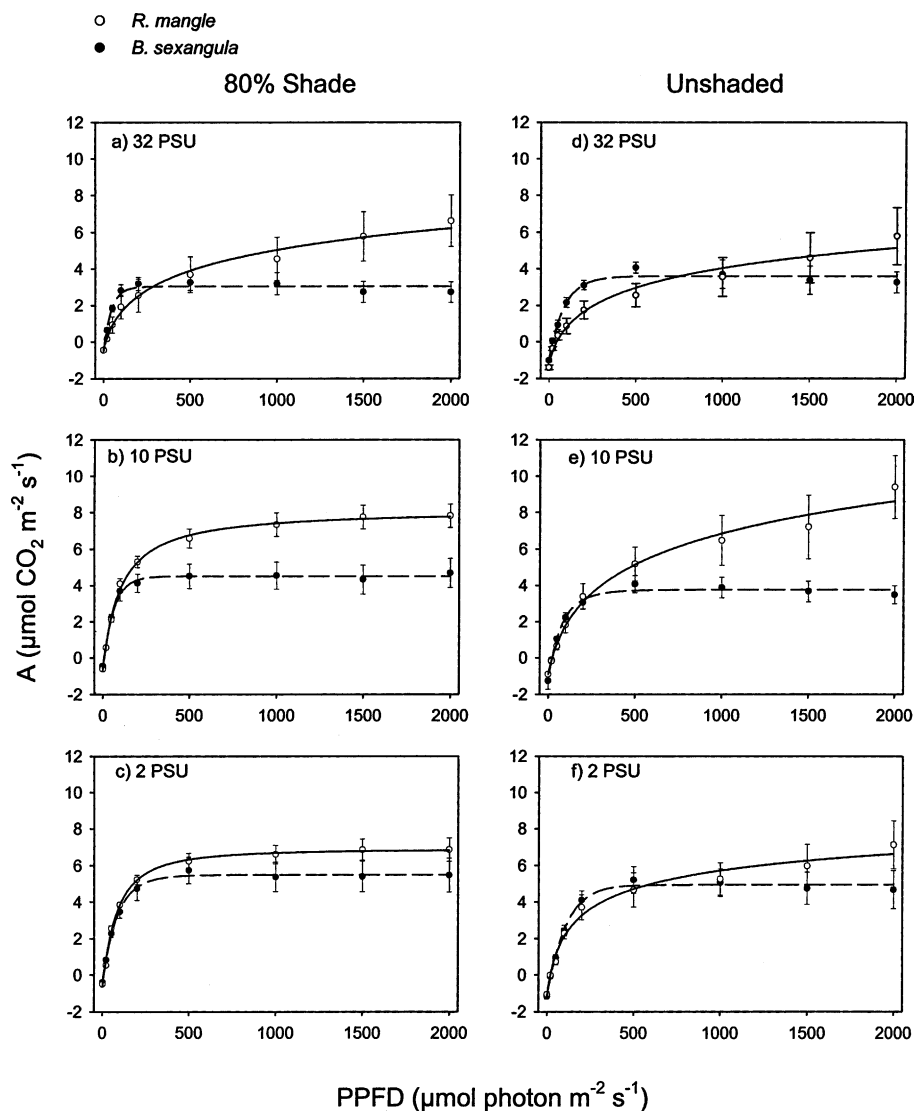


Fig. 1. Leaf-level photosynthetic assimilation response curves for *R. mangle* and *B. sexangula* seedlings grown under contrasting sunlight and salinity environments ($5 \leq N \leq 7$ for each measurement point). Calculated parameters from curves are presented in Table 2. Error bars represent 1 S.E. of the mean for untransformed data.

proportionately more resources to leaves and less to roots. Both species increased the ratio of leaf area to leaf mass (i.e., specific leaf area) under lower light regimes presumably to maximize light capture; significant interactions between species and light corroborated these findings.

The effects of salinity on either species differed, but with comparative growth sensitivity of *R. mangle* to salinity extremes not paralleling the responses to light. *R. mangle* seedlings

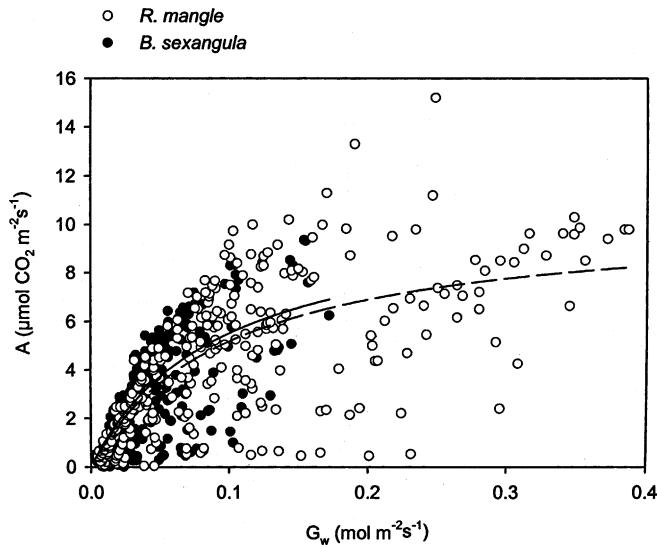


Fig. 2. Photosynthetic assimilation (A) as a function of stomatal conductance (G_w) for *R. mangle* and *B. sexangula* seedlings growing among different combinations of sunlight and salinity.

attained greater height, leaf area, and specific leaf area as well as lower root and stem biomass with increased light but were nearly unaffected by salinity (Tables 1 and 3). While only specific leaf area decreased at 32 PSU with increased salinity from 2 and 10 PSU, relative growth rates did peak at 10 PSU (Fig. 3). *B. sexangula* seedlings, on the other hand, were similarly sensitive to light and salinity. In general, higher salinity decreased growth in *B. sexangula* but had a dampened effect on *R. mangle* seedlings relative to 2 or 10 PSU

Table 3

Means of growth parameters (\pm S.E.) and biomass ratios (excluding propagule mass) measured for *R. mangle* and *B. sexangula* seedlings growing in unshaded and shaded environments (pooled for salinity)

Variable	<i>R. mangle</i>		<i>B. sexangula</i>	
	Unshaded	Shade	Unshaded	Shade
Height (cm)	39.5 \pm 0.8	52.4 \pm 1.0	29.8 \pm 0.8	36.2 \pm 0.9
Root biomass (g dry wt)	8.8 \pm 0.3	2.7 \pm 0.1	5.9 \pm 0.3	1.3 \pm 0.1
Stem biomass (g dry wt)	3.4 \pm 0.1	2.2 \pm 0.1	2.9 \pm 0.1	1.3 \pm 0.1
Leaf biomass (g dry wt)	5.0 \pm 0.1	3.8 \pm 0.2	4.0 \pm 0.1	2.5 \pm 0.1
Relative growth rate (g g ⁻¹ per week)	0.017 \pm 0.001	0.004 \pm 0.001	0.027 \pm 0.001	0.009 \pm 0.001
Leaf area (cm ²)	252.9 \pm 6.7	315.2 \pm 12.9	302.0 \pm 11.7	306.8 \pm 13.1
Specific leaf area (cm ² g ⁻¹)	51.1 \pm 0.6	83.3 \pm 0.9	77.5 \pm 2.7	121.3 \pm 2.1
Root biomass ratio	0.51	0.31	0.46	0.26
Stem biomass ratio	0.20	0.25	0.23	0.26
Leaf biomass ratio	0.29	0.44	0.31	0.49

Measurement replication was 85 to 90 for each treatment combination.

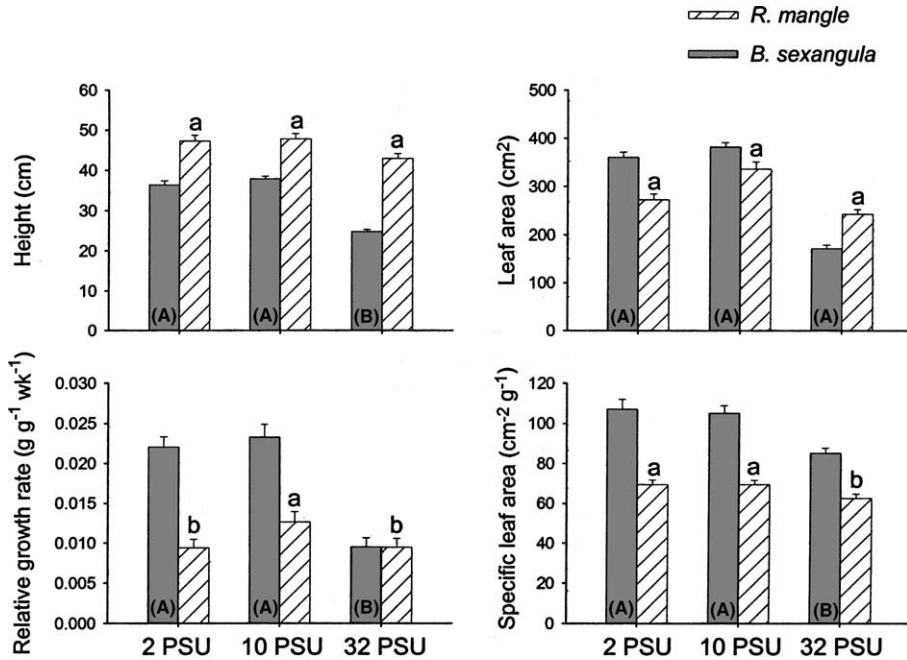


Fig. 3. Height, relative growth rate, leaf area, and specific leaf area for *R. mangle* and *B. sexangula* seedlings grown under contrasting salinity environments ($N = 59$ – 60 for each measurement bar). Contrasting letters of similar case for a species by treatment salinity represent significant differences at $\alpha = 0.05$. Error bars represent 1 S.E. of the mean for untransformed data.

treatments (Table 1; Fig. 3). Interactions between species and salinity were significant for all growth parameters measured (Table 1).

Foliar Na/K ratios for *R. mangle* (0.32 ± 0.03 S.E.) were significantly lower than for *B. sexangula* (1.28 ± 0.10 S.E.: $F(1, 4) = 271.61$; $P \leq 0.001$). Na/K ratios of *B. sexangula* were unaffected by light ($F(1, 4) = 0.18$; $P = 0.716$) and salinity ($F(2, 8) = 1.10$; $P = 0.418$). Na/K ratios in *R. mangle* seedlings were also unaffected by light level ($F(1, 4) = 7.40$; $P = 0.113$), but increased at a salinity of 32 PSU relative to 2 and 10 PSU treatments ($F(2, 8) = 16.52$; $P = 0.012$).

4. Discussion

4.1. Salinity and shade interactions

Both species exhibited patterns that are broadly typical of halophytes (cf. Cheeseman, 1994). Dark respiration (R_{day}) rates and light compensation points were low, while apparent quantum yields (Φ) were high (Table 2). *B. sexangula* seedlings, however, had significantly lower rates of A_{max} relative to seedlings of *R. mangle* across the range of light and salinity

levels tested (Table 2, Fig. 1), indicating a greater overall photosynthetic potential for *R. mangle*. This result, along with *B. sexangula*'s lower LCP and a reduced assimilation rate at light saturation, strongly suggests the species is well adapted to a low light regime but at the expense of being able to respond positively under more favorable conditions (i.e., higher light levels or "optimal" salinity levels). Other findings, such as the greater mean specific leaf area of *B. sexangula* under low light, the lack of an effect of shading on height growth, and, most importantly, the more efficient biomass allocation from roots to leaf structure under shade, lend further support to the conclusion that *B. sexangula* is a relatively shade tolerant species.

Our results strongly suggest that *R. mangle* is much better suited to take advantage of high light even at relatively high salinity levels. Significant differences between the two species in A_{\max} at high incident light levels are readily apparent in most of the assimilation response curves (Fig. 1). Also apparent is the reduced tendency for A_{\max} to level off at high light levels as it does for *B. sexangula*.

Evidence for less salt sensitivity in *R. mangle* includes the reduced effect of salinity on height growth (Fig. 3) and the generally insignificant effect of salinity on other physiological and growth variables, other than relative growth rates (Table 1; Fig. 3). Also, *R. mangle* maintained a much lower and presumably more favorable foliar Na/K ratio (0.32) relative to *B. sexangula* (1.28) across the range of salinities tested. Lower Na/K ratios generally indicate a lower level of interference of salinity with cellular functions (Wyn Jones et al., 1979; Greenway and Munns, 1980; Popp et al., 1985). Ratios above 1.0 are believed to be high enough to cause significant physiological impairment, at least in non-halophytes (Wyn Jones et al., 1979).

Over the 9-month duration of the study, there was no seedling mortality and few visible signs of stress, suggesting that both species are capable of at least short-term persistence under the range of conditions we tested. We did notice that *B. sexangula* seedlings growing in the unshaded treatments developed a reddening of their abaxial leaf surfaces, a response not noted for *R. mangle*. If this response is due to the synthesis of pigments to protect the photosynthetic apparatus of the plants and reduce photoinhibition (Björkman et al., 1988), it may represent an energy cost that would lend a further advantage to *R. mangle* in high light and high salinity environments. The protection of leaf photochemistry generally requires lower rates of Φ at high light in order to provide appropriate energy dissipation (Cheeseman et al., 1991). However, we did not detect a significant decrease in Φ for unshaded seedlings nor did we measure pigment concentrations directly. In addition, *B. sexangula* seedlings appear to be under fairly strong stomatal control (Fig. 2), which limits their responsiveness to light. Hence, any adjustments in assimilation beyond the light saturation points will have to involve an increase in efficiency of leaf-level carbon assimilation relative to stomatal conductance. Stomatal control may not be as important for *R. mangle*.

While most of our results fit a pattern that is predictable for species with differing tolerances to light and sensitivities to salinity, some results are not consistent. For example, the two comparative assimilation response curves for seedlings grown at 32 PSU (Fig. 1a and d) show a greater CO_2 assimilation rate for *B. sexangula* than for *R. mangle* seedlings at low light. While we might expect this pattern at lower salinity levels, such a result at the highest salinity level, where reduced growth indicated an overall negative response, was unexpected. Perhaps the leaf is compensating photosynthetically for a decreased specific leaf area at high salinity? An overall low response to both stress and favorable conditions

may promote persistence of *B. sexangula* in low resource environments, but may limit its ability to exploit more favorable ones.

4.2. Implications for species zonation and mangrove understory development

On exposed intertidal sites in Hawaii only a few potentially competitive species are present, including *Batis maritima* L., *Paspalum vaginatum* Sw., and on extreme landward edge locations, *Hibiscus tiliaceus* L. and *Thespesia populnea* (L.) Sol. Ex Corrêa (see Egler, 1947). While these species co-occur with mangroves, either their herbaceous nature, sparse density, or salt intolerance limit direct competition with introduced mangroves. Likewise, the mangrove understory in Hawaii is not atypical of neotropical mangrove forests in lacking a prominent understory (Janzen, 1985; Corlett, 1986; Lugo, 1986; Snedaker and Lahmann, 1988), and is composed mostly of seedlings and saplings of *R. mangle* and *B. sexangula*.

Differences in sensitivity of *R. mangle* and *B. sexangula* to salinity and tolerance to shade may be sufficient, therefore, to explain current species distribution patterns and the relative success of *R. mangle* in Hawaii. In our study, *R. mangle* seedlings exhibited a significantly greater photosynthetic and growth capacity than did *B. sexangula* over a wide range of light and salinity conditions. These interspecific differences include a much greater capacity of *R. mangle* to tolerate high salinity environments (Table 1, Fig. 3) and a much greater ability to respond to sustained, high light delivery (Fig. 1). The latter trait may help *R. mangle* to colonize new sites and canopy gaps. Because most Hawaiian mangrove stands are young, a species such as *R. mangle* that is best adapted to a high light environment and also less sensitive to the detrimental effects of salt would have an advantage. The apparent advantage to growth at higher salinity levels may be especially important in Hawaii, where most sites have a narrow intertidal zone with little or no area with a moderate to low salinity regime.

We considered several alternate explanations for the patterns of mangrove species distribution observed in Hawaii. Differential propagule predation by crabs or other animals was one possibility, but patterns of relative and inferred influence on forest structure among studies from other mangrove systems are inconsistent (see Allen et al., 2003). Also, in the case of *R. mangle*, both high rates of propagule production (Cox and Allen, 1999) and low rates of propagule predation (Steele et al., 1999) have been documented. Similar data are lacking for *B. sexangula*, although mature *B. sexangula* trees produce healthy crops of propagules that are not heavily consumed by predators. Still, the possibility of differential predation warrants further investigation. Our observations also suggest that a tidal sorting of propagules across the intertidal zone does not occur (Rabinowitz, 1978), although this effect also remains unexamined at our sites. Finally, selective cutting of mature *B. sexangula* trees, presumably to facilitate harvesting of the flowers (Allen, 1998), also has the potential to reduce the already small population of *B. sexangula*. Selective cutting, however, is believed to be a factor in just a few locations (e.g., Heeia Swamp, Oahu) that have relatively wide intertidal zones and extensive areas of moderate to low salinity.

4.3. Strategies of light and salinity tolerance

Data suggest that trade-offs may exist in a species' response to two factors simultaneously. *B. sexangula* exhibited responses typical of a highly shade tolerant species, but it grew

relatively poorly at the highest salinity level. *B. sexangula*'s strategy can be characterized by slow whole-plant growth with little variation under unstressful environmental conditions. Morphological plasticity allows for adjustments in carbon gain efficiency, which may be at least partially necessitated by the reduced capacity of stomates for gas exchange at the individual leaf-level (morphological strategy).

In contrast, *R. mangle* may be somewhat less adapted than *B. sexangula* to low light levels but less affected by salinity. This species' strategy involves faster whole-plant growth over a wide range of environmental conditions, which is enhanced by leaf-level physiological adjustments (physiological strategy). Ball (1998) proposed an ecophysiological hypothesis related to salt tolerance and species' coexistence along salinity gradients that seems remarkably applicable to Hawaii, where mean separations in the physiological response of the two species were greatest at moderate salinity levels. Hence, even in mangrove species growing in a non-native environment, physiological competition between these two species is potentially reduced by greater mean separations in assimilation response at salinities corresponding to moderate salinity ranges in Hawaii.

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