CrossMark

COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Environmental tolerances of rare and common mangroves along light and salinity gradients

Emily M. Dangremond[1,2] · Ilka C. Feller[2] · Wayne P. Sousa[1]

Abstract Although mangroves possess a variety of morphological and physiological adaptations for life in a stressful habitat, interspecific differences in survival and growth under different environmental conditions can shape their local and geographic distributions. Soil salinity and light are known to affect mangrove performance, often in an interactive fashion. It has also been hypothesized that mangroves are intrinsically shade intolerant due to the high physiological cost of coping with saline flooded soils. To evaluate the relationship between stress tolerance and species distributions, we compared responses of seedlings of three widespread mangrove species and one narrow endemic mangrove species in a factorial array of light levels and soil salinities in an outdoor laboratory experiment. The more narrowly distributed species was expected to exhibit a lower tolerance of potentially stressful conditions. Two of the widespread species, *Avicennia germinans* and *Lumnitzera racemosa*, survived and grew well at low–medium salinity, regardless of light level, but performed poorly at high salinity, particularly under high light. The third widespread species, *Rhizophora mangle*, responded less to variation in light and salinity. However, at high salinity, its relative growth rate was low at every light level and none of these plants flushed leaves. As predicted, the rare species, *Pelliciera rhizophorae*, was the most sensitive to environmental stressors, suffering especially high mortality and reduced growth and quantum yield under the combined conditions of high light and medium–high salinity. That it only thrives under shaded conditions represents an important exception to the prevailing belief that halophytes are intrinsically constrained to be shade intolerant.

Keywords Mangrove · Distribution · Rarity · Stress tolerance · *Pelliciera rhizophorae*

Communicated by Amy Freestone.

✉ Emily M. Dangremond
dangremonde@si.edu

1 Department of Integrative Biology, University of California, 3040 VLSB MC 3140, Berkeley, CA 94720-3140, USA

2 Present Address: Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, MD 21037, USA

Introduction

Narrow endemic and widespread potentially invasive species represent opposite ends of the continuum of species distribution–abundance patterns, and both present major challenges to the design of effective environmental management and conservation efforts. How species distribution patterns at different spatial scales are shaped and maintained by life history, demographic, genetic, and environmental processes is a fundamental focus of research in ecology and evolutionary biology (Rabinowitz 1981; Kruckeberg and Rabinowitz 1985; Gaston 1994, 2003; Gaston and Kunin 1997; Rosenzweig and Lomolino 1997). Recognizing that assessments of species rarity are scale dependent (Harper 1981), Rabinowitz (1981; see also Rabinowitz et al. 1986; Gaston 1994) distinguished different categories of rare species. These were defined by seven out of the eight combinations of three distribution–abundance characteristics: geographic range (wide or narrow), habitat specificity (broad or restricted), and local abundance

🔗 Springer

(somewhere dense or everywhere sparse). Any species that has a narrow geographic range, lives in a restricted number of habitats, or typically lives at low density exhibits a form of rarity. Common species comprise the eighth combination: they have wide geographic ranges and occupy a broad range of habitats, in which they are generally abundant. These eight classifications were presented as simplified, heuristic divisions of what is really a continuum of distribution–abundance patterns.

Species whose populations are typically sparse and patchily distributed tend to have narrower geographical ranges than common species (Hanski 1982; Gotelli and Simberloff 1987; Collins and Glenn 1990; Gaston and Lawton 1990; Hanski et al. 1993; Boulangeat et al. 2012). Among the hypothesized explanations for the restricted distributions of rare endemics compared to common widespread species is that the former have smaller fundamental niches, possessing more limited ranges of physiological tolerance or more specialized resource or other habitat requirements (Kruckeberg and Rabinowitz 1985; Boulangeat et al. 2012; Slatyer et al. 2013). If these requisite conditions and resources are of limited spatial extent, or are otherwise difficult to access, then the distribution and abundance of a species that depends on them will be constrained as well. This study tests the hypothesis that widespread species are more stress tolerant than narrow endemics, examining the specific case of mangrove trees, a taxonomically diverse collection of taxa that have evolved convergently to live under the stressful edaphic conditions at the interface of tropical marine and terrestrial environments. We compared the performances of four species of seedlings establishing across an array of experimental environmental conditions that are typical of natural mangrove habitats.

Mangrove forests offer an excellent system in which to investigate the relationship between the stress tolerance of species and their spatial distributions, as these forests occupy a habitat that is physically challenging to both plant establishment and growth (Ball 1988a; Smith 1992; Krauss et al. 2008), and component tree species range from rare endemic to common, and may include non-native invasives. The tidally influenced mangrove habitat is characterized by flooded, hypoxic, and saline soils. Adaptations that allow plants to live in such severe edaphic conditions are varied, but have evolved in 16 different plant families (Tomlinson 1986; Hogarth 2007). These adaptations include morphological traits such as aerial roots, lenticels, and pneumatophores that aerate the rhizosphere in hypoxic soils, and regulation of tissue salt concentrations by specialized salt-excreting leaf glands or exclusion of salt at root surfaces. Physiological and growth responses to gradients in salinity vary among mangrove species and can ultimately affect their distributions and abundances (Ball 1988a, b, 2002; Smith 1992; Ball and Pidsley 1995; Krauss et al. 2008).

It has previously been proposed that halophytes inhabiting the intertidal zone are shade intolerant, which explains why mangrove forests typically lack an understory layer of plant species that mature and reproduce beneath the closed canopy (Janzen 1985; Lugo 1986; Snedaker and Lahmann 1988). The high metabolic costs of tolerating salt and inundation are hypothesized to preclude the evolution of morphological and physiological traits that allow growth and reproduction in a low-light environment. However, the rare neotropical mangrove *Pelliciera rhizophorae* (Tetrameristaceae) often occurs as a reproducing understory species in forests where *Rhizophora mangle* (Rhizophoraceae) dominates the canopy, indicating that *Pelliciera* may be shade tolerant throughout its life. *Pelliciera* is largely restricted to sites of low to moderate soil salinity, where it typically grows in partial shade beneath a mixed-species canopy of adult conspecifics and *Rhizophora mangle* (Jiménez 1984; E. Dangremond, pers. obs.).

In this study, we investigated the independent and potentially interacting effects of two environmental factors, salinity and light, on the establishment, early growth, and survival of four mangrove species. We compared *Pelliciera rhizophorae* to three mangrove species that are common throughout their native ranges: two neotropical species, *Rhizophora mangle* (Rhizophoraceae) and *Avicennia germinans* (Acanthaceae), and the Indo-West Pacific species, *Lumnitzera racemosa* (Combretaceae). All three have also become established, either accidentally or intentionally, as reproducing populations outside their native ranges (see "Discussion"). The study focused on the responses of seedlings in the first 12 weeks of life to the tested environmental factors, because variation in seedling demography is a major driver of forest dynamics and structure (Smith 1992; McKee 1995; Krauss et al. 2008). We expected light and salinity to exert a synergistic impact on mangrove seedling performance (Ball 2002; López-Hoffman et al. 2006, 2007), with the interactive impact being strongest for the rare species *Pelliciera rhizophorae*.

Materials and methods

Study species

As noted above, three of the study species are native to the Atlantic–East Pacific (AEP) biogeographic region, and one to the Indo-West Pacific (IWP) region (Tomlinson 1986). *Rhizophora mangle* occurs from northern Florida to southern Brazil on the Atlantic coast of North America, and from Mexico to Peru on the Pacific coast. It also inhabits the shores of West Africa, from Senegal to Angola. Its propagules are large; the average fresh mass (± 1SE) of propagules used in this experiment was 14.5 g (± 0.40)

(corresponding to a dry mass of 8.1 g), and were collected from the Indian River Lagoon (27.56°N, 80.33°W), Fort Pierce, FL, USA on 10 August 2010. *Avicennia germinans* has a geographic range similar to that of *Rhizophora mangle*, extending from southern Florida to Brazil on the Atlantic coast of North America, Mexico to Peru on the Pacific coast, and along the coast of West Africa. Local Florida populations were not fruiting at the start of the experiment, so we used propagules from Panama, where the species fruits earlier in the year. Propagules were collected from Punta Galeta, near Colón, Panama (9.38°N, 79.87°W) on 27 July 2010; their average fresh mass was 1.78 g (±0.16) (dry mass of 0.67 g). The third AEP species, *Pelliciera rhizophorae*, has a much more restricted and patchy geographic range than the other study species; it is only found on the Caribbean and Pacific coasts of Central America. In the Caribbean, small populations exist in Nicaragua, Panama, and Columbia. Larger, but still discontinuous, populations can be found along the Pacific coast, from Costa Rica to Ecuador. This species does not occur in Florida; propagules used in the experiment were collected from Souli Creek (9.01ºN, 81.97ºW) and Cilico Creek (9.07ºN, 82.24ºW), Bocas del Toro, Panama on 22 and 24 July 2010. Their average fresh mass was 69.5 g (±2.73) (dry mass of 24.1 g).

Native to the IWP, *Lumnitzera racemosa* has a wide distribution along the shores of South Asia, northern Australia, New Guinea, southern India, and East Africa. It was introduced to Florida at least three times during the 1960s and 1970s, when it was planted into the living collections of the Fairchild Tropical Botanic Garden, Coral Gables, FL, USA (Fourqurean et al. 2010). At all three planting sites, the species reproduced prolifically, spread beyond the boundaries of the gardens, and became a naturalized invasive in the surrounding area, where it came to dominate local stands of mangroves and was estimated to have a population growth rate of 17–23 % per year (Fourqurean et al. 2010). Ongoing eradication efforts have eliminated most reproductive individuals, so we collected young-of-the-year seedlings and transplanted them into treepots for use in the experiment (see below). Seedlings were collected from Matheson Hammock County Park (25.67°N, 80.26°W), FL, USA on 2 August 2010. The average initial fresh mass of *Lumnitzera racemosa* seedlings was 1.29 g (±0.10) (dry mass of 0.33 g). Hereafter, the study species will be referred to by their generic names.

Experimental design

We tested the survival and growth responses of the four seedling species to different combinations of light and salinity in an enclosed sunlit patio area adjacent to the Smithsonian Marine Station at Fort Pierce, FL, USA (27.46°N,

80.31°W). The experiment had a three-way factorial design, examining the independent and interactive effects of light level and salinity on seedling growth and survival of the four mangrove species. Three daytime light treatments were established, spanning the range of field light levels from open sky to forest understory (Ball and Critchley 1982; Cheeseman et al. 1991). Photosynthetic photon flux density maxima, measured under clear sky conditions at midday, were: high light (1200 µmol m^{-2} s^{-1}), medium light (400 µmol m^{-2} s^{-1}), and low light (130 µmol m^{-2} s^{-1}). The high-light treatment was ambient, open-sky conditions, while the medium- and low-light treatments were achieved with a shade-cloth roof (Gempler's® 50 % shade cloth and Home Depot® 90 % shade cloth, respectively). These three light treatments were crossed with three salinity treatments: freshwater (0 psu), seawater (35 psu), or hypersaline (60 psu). These salinities represent a typical range of field porewater salinities experienced by mangroves (Smith 1992); salt concentrations (measured with a handheld refractometer) were achieved by adding Instant Ocean® aquarium salt to fresh tap water. All treatments were refreshed with new water of the appropriate salinity each week. To minimize the effects of rainfall and evaporation, salinity was checked in-between weekly water changes and adjusted if necessary. Although we did not fertilize our plants, the tap water used in the experiment contained higher concentrations (±1SE) of nitrate (0.585 mg/L ± 0.15) and phosphate (78 µg/L ± 1.15) than were contributed by the added Instant Ocean® salts. Instant Ocean® mixed with distilled water to 35 psu has nitrate levels of 0.141 mg/L ± 0.003 and phosphate levels of 14.3 µg/L ± 2.4 (Demes et al. 2009). Thus, the admixture of Instant Ocean salts had only a modest effect on nutrient availability across the salinity treatments.

On 13 August 2010, each of the nine light–salinity treatment combinations was established in three plastic tubs (55 cm (L) × 40 cm (W) × 25 cm (D)), and each tub was stocked with 16 potted early-stage seedlings (or transplanted young-of-the-year seedlings in the case of *Lumnitzera*), four of each species. Prior to planting, collected propagules were floated in freshwater for 1–2 weeks. This allows *Avicennia and Pelliciera* propagules to shed their pericarps, and enhances establishment rates of *Rhizophora* propagules. At the time of planting, the early-stage *Avicennia* and *Pelliciera* seedlings still retained their cotyledons and had not yet developed true leaves. *Rhizophora* propagules exhibited no elongation of the epicotyl. Seedlings were planted into 12.7-cm-wide, 24.1-cm-deep plastic treepots (Steuwe and Sons, Inc. #CPOT10R) that were filled with unamended topsoil (Timberline®). Developing seedlings of *Avicennia* and *Pelliciera* were shallowly inserted into the soil so that the root apical meristem was approximately 1 cm below the soil surface. The elongate propagules of *Rhizophora* were inserted into the soil just

far enough to stay upright (~4 cm). At planting, the average heights (soil surface to base of the primary apical stipule or leaf-pair) of the four species of seedlings were: 5.3 cm for *Avicennia*, 6.3 cm for *Pelliciera*, 7.4 cm for *Lumnitzera*, and 18.3 cm for *Rhizophora*. All seedlings were weighed before potting.

Pots of the different species were randomly interspersed within each tub, and the 27 tubs (9 treatments × 3 replicates each) were randomly interspersed across the common garden. Seedlings were watered once a week with water of the same salinity as the respective tub; the water level maintained in the tubs covered the lower 3–5 cm of each pot, keeping the soil continually moist but not inundating it. Over the duration of the experiment, the temperature regimes of the experimental site in Florida and the coastal Caribbean site in Panama from which the *Pelliciera* and *Avicennia* propagules had been collected were very comparable. During the experimental period, mean air temperature (±1SE) at the experimental site was 27.3 °C ± 0.05, with a minimum of 18.1 °C and a maximum of 32.6 °C (Smithsonian Physical Monitoring Network, Smithsonian Marine Station at Fort Pierce, FL, USA, http://nmnhmp.riocean.com/arc_vision.php). During the same period, the mean air temperature at Punta Galeta, Panama was 26.9 °C ± 0.02, with a minimum of 23.3 °C and a maximum of 32.4 °C (Smithsonian Tropical Research Institute, Physical Monitoring Program, Galeta Marine Laboratory, Panama, http://biogeodb.stri.si.edu/physical_monitoring/research/galeta).

Measurements and statistical analysis

We assessed seedling condition (alive or dead) and measured seedling height at weekly intervals over a period of 12 weeks (82 days). In association with the final set of height measurements, we assayed light-adapted photosynthetic yield (i.e., quantum efficiency of Photosystem II photochemistry) on a subsample of plants from each treatment as an index of plant stress (Genty et al. 1989; Maxwell and Johnson 2000; Baker and Oxborough 2004). This index (Φ_{PSII}) is calculated as $(F_m - F_t)/F_m$, where F_m and F_t are the maximal and steady-state fluorescence yields, respectively (following the notation of Maxwell and Johnson 2000). It measures the proportion of light absorbed by PSII chlorophyll that is used in photochemistry. A pulse amplitude modulation (PAM) fluorometer (Opti-Sciences OS5-FL, Hudson, NH, USA) was used to measure fluorescence values for three randomly chosen plants of each species in each treatment; however, no surviving *Pelliciera* plants remained in the high-light hypersaline or high-light seawater treatments, and the leaves on the freshwater plants were too small to make an accurate measurement. *Rhizophora* seedlings growing in hypersaline treatments did not flush leaves, so measurements could not be taken on those plants. Following these fluorescence measurements, surviving seedlings were carefully extracted from their pots and the soil washed from their roots. They were then dried for 3 days to a constant mass in a 60 °C drying oven, and weighed to determine dry biomass.

We analyzed the independent and interacting effects of species, light level, and salinity on plant survival and growth. Three growth measures were evaluated: plant height, dry biomass, and relative growth rate. All plants that rooted (see below) were included in the height and biomass analyses, using measurements taken either at the time of their death within the 12-week experimental period or when they were harvested alive at 12 weeks. This approach produced an integrated measure of the combined influence of life span and growth rate on the mean final height and biomass attained by plants under the different environmental conditions. We re-ran the same analyses, examining only those individuals that survived to be harvested alive at 12 weeks. In this case, observed differences would reflect solely the influence of environmental conditions on plant growth over 12 weeks. These age-restricted analyses produced qualitatively identical patterns of response to the treatments, so are not reported here. Weekly relative growth rate (RGR) in dry biomass was calculated as $(\ln W_2 - \ln W_1)/(t_2 - t_1)$ where W_1 and W_2 are the dry masses of a plant (or propagule) at the beginning and end of the experimental period $(t_2 - t_1)$, or 12 weeks. RGR was compared among treatments only for individuals that survived the entire experimental period. We adopted this protocol because, for most organisms, RGR changes as individuals grow; typically it declines with size/age (Rees et al. 2010; Paine et al. 2012). Therefore, using all individuals regardless of the size/age at death to compute a mean weekly RGR might have introduced a bias into the treatment comparisons. Since the dry masses of planted propagules could not be determined prior to planting, we used a wet-to-dry mass conversion to calculate approximate dry masses of propagules and seedlings (W_1) at the beginning of the experimental period. We collected extra propagules of each species (seedlings in the case of *Lumnitzera*), weighed them while they were fresh, and then weighed them again after they dried to constant mass at 60 °C for 3 days. Linear regressions converted wet to dry mass for each species (see Appendix A in the Electronic supplementary material, ESM).

Rates of seedling survival to 12 weeks were compared among species and treatments by multidimensional contingency table analysis (Fienberg 1970; Bishop et al. 1975; Agresti 2013). Preliminary *G* tests comparing rates of mortality among the three tubs assigned to each light–salinity combination detected no significant differences

($G_{df=2}$ ranged from 0.00 to 4.79, $P > 0.05$ in all cases), so we pooled the data (i.e., counts of dead and surviving seedlings) across tubs within each cell of the design to obtain an adequate sample size for multiway categorical data analysis. Reported G values are those associated with deletion of the indicated terms from the model; a P value ≤ 0.05 indicates that removal of the term significantly reduced model fit.

Final height and biomass, RGR, and Φ_{PSII} were compared among species and experimental treatments with mixed-model, factorial ANOVA. In these analyses, species, light level, and salinity were treated as fixed factors, and tub as a nested random factor (within each light and salinity combination). Cochran's tests confirmed homoscedasticity of variance for RGR and quantum yield; final height and biomass were $\ln(X)$ and $\ln(X + 1)$ transformed, respectively, to equalize variances prior to analysis. In analyses that detected significant interaction effects, species-specific patterns were explored post hoc with simple effects analyses (Winer et al. 1991).

Several of the planted propagules never developed roots. Whether this was an effect of treatment or propagule inviability could not discerned, so these individuals were dropped from the analysis. Also eliminated was a supposed

Lumnitzera seedling that proved to be a seedling of the morphologically similar native mangrove *Laguncularia racemosa*.

Results

Survival

The combination of high-light and hypersaline conditions was particularly stressful to developing seedlings (Fig. 1), as evidenced by a significant light × salinity interaction effect on survival rates (G to remove = 12.83, $df = 4$, $P = 0.012$). High light was especially harmful to *Pelliciera* seedling survival (species × light, G to remove = 21.47, $df = 6$, $P = 0.002$), which suffered 83.3 % mortality (pooled across salinity levels), compared to 22.2, 19.4, and 14.3 %, mortality for *Rhizophora*, *Lumnitzera*, and *Avicennia*, respectively. *Pelliciera* and *Rhizophora* appeared to be more stressed by high salinity (60 psu) than the other two species, with 61.1 and 23.7 % dying (pooled across light levels), respectively, compared to 9.4 % for *Avicennia* and 8.6 % for *Lumnitzera*. However, the species × salinity interaction was not statistically significant (G to remove = 6.06, $df = 6$, $P = 0.416$).

Growth

High light and high salinity caused a reduction in seedling growth compared to other treatments, though individual species responded differently to these environmental conditions. Mean final height was shaped by a three-way interaction of species, light, and salinity effects (Fig. 2; $F_{12,54} = 2.15$, $P = 0.028$). Posthoc examination of the effects of light and salinity levels on the mean height attained by each species (Table 1) revealed strongly interactive effects of these variables on *Pelliciera* seedling height. As for survival rates, the combination of high light and high salinity disproportionally limited the final height of this species' seedlings (Fig. 2d). The final heights of *Lumnitzera* and *Avicennia* seedlings were also reduced by high light and high salinity, but these effects were additive, not interactive (Fig. 2a, b). Finally, neither light level nor salinity affected the terminal heights of *Rhizophora* seedlings (Fig. 2c).

Final seedling biomass was affected by the treatments in a very similar manner to plant height (Fig. 2), with significant interactions between species and light ($F_{6,54} = 20.49$, $P < 0.001$) and species and salinity ($F_{6,54} = 3.51$, $P = 0.005$). *Pelliciera* biomass exhibited a marked sensitivity to the combination of high light and hypersalinity (Table 1; Fig. 2h). *Lumnitzera* seedling biomass was depressed by high salinity, but showed no consistent
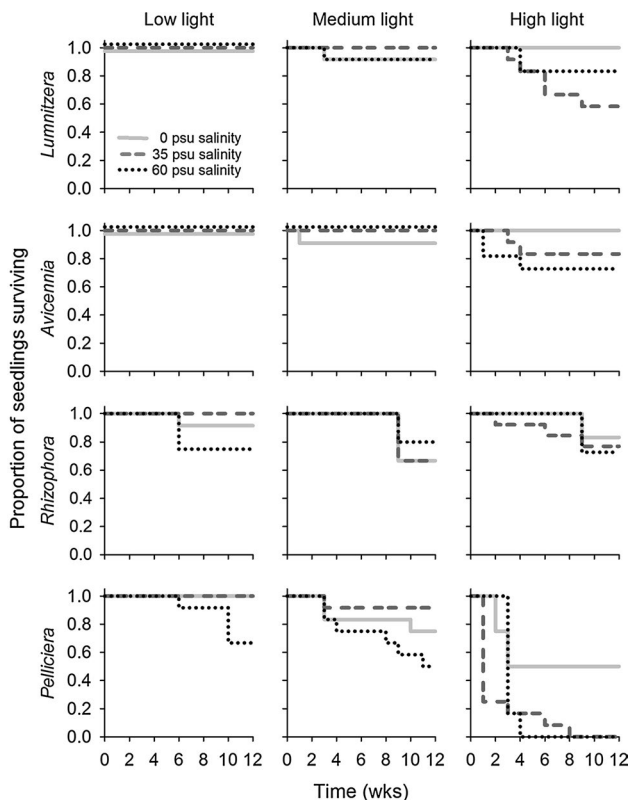

Fig. 1 Survival curves for seedlings of four mangrove species grown under three light and salinity treatments for 12 weeks

response to light level (Fig. 2e). *Avicennia* biomass exhibited a hump-shaped response to salinity; it was higher at 35 psu than 0 psu, and lowest at 60 psu (Fig. 2f). At every salinity, high light levels depressed seedling biomass of *Avicennia*. The final biomass of *Rhizophora* seedlings was unaffected by salinity or light level (Fig. 2g).

Because none of the *Pelliciera* growing under high-light conditions in either seawater or hypersaline treatments lived past 7 weeks, a full factorial analysis of RGR, comparable to those conducted on final height and biomass, was not possible. Instead, we conducted two three-way ANOVAs on subsets of the experimental design: (A) with *Pelliciera* removed from the analysis, and (B) with the high-light treatment removed from the analysis. Analysis A showed that high light and hypersalinity reduced the RGR of both *Lumnitzera* and *Avicennia*, with no evidence of an interaction between the factors (Table 1; Fig. 3a, b). The RGR of *Avicennia* peaked at 35 psu, which is consistent with biomass patterns (see above). The RGR of *Rhizophora* did not differ statistically across salinities or light levels (Fig. 3c), but several elements of its response warrant further investigation with greater replication. Regardless of

light level, its RGR was lowest at 60 psu, and none of these plants flushed leaves. In contrast, its highest RGR occurred in the high-light freshwater treatment (Fig. 3c). The latter response was also weakly evident in the final height and biomass data.

When the high-light treatment was excluded, allowing all four species to be considered in the analysis (analysis B), only salinity was found to affect RGR, and its influence varied among the species (Table 1). At the low to medium light levels considered in the analysis, the RGRs of *Lumnitzera* and *Avicennia* were reduced at high salinity (Fig. 3a, b), whereas no significant effect of salinity on RGR was detected for *Rhizophora* or *Pelliciera* (Fig. 3c, d).

Quantum yield

Quantum yield varied with the treatments in a species-specific manner (Fig. 3). As noted above, due to treatment-related mortality, measurements were missing for certain species-treatment combinations, so separate ANOVAs examining the effects of light level, salinity, and their interaction were conducted for each species (Table 2). Quantum yield was generally higher at the lowest light level for all four species, ranging close to 0.8 in seawater for all four species. A value of ~0.83 is considered optimal photosynthetic performance for most plant species (Maxwell and Johnson 2000). The quantum yield of *Lumnitzera* showed no significant response to salinity, regardless of light level (Fig. 3e). *Pelliciera*'s photosynthetic yield declined with increasing salinity under both medium and low light levels (Fig. 3h). Both *Avicennia* and *Rhizophora* exhibited light × salinity interactions that were difficult to interpret. *Avicennia*'s quantum yield increased with a rise in salinity from 0 to 35 psu, especially under low light, and then changed little at higher salinity (Fig. 3f). The pattern for *Rhizophora* with respect to salinity was unclear, since seedlings in the high-salinity treatments did not flush leaves and quantum yield could not be measured (Fig. 3g).

Discussion

Our main prediction was that the widely distributed species *Lumnitzera*, *Rhizophora*, and *Avicennia* would have broader environmental tolerances than the narrow endemic *Pelliciera*. The experimental results confirm this general prediction; however, the widely distributed species did exhibit individualistic responses that varied with the specific performance measure.

Pelliciera was clearly more sensitive to high salinity and light than the other three species. It suffered higher mortality than the other species in hypersaline treatments, and this difference was accentuated at high light levels. High-light
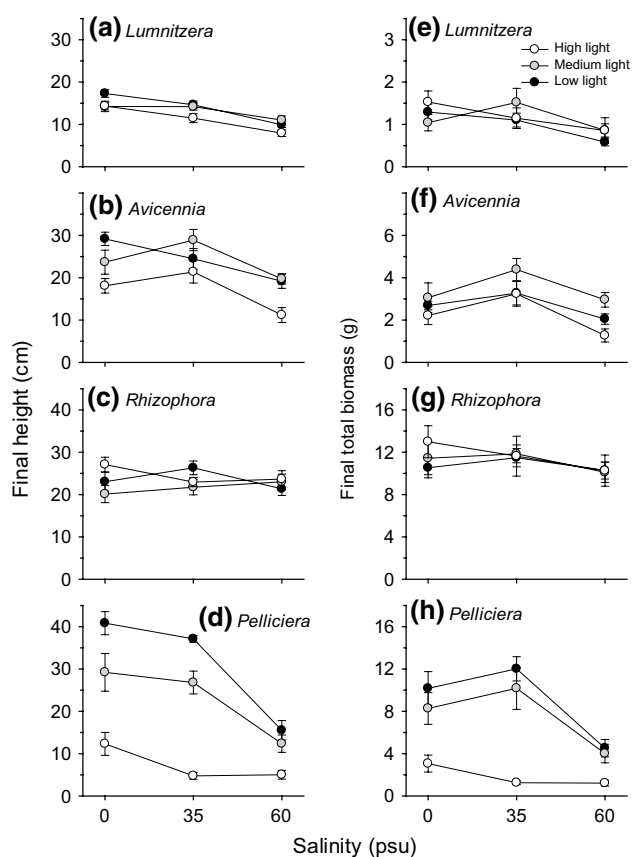

Fig. 2 Effects of light and salinity treatments on height (*left*) and dry biomass of seedlings (*right*) at the time of their death (if prior to 12 weeks) or when harvested at 12 weeks. Values are means ±1SE

Table 1 Effects of species, light level, and salinity on final height, final biomass, and RGR of mangrove seedlings. Significant full-model ANOVA interactions are reported for each response variable, followed by post hoc simple effects analyses for individual species (see text for details)

Factor	df	Lumnitzera	Avicennia	Rhizophora	Pelliciera
Final height: species × light × salinity ($F_{12,54} = 2.15^*$)					
Light	2, 54	3.44*	13.79***	1.31	150.98***
Salinity	2, 54	12.94***	10.68***	0.16	47.76***
Light × salinity	4, 54	0.79	1.70	0.90	6.33***
Final biomass: species × light ($F_{6,54} = 20.49^{***}$); species × salinity ($F_{6,54} = 3.51^{**}$)					
Light	2, 54	0.11	6.67**	0.01	86.29***
Salinity	2, 54	4.29*	7.23**	1.02	23.56***
Light × salinity	4, 54	0.66	1.04	0.48	4.42**
RGR: analysis A (Pelliciera excluded): species × light ($F_{4,36} = 3.01^*$); species × salinity ($F_{4,36} = 4.31^{**}$)					
Light	2, 36	4.59*	9.84***	0.02	
Salinity	2, 36	27.18***	12.95***	1.18	
Light × salinity	4, 36	0.62	0.57	0.47	
RGR: analysis B (high-light trt excluded): species × salinity ($F_{6,36} = 2.17$, $P = 0.069$)					
Salinity	2, 12	18.19***	8.29**	0.60	0.64

Data are F ratios and probability levels: $* P \leq 0.05$, $** P \leq 0.01$, $*** P \leq 0.001$

and salinity conditions also reduced its final height, biomass, and relative growth rate compared to other treatments. Of the four species, *Pelliciera* exhibited the greatest
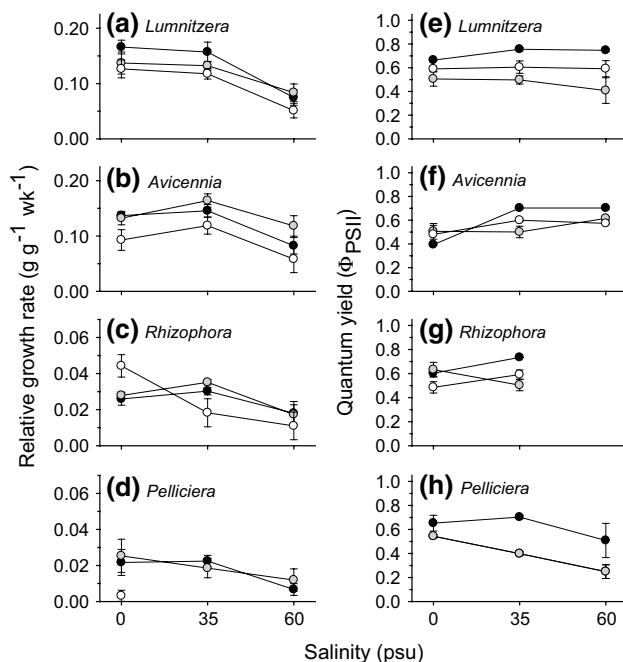

Fig. 3 Effects of light and salinity treatments on the dry biomass relative growth rate (*left*) of surviving seedlings to 12 weeks. Values are means ±1SE. Symbol legend for light level as in Fig. 2. No *Pelliciera* seedlings survived at medium or high salinity under high light, so neither RGR nor quantum yield could be measured for these treatments. Seedlings growing in freshwater under high light flushed leaves that were too small for accurate measurement of quantum yield. *Rhizophora* propagules growing at high salinity did not flush leaves at any light level, so quantum yield measurements could not be made

reduction in quantum yield with increasing salinity. High salinity continues to be stressful for the ensuing size/age-class of this species: rates of carbon dioxide exchange in two- to seven-year-old *Pelliciera* saplings grown hydroponically in 17.5 and 35 psu were reduced by 10 and 26 %, respectively, compared to those grown in 3.5 psu (Naidoo and von Willert 1999). With respect to light environment, we found that *Pelliciera's* quantum yield was highest under shaded conditions at all three salinities, which was generally also the case for *Lumnitzera* and *Avicennia*. The only exception was *Avicennia* growing in freshwater, where quantum yields were similar across light levels. Therefore, energy conversion was generally most efficient in the shade, a pattern observed in other mangrove studies (Björkman et al. 1988; Krauss and Allen 2003).

The invasive *Lumnitzera* and native *Avicennia* performed quite similarly across the treatments. They both exhibited >90 % survival at all salinity levels under low to medium light, with their survival declining to 58–83 % in saline treatments under high light. Both species showed a strong reduction in final height, biomass, and RGR under high-salinity conditions; *Avicennia* performed best at intermediate salinity (35 psu), whereas *Lumnitzera's* growth differed little between freshwater and seawater. *Avicennia* seedlings have been shown to be less sensitive to salt than other mangroves because of their high water-use efficiency. This conservative use of water limits their growth rate but allows *Avicennia* species to live in highly saline environments (Jiménez 1984; Ball 1988b; Lovelock and Ball 2002).

Both *Avicennia* and *Lumnitzera* had depressed growth under high-light conditions, with *Avicennia* being the more sensitive of the two species. All three measures of *Avicennia's* growth were reduced by high light; *Lumnitzera's* response was smaller in magnitude and only detectable in

Table 2 Results of ANOVA for the independent and interactive effects of light and salinity on the quantum yields of the four species of mangrove seedlings

Species	Light		Salinity		Light × salinity	
	df	F	df	F	df	F
Lumnitzera	2, 18	17.35***	2, 18	0.45	4, 18	0.78
Avicennia	2, 17	1.74	2, 17	14.56***	4, 17	4.21*
Rhizophora	2, 12	5.33*	1, 12	1.13	2, 12	5.93*
Pelliciera	1, 10	25.11***	2, 10	7.90**	2, 10	2.00

Probability levels are: * $P < 0.5$, ** $P < 0.1$, *** $P < 0.001$

final height and RGR. The quantum yields of both species tended to decline with increasing light, but this effect was not seen at 0 psu for *Avicennia*. At a given light level, the quantum yield of *Lumnitzera* showed little response to salinity. *Rhizophora* suffered greater mortality (up to 33 %) than *Lumnitzera* or *Avicennia* in saline treatments under low and medium light, but similar levels to these two species under high light. We did not detect any statistically significant influence of light level or salinity on the final height, biomass, or RGR of *Rhizophora*; at high salinity, however, none of the plants flushed leaves, and RGRs at all light levels were low. Its quantum yield responded in a limited and complex manner to light and salinity; confirmation and interpretation of the patterns beg additional data. Taken together, these findings indicate that *Rhizophora* is negatively affected by high salinity and must establish in more moderate salinity conditions.

It is important to note that our results pertain only to the seedling stage of the study species' life histories. Optimal conditions for growth may change during a plant's ontogeny (Ball 1988a, b, 2002; Lovelock and Ball 2002). In addition, our treatments were imposed as fixed conditions of light and salinity; different patterns and rates of temporal variation in soil salinity can affect the tolerance and performance of developing mangrove seedlings (Lin and Sternberg 1993; Bompy et al. 2014).

Due to the physiological constraints of living in saline flooded soil, mangroves often exhibit a reduction in photosynthetic rates and carbon assimilation (i.e., growth) under high soil salinity conditions (Ball 1988a; Lovelock and Ball 2002; Reef and Lovelock 2014). Additionally, because the photosynthetic rates of mangroves saturate at relatively low light intensities (typically 40 % irradiance or less; Krauss et al. 2008), exposure of leaves to direct sunlight can result in a large excess of excitation energy and a stressful increase in leaf temperature. Such conditions increase the potential for photooxidative damage to Photosystem II, or photoinhibition, under high-light conditions (Björkman et al. 1988). While much more detailed physiological measurements would be required to identify the precise mechanisms accounting for the marked vulnerability of *Pelliciera* to high-light and hypersaline conditions, quantum yield values

demonstrate a clear reduction in its photosynthetic efficiency. Mangroves employ a variety of photoprotective mechanisms (Ball 1988a, 1996; Björkman et al. 1988; Ball and Passioura 1995; Cheeseman et al. 1997; Krauss et al. 2008), but *Pelliciera* has not been studied in this regard.

Our results are in agreement with the conclusion of Krauss and Ball (2013) that few mangrove species are obligate halophytes. While our study only monitored survival and growth for 12 weeks, seedlings of all four species survived well in freshwater at all light levels. In fact, in high light, all survived better in freshwater than either saline treatment. *Lumnitzera* and *Pelliciera* tended to grow better in fresh than saline water at a given light level. *Avicennia* grew slightly better in seawater than freshwater, but most slowly in hypersaline conditions. *Rhizophora* growth was little affected by salinity, possibly because the plants were still drawing heavily on hypocotyl reserves (Ball 1988a, b, 2002). This species' highest RGR was attained under high light in freshwater. To better define the shape of the relationships between growth or physiological performance and salinity for these species, future experiments should employ a greater number of salinity levels than the three used here.

Responses of mangrove seedlings to covarying levels of light and salinity have been studied in both field and greenhouse settings (Ball 2002; Krauss and Allen 2003; López-Hoffman et al. 2006, 2007). Those investigations focused exclusively on species that are abundant and widely distributed, so do not provide tests of the specific hypothesis we examined. Further, performing a meaningful comparison of our findings with theirs is a challenging task due to lack of a common experimental protocol. Nonetheless, that collection of studies sheds light on patterns of mangrove species tolerance of variation in those particular physical conditions. Here, we examine two studies that included one or more of our study species.

Krauss and Allen (2003) measured photosynthetic and growth responses of two invasive mangrove species in Hawaii, *Rhizophora mangle* and *Bruguiera sexangula*, to six combinations of light (2 levels) and salinity (3 levels) in a greenhouse. Propagules were planted into commercial potting mix and fertilized every 28 days. No plants died

in any treatment over the course of the study. In general, growth of *Bruguiera* was more negatively affected by high salinity than that of *Rhizophora*, and *Rhizophora* showed an increase in photosynthetic assimilation with rising light levels, even at high salinity, while *Bruguiera*'s photosynthetic response plateaued at relatively low light levels, irrespective of salinity.

We also found *Rhizophora* to be relatively insensitive to variations in light and salinity. Its final height and biomass did not differ across our treatments; RGR appeared to decline under hypersaline conditions, but the trend was not significant. *Bruguiera*'s sensitivity to saline conditions but tolerance of a range of light levels is similar to what we observed for *Avicennia* and *Lumnitzera*. Both of the latter species suffered higher rates of mortality under high-light, high-salinity conditions than did either of Krauss and Allen's study species. However, our hypersaline treatment was essentially twice the salt concentration of their highest salinity level, so it is not surprising that we observed greater mortality.

The study most similar to ours in terms of taxa was López-Hoffman et al.'s (2006, 2007) greenhouse and field investigation of salinity and light effects on the photosynthesis, growth, and survival of *Avicennia germinans* and *Rhizophora mangle*. Seedlings used in their greenhouse experiment were pre-grown from propagules hydroponically for 3 months in 20 % seawater, prior to being transplanted into individual pots containing 1:1 sand and topsoil. Four light levels and three salinities were tested in a full factorial design. Experimental salinities were imposed gradually over a 3-week acclimation period to avoid osmotic shock. Plants were fertilized monthly, and experienced a simulated tidal regime. In parallel field experiments, the investigators monitored growth and mortality of *Avicennia* and *Rhizophora* seedlings planted in two tidal zones that differed markedly in salinity (0–5 vs. 35–70 psu) at a site on the coast of northwestern Venezuela. Within each zone, seedlings were planted in twelve plots representing a gradient of light levels. *Avicennia* seedlings were grown for 6 weeks at 20 % seawater prior to being transplanted onto the plots, while *Rhizophora* propagules were planted directly in the plots.

The responses of *Avicennia* and *Rhizophora* to the light and soil salinity regimes documented by López-Hoffman et al. differed considerably from those we observed. We recorded the highest rates of mortality under high-light, high-salinity conditions, while López-Hoffman et al. found low light, low salinity to be most lethal to *Rhizophora* and low light, high salinity to be most harmful to *Avicennia*. We found that high-light, high-salinity conditions also depressed the growth of at least three of our four species, whereas López-Hoffman et al. found that *Rhizophora* growth was lowest under low-light, low-salinity conditions

and *Avicennia* growth was poorest under low light—equally so for plants growing at low or high salinity. They observed the peak growth of *Avicennia* and *Rhizophora* to occur under high-light, low-salinity conditions, while we observed maximal growth under low–medium light in either freshwater or seawater, depending on the species. Only in the aforementioned case of *Rhizophora* growing in freshwater did we observe high-light conditions to possibly enhance growth. We do not have a concrete explanation for these contrasting findings; however, differences in experimental protocol might have contributed to them. In our experiment, three of the four species were introduced to the treatments as early-stage (1–2 week-old) seedlings and monitored as they matured over the course of the study, while López-Hoffman et al. initiated most of their experiments with seedlings that were substantially older: 12-week-old seedlings in the greenhouse and 6-week-old seedlings in the field. The younger stages we studied may exhibit quantitatively or qualitatively different responses to stressors than the older plants used by López-Hoffman et al. In addition, their plants were fertilized monthly while ours were not, and their growth measurements were made over 2- to 4-times-longer time spans than ours. Growth responses to variation in salinity are known to vary with nutrient supply (Lin and Sternberg 1992; Feller et al. 2003a, b).

Previous studies have shown that when introduced to a new locale, species with large native ranges are more likely to become naturalized in the novel habitat than species with smaller native geographic ranges, possibly because of the ability to tolerate a wider range of environmental conditions (Croci et al. 2007; Pemberton and Liu 2009; Shah et al. 2012). *Lumnitzera* appears to meet this expectation; it was arguably the species least affected by the treatments. However, the widespread native species *Avicennia* and *Rhizophora* were only slightly more sensitive to alterations in light and salinity, and they too have proven to be effective invaders outside their native range. *Avicennia germinans* has recently spread north through the Texas Gulf Coast and Florida salt marshes (Stevens et al. 2006; Perry and Mendelssohn 2009; Cavanaugh et al. 2014), and *A. marina*, intentionally introduced from New Zealand to Mission Bay in San Diego, CA, USA in 1968, became invasive during the 1970s and again in 2006, despite removal efforts (Moran 1980; Sauer 1988; Moseman et al. 2008). *Rhizophora mangle* was introduced to Hawaii in 1902, where it is now well established and vigorously expanding its local distribution (Krauss and Allen 2003; Chimner et al. 2006), as is *R. stylosa*, which was introduced to two of the Society Islands of French Polynesia in about 1946 (Taylor 1979; Smith 1996). Several broadly comparative analyses have detected little or no difference between traits of invasive exotic species and common native species, including

carbon capture strategy (Leishman et al. 2010; Tecco et al. 2010), growth response to nutrients, and survival in a competitive environment (Dawson et al. 2012).

It has been hypothesized that the patchy geographic distribution and limited range of *Pelliciera* are a consequence of its low tolerance of saline soil conditions (Fuchs 1970; Jiménez 1984). This hypothesis originated from the observation that stands of this species are typically located near freshwater drainages or brackish lagoons, where soil salinities are lower than seawater. Such habitats are distributed patchily along coastlines, hence the restricted and discontinuous distribution of the species. Fossil pollen records indicate that *Pelliciera* was widely distributed in the Caribbean region through much of the Tertiary, but its range began to shrink dramatically in the Early to Middle Miocene (Graham 1977; Gentry 1982; Jiménez 1984; Rull 2001). The present-day distribution of the species in the Caribbean comprises small, isolated populations in Nicaragua, Panama, and Columbia, located near sources of freshwater. Larger, but still discontinuous, populations can be found along the Pacific coast from Costa Rica to Ecuador, generally at sites with relatively high precipitation and abundant runoff. Several explanations have been proposed for this large reduction in range and abundance, including the combined effects of sea-level fluctuations, interspecific competition with *Rhizophora*, and the cooler, drier climate of the late Miocene and Pleistocene. Reduced rainfall, lower runoff, and associated increases in soil salinity are hypothesized to have played a primary role in narrowing and fragmenting the species distribution.

Our experiment showed that *Pelliciera* seedlings can tolerate water salinity levels of 35 psu and, more surprisingly, can survive in water with salt levels of 60 psu, if growing in shade. Because the experiment only ran for 12 weeks, it remains unknown if *Pelliciera* could survive to adulthood or reproduce under high-salinity conditions. Jiménez (1984) observed that *Pelliciera* did not occur at sites with >37 psu salinity along the Pacific coast of Costa Rica. Nevertheless, sites with salinity levels of 35 psu or less are common along the coasts of Central America. *Rhizophora* typically occupies such sites and is widespread throughout the Neotropics. Therefore, something in addition to suitable edaphic conditions is contributing to the rarity of *Pelliciera*. We found that high light intensity was the most stressful treatment in terms of *Pelliciera* survival; in the high-light treatment, 50 % of the seedlings in freshwater died, and none survived in either salt treatment. These results have important consequences for understanding the capability of *Pelliciera* to colonize new areas and expand existing populations. *Pelliciera* produces a small number of very large propagules and therefore has weak dispersal ability (Fuchs 1970). This, together with the required combination of low-light and moderate-salinity conditions, greatly limits the

potential distribution of *Pelliciera*. The species is unable to establish in sites with an open canopy; it recruits most successfully to shaded understory environments beneath the canopy of established trees; typically these are mixed stands of adult conspecifics and *Rhizophora* growing along creeks or brackish lagoons (Jiménez 1984; E. Dangremond, pers. obs.).

Our findings were consistent with the proposition that widely distributed mangrove species are more stress tolerant that those with limited geographic ranges. The rare endemic *Pelliciera* is considerably less tolerant of potentially stressful high-salinity and -light conditions than the three widespread mangrove species we studied, two of which are native and one of which was introduced to *Pelliciera*'s range. To determine if this is a general pattern will require additional studies of mangrove stress tolerance that specifically include species with relatively small geographic ranges.

Author contribution statement EMD and ICF conceived and designed the experiment. EMD performed the experiment. EMD and WPS analyzed the data and wrote the manuscript; ICF provided editorial advice.

References

Agresti A (2013) Categorical data analysis, 3rd edn. Wiley, Hoboken

Baker NR, Oxborough K (2004) Chlorophyll fluorescence as a probe of photosynthetic productivity. In: Papageorgiou GC, Govindjee (eds) Chlorophyll a fluorescence: a signature of photosynthesis. Kluwer Academic, Dordrecht, pp 65–82

Ball MC (1988a) Ecophysiology of mangroves. Trees 2:129–142. doi:10.1007/BF00196018

Ball MC (1988b) Salinity tolerance in the mangroves *Aegiceras corniculatum* and *Avicennia marina* I. Water use in relation to growth, carbon partitioning, and salt balance. Aust J Plant Physiol 15:447–464. doi:10.1071/PP9880447

Ball MC (1996) Comparative ecophysiology of mangrove forest and tropical lowland moist rainforest. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman and Hall, New York, pp 461–496

Ball MC (2002) Interactive effects of salinity and irradiance on growth: implications for mangrove forest structure along salinity gradients. Trees Struct Funct 16:126–139. doi:10.1007/s00468-002-0169-3

Ball MC, Critchley C (1982) Photosynthetic responses to irradiance by the grey mangrove, *Avicennia marina*, grown under different light regimes. Plant Physiol 70:1101–1106. doi:10.1104/pp.70.4.1101

Ball MC, Passioura JB (1995) Carbon gain in relation to water use: photosynthesis in mangroves. In: Schulze ED, Caldwell NM (eds) Ecophysiology of photosynthesis. Springer, Heidelberg, pp 247–257

Ball MC, Pidsley SM (1995) Growth responses to salinity in relation to distribution of two mangrove species, *Sonneratia alba* and *S. lanceolata*, in northern Australia. Funct Ecol 9:77–85. doi:10.2307/2390093

Bishop YM, Fienberg SE, Holland PW (1975) Discrete multivariate analysis: theory and practice. MIT Press, Cambridge

Björkman O, Demmig B, Andrews TJ (1988) Mangrove photosynthesis: response to high-irradiance stress. Aust J Plant Physiol 15:43–61. doi:10.1071/PP9880043

Bompy F, Lequeue G, Imbert D, Dulormne M (2014) Increasing fluctuations of soil salinity affect seedling growth performances and physiology in three Neotropical mangrove species. Plant Soil 380:399–413. doi:10.1007/s11104-014-2100-2

Boulangeat I, Lavergne S, Van Es J, Garraud L, Thuiller W (2012) Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. J Biogeogr 39:204–214. doi:10.1111/j.1365-2699.2011.02581.x

Cavanaugh KC, Kellner JR, Forde AJ, Gruner DS, Parker JD, Rodriguez W, Feller IC (2014) Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proc Natl Acad Sci USA 111:723–727. doi:10.1073/pnas.131580011

Cheeseman J, Clough BF, Carter DR, Lovelock CE, Eong OJ, Sim RG (1991) The analysis of photosynthetic performance in leaves under field conditions: a case study using *Bruguiera* mangroves. Photosynth Res 29:11–22. doi:10.1007/BF00035202

Cheeseman JM, Herendeen LB, Cheeseman AT, Clough BF (1997) Photosynthesis and photoprotection in mangroves under field conditions. Plant Cell Environ 20:579–588. doi:10.1111/j.1365-3040.1997.00096.x

Chimner RA, Fry B, Kaneshiro MY, Cormier N (2006) Current extent and historical expansion of introduced mangroves on O'ahu, Hawai'i. Pac Sci 60:377–383. doi:10.1353/psc.2006.0013

Collins SL, Glenn SM (1990) A hierarchical analysis of species' abundance patterns in grassland vegetation. Am Nat 135: 633–648. http://www.jstor.org/stable/2462027

Croci S, Le Quilliec P, Clergeau P (2007) Geographical range as predictor of spatial extent of invading birds. Biodivers Conserv 16:511–524. doi:10.1007/s10531-006-6732-2

Dawson W, Fischer M, van Kleunen M (2012) Common and rare plant species respond differently to fertilization and competition, whether they are alien or native. Ecol Lett 15:873–880. doi:10.1111/j.1461-0248.2012.01811.x

Demes K, Bell SS, Dawes CJ (2009) The effects of phosphate on the biomineralization of the green alga, *Halimeda incrassata* (Ellis) Lam. J Exp Mar Biol Ecol 374:123–127

Feller IC, McKee KL, Whigham DF, O'Neill JP (2003a) Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. Biogeochemistry 62:145–175. doi:10.1023/A:1021166010892

Feller IC, Whigham DF, McKee KL, Lovelock CE (2003b) Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. Oecologia 134:405–414. doi:10.1007/s00442-002-1117-z

Fienberg SE (1970) The analysis of multidimensional contingency tables. Ecology 51:419–433. doi:10.2307/1935377

Fourqurean JW, Smith TJ III, Possley J, Collins TM, Lee D, Namoff S (2010) Are mangroves in the tropical Atlantic ripe for invasion? Exotic mangrove trees in the forests of South Florida. Biol Invas 12:2509–2522. doi:10.1007/s10530-009-9660-8

Fuchs HP (1970) Ecological and palynological notes on *Pelliciera rhizophorae*. Acta Bot Neerl 19:884–894

Gaston KJ (1994) Rarity. Chapman and Hall, London

Gaston KJ (2003) The structure and dynamics of geographic ranges. Oxford University Press, Oxford

Gaston KJ, Kunin WE (1997) Rare-common differences: an overview. In: Gaston KJ, Kunin WE (eds) The biology of rarity. Population and Community Biology, vol 17. Springer, Dordrecht, pp 12–29

Gaston KJ, Lawton JH (1990) Effects of scale and habitat on the relationship between regional distribution and local abundance. Oikos 58:329–333. doi:10.2307/3545224

Gentry AH (1982) Phytogeographic patterns as evidence for a Chocó refuge. In: Prance GT (ed) Biological diversification in the tropics. Columbia University Press, New York, pp 112–136

Genty B, Briantais J-M, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. BBA-Gen Subj 990:87–92. doi:10.1016/S0304-4165(89)80016-9

Gotelli NJ, Simberloff D (1987) The distribution and abundance of tallgrass prairie plants: a test of the core-satellite hypothesis. Am Nat 130:18–35. http://www.jstor.org/stable/2461878

Graham A (1977) New records of *Pelliciera* (Theaceae/Pelliciericeae) in the Tertiary of the Caribbean. Biotropica 9:48–52. doi:10.2307/2387858

Hanski I (1982) Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38:210–221. http://www.jstor.org/stable/3544021

Hanski I, Kouki J, Halkka A (1993) Three explanations of the positive relationship between distribution and abundance of species. In: Ricklefs RE, Schluter D (eds) Community diversity: historical and geographical perspectives. University Chicago Press, Chicago, pp 108–116

Harper JL (1981) The meanings of rarity. In: Synge H (ed) The biological aspects of rare plant conservation. Wiley, New York, pp 189–203

Hogarth PJ (2007) The biology of mangroves and seagrasses, 2nd edn. Oxford University Press, Oxford

Janzen DH (1985) Mangroves: where's the understory? J Trop Ecol 1:89–92. doi:10.1017/S0266467400000122

Jiménez JA (1984) A hypothesis to explain the reduced distribution of the mangrove *Pelliciera rhizophorae* Tr and Pl. Biotropica 16:304–308. http://www.jstor.org/stable/2387939

Krauss KW, Allen JA (2003) Influences of salinity and shade on seedling photosynthesis and growth of two mangrove species, *Rhizophora mangle* and *Bruguiera sexangula*, introduced to Hawaii. Aquat Bot 77:311–324. doi:10.1016/j.aquabot.2003.08.004

Krauss KW, Ball MC (2013) On the halophytic nature of mangroves. Trees 27:7–11. doi:10.1007/s00468-012-0767-7

Krauss KW, Lovelock CE, McKee KL, López-Hoffman L, Ewe SML, Sousa WP (2008) Environmental drivers in mangrove establishment and early development: a review. Aquat Bot 89:105–127. doi:10.1016/j.aquabot.2007.12.014

Kruckeberg AR, Rabinowitz D (1985) Biological aspects of endemism in higher plants. Ann Rev Ecol Syst 16: 447–479. http://www.jstor.org/stable/2097056

Leishman MR, Thomson VP, Cooke J (2010) Native and exotic invasive plants have fundamentally similar carbon capture strategies. J Ecol 98:28–42. doi:10.1111/j.1365-2745.2009.01608.x

Lin G, Sternberg LSL (1992) Effect of growth form, salinity, nutrient and sulfide on photosynthesis, carbon isotope discrimination and growth of red mangrove (*Rhizophora mangle* L.). Aust J Plant Physiol 19:509–517. doi:10.1071/PP9920509

Lin G, Sternberg LSL (1993) Effects of salinity fluctuation on photosynthetic gas exchange and plant growth of the red mangrove (Rhizophora mangle L.). J Exp Bot 44:9–16. doi:10.1093/jxb/44.1.9

López-Hoffman L, DeNoyer JL, Monroe IE, Shaftel R, Anten NPR, Martínez-Ramos M, Ackerly DD (2006) Mangrove seedling net photosynthesis, growth, and survivorship are interactively affected by salinity and light. Biotropica 38:606–616. doi:10.1111/j.1744-7429.2006.00189.x

López-Hoffman L, Anten NPR, Martínez-Ramos M, Ackerly DD (2007) Salinity and light interactively affect neotropical mangrove seedlings at the leaf and whole plant levels. Oecologia 150:545–556. doi:10.1007/s00442-006-0563-4

Lovelock CE, Ball MC (2002) Influence of salinity on photosynthesis of halophytes. In: Lauchli A, Luttge U (eds) Salinity: environment—plants—molecules. Kluwer, Dordrecht, pp 315–339

Lugo AE (1986) Mangrove understory: an expensive luxury? J Trop Ecol 2:287–288. doi:10.1017/S0266467400000912

Maxwell K, Johnson GN (2000) Chlorophyll fluorescence—a practical guide. J Exp Bot 51:659–668. doi:10.1093/jexbot/51.345.659

McKee KL (1995) Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physico-chemical factors. Oecologia 101:448–460. doi:10.1007/BF00329423

Moran, R (1980) Noteworthy collections: *Avicennia marina* var. *resinifera.* Madroño 27:143. http://www.jstor.org/stable/41426134

Moseman SM, Zhang R, Qian PY, Levin LA (2008) Diversity and functional responses of nitrogen-fixing microbes to three wetland invasions. Biol Invas 11:225–239. doi:10.1007/s10530-008-9227-0

Naidoo G, von Willert DJ (1999) Gas exchange characteristics of the tropical mangrove, *Pelliciera rhizophorae*. Mangroves Salt Marshes 3:147–153. doi:10.1023/A:1009943408779

Paine TCE, Marthews TR, Vogt DR, Purves D, Rees M, Hector A, Turnbull LA (2012) How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. Method Ecol Evol 3:245–256. doi:10.1111/j.2041-210X.2011.00155.x

Pemberton RE, Liu H (2009) Marketing time predicts naturalization of horticultural plants. Ecology 90:69–80. doi:10.1890/07-1516.1

Perry CL, Mendelssohn IA (2009) Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. Wetlands 29:396–406. doi:10.1672/08-100.1

Rabinowitz D (1981) Seven forms of rarity. In: Synge H (ed) The biological aspects of rare plant conservation. Wiley, New York, pp 205–217

Rabinowitz D, Cairns S, Dillon T (1986) Seven forms of rarity and their frequency in the flora of the British Isles. In: Soulé ME (ed) Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, pp 182–204

Reef R, Lovelock CE (2014) Regulation of water balance in mangroves. Ann Bot–London. doi:10.1093/aob/mcu174

Rees M, Osborne CP, Woodward FI, Hulme SP, Turnbull LA, Taylor SH (2010) Partitioning the components of relative growth rate: how important is plant size variation? Am Nat 176:E152–E161. doi:10.1086/657037

Rosenzweig ML, Lomolino MV (1997) Who gets the short bits of the broken stick? In: Gaston KJ, Kunin WE (eds) The biology of rarity. Population and Community Biology, vol 17. Springer, Dordrecht, pp 63–90

Rull V (2001) A quantitative palynological record from the early Miocene of western Venezuela, with emphasis on mangroves. Palynology 25:109–126. doi:10.2113/0250109

Sauer JD (1988) Plant migration: the dynamics of geographic patterning in seed plant species. University of California Press, Berkeley

Shah M, Reshi ZA, Lavoie C (2012) Predicting plant invasiveness from native range size: clues from the Kashmir Himalaya. J Plant Ecol 5:167–173. doi:10.1093/jpe/rtr021

Slatyer R, Hirst M, Sexton JP (2013) Niche breadth predicts geographical range size: a general ecological pattern. Ecol Lett 16:1104–1114. doi:10.1111/ele.12140

Smith TJ III (1992) Forest structure. In: Robertson AI, Alongi DM (eds) Tropical mangrove ecosystems. American Geophysical Union, Washington, DC, pp 101–136

Smith JMB (1996) Perspectives on an invasion of paradise: *Rhizophora stylosa* on Moorea, French Polynesia. Aust Geog Stud 34:81–87. doi:10.1111/j.1467-8470.1996.tb00104.x

Snedaker SC, Lahmann EJ (1988) Mangrove understorey absence: a consequence of evolution? J Trop Ecol 4:311–314. doi:10.1017/S0266467400002881

Stevens PW, Fox SL, Montague CL (2006) The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. Wetl Ecol Manage 14:435–444. doi:10.1007/s11273-006-0006-3

Taylor FJ (1979) *Rhizophora* in the Society Islands. Pac Sci 33:173–176

Tecco PA, Diaz S, Cabido M, Urcelay C (2010) Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? J Ecol 98:17–27. doi:10.1111/j.1365-2745.2009.01592.x

Tomlinson PB (1986) The botany of mangroves. Cambridge University Press, Cambridge

Winer BJ, Brown DR, Michels KM (1991) Statistical principles in experimental design, 3rd edn. McGraw-Hill, New York