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Biotic and abiotic factors constraining the distribution and abundance of the rare mangrove *Pelliciera rhizophorae* in Panamá

By

Emily Margaret Dangremond

A dissertation submitted in partial satisfaction of the requirements for the degree of

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in

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University of California, Berkeley

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Fall 2013

Biotic and abiotic factors constraining the distribution and abundance of the rare mangrove *Pelliciera rhizophorae* in Panamá

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by Emily Margaret Dangremond

Abstract

Biotic and abiotic factors constraining the distribution and abundance of the rare mangrove
Pelliciera rhizophorae in Panamá

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Emily Margaret Dangremond

Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Professor Wayne Sousa, chair

Pelliciera rhizophorae is a Neotropical mangrove species with a narrow geographic distribution. Despite having a wide fossil distribution around the Caribbean Sea, extant populations of *P. rhizophorae* are rare on the Caribbean coast of Central and South America. The current extent of the distribution of *P. rhizophorae* on the Caribbean coast of Panamá was investigated. Populations are small and isolated, with seven populations occurring on freshwater streams in Bocas del Toro and Colón provinces. A shadehouse experiment was conducted to test the shade and salinity tolerances of *P. rhizophorae* compared to three widespread mangrove species: *Avicennia germinans*, *Rhizophora mangle*, and *Lumnitzera racemosa*. *Pelliciera rhizophorae* is more sensitive to soil salinity and high light conditions than other, more common mangroves but its salinity tolerance does not explain its narrow distribution. Obstacles to recruitment for *P. rhizophorae* were examined by quantifying propagule predation by crabs and seedling survival in different forest types. Crab predation of *P. rhizophorae* propagules was much higher in mangrove forests where *P. rhizophorae* does not occur than where it does occur. Seedlings were planted that were protected from predation by crabs, and seedling survival did not differ between forest types, suggesting that crab predation limits recruitment in areas dominated by other mangrove species. Nutrient dynamics and biomass allocation ratios were studied in *P. rhizophorae* from populations on the Pacific and Caribbean coasts of Panamá. There are two growth forms that occur on each coast: a stunted “dwarf” form and a taller “fringe” form. In other species the stunted form is caused by nutrient limitation, but the nutrient status of *P. rhizophorae* had never been studied. Dwarf trees had lower nutrient content than fringe trees, and also allocated more biomass to stems than leaves relative to fringe trees. A combination of abiotic (e.g., shade availability) and biotic factors (e.g., propagule predation by crabs) are responsible for the narrow distribution of *P. rhizophorae*.

For Ian

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Introduction

The life history, demographic, and environmental features that determine different forms of species rarity are a main focus of investigations in ecology and evolutionary biology (Rabinowitz 1981, Kruckeberg and Rabinowitz 1985, Gaston 1994, 2003). Rare species are interesting from an academic perspective, but also in terms of conservation, as rapid global change makes it important to understand the threats to biodiversity and possible conservation solutions.

Deborah Rabinowitz (1981) defined seven forms of rarity according to three axes: geographic range (large vs. small), habitat specificity (generalist or specialist), and local abundance (abundant or sparse). This dissertation explores abiotic and biotic factors contributing to the abundance and distribution of a plant species that is rare on all three of these axes. *Pelliciera rhizophorae* is a Neotropical mangrove with a narrow geographical range, specialized habitat, and generally sparse local abundance. I chose to study this species because it is an example of the rarest of the rare, and before I started this work, very little was known about the current distribution and autecology of *P. rhizophorae*.

There are challenges associated with investigating the population ecology of long-lived organisms, since an observation period of a few years is not long enough to observe individuals mature to reproduction, rates of adult mortality, or many transitions between life stages. For this reason, I focused on seedling establishment for two chapters. For the other two chapters, I examined the functional traits of adult trees and mapped the size and location of this rare tree throughout Panamá.

Pelliciera rhizophorae was thought to be extinct from the Caribbean until 1981, but the fossil pollen record showed it was once widespread throughout the Caribbean region. In the first chapter, I describe the current extent of *P. rhizophorae* occurrence on the Caribbean coast of Panamá. Populations are small and isolated, occurring on freshwater streams in Bocas del Toro and Colón provinces.

In 1984, Jorge Jimenez suggested the current reduced distribution of *P. rhizophorae* was due to a lack of suitable habitat on the Caribbean coast. He observed that the species was only found in areas with low soil salinity. However, the ability of *P. rhizophorae* to establish and grow in a range of habitat conditions had never been tested. I conducted a shadehouse experiment to test the shade and salinity tolerances of *P. rhizophorae*; two mangrove species common throughout the Neotropics, *Avicennia germinans* and *Rhizophora mangle*; and one mangrove in the early stages of becoming invasive in Florida, *Lumnitzera racemosa*. I found *P. rhizophorae* to be more sensitive to soil salinity and high light conditions than other, more common mangroves.

Having tested seedling establishment in a controlled shadehouse environment, I then studied seedling establishment under field conditions. In the third chapter I compared rates of seedling establishment in different forest types to investigate whether *P. rhizophorae* could survive and grow in forests other than those in which it is currently found. *Pelliciera rhizophorae* survived in other forest types as well as it survived in its own forest zone. I also quantified rates of propagule predation by crabs and found a strong influence of crabs limiting seedling establishment in forests that are not occupied by *P. rhizophorae*.

In the last chapter, I examined the nutrient status and biomass allocation of *P. rhizophorae* trees from populations on both coasts of Panamá. Like other mangroves, *P. rhizophorae* grows as a stunted “dwarf” form in addition to a taller “fringe” form. In other

species the stunted form is caused by nutrient limitation, but the nutrient status of *P. rhizophorae* had never been studied. Dwarf trees had lower nutrient content than fringe trees, and also had a different architecture, devoting more biomass to stems than leaves relative to fringe trees. My results indicate that dwarf trees on both coasts and fringe trees on the Caribbean coast of Panamá are nutrient-limited.

Taken together, the results presented here give a clearer picture of the abiotic and biotic factors influencing the distribution of *P. rhizophorae*. Propagules are limited to establishing in shaded, low salinity sites. Additionally, they must escape predation by crabs, which are abundant throughout all Panamanian mangrove forests. Adult trees are nutrient-limited on the Caribbean coast of Panamá, and the dwarf growth form is caused by nutrient-limitation. The naturally occurring environment provides many challenges to *P. rhizophorae* population growth and expansion. Coupled with anthropogenic climate change, coastal development and habitat destruction, the future of this species may appear bleak. However, *Pelliciera* fossil pollen has been found from 50 mya (Graham 1977), so the *Pelliciera* lineage has survived past climate changes and may continue to exist in future climates. Current and future conservation efforts should focus on protecting *P. rhizophorae* habitat from destruction.

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Chapter 1

A census of Caribbean *Pelliciera rhizophorae* populations in Panamá

Abstract

Pelliciera rhizophorae is a neotropical mangrove with a narrow geographical range. This study assessed species composition and demographic structure of *P. rhizophorae* forests on the Caribbean coast of Panamá. Previous work has suggested that the distribution of *P. rhizophorae* is limited by soil salinity. *Pelliciera rhizophorae* usually occurs in monospecific zones along freshwater streams. Populations sampled were Cilico Creek and Souli Creek in Bocas del Toro, Quebrada Las Mercedes in Colón, and the Quebro River in Veraguas. Other common mangrove species, *R. mangle*, *L. racemosa*, and *A. germinans*, were present at most sites where *P. rhizophorae* occurs, and abundance of other species varied from site to site. Size structure was generally consistent among sites, with the majority of trees in the 0-5 cm DBH class.

Introduction

Pelliciera is a monotypic genus in the family Tetrameristaceae (APG II 2003), first described in 1862 by Triana and Planchon. *Pelliciera* was originally placed in the Theaceae, but its inclusion there was not universally accepted due to anatomical differences in wood and other structures. Beauvisage (1920) suggested *Pelliciera* should be assigned to its own family and was supported by Record (1942), Metcalfe and Chalk (1950) and Kobuski (1951), which resulted in the formation of the family Pellicieraceae. Molecular analysis placed *Pelliciera* in the family Tetrameristaceae in 2003 (APG II 2003), where it remains currently (APG 2009). The other genera of the Tetrameristaceae are *Pentamerista*, which is endemic to South America, and *Tetramerista*, endemic to Malaysia.

The sole member of the genus, *P. rhizophorae*, is a mangrove endemic to the Neotropics. The lineage originated in the Tethys Sea in the early Tertiary (Ellison et al. 1999), and fossil pollen has been found in the Caribbean dating back to the Eocene (Graham 1977). The fossil record indicates that *Pelliciera* was once widespread throughout the region. However, the modern distribution of *Pelliciera* is much narrower than its former distribution, and it is a rare component of the Neotropical mangrove flora. In fact, until 1982 *P. rhizophorae* was thought to be extinct from the Caribbean Sea. Calderón-Saenz in 1982 and Winograd in 1983 identified populations on the Caribbean coast of Colombia. Another small population was identified on the Caribbean coast of Nicaragua in 1991 (Roth and Grijalva 1991), but they only counted ten seedlings and one sapling that had survived the severe hurricane of 1988. (The current status of this population is unknown.) Caribbean populations are considered to be relicts of a once wider distribution, which may have been reduced due to cooler climates in the late Miocene (Graham 1977) or dry periods in the Pleistocene (Gentry 1981) and/or changing salinity of the Caribbean (Haug et al. 2001).

Caribbean populations of *P. rhizophorae* are small and isolated relative to Pacific populations. Castillo-Cardenas and Toro-Perea (2012) found low genetic diversity in the Caribbean populations and evidence of a recent bottleneck in Panamanian populations. Jimenez (1984) observed that *P. rhizophorae* occurs in areas of low soil salinity with a freshwater input. The maximum salt concentration of *P. rhizophorae* habitats Jimenez observed on the Pacific coast of Costa Rica was 37 parts per thousand (ppt), though other mangroves can be found in soil salinities of 100 ppt. He suggested that the current distribution of *P. rhizophorae* may result from a low salinity tolerance and the species may therefore be restricted to sites with high precipitation and abundant runoff. After the isthmus of Panamá emerged, salinity in the Caribbean increased by 1 ppt (Haug et al. 2001). Jimenez posits that *P. rhizophorae* expanded

its range on the Pacific coast after more humid climates returned to the region, but unlike other mangroves, did not re-expand on the Caribbean because of a lack of suitable habitat. However, Jimenez carried out no tests of his hypothesis, did not sample Caribbean populations, and did not test the physiological tolerance of *P. rhizophorae* to environmental conditions.

The purpose of this study was to assess size, species composition and demographic structure of *P. rhizophorae* forests on the Caribbean coast of Panamá. *Pelliciera rhizophorae* is found on tidal streams on the Caribbean coast of Panama, and in estuaries on the Pacific coast (E. Dangremond, pers. obs.). All known populations on the Caribbean coast of Panamá were surveyed. Populations on the Pacific coast were also identified, and one was chosen based on its accessibility to compare forest structure to the Caribbean populations. Other Pacific populations have been surveyed in Costa Rica (Jimenez 1984 and Mainardi Grellet 1995).

Methods

Creeks on the Caribbean coast of Panama were surveyed between June 2010 and February 2012. Locations were identified that appeared suitable for *P. rhizophorae*, based on the presence of freshwater creeks and *Rhizophora mangle*, which indicates mangrove as opposed to terrestrial vegetation. Caribbean populations were surveyed in Colón and Bocas del Toro provinces. The sampled Pacific population was on the Azuero peninsula (Fig. 1). The perimeter of each site was delineated with a handheld GPS unit (Garmin Oregon 300) and then the area was calculated with ArcGIS.

In four mangrove stands (Souli Creek, Cilico Creek, Quebrada Las Mercedes and Quebro), transects were used to sample species composition, density and population structure. The Souli Creek population was sampled in June 2009 and October 2011; the Quebro population was sampled in June 2010; the Quebrada Las Mercedes (QLM) population was sampled in July 2010 and the Cilico Creek population was sampled in October 2011. At each site, two types of transects were used: a 10-m wide tree transect, in which all trees above 1 m tall were counted, and a 1-m wide seedling transect nested inside the 10-m transect in which all seedlings were counted. Five parallel transects of 80 m (60 m at Cilico Creek) spaced 20 m apart were established perpendicular to the creek from the water's edge to the point where the mangrove stand intersected with *terra firme* forest. Diameter at breast (DBH) height measurements were taken within 4 m segments for all *P. rhizophorae* trees taller than 1.3 m. Individuals of all species were recorded in 5-m intervals within each transect. Reproductive phenology was also observed in each population. At QLM, all naturally-occurring seedlings in a 8 x 8 m plot were tagged and followed over two years. Population sizes were estimated by multiplying the average density of individuals in the transects by the total population area calculated by GPS measurements.

Size distributions were compared with a two-sample Kolmogorov-Smirnov test between each pair of sites and then p-values were adjusted with a Bonferroni correction. This analysis was done in R version 2.7.2 (R Core Development Team, 2013).

Results

Pelliciera rhizophorae was found on seven tidal creeks on the Caribbean coast of Panama (Fig. 1). No *P. rhizophorae* was found in the Fort Sherman area (9.36° N, 79.96° W) west of the city of Colón. East of Colón, no *P. rhizophorae* was found between Maria Chiquita (9.44° N,

79.75° W) and Portobelo (9.55° N, 79.64° W). The locations, area, and size estimates of all Caribbean populations are presented in Table 1. Specific information about each site, in addition to locations of Pacific populations, can be found in Appendix A.

Size structure for the Souli Creek, Cilico Creek, QLM and Quebro populations is presented in Fig. 2. In general, *P. rhizophorae* populations are dominated by smaller individuals, with most in the 0-5 cm range and very few in each population above 30 cm DBH. The size distributions of these four populations were not significantly different from each other (Table 2).

Seedling densities and distributions with respect to the creek edge for the four populations sampled are presented in Fig. 3. I did not find a consistent pattern in seedling abundance with distance from creek edge—in some cases, seedlings were densest close to the creek (e.g. Cilico), while at other sites, seedling densities peaked at 40 or more meters away from the creek (e.g. QLM and Quebro). At Souli Creek, seedlings were densest between 10 and 40 m from the creek.

Species composition for the mangrove forests sampled are presented as average number of individuals per transect point in Figs. 4-7. Both Souli and Cilico Creek stands were dominated by *P. rhizophorae* within 20 m of the creek. Souli Creek had terrestrial species throughout the forest, with the highest concentration 60-80 m from the creek. Cilico Creek had a mix of the common mangrove species, *R. mangle*, *L. racemosa*, and *A. germinans*, at an intermediate distance from the creek where *P. rhizophorae* was not abundant. QLM had the highest density of *P. rhizophorae* individuals at 20-45 m from the creek, and *R. mangle* occurred at highest densities < 10 m and 60-80 m from the creek. Other mangrove species were present at QLM but not at high densities. Quebro was dominated by *R. mangle* close to the creek, with *P. rhizophorae* densest in the zone furthest from the creek before *terra firme* vegetation replaces mangroves. Caribbean populations exhibited some flowering and propagules throughout the year, with propagule production peaking in October. The Pacific population had peak propagule production in July.

Discussion

The rare mangrove *P. rhizophorae* was found on seven tidal creeks on the Caribbean coast of Panama. Five populations of *P. rhizophorae* were identified in Bocas del Toro, and two in Colón province. Sites were not surveyed in Kuna Yala or anywhere east of Portobelo, so it is possible there are more populations on Panama's Caribbean coast. Population size estimates ranged from 22 individuals at Bahia Escondida to 127,677 individuals at Souli Creek. Jimenez (1984) found that soil salinity was 37 ppt or lower in *P. rhizophorae* populations in Costa Rica. My results support his results; 32 ppt was the maximum soil salinity I measured in a *P. rhizophorae* population.

Pelliciera rhizophorae populations varied in forest structure and species composition. At Souli Creek and Cilico Creek, *P. rhizophorae* individuals were densest close to the creek edge. Souli Creek had other mangroves in low densities within the first 40 m from the creek, but then changed to terrestrial vegetation. At Souli Creek, seedlings were densest between 10 and 40 m from the creek. *Pelliciera rhizophorae* may be outcompeted further from the creek, as terrestrial vegetation becomes denser. Seedlings at Cilico Creek are densest close to the creek edge. Larger *P. rhizophorae* individuals are also densest close to the creek, which may explain seedling density if seedlings establish close to parent trees. This is a different pattern than the other sites, where *P. rhizophorae* increases in abundance with distance from the creek. At both

Quebro and QLM, seedlings were densest around 40 m from the creek. This could be because floating propagules are moved inland by the tide before they are firmly rooted and deeper water at the creek bank may make it difficult to establish a root-hold. This is most likely the case at Quebro, where Pacific tides flood the entire forest and limit seedling establishment close to the water's edge. Tidal inundation could also prevent establishment close to the creek at QLM—the creek is bordered by mature *R. mangle* trees with occasional *R. mangle* seedlings, which seem to establish in deep water more often than *P. rhizophorae* (E. Dangremond, pers. obs.).

The low frequency of individuals with trunks greater than 30 cm suggests younger individuals dominate the forests. In general, mature *P. rhizophorae* has smaller average DBH than other mangroves in the region (Jimenez 1990, Jimenez and Sauter 1991, Mainardi Grellet 1995). Individuals can be reproductively mature with a DBH of <10 cm. Though a few trees in Caribbean populations reached extremes of about 40 cm DBH, the Quebro population on the Pacific coast had more individuals in the 20-30 cm range than the Caribbean populations. However, in other areas of the Pacific coast (e.g. the Darién region), *P. rhizophorae* may grow wider and taller (IC Feller, pers. comm.).

The determining factors for the current distribution of *P. rhizophorae* remain unknown. Jimenez (1984) suggested *P. rhizophorae* is more abundant on the Pacific coast because it is restricted to sites with high precipitation and low salinity due to a physiological intolerance to highly saline soils. In Panamá, the Caribbean coast actually receives more annual rainfall than the Pacific coast (Condit 1998). However, this may favor terrestrial vegetation over mangroves in some areas, such as Cilico Creek and Souli Creek. Research on *P. rhizophorae* forests on the Pacific coast of Costa Rica found that distance from the mouth of an estuary best predicted *P. rhizophorae* stand structure and floristic composition (Mainardi Grellet 1995), with abundant pure stands of *P. rhizophorae* located at the edges of the estuary, and *R. racemosa* replacing *P. rhizophorae* in the central estuarine stands. The Pacific populations of Panamá also tend to be on the landward side of their estuaries. On the Pacific coast of Costa Rica, *P. rhizophorae* is sometimes found in estuaries as far inland as 18 km (Mainardi Grellet 1995). On the Caribbean coast of Panamá, there are fewer large estuaries than the Pacific coast, and so *P. rhizophorae* occurs on freshwater streams and is never found more than 1 km inland. In many of the Caribbean populations, *P. rhizophorae* extends 100 m or less from the creek's edge before the vegetation turns to terrestrial forest.

The populations in each Caribbean province could be called subpopulations of two regional populations (Bocas del Toro and Colón), as they are within a few kilometers of each other. Castillo-Cardenas and Toro-Perea (2012) treated them as one Bocas del Toro population and one Bahia Las Minas (Colón) population. However, each site occurs on a separate stream with no continuity between them. It remains unknown if dispersal occurs, and with what frequency, between plants on separate streams in the same region. The low intrapopulation genetic diversity Castillo-Cardenas and Toro-Perea (2012) found suggests there is little, if any, dispersal between populations. Interestingly, Castillo-Cardenas (2009) found evidence of transisthmian gene flow between a Pacific population in Panama and two Caribbean populations in Colombia. There was no evidence of gene flow between Pacific and Caribbean populations within Panama or within Colombia, despite at least one Caribbean population in Panama being closer than the Colombian Caribbean populations. Gene flow does not occur between other species of mangroves on the two coasts of Central America, including *Rhizophora mangle* and *Avicennia germinans* (Dodd et al. 2002, Cerón-Souza et al. 2012).

Pelliciera rhizophorae likely experienced reductions in its range due to past climate changes. Future climate change may present more challenges for this rare species. Valiela and others (2012) observed that rainfall on the Pacific coast of Panama is slowly increasing, freshening the water in estuaries and near shore waters. This could result in increased habitat for *P. rhizophorae*, but they observed individuals growing on stream banks being swept away by erosion during large discharge events, such as the heavier than normal precipitation during 2010. Heavier runoff could make *P. rhizophorae* more vulnerable to climate change-induced loss of habitat. On the other hand, the Caribbean is predicted to become drier (Campbell et al. 2011, Karmalkar et al. 2011, Biasutti et al. 2012, Hall et al. 2012), placing those populations at even greater risk of extinction.

In the Caribbean, *P. rhizophorae* is an excellent example of one of Rabinowitz' (1981) seven forms of rarity: geographically restricted, but locally abundant. That pattern of rarity appears to be driven by its dependence on low salinity conditions afforded by coastal streams or creeks for maximal growth, reproduction, and survival (Chapter 2). The species has low fecundity and modest dispersal ability, which means that its persistence in the Caribbean depends on the protection of coastal creeks from water diversion and pollution.

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Table 1. Locations, area, and estimates of population sizes (trees ≥ 1.3 m tall) of Caribbean populations of *Pelliciera rhizophorae* in Panama. Coordinates are in decimal degrees.

Creek	Latitude	Longitude	Area (ha)	Population Size
Bahia Azul	9.143	-81.879	3.75	11,264
Bahia Escondida	9.282	-82.284	0.19	22
Bahia Las Minas	9.383	-79.807	3.25	4,490
Cilico Creek	9.076	-82.246	0.92	7,866
Patterson Creek	9.100	-81.889	0.94	9,909
Quebrada Las Mercedes	9.435	-79.785	9.92	79,360
Souli Creek	9.010	-81.791	6.74	127,677

Table 2. Pairwise comparisons of size distributions of *Pelliciera rhizophorae* populations. Each pair of distributions was compared with two-sample Kolmogorov-Smirnov test, and p-values were adjusted using a Bonferroni correction. D = KS distance.

	Cilico	Quebro	QLM
Souli	D = 0.144, p = 1	D = 0.1654, p = 0.49	D = 0.1262, p = 1
Cilico		D = 0.1032, p = 1	D = 0.1600, p = 1
Quebro			D = 0.1935, p = 0.20

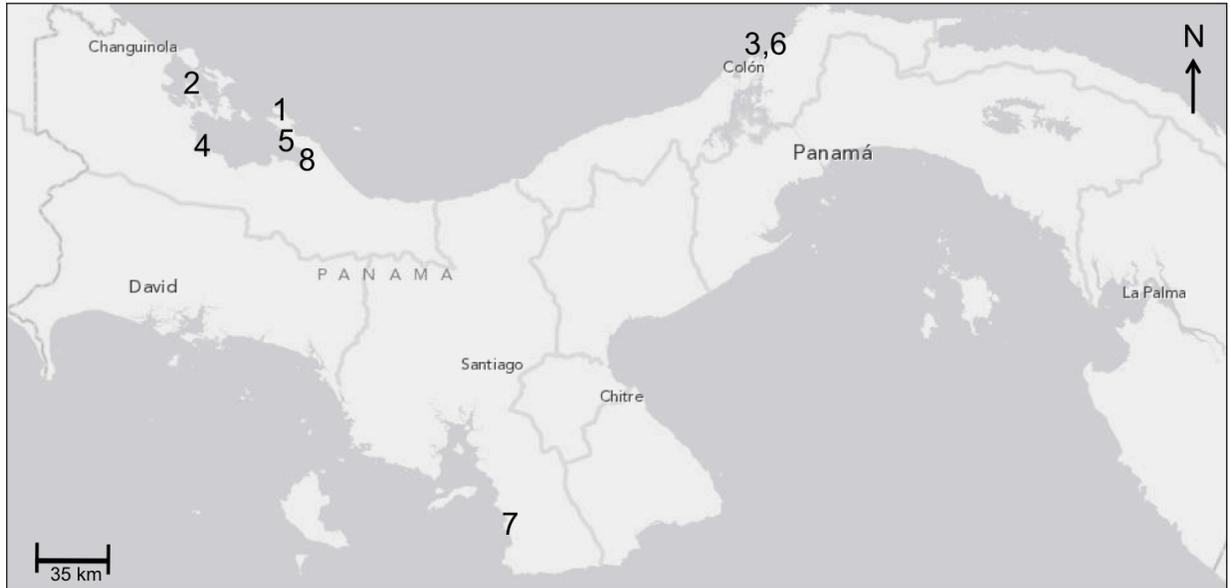


Figure 1. Map of *Pelliciera rhizophorae* populations surveyed in Panama, including all known Caribbean populations. 1-Bahía Azul, 2-Bahía Escondida, 3-Bahía Las Minas, 4-Cilico Creek, 5-Patterson Creek, 6-Quebrada Las Mercedes, 7-Quebro River, 8-Souli Creek.

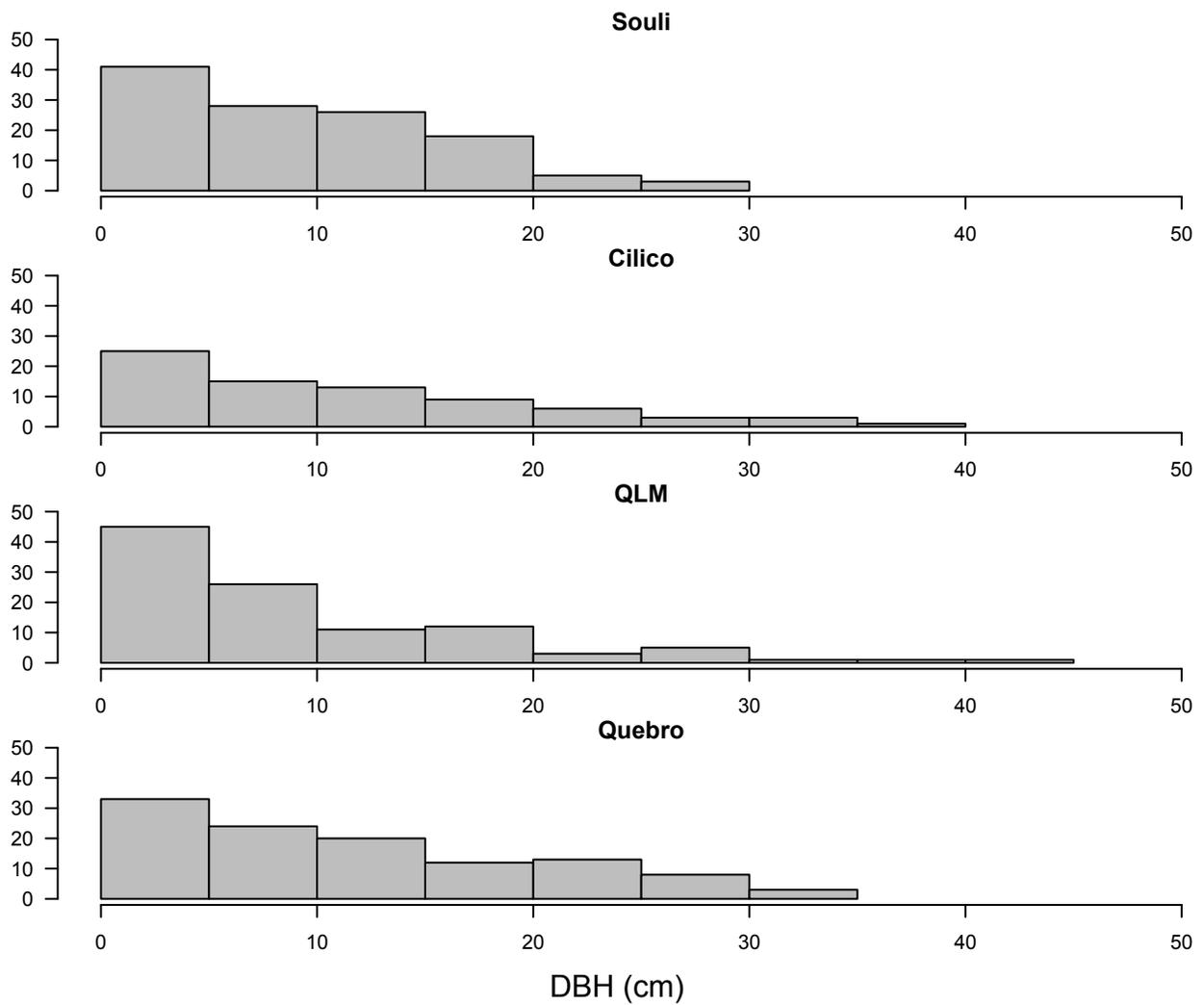


Figure 2. Diameter at breast height (DBH) of *Pelliciera rhizophorae* trees ≥ 1.3 m tall in four populations in Panama. Souli, Cilico and QLM are on the Caribbean coast and Quebro is on the Pacific coast. Y-axis is average number of individuals per 10 m transect.

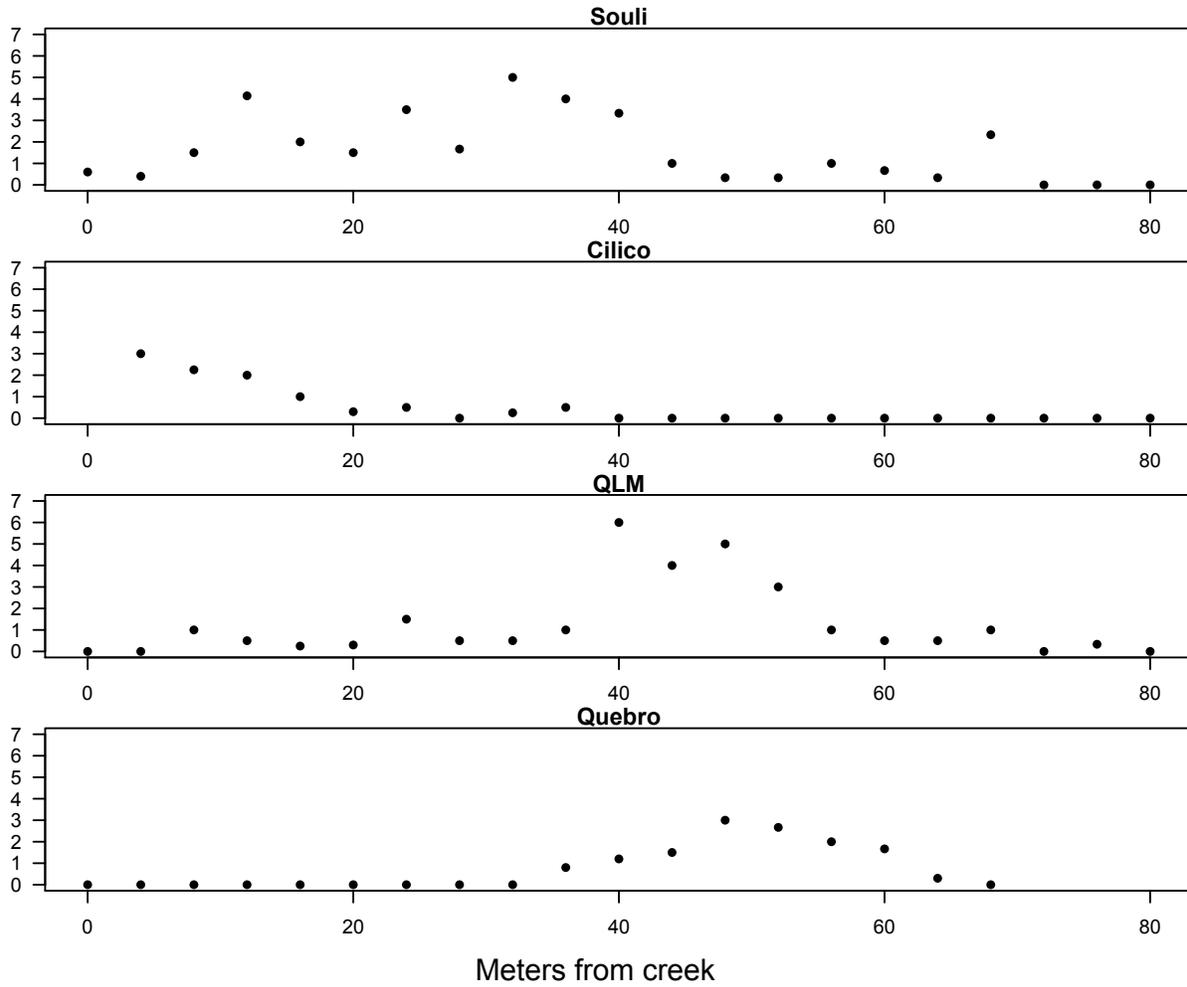


Figure 3. Average seedling density (# of individuals per square meter) in four populations in Panama. Seedlings were measured in 4-m segments on transects perpendicular to the creek.

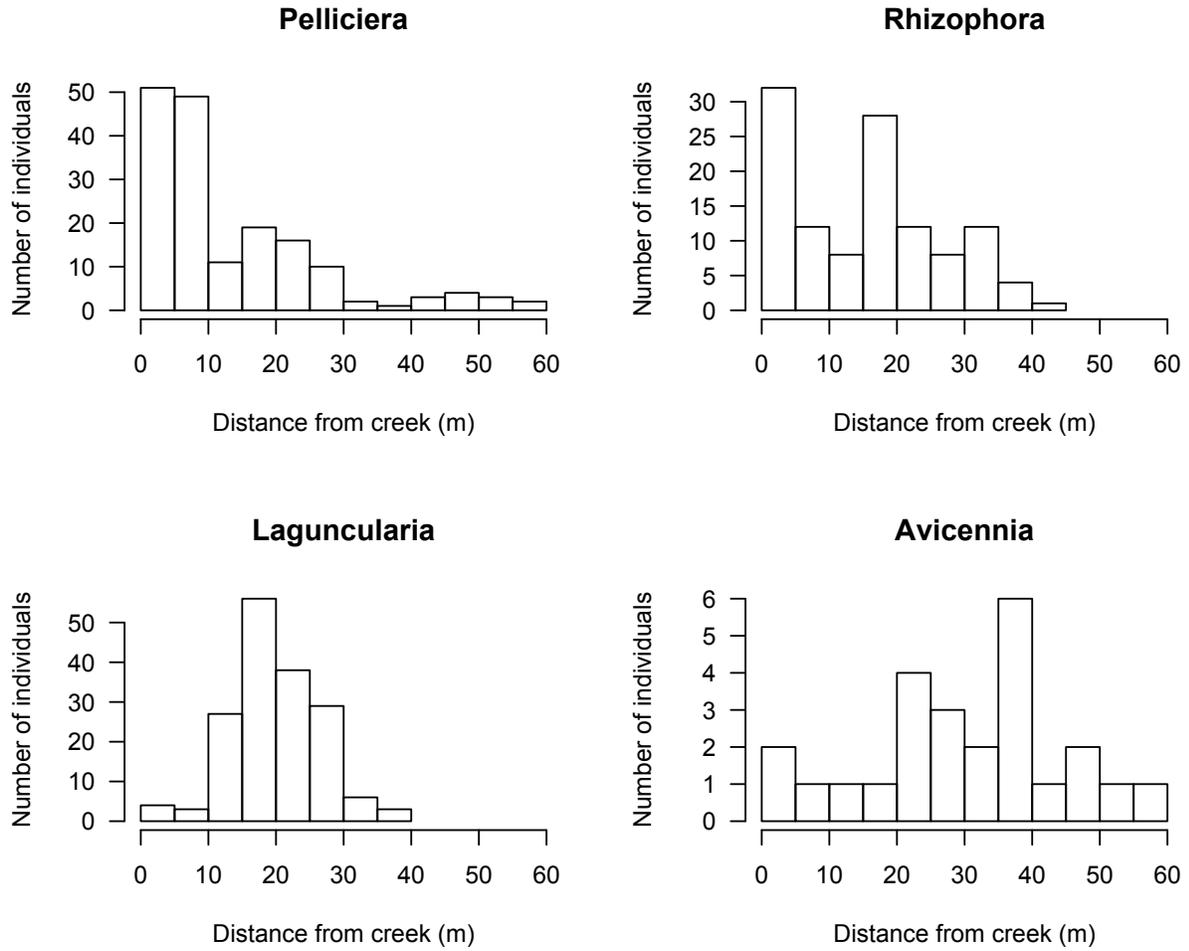


Figure 4. Species composition of Cilico Creek population. Y-axis is average number of individuals per 10 m transect.

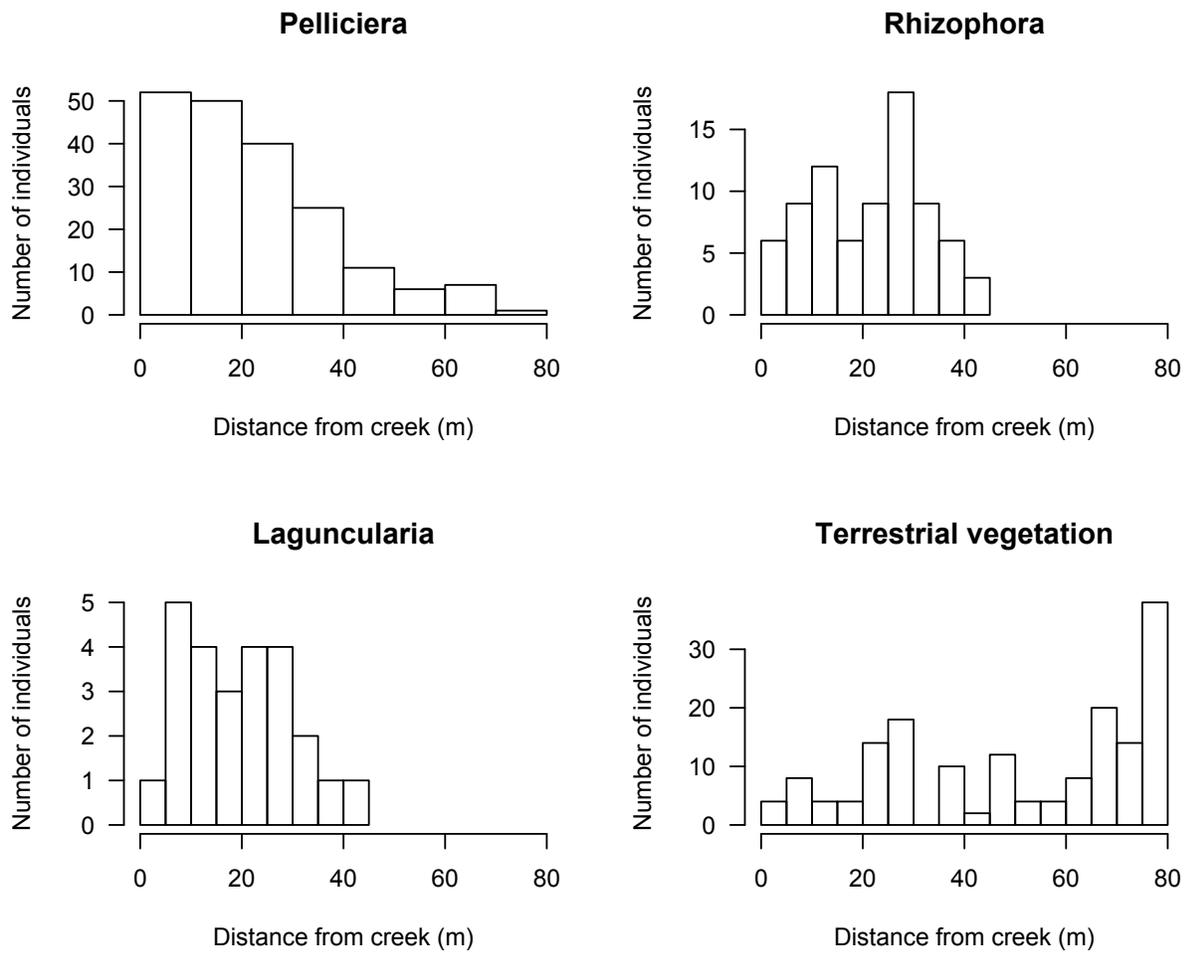


Figure 5. Species composition of Souli Creek population. Y-axis is average number of individuals per 10 m transect.

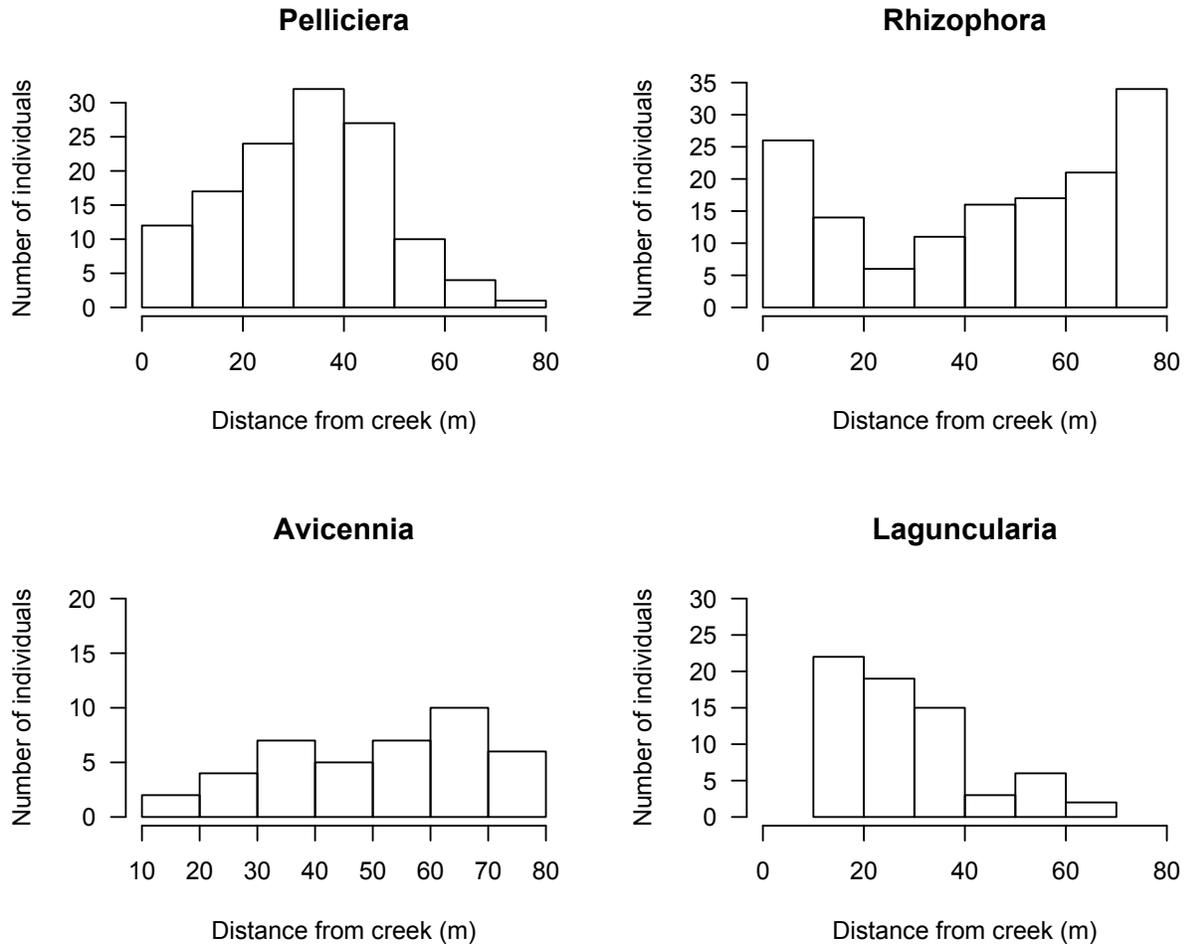


Figure 6. Species composition of QLM population. Y-axis is average number of individuals per 10 m transect.

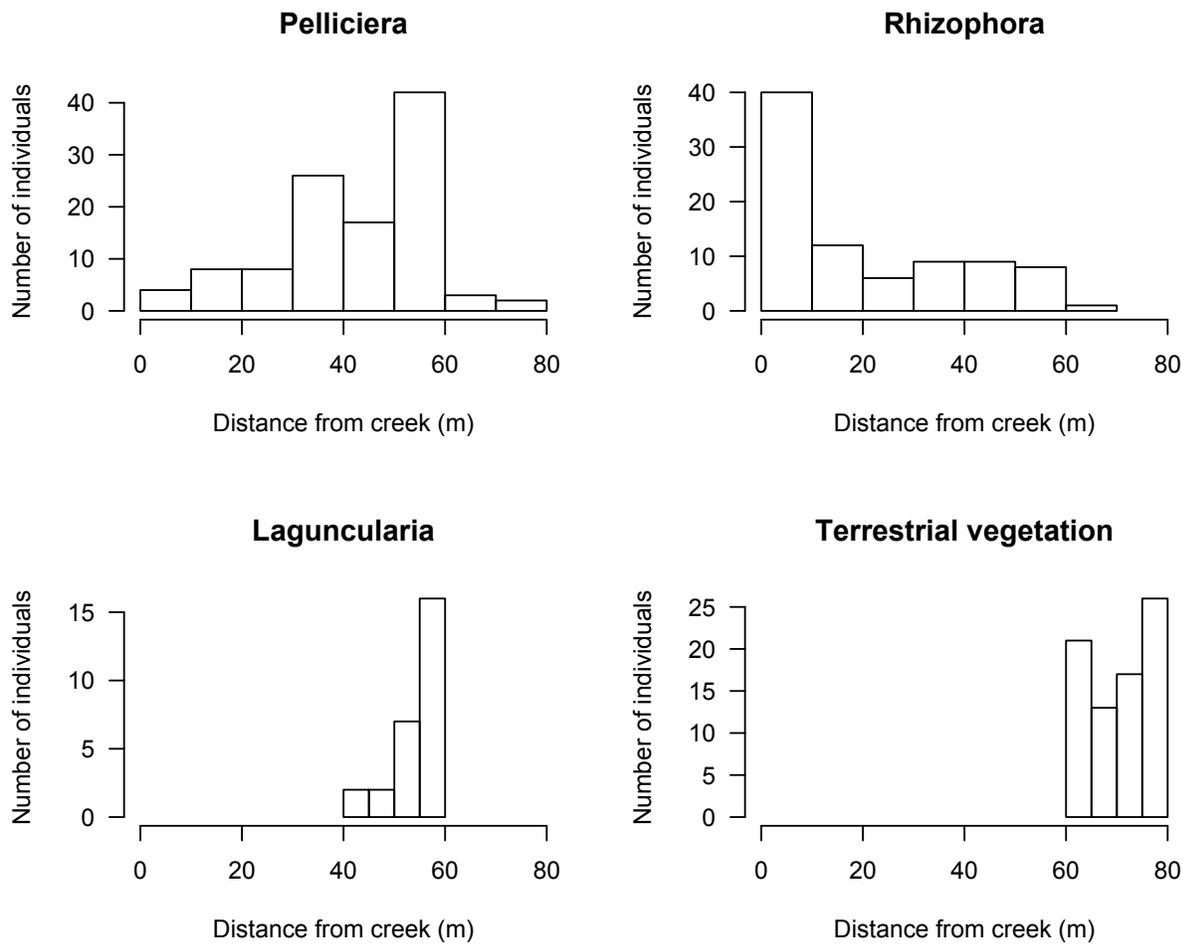


Figure 7. Species composition of Quebro population. Y-axis is average number of individuals per 10 m transect.

Appendix A. Locations, extent and salinity of *Pelliciera rhizophorae* populations in Panama.

Water samples were taken to measure interstitial soil salinity using the soil sipper method described by McKee et al. (1988). Salinity was measured with a handheld refractometer (Leica, Buffalo NY). NS = not sampled.

Site	Location	Extent of <i>P. rhizophorae</i> along creek (distance from mouth)	Salinity range (‰)
<i>Bocas del Toro</i>			
Bahia Azul	9.14° N 81.88° W	640 m	7-10
Bahia Escondida	9.28° N 82.28° W	125 m	12-15
Cilico Creek	9.08° N 82.25° W	460 m	0-10
Patterson Creek	9.10° N 81.90° W	300 m	7
Souli Creek	9.01° N 81.79° W	850 m	5-13
<i>Colón</i>			
Bahia Las Minas	9.38° N 79.81° W	258 m	11-29
Quebrada Las Mercedes	9.44° N 79.79° W	280 m	3-25
<i>Chiriquí</i>			
Chorcha	8.35° N 82.28° W	NS	NS
Pedregal	8.36° N 82.43° W	NS	NS
Playa La Barqueta	8.30° N 82.54° W	NS	5-14
<i>Veraguas</i>			
Arenas	7.35° N 80.89° W	NS	NS
Quebro river	7.44° N 80.91° W	2 km	4-32
Tebario river	7.72° N 80.99° W	NS	NS
<i>Panamá</i>			
Punta Chame	8.63° N 79.71° W	NS	NS

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McKee, K.L., Mendelssohn, I.A., and Hester, M.W. 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *American Journal of Botany*. 75: 1352-1359.

Chapter 2

Environmental tolerances of rare, common and invasive mangroves

Abstract

The Caribbean region is home to both native and exotic mangrove species. Mangrove forests are generally considered to be resistant to invasion because of the stressful edaphic conditions that characterize their habitat—most plants cannot survive in saline, flooded soils. However, nonnative mangroves, which are already adapted to these harsh conditions, may be able to replace native species. In this study, I experimentally compared the responses of native and invasive mangrove species to two abiotic conditions that affect their physiology, growth, and survival: shade and salinity. I grew seedlings of four species (two common and one rare species from the Caribbean and one invasive species native to the Indo-West Pacific) in three shade treatments and three salinity treatments at the Smithsonian Marine Station in Fort Pierce, Florida. The common Caribbean mangroves, *Avicennia germinans* and *Rhizophora mangle* responded differently to the treatments. *Avicennia germinans* had 80-100% survival in all treatments except the most stressful—high light and hypersaline water. *Rhizophora mangle* was not tolerant of high salt levels, with less than 50% survival in hypersaline treatments. The invasive species *Lumnitzera racemosa* had 75-100% survival in all treatments, but had the highest relative growth rate in freshwater and seawater treatments. The rare Caribbean species, *Pelliciera rhizophorae*, had survival between 0 and 50% in the high light treatment, and achieved the highest growth rates, height, and leaf areas in shaded freshwater and seawater treatments. These results show differential performance and mortality for each mangrove species when subjected to different combinations of light and salinity. In addition to contributing to our understanding of mangrove distributions, the results from this study may aid management efforts to control the newly invasive species *Lumnitzera racemosa*.

Introduction

The life history, demographic, and environmental features that determine different forms of species rarity have long been a focus of investigations in ecology and evolutionary biology (Rabinowitz 1981, Kruckeberg and Rabinowitz 1985, Gaston 1994, 2003). Understanding how these mechanisms affect the temporal and spatial dynamics of rare species is also central to the design of effective conservation efforts. Suggested explanations for differences in the distributions of rare versus common species, particularly among closely related species, include the degree of habitat specialization, differences in resource use, genetic variation, and vulnerability to enemies (Grime 1977, 1979, Gaston 1994, 2003). For example, weak competitors may be relegated to undesirable habitat where they experience less intense competition, and are more likely to become narrow endemics than closely related, stronger competitors (Lavergne et al. 2004, Thompson et al. 2005, Poot and Lambers 2008, Anacker et al. 2011).

Even in stressful habitats such as deserts and salt marshes, plant species exhibit variation in their ability to cope with stress (e.g. Wang et al. 2010, Martinez-Tillería et al. 2012). Within a habitat, species' variation in ability to cope with environmental conditions may have consequences for patterns of distribution. There may be tradeoffs in tolerance of different stressors, such as a tradeoff between drought and shade tolerance (Smith and Huston 1989). The link between stress tolerance and abundance within a habitat type is not yet established, though it has been suggested that the two are related (Fourqurean et al. 2010). In harsh environments, are widespread species more stress-tolerant than narrow endemics? Alternatively, there may be fine-

scale heterogeneity within a habitat type and species have tradeoffs in their ability to live in a range of conditions but then that heterogeneity may not be evenly distributed across the landscape. However, most mangrove habitats have a gradient of low to high salinity distributed from the ocean inland, and if a freshwater source is present, may have even lower salinity water further from the coast.

Mangrove forests offer an excellent system in which to investigate the stress tolerance of species with varying distributions, as they provide a physically challenging habitat for plant establishment and growth, and species distributions vary greatly from rare endemics to common or even invasive. The tidally influenced mangrove habitat is characterized by flooded, hypoxic and saline soils. Adaptations that allow plants to live in such a habitat are varied, but have evolved in 16 different plant families (Hogarth 1999). These adaptations include morphological traits such as aerial roots, lenticels, and pneumatophores for obtaining oxygen in hypoxic soils, and regulation of tissue salt concentrations by specialized salt excreting glands or exclusion of salt at root surfaces.

Mangrove communities in the Neotropics are composed predominantly of three abundant species, *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*, which are common and occur from Florida to Brazil. Another species, *Pelliciera rhizophorae*, is relatively rare, with a distribution from Nicaragua to Ecuador. Recently, two potentially invasive mangroves were identified in Florida, *Lumnitzera racemosa* and *Bruguiera gymnorrhiza* (Fourqurean et al. 2010); both are native to the Indo-West Pacific. Hereafter, these species will be referred to by their generic names only.

Since native mangrove species encounter and tolerate a broad range of environmental conditions, including chronic drought stress from living in a saline environment (Ball and Farquhar 1984, Ball 1988) and fluctuations in salinity, temperature, and light, a successful invader would also have to tolerate a wide range of conditions. The interacting effects of shade and salinity are particularly important for mangrove performance: growth and survival in high salinity environments is greatly reduced when accompanied by low light, probably because of the high metabolic cost of coping with salt (Ball 2002, Krauss and Allen 2003, Krauss et al. 2008). Low light is a common characteristic of the understory, and may account for interspecific differences in seedling survival (Rabinowitz 1978a, McKee 1995a). Very high light levels can be another source of stress to plants; excess light can damage or inactivate photosystem II (Osmond et al. 1999, Chow et al. 2005), adding another stressor to already drought-stressed plants. If an exotic plant can grow better in stressful conditions than the natives can, it may be able to take advantage of sites where natives are unable to grow. Therefore, to understand the success of these non-native species and prevent further spread, it is vital to first examine their tolerances of abiotic conditions.

Shade tolerance varies among mangrove species; for example, *Laguncularia* seedlings have high mortality in shade (Rabinowitz 1978a, W.P. Sousa, pers. comm.) but *Pelliciera* seedlings and reproductive individuals often occur in the shaded understory beneath a *Rhizophora*-dominated canopy (E. Dangemond, pers. obs.). Tolerance of salinity also varies among mangrove species and can affect their distributions and abundances (Smith 1992). For example, *Avicennia* has been shown to tolerate up to 100 ppt salt and *Pelliciera* tolerated only up to 37 ppt salt in a previous experiment (Jimenez 1984). The optimal salt concentration may vary among even closely related species—two species of *Sonneratia* both survived in 0-50% seawater, but *S. lanceolata* performed best in 0-5% seawater and *S. alba* performed best in 5-50% seawater (Ball and Pidsley 1995). The rare species *Pelliciera rhizophorae* has been

hypothesized to have a restricted range due its low salinity tolerance, as it occurs only in habitats with salinity less than that of seawater (Jimenez 1984). There are other mangrove areas with salinity this low but typically *Rhizophora* and *Laguncularia* occupy the low salinity sites. Other mangroves, such as *Avicennia* spp., occur in habitats with salinity three times that of seawater. However, the tolerance to environmental stressors has never been tested in the narrow endemic *Pelliciera rhizophorae* nor in the invasive mangrove *Lumnitzera racemosa*.

In this study, I investigated the strength of two environmental stresses influencing the survival and growth of four different mangrove species, including the invasive *Lumnitzera racemosa*, two widespread species common throughout the Caribbean and south Florida, *Rhizophora mangle* and *Avicennia germinans*, and one rare species, *Pelliciera rhizophorae*, endemic to the Pacific and Caribbean coasts of Central America. Since differential seedling establishment is an important factor in forest structure (McKee 1995b), I focus here on seedling response to shade and salinity. I hypothesized that the invasive species *Lumnitzera racemosa* would have broader environmental tolerances than the two common native species, *Rhizophora mangle* and *Avicennia germinans*, but that the narrow endemic *Pelliciera rhizophorae* would be the least tolerant of environmental stress.

Methods

Study system: The red mangrove *Rhizophora mangle* has a broad geographical range, occurring from northern Florida to Brazil on the Atlantic coast of North America, and from Baja California to Peru on the Pacific coast. Its propagules are large; the average mass of propagules used in this experiment was 14.5 g (± 0.03). *Rhizophora* propagules were collected from the Indian River Lagoon (27.56° N, 80.33° W), Fort Pierce, Florida on 10 August 2010. The black mangrove *Avicennia germinans* is native to Florida but was not fruiting at the beginning of the experimental period, so the propagules used were from Panama, where *Avicennia* fruits earlier in the year. Average propagule mass was 1.78 g (± 0.01). Propagules were collected from the Rio Coco Solo, Colón, Panama (9.38° N, 79.87° W) on 27 July 2010. *Laguncularia racemosa*, another species common throughout the Neotropics, was not used because mature propagules were not available at the start of the experiment. Originally from the Indo-Pacific, *Lumnitzera racemosa* has been introduced to Florida numerous times (Fourqurean et al. 2010). It escaped from the Fairchild Tropical Botanic Garden, Coral Gables, FL, and has become invasive in the surrounding area. Eradication efforts have eliminated reproductive individuals of *Lumnitzera*, so I collected seedlings and transplanted them to the experimental garden. Seedlings were collected from Matheson Hammock County Park (25.67° N, 80.26° W), Florida on 2 August 2010. Average initial mass of *Lumnitzera* seedlings was 1.29 g (± 0.01). *Pelliciera rhizophorae* does not occur in Florida, and propagules were collected from Souli Creek (9.01°N, 81.97°W) and Cilico Creek (9.07°N, 82.24°W), Bocas del Toro, Panama on 22 and 24 July 2010. All propagules were kept moist until they were planted in potting soil. Average initial mass was 69.5 g (± 0.22).

Experimental design: The experiment was a two-factorial design examining the independent and interactive effects of light-level and salinity on seedling survival and growth. The plants were grown in the outdoor shadehouse at the Smithsonian Marine Station in Fort Pierce, Florida (27.46° N, 80.31° W). Three daytime light treatments were established: high (PAR = 1200 $\mu\text{E}/\text{m}^2/\text{sec}$), medium (PAR = 400 $\mu\text{E}/\text{m}^2/\text{sec}$), and low (PAR = 130 $\mu\text{E}/\text{m}^2/\text{sec}$). These light

levels are within the range of those in naturally occurring field conditions in the open and underneath a canopy (Cheeseman et al. 1991). Low and medium light treatments were achieved with a shade-cloth roof (Home Depot 90% shade cloth and Gempler's 50% shade cloth); whereas high light was ambient, open sky conditions.

Plants were potted and the experimental treatments initiated on 13 August 2010. Propagules and seedlings were planted individually in topsoil-filled four-inch wide plastic treepots (Steuwe and Sons CPOT10R) with drainage holes. Propagules were inserted into the soil so that the root apical meristem was at least 1 cm below the soil surface. *Rhizophora* propagules were inserted into the soil just far enough to stay upright. All propagules and seedlings were weighed before potting; in addition, because *Lumnitzera* seedlings already had roots, root length was also measured before potting. The pots were placed in tubs, 16 pots per tub. Each tub was assigned a salinity treatment: freshwater, seawater (35 ppt) or hypersaline (60 ppt), with four tubs per salinity level. These salinities were chosen to represent the range of salinities in which mangroves are usually found (Smith 1992); salt levels (measured with a handheld refractometer) were achieved by adding Instant Ocean to water. All four species were mixed in each tub, and there were 12 replicates per species per treatment, distributed among three tubs. Seedlings were watered once a week with water of the same salinity as the respective tub; the water in the tubs kept the soil continually moist but pots were not completely flooded. Every week I measured height of all plants, and at the end of the experiment plants were dried for three days in a 60° C drying oven. Each plant was weighed to determine final biomass, with shoots and roots measured separately.

Relative growth rate (RGR) was calculated to allow comparisons among the different species. RGR is $(W_2 - W_1)/(t_2 - t_1)$ where W_1 and W_2 are the dry weights of a plant (or propagule) at the beginning and end of the experimental period, $t_2 - t_1$. Since the dry-weights of planted propagules could not be determined prior to planting, I used a wet-to-dry weight conversion to calculate approximate dry weights of propagules and seedlings (W_1) at the beginning of the experimental period. I 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 at 60° C for three days. Linear regressions converted wet to dry weights for each species (Appendix A). Total leaf area of each plant at the end of the experiment was measured with a leaf area meter (LI-3000 Area Meter, LI-COR, Lincoln, Nebraska).

At week 12, a pulse amplitude modulation (PAM) fluorometer (Opti-Sciences OS5-FL, Hudson, New Hampshire) was used to measure light-adapted photosynthetic yield ($F_{ms} - F_s / F_{ms}$, where F_s and F_{ms} are the steady state and maximal fluorescence values of the sample during exposure to light). Measurements were taken on three 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 had no leaves, so measurements could not be taken on those plants.

Statistical Analysis:

All analyses were done in R (Version 3.0, R Development Core Team 2013). Survival (time-to-event) analysis was used to estimate the effects of shade, salinity and species on a hazard function, which is an individual's instantaneous risk of dying. The effects of shade, salinity and species on seedling survival were analyzed with an extended Cox model, which extends the Cox proportional hazards model to allow for non-proportional hazards, i.e., hazard

functions that change over time. A heaviside function was defined that allowed the hazard ratio to change over different time periods (Kleinbaum and Klein 2012). A cut-point of 30 days was chosen because most survival curves diverge after that point, indicating separate hazard functions before and after 30 days. The extended Cox model included a main effects of shade, salinity and species, and one heaviside function as a product with species. The model used was

$$h(t, \mathbf{X}(t)) = h_0(t)e^{[\beta_1(\text{Shade})+\beta_2(\text{Salinity})+\beta_3(\text{Species})+\delta(\text{Species})g(t)]}$$

where $g(t) = 1$ if $t < 30$ days

0 if $t \geq 30$ days

$h(t)$ is the hazard function at time t and $h_0(t)$ is the baseline hazard. For the baseline hazard, the shade treatment was chosen to be low light and salinity was chosen to be freshwater, as those were the least-stressful treatments. *Avicennia* was chosen as the baseline species because it had very little mortality over the course of the experiment. All two-way interactions between shade, salinity and species were tested, but none of the interaction terms were significant, so they were removed from the model.

Growth measures for plants that died during the experiment were calculated for the period in which they were alive. Growth rates were compared with analysis of variance. The variation in salinity between tubs of the same treatment was < 0.5 ppt; because the differences between tubs were minimal, treatment replicates in different tubs were pooled. Final height, root-to-shoot ratio, relative growth rate, final biomass and leaf area were analyzed with a factorial ANOVA with species, light and salinity as factors. The Bartlett test was used to assess homoscedasticity, and when unequal variances were present, data were log-transformed to achieve homogeneity of variances. The analyses for height, final biomass and leaf area included initial propagule mass as a covariate because it was expected to influence seedling growth. Where an ANOVA found a significant treatment effect, Tukey's HSD test was used to determine differences between groups.

Results

Survival

Estimated coefficients for the extended Cox model are presented in Table 1. Shade, salinity and species all had significant effects on the hazard function. The estimated coefficient for the heaviside function was also significantly different from zero, suggesting the hazard ratios for species are different over the two time periods of $t < 30$ and $t \geq 30$. The hazard ratios for each species compared to *Avicennia* are presented in Table 2.

Overall, *Avicennia* and *Lumnitzera* experienced low mortality, with the highest mortality in the high light-seawater and high light-hypersaline treatments (Fig. 1). These were also the most stressful for *Pelliciera* and *Rhizophora*. By the end of 12 weeks, all *Pelliciera* seedlings in the high light-seawater and high light-hypersaline treatments died. More than 50% of *Rhizophora* individuals in all hypersaline treatments died by the end of the experimental period.

Growth

Growth responses of each of the four species to the light and salinity treatments are examined separately below.

Avicennia germinans

Initial propagule mass had a significant effect on relative growth rate and height of *Avicennia germinans*. Shade and salinity significantly affected RGR, height, leaf area (Table 3) and root to shoot ratio (Table 4). Seedlings grew taller in the freshwater and seawater treatments than the hypersaline treatments (Fig. 2). Seedling height ranged from 10.6 cm in the high light-hypersaline treatment to 29.3 cm in the medium light, seawater treatment. RGR was highest in the medium light-seawater treatment and lowest in the high light-hypersaline treatment (Fig. 3). Root-to-shoot ratio was lowest in the low light-seawater treatment and highest in the high light-freshwater treatment (Fig. 4). Average leaf area per plant was lowest in the high light-freshwater treatment (mean = $2.48 \text{ cm}^2 \pm 0.09$) and highest in the medium light-hypersaline treatment (mean = $6.61 \text{ cm}^2 \pm 0.14$, Fig. 5). Final biomass was highest in seawater treatments across light levels (Fig. 6). Shade, salinity and their interaction had significant effects on light-adapted photosynthetic yield (Table 5, Fig. 7). Photosynthetic yield was significantly lower in freshwater than in hypersaline (Tukey HSD, $p = 0.001$) or seawater (Tukey HSD, $p = 0.006$), and lower in low light than medium light (Tukey HSD, $p = 0.047$).

Lumnitzera racemosa

Initial seedling mass affected RGR, but not height or leaf area. Shade and salinity significantly affected RGR, height and leaf area (Table 3). Seedlings in the low light-freshwater treatment had the highest RGR and were tallest (mean height = $16.74 \text{ cm} \pm 0.38$; Fig. 2 and 3) and seedlings in the high light-hypersaline treatment had the lowest RGR and were shortest (mean height = $7.96 \text{ cm} \pm 0.26$) (Table 4). Root-to-shoot ratios were highest in the high light treatments, and decreased as salinity decreased (Fig. 4). Average leaf area was lowest in the high light-hypersaline treatment (mean = $1.47 \text{ cm}^2 \pm 0.07$) and highest in the low light-freshwater treatment ($3.67 \text{ cm}^2 \pm 0.07$, Fig. 5). Final biomass was highest in the high light treatments and lowest in hypersaline treatments (Fig. 6). Light-adapted photosynthetic yield was greater in low light than in high (Tukey HSD, $p = 0.038$) or medium light (Tukey HSD, $p = 0.001$) but salinity did not significantly affect yield (Table 5, Fig. 7).

Pelliciera rhizophorae

Pelliciera propagules are very large with extremely fleshy cotyledons, and initial propagule mass affected RGR, height and leaf area. Salinity had a negative effect on RGR, but shade did not significantly affect RGR (Table 4, Fig. 3). RGR was lowest in the high light-hypersaline plants and highest in the medium and high light-freshwater treatments. Shade, salinity and their interaction had significant effects on height; *Pelliciera* seedlings were tallest when growing in low light and freshwater (mean height = $40.83 \text{ cm} \pm 0.78$), and shortest in the high light-hypersaline treatment (mean height = $5.02 \text{ cm} \pm 0.29$) (Fig. 2). Root-to-shoot ratios were above 1 in all the full sun treatments and all the hypersaline treatments, and decreased as salinity decreased (Fig. 4). Average leaf area ranged from $0.35 \text{ cm}^2 \pm 0.07$ in the high light-hypersaline treatment to $14.8 \text{ cm}^2 \pm 0.57$ in the medium light-freshwater treatment (Fig. 5). Final biomass depended on shade and salt treatment (Fig. 6). Both shade and salinity affected

photosynthetic yield (Table 5, Fig. 7). Yield was greater in low light than in medium light (Tukey HSD, $p = 0.001$) and greater in freshwater (Tukey HSD, $p = 0.008$) and seawater (Tukey HSD, $p = 0.03$) than hypersaline water.

Rhizophora mangle

Rhizophora propagules are very large, and initial propagule mass affected RGR, but not height or leaf area. Shade, salinity and their interaction had significant effects on RGR and height (Table 3, Fig. 2 and 3). RGR was highest in the medium light-seawater treatment and lowest in the low light hypersaline treatment. *Rhizophora* seedlings were tallest in the low light-freshwater treatment (mean height = $29.85 \text{ cm} \pm 0.84$) and shortest in the medium and high light-hypersaline treatments (mean height = $18.04 \text{ cm} \pm 0.16$). Shade and salinity affected leaf area quite drastically (Table 3). Root-to-shoot ratios were much lower in hypersaline treatments than in freshwater or seawater (Fig. 4). *Rhizophora* average leaf area ranged $0.15 \text{ cm}^2 \pm 0.03$ in the high light-hypersaline treatment to $7.92 \text{ cm}^2 \pm 0.37$ in the low light-freshwater treatment (Fig. 5). Final biomass depended on the interaction of shade and salt (Fig. 6). *Rhizophora* seedlings growing in hypersaline treatments flushed no leaves, so photosynthetic yield could not be measured on those plants. However, for the plants that were measured, shade and the interaction of shade and salinity significantly affected photosynthetic yield (Table 5, Fig. 7). Seedlings growing in freshwater and seawater had greater yield in low light than in high light (Tukey HSD, $p = 0.02$).

Discussion

Avicennia germinans and *Lumnitzera racemosa* had high survival in all treatments, and even in the most stressful treatment (high light-hypersaline), survival was above 60% for *Avicennia* and above 70% for *Lumnitzera*. *Rhizophora* and *Pelliciera* had very high hazard ratios, demonstrating their lower tolerance of high light and salt compared to *Avicennia* and *Lumnitzera*. *Pelliciera* survival was very low in high light environments; combined with the almost-always lethal effects of salinity, this could be a major factor limiting colonization of new sites by *Pelliciera*, which naturally often occurs in the understory of *Rhizophora*-dominated forests. *Rhizophora* survival was similar across light treatments, with large differences in survival across salinity treatments. As *Rhizophora* often occurs as the only tree species on small islands, it is not surprising that it can tolerate high light environments well.

Root-to-shoot ratio is related to resource capture and can vary in relation to nutrient availability and stress. In the four species studied here, the effects of treatments on root-to-shoot ratio varied among species. For *Avicennia*, *Rhizophora*, and *Lumnitzera*, root-to-shoot ratios were highest in freshwater and values were well below 1 for all treatments. Ball (1988) found that root-to-shoot ratio in *Avicennia marina* increased with higher salinities at the expense of height and leaf growth; in this study, *A. germinans* decreased its root-to-shoot ratio as salinity increased. However, Ball investigated a lower range of salinities. The optimal growth range of *A. marina* is from 0-30 ppt (Smith 1992), and *Pelliciera* exhibited a similar response to *A. marina*. In the shade, *Pelliciera* had highest root-to-shoot ratios in the hypersaline treatments. In the high light treatment, *Pelliciera* seedlings grown in seawater had significantly higher root-to-shoot ratios than plants grown in freshwater. In other studies, halophytes have maintained relative constant root-to-shoot ratios across a range of salinities (Barbour 1970; Parrondo et al. 1978; Kenkel et al. 1991, Gilbert and Fraser 2013), which is not consistent with my results.

Previous studies have shown that when introduced to a new range, 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 range of environmental conditions (Croci et al. 2007, Pemberton and Liu 2009, Shah et al. 2012). *Avicennia germinans* has recently spread north through the Texas gulf coast and Florida salt marshes (Stevens et al. 2006, Perry and Mendelssohn 2009) and *A. marina* became invasive in the San Diego area in the 1970s and again in 2006 despite removal efforts (Moseman et al. 2008). Recent comparisons have detected 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). Thompson and Davis (2011) suggest that plants can be separated into “winners” and “losers” based on their traits and their success in spreading, regardless of exotic or native status. In this study, one common species, *Avicennia germinans*, had similar patterns of survival and growth to an invasive exotic species, *Lumnitzera racemosa*, but another common species, *Rhizophora mangle*, was more similar in its survival and growth to the narrow endemic, *Pelliciera rhizophorae*.

Species responded differently to the various treatments in this experiment, but the invasive species (*Lumnitzera racemosa*) was also the least affected by the treatments, while the rare species (*Pelliciera rhizophorae*) was sensitive to the most stressful conditions. The two common species, *Avicennia germinans* and *Rhizophora mangle*, tolerated a broad range of salt and light levels, but performed best under less stressful conditions, *i.e.* shade and freshwater. McKee (1995) found that differences in growth among mangrove species (including *Avicennia germinans* and *Rhizophora mangle*) were apparent at high light levels and minimized at low light levels.

Hypotheses to explain the limited distribution of *Pelliciera* observe that this species is usually found in areas with a freshwater input and low interstitial soil salinity (Jimenez 1984). Jimenez suggests that this species has a low salinity tolerance and therefore is greatly limited in its available habitat. However, my results show that *Pelliciera* seedlings can tolerate water salinity levels of 35 ppt and more surprisingly, can survive in water with salt levels of 60 ppt if growing in shade. Sites with salinity levels of 35 ppt or less are common throughout mangrove habitat, as *Rhizophora* typically only occurs in such sites and is widespread throughout the Neotropics. The “preferred” habitat of *Pelliciera* (*i.e.*, salinity less than 35 ppt) is not rare throughout its range, so something other than fine-scale specialization to microhabitat is driving rarity in this species. This experiment only examined seedling survival to 12 weeks, so it remains unknown if *Pelliciera* could survive to adulthood or reproduce under these conditions. Older seedlings may be less tolerant of stressful conditions once they use up their cotyledon reserves (Ball 1988, Ball and Pidsley 1988). Naidoo and Willert (1999) found that growing in 100% seawater (corresponding to ~35 ppt salt) caused a 26% reduction in CO₂ exchange in *Pelliciera* saplings that were two to seven years old. However, high light level was the most stressful of the conditions tested for *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 a limited number of dispersal units. They are thus limited in the new areas they can colonize not because of high salinity but because of their need for shade—many sites with an open canopy, such as a beach or small mangrove island, are uninhabitable to this species.

Rhizophora mangle and *Avicennia germinans* are both widespread species, but exhibited different responses to these environmental stresses. *Rhizophora* had high mortality in hypersaline soil. *Rhizophora* seedlings grew best in shade and freshwater, but growth rates and biomass allocation did not vary much among treatments. *Avicennia* tolerated all the conditions, and was least sensitive to the salt level. Between freshwater and seawater treatments, there was very little change in plant performance. *Avicennia* seedlings have been shown to be less sensitive to salt than other mangroves because of their high water use efficiency. This water use efficiency slows growth rate, but allows *Avicennia* species to live in highly saline environments (Ball 1988, Smith 1992).

Lumnitzera has a different salt-tolerance strategy; it changes its leaf succulence in response to salt, allowing it to endure hypersaline conditions (Parida and Jha 2010). *Lumnitzera* tolerated all the conditions well but especially thrived in the full sun. This is surprising because all the other species grew slightly better in the shade than the full sun. The fact that *Lumnitzera* performs best in the full sun might explain why it has had success invading Florida—by not having to rely on the shade of other plants, *Lumnitzera* can colonize areas where few or no woody plants already occur, and avoid competition for resources. The Fairchild Tropical Botanic Garden removed reproductive *Lumnitzera* individuals in 2010 (J. Possley, pers. comm.), but seedlings survived in the adjacent Matheson Hammock county park despite removal efforts (pers. obs.). There, *Lumnitzera* seedlings are camouflaged among other mangroves, particularly the native species *Laguncularia racemosa*. The concern that *Lumnitzera racemosa* may become more widespread in Florida (Fourqurean et al. 2010) is valid and seems likely, given its resilience in a variety of growth conditions and the difficulty in extirpating its seedlings. When introduced by humans, mangrove species have successfully invaded both mangrove and non-mangrove habitat (Table 6).

In this study, the species with broader native ranges had broader tolerances of environmental conditions. Another rare Neotropical mangrove, *Avicennia bicolor*, also has low tolerance to salinity compared to other mangroves, and displaces *A. germinans* in low salinity sites of the Pacific coast of Costa Rica (Jimenez 1990). However, the rare species *Pelliciera rhizophorae* tolerated more extreme conditions than expected, as it grew well in seawater when it was grown in the shade. Some seedlings even survived the hypersaline conditions, though it is unknown if they would survive to maturity. Though there are other narrowly endemic mangrove species, there have been very few ecological studies on their growth preferences and distributions. Biotic interactions were not examined in this study, but can influence invasion success, through processes such as escape from natural enemies and evolution of increased competitive ability. This is the first experimental test of the salinity tolerance of *Pelliciera*, and shows that *Pelliciera* is affected by the interaction of salt and light. Therefore, salinity tolerance alone does not seem to fully explain the narrow geographic range of *Pelliciera*, but the interaction of environmental conditions may contribute to its patchy, disjunct distribution in the Caribbean.

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Table 1. Extended Cox model for seedling survival. Robust standard errors take into account multiple observations for each individual. HV30 is the heaviside function that takes on the value 1 if $t < 30$ and 0 if $t \geq 30$.

	Coefficient	$e^{(\text{Coeff.})}$	SE	Robust SE	z	p
Shade	0.024	1.024	0.003	0.003	7.45	9.6×10^{-14}
Salinity	0.039	1.040	0.005	0.005	7.10	1.2×10^{-12}
HV30	-2.029	0.131	0.409	0.346	-5.86	4.7×10^{-9}
<i>Lumnitzera</i>	2.193	8.964	0.661	0.642	3.41	6.4×10^{-4}
<i>Pelliciera</i>	6.140	464.2	0.949	0.819	7.50	6.5×10^{-14}
<i>Rhizophora</i>	6.495	661.6	1.180	1.021	6.36	2.0×10^{-10}

Table 2. Hazard ratios for seedling survival compared to *Avicennia germinans*.

Species	Hazard ratio
<i>Lumnitzera racemosa</i>	1.78 for $t < 30$ 2.19 for $t \geq 30$
<i>Pelliciera rhizophorae</i>	61.0 for $t < 30$ 464 for $t \geq 30$
<i>Rhizophora mangle</i>	87.0 for $t < 30$ 661 for $t \geq 30$

Table 3. Analysis of Variance table for mangrove seedling growth after 12 weeks. Starting mass was included as a covariate.

	Relative growth rate (mg g ⁻¹ day ⁻¹)						Height (cm)						Leaf area (cm ²)					
	Df	SS	MS	F	P		Df	SS	MS	F	P		df	SS	MS	F	P	
Avicennia																		
Starting mass	1	14555	14555	23.57	< 0.001		1	439.11	439.11	12.513	< 0.001		1	0.09	0.09	0.022	0.884	
Shade	2	7682	3841	6.219	0.003		2	685.80	342.90	9.771	< 0.001		2	142.19	71.10	17.61	< 0.001	
Salinity	2	12790	6395	10.35	< 0.001		2	1204.91	602.45	17.167	< 0.001		2	26.69	13.34	3.305	0.042	
Shade x Salinity	4	1662	415	0.673	0.612		4	275.55	68.89	1.963	0.197		4	7.82	1.95	0.484	0.747	
Residuals	88	54351	618				74	2596.9	35.09				82	331.07	4.04			
Lumnitzera																		
Starting mass	1	19484	19484	22.33	< 0.001		1	6.82	6.82	1.416	0.238		1	1.151	1.151	1.622	0.207	
Shade	2	7293	3646	4.18	0.018		2	83.02	41.51	8.618	< 0.001		2	22.352	11.176	15.749	< 0.001	
Salinity	2	27445	13722	15.73	< 0.001		2	474.46	237.23	49.250	< 0.001		2	9.738	4.869	6.861	0.002	
Shade x Salinity	4	5305	1326	1.52	0.203		4	14.10	3.53	0.732	0.573		4	4.481	1.120	1.579	0.188	
Residuals	93	81155	873				80	385.35	4.82				79	56.062	0.710			
Pelluciera																		
Starting mass	1	283.72	283.72	40.592	< 0.001		1	526.8	526.8	5.963	0.017		1	297.68	297.68	10.213	0.002	
Shade	2	34.32	17.16	2.455	0.091		2	5362.8	2681.4	30.352	< 0.001		2	661.03	330.51	11.340	< 0.001	
Salinity	2	46.59	23.30	3.333	0.040		2	3650.2	1825.1	20.659	< 0.001		2	1026.89	513.44	17.616	< 0.001	
Shade x Salinity	4	62.76	15.69	2.245	0.070		2	334.0	167.0	1.891	< 0.001		2	109.80	54.90	1.884	0.162	
Residuals	97	677.99	6.99				76	6714.2	88.3				55	1603.06	29.15			
Rhizophora																		
Starting mass	1	41.43	41.43	5.89	0.017		1	1.57	1.57	0.1114	0.739		1	4.01	4.01	1.117	0.293	
Shade	2	52.55	26.27	3.74	0.026		2	273.30	136.65	9.669	< 0.001		2	200.91	100.45	27.983	< 0.001	
Salinity	2	90.11	45.06	6.41	0.002		2	2465.0	1232.5	87.206	< 0.001		2	610.48	305.24	85.029	< 0.001	
Shade x Salinity	4	95.60	23.90	3.40	0.011		4	27.80	6.95	0.291	0.029		4	30.10	7.53	2.096	0.087	
Residuals	116	814.89	7.02				116	1639.45	14.13				98	351.81	3.59			

Table 4. Factorial ANOVA table for root to shoot ratio.

	df	SS	MS	F	p
Species	3	54.008	18.00	441.2742	< 0.001
Light	2	0.650	0.325	7.9658	< 0.001
Salt	2	0.086	0.043	1.0533	0.349
Species x Light	6	0.436	0.073	1.7830	0.101
Species x Salt	6	0.541	0.090	2.2086	0.041
Light x Salt	4	0.556	0.139	3.4074	0.009
Species x Light x Salt	12	1.748	0.146	3.5703	< 0.001
Residuals	397	16.196	0.041		

Table 5. ANOVA table for light-adapted photosynthetic yield.

	df	SS	MS	F	p
Avicennia					
Shade	2	0.038	0.019	3.799	0.043
Salinity	2	0.112	0.056	11.326	0.001
Shade x salinity	4	0.083	0.021	4.210	0.015
Residuals	17	0.084	0.005		
Lumnitzera					
Shade	2	0.326	0.163	16.116	<0.001
Salinity	2	0.002	0.001	0.106	0.900
Shade x salinity	4	0.028	0.007	0.698	0.603
Residuals	18	0.182	0.010		
Pelliciera					
Shade	1	0.194	0.194	25.013	0.001
Salinity	2	0.122	0.061	7.879	0.008
Shade x salinity	2	0.031	0.015	1.980	0.189
Residuals	10	0.077	0.008		
Rhizophora					
Shade	2	0.056	0.028	5.300	0.022
Salinity	1	0.006	0.006	1.127	0.309
Shade x salinity	2	0.062	0.031	5.905	0.016
Residuals	12	0.063	0.005		

Table 6. Examples of invasive mangrove species.

Species	Location	Reference
<i>Avicennia marina</i>	San Diego, USA	Moseman et al. 2008
<i>Bruguiera gymnorhiza</i>	Miami, USA	Fourqurean et al. 2010
<i>Conocarpus erectus</i>	Hawaii	Chimner et al. 2006
<i>Lumnitzera racemosa</i>	Tonga Bangladesh Miami, Florida, USA	Clark and Thaman 1993 Biswas et al. 2007 Fourqurean et al. 2010
<i>Rhizophora mangle</i>	Hawaii	Chimner et al. 2006
<i>Rhizophora stylosa</i>	Moorea, French Polynesia	Langer and Lipps 2006
<i>Sonneratia apetala</i>	Macau and Hong Kong	Ng and Richard 2002

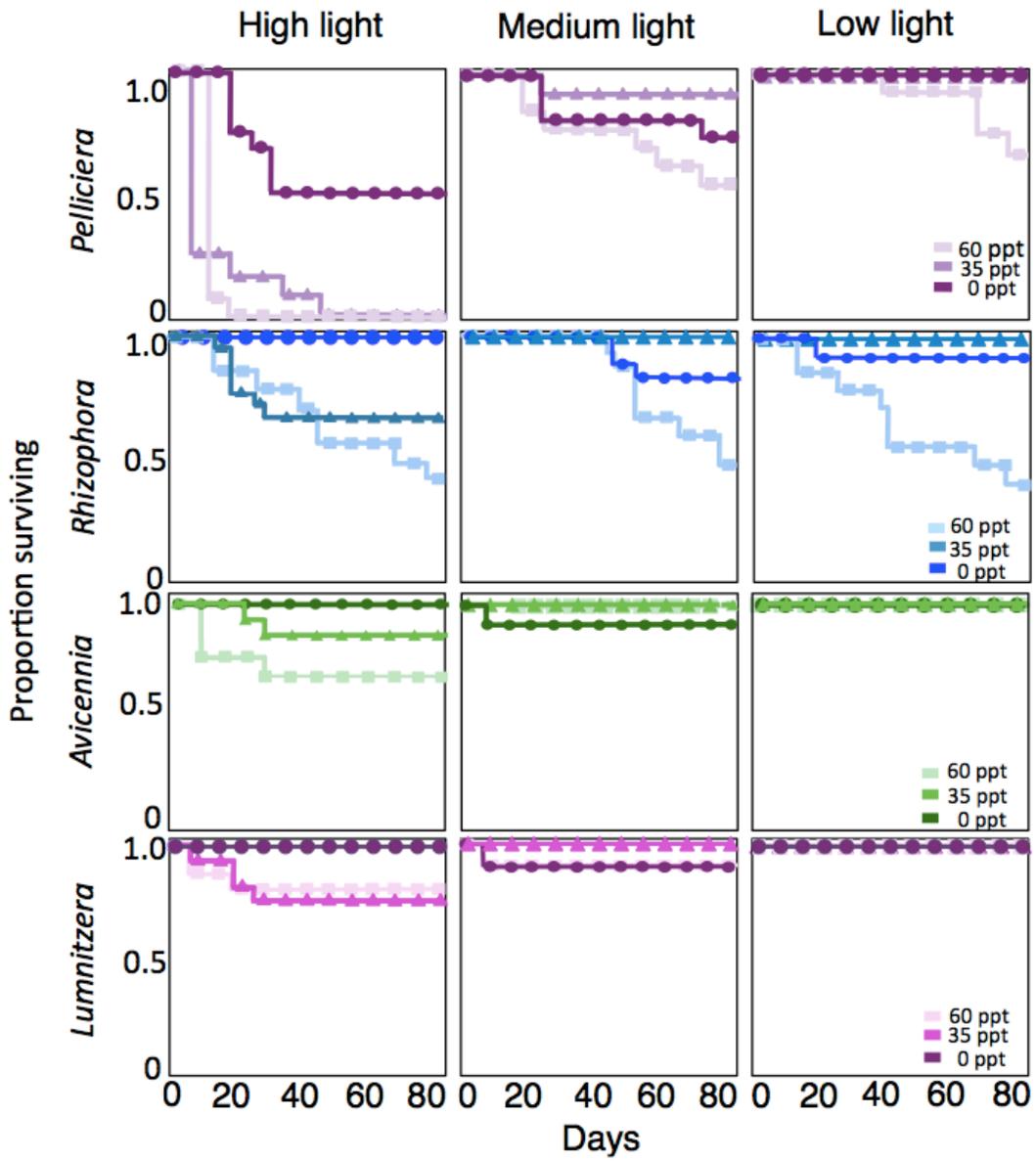


Figure 1. Kaplan-Meier survival curves for mangrove seedlings over 12 weeks.

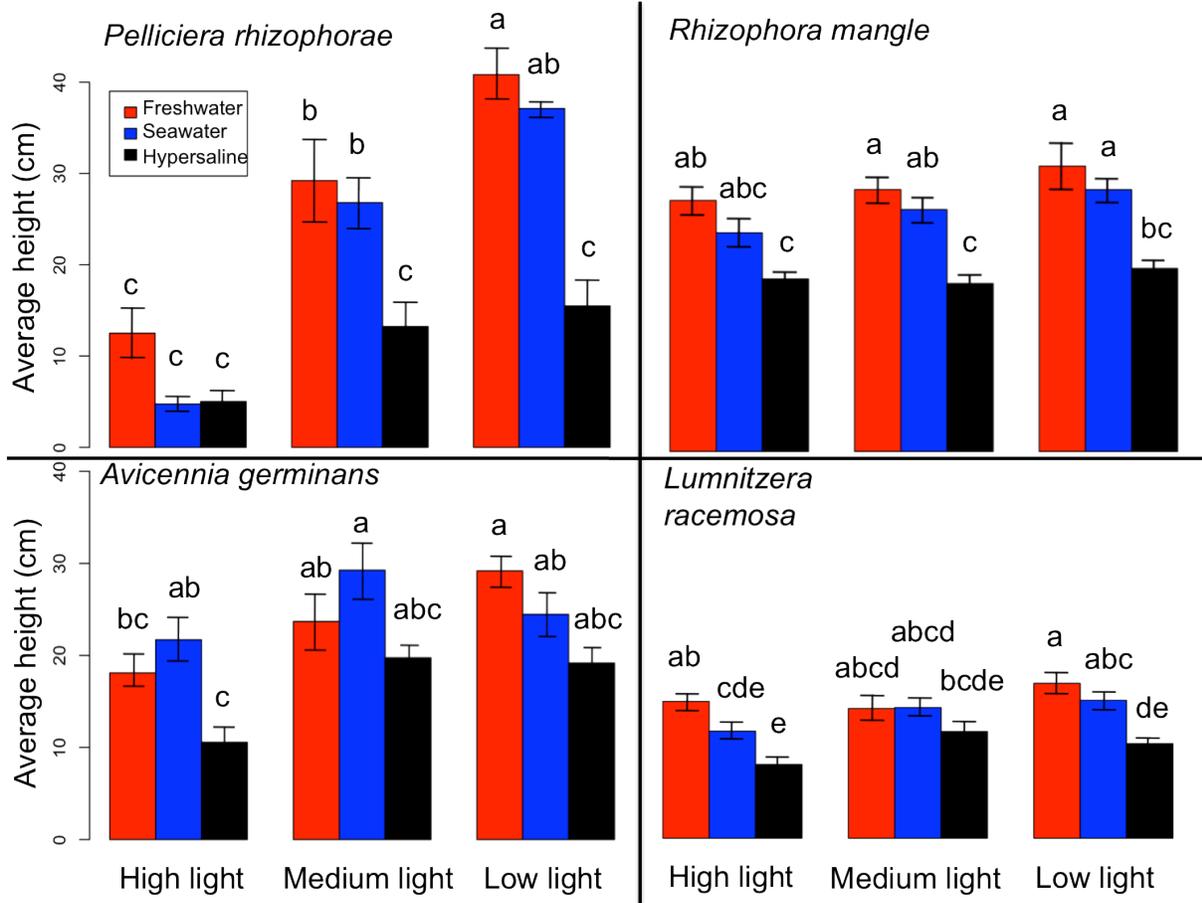


Figure 2. Average height of plants in each treatment at the end of the experimental period. Error bars are \pm one standard error of the mean. Letters above bars summarize results of a Tukey HSD test. Within each species, means with the same letter are not significantly different at $P = 0.05$.

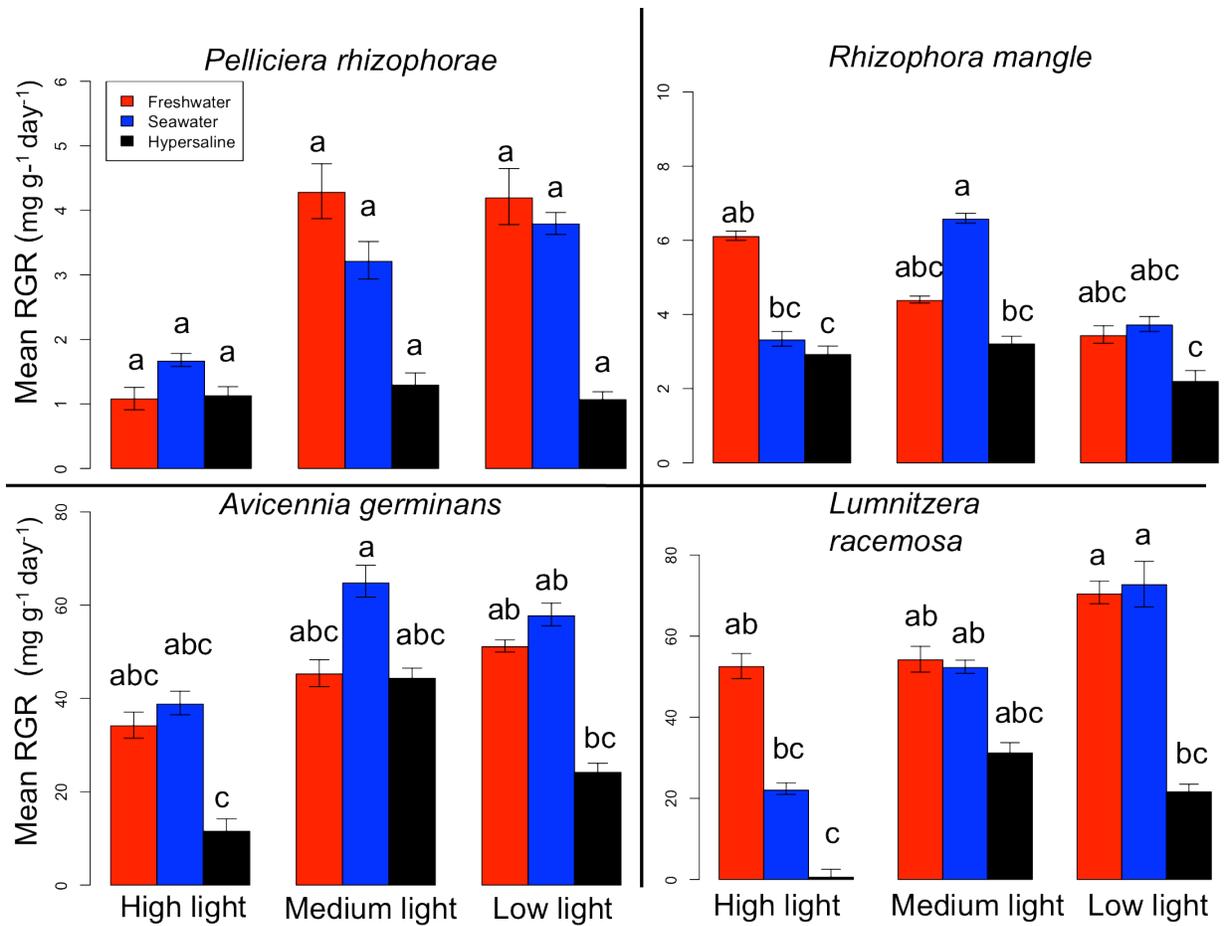


Figure 3. Relative growth rate (RGR) for plants after 12 weeks in treatments. Values are means \pm one standard error of the mean. Letters above bars summarize results of a Tukey HSD test. Within each species, means with the same letter are not significantly different at $P = 0.05$.

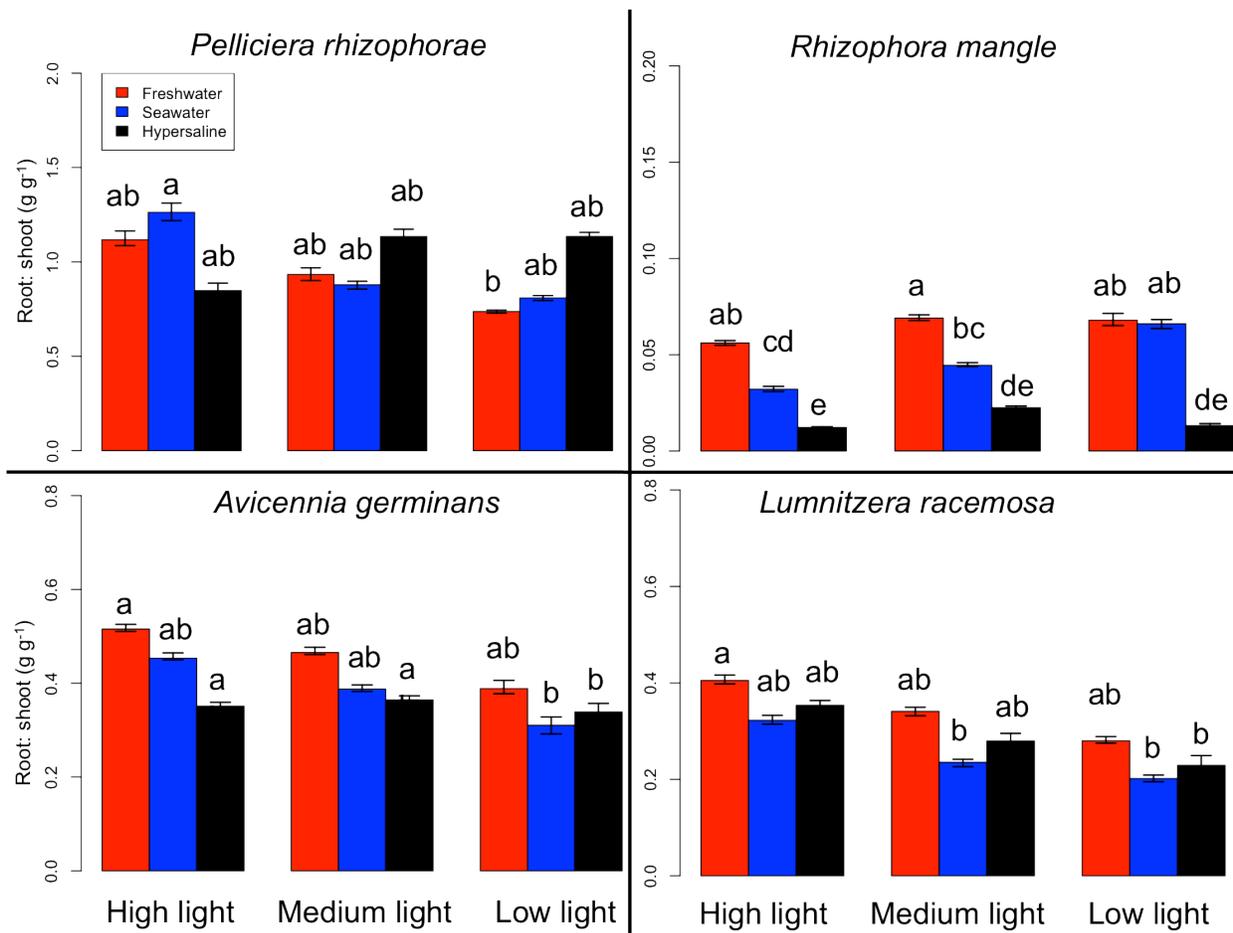


Figure 4. Root to shoot ratios for mangrove seedlings after 12 weeks of treatments. Values are treatment means. Error bars are \pm one standard error of the mean. Letters above bars summarize results of a Tukey HSD test. Within each species, means with the same letter are not significantly different at $P = 0.05$.

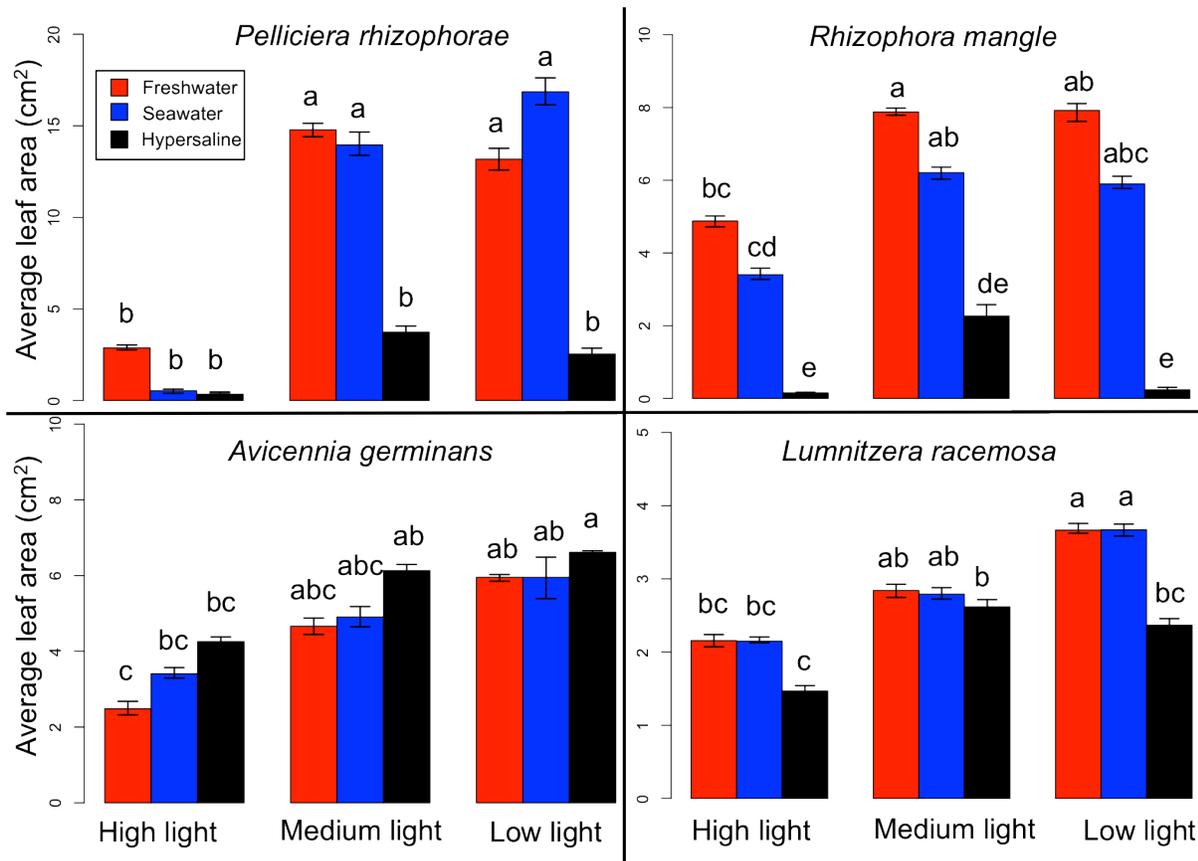


Figure 5. Average size of leaves on seedlings after 12 weeks in treatments. Values are treatment means. Error bars are \pm one standard error of the mean. Letters above bars summarize results of a Tukey HSD test. Within each species, means with the same letter are not significantly different at $P=0.05$.

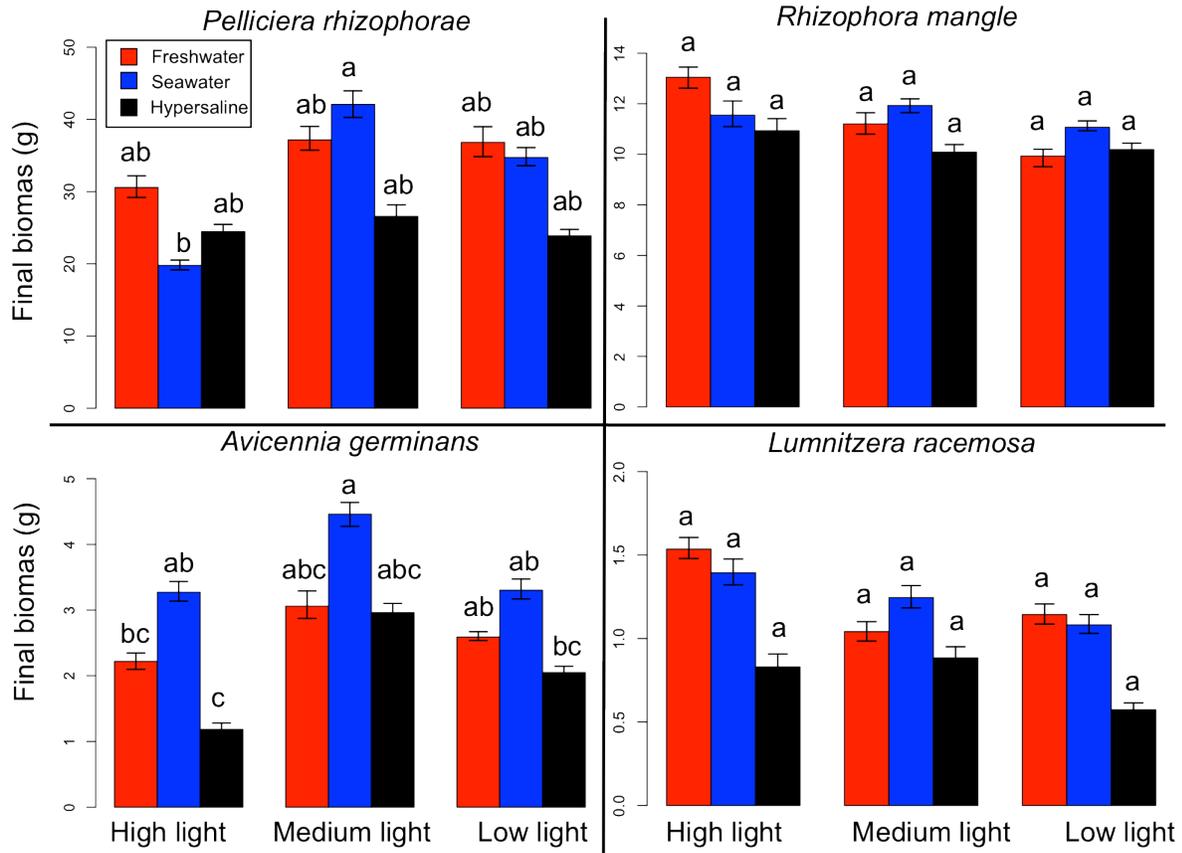


Figure 6. Final biomass of plants after 12 weeks in treatments. Values are treatment means. Error bars are \pm one standard error of the mean. Letters above bars summarize results of a Tukey HSD test. Within each species, means with the same letter are not significantly different at $P = 0.05$.

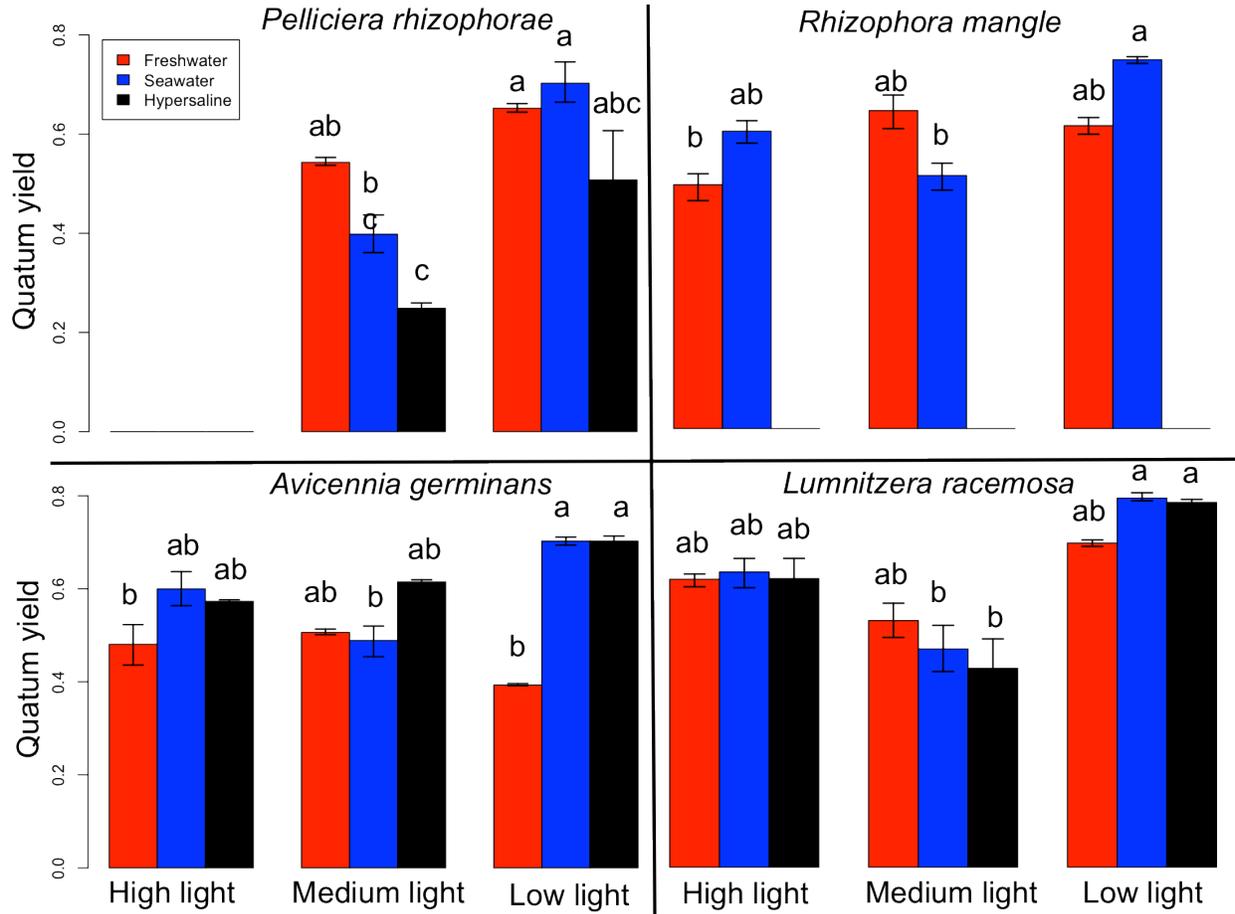


Figure 7. Light-adapted photosynthetic yield based on leaf fluorescence of seedlings after 12 weeks in treatment. Values are means \pm one standard error of the mean. Letters above bars summarize results of a Tukey HSD test. Within each species, means with the same letter are not significantly different at $P=0.05$. *Rhizophora* plants in the hypersaline treatments had no leaves, so yield could not be measured. In high light, no *Pelliciera* plants were alive in the hypersaline or seawater treatments, and the leaves on the freshwater plants were too tiny to get an accurate measurement.

Appendix A. Wet to dry weight conversion of mangrove seedlings and propagules. Propagules were converted to dry weights by $Y = \alpha + \beta x$, where x is the wet weight, Y is the dry weight and α and β are as follows:

Species	α	β	R^2
<i>Avicennia germinans</i>	-0.065	0.432	0.976
<i>Lumnitzera racemosa</i>	-0.089	0.327	0.944
<i>Pelliciera rhizophorae</i>	1.268	0.328	0.830
<i>Rhizophora mangle</i>	-1.112	0.637	0.865

Chapter 3

Propagule predation by crabs limits establishment of the endemic neotropical mangrove,
Pelliciera rhizophorae

Abstract

Recruitment of seedlings is crucial to the establishment and maintenance of plant populations and species ranges. Though propagule predation by crabs is prevalent in mangroves around the world, it has never been examined for the rare mangrove species *Pelliciera rhizophorae*. This study examined propagule and seedling fate of *P. rhizophorae* to understand population dynamics of this species in Panamá. A propagule predation experiment was conducted at sites on the Caribbean and Pacific coasts of Panamá. Propagules were placed in either *R. mangle* or *P. rhizophorae* forests on both coasts. At the Caribbean sites, crabs consumed 86.7% of propagules in the *R. mangle* forest but only 3.3% of propagules in the *P. rhizophorae* zone. At the Pacific site, crabs consumed 90% of propagules in the *R. mangle* zone and 66.7% in the *P. rhizophorae* zone. Propagules of both species were planted in the different forest types to examine survival without crab predation. Seedling survival did not vary between cohorts or with forest type, suggesting that predation, rather than seedling survival once established, limits *P. rhizophorae* populations. Overall, *P. rhizophorae* had fewer propagules eaten than *R. mangle*. At face value, this result is inconsistent with the fact that *R. mangle* is a much more common species, however it produces an order of magnitude more propagules per capita than *P. rhizophorae* and may well satiate its crab predators.

Introduction

Species composition of local communities can be thought of as the product of multiple abiotic and biotic filters acting on the species pool. Species that successfully pass through the filters are present in the local species assemblage (Keddy 1992, Poff 1997, Stutzner et al. 2001). A paradigm that has gained wide acceptance is that abiotic factors such as temperature, precipitation and soil type determine large-scale patterns of species distributions, while the influence of biotic interactions occurs primarily at the local level (Wiens 2011). Consistent with this expectation, Boulangeat et al. (2012) found that for plant species in the French Alps abiotic factors and dispersal determine presence or absence of a species, but abundance is determined by biotic interactions at the community level.

One of the biotic filters increasingly recognized as important for recruitment and plant population dynamics on a local scale is the role of seed predators (Louda 1982, 1989, Kauffman and Maron 2006, Maron and Kauffman 2006, Maron et al. 2012). Seed consumers limit establishment and ultimately the growth rate of a population, and these effects can impact species-level persistence in the case of rare species comprised of small, isolated populations (Dangremond et al. 2010). Land crabs that eat seeds are major limiting factors of tree recruitment in tropical forests, including mangrove forests (e.g. Smith 1987, Smith et al. 1989, Sousa and Mitchell 1999), coastal terrestrial forests (Lindquist and Carroll 2004) and island forests (Lindquist et al. 2009). Though mangroves and other coastal forests are heavily influenced by abiotic conditions such as the tidal gradient and flooding regime, Lindquist et al. (2009) argue that crabs take precedence over local abiotic conditions in their effects on local species composition. Indeed, rates of seed predation by crabs can be very high (Smith 1987, Smith et al. 1989, McKee 1995, Sousa and Mitchell 1999), ranging up to 100% in some sites (Smith 1987, 1989, Clarke and Kerrigan 2002).

Mangrove forests are characterized by zones of differing tree species composition along the tidal gradient (Smith 1992). Three main hypotheses have been introduced to explain how crab predation influences mangrove zonation. First, the dominance-predation model proposed

by Smith (1987) hypothesizes that crabs consume seeds of mangrove species in an inverse relationship to the tree's dominance or zonation in the forest—highest rates of seed predation occur in zones where a species does not occur or dominate. Second, the canopy gap hypothesis posits that propagule predation is higher under closed canopies than in adjacent gaps, where crabs are at risk of exposure to high air temperatures and desiccation, creating a refuge from propagule predation in gaps (Osborne and Smith 1990, Clarke and Kerrigan 2002). Third, the flooding regime hypothesis, suggests predation is lowest in the low intertidal region because it is flooded there more. This leaves crabs less time to forage there than in the upper intertidal region, which is predicted to have high rates of crab predation (Osbourne and Smith 1990, Clarke and Myerscough 1993).

Previous studies have yielded mixed results in support of these three hypotheses. The dominance-predation model has been tested in multiple sites around the world (Smith et al. 1989, McKee 1995, McGuinness 1997, Sousa and Mitchell 1999, Allen et al. 2003, Sousa and Dangremond 2011), and evidence does not support this as a general model of mangrove zonation. However, the patterns of seed predation proposed in this model are observed for some species, namely in the genus *Avicennia*. Similarly, support for crab predation determining species composition around gaps is mixed (Sousa and Mitchell 1999, Clarke and Kerrigan 2002). Osborne and Smith (1990) found lower predation of *A. marina* propagules in large light gaps than small ones, but Sousa and Mitchell (1999) found that propagule predation by crabs was not influenced by the environment of light gaps, and Clarke and Kerrigan (2002) found no consistent pattern of crab predation in light gaps. Finally, evaluations of the flooding regime hypothesis in the Neotropics (Smith et al. 1989, McKee 1995, and Sousa and Mitchell 1999), where tidal ranges are small, have found rates of predation to be highest in the low intertidal zone, where herbivorous species comprise the majority of the crab assemblage, as compared to the upper intertidal where detritivorous species predominate. While these previous studies have all shown that crabs play a large role in removing viable propagules and thereby limiting seedling establishment, the effects of crab removal on mangrove forest structure are not well understood. Despite the large number of propagules lost to predation, other factors may influence the recruitment and ultimate survival of mangrove seedlings (Krauss et al. 2008). If, for example, mangrove propagules that escape predation cannot establish in the environmental conditions in which they find themselves, or die because of resource competition with co-occurring individuals, then seed predators will not have a large effect on the demography of the plant.

This study examines factors that affect seedling establishment of a rare neotropical mangrove species, *Pelliciera rhizophorae*. *Pelliciera rhizophorae* usually co-occurs either in monospecific adjacent zones or mixed together in the same forest with *Rhizophora mangle*, a common mangrove that dominates the canopy of low intertidal forests in the Caribbean. The amount of seed predation *P. rhizophorae* experiences has never been measured, and therefore it is unknown how crabs affect the abundance and distribution of this species. The objectives of this study were to determine the effects of two potential filters on establishment: propagule predation by crabs, which prevents seedling establishment, and forest type, which could affect establishment success and seedling survival. The questions addressed were: 1) how does propagule predation of *P. rhizophorae* differ in different forest types? 2) if protected from crab predation, how does seedling survival vary in different forest types? Because *P. rhizophorae* usually co-occurs with *R. mangle* and their seedlings may compete for resources, propagule and seedling survival of both species was studied.

Methods

Study species:

Pelliciera rhizophorae has a narrow geographic distribution (Graham 1997, Jimenez 1984, Tomlinson 1986), with populations on the Caribbean coast of Panamá and Colombia and Pacific coast from Costa Rica to northern Ecuador. In Panamá, *P. rhizophorae* occurs in a few small isolated populations on the Caribbean coast and in larger, more contiguous populations on the Pacific coast. *Pelliciera rhizophorae* only occurs in areas near freshwater, such as streams or estuaries. Where it does occur, it ranges from rare to locally abundant, and usually occurs in monospecific zones adjacent to *R. mangle* or in their understory. Like other mangroves, *P. rhizophorae* produces propagules that are buoyant and water-dispersed. Peak propagule production occurs in June and July in Pacific sites of Panamá and October in Caribbean sites, though Caribbean trees produce some fruit all throughout the rainy season (IC Feller, pers. comm.). *Pelliciera rhizophorae* propagules are larger than other mangrove propagules, with large fleshy cotyledons making up the bulk of the propagule. In Panamá, *P. rhizophorae* propagules have an average mass of 86.2 (± 6.3) g and a length of 7.76 (± 0.24) cm (Rabinowitz 1978a).

Rhizophora mangle is widespread and locally abundant throughout the Neotropics (Tomlinson 1986). Its long slender, viviparous propagules are also water-dispersed. *Rhizophora mangle* typically occurs lowest in the intertidal zone, with its large prop roots partially submerged in water. In Panamá its propagules have an average mass of 14.0 (± 1.1) g and a length of 22.1 (± 1.0) cm (Rabinowitz 1978a).

Study sites:

Propagule predation experiments were carried out in Pacific and Caribbean populations of *P. rhizophorae*. The Pacific experiment was conducted in the mangroves near the Quebro River (7.44° N, 80.92° W), in Veraguas province of Panamá. *Pelliciera rhizophorae* and *R. mangle* are the dominant species of this forest, with occasional *Avicennia germinans* and *Laguncularia racemosa* individuals. The mangroves are bordered by the Quebro River on the east and by coconut palms and a narrow strip of pasture land on the west, giving way to sandy beach. Crab species observed there were *Aratus pisonii*, *Ucides occidentalis*, *Goniopsis pulchra*, and a large number of small hermit crabs, *Clibanarius lineatus*.

The Caribbean sites were in Bahia Las Minas (9.43° N, 79.79° W) and Punta Galeta (9.40° N, 79.86° W) in Colón province. A crab predation experiment and a seedling establishment experiment were conducted at these sites. In this area, *P. rhizophorae* occurs in small populations along slow-moving freshwater streams. *Rhizophora mangle*, *A. germinans* and *L. racemosa* are abundant in the surrounding mangrove forest. *Pelliciera rhizophorae* occurs either in monospecific zones or scattered among *R. mangle*-dominated stands. Crab species observed at the Caribbean sites were *Goniopsis cruentata*, *Ucides cordatus*, *Aratus pisonii*, *Cardiosoma guanhumii* and *Uca rapax*.

Crab predation experiment:

Experiments were conducted during peak propagule production in June 2010 (Pacific) and September to October 2012 (Caribbean). On both the Caribbean and Pacific coasts, I collected 60 propagules from reproductive *P. rhizophorae* trees. No more than two propagules were collected from each tree. To avoid using immature propagules, propagules were chosen

that were easily abscised from the tree. Propagules ranged in size from 6.0 to 8.5 cm wide. Sixty was the maximum number of mature propagules that met these criteria and were accessible (i.e. not too high in the canopy) during experimental setup.

On each coast, I haphazardly selected three sites of pure *P. rhizophorae* canopy and three paired sites where *R. mangle* dominated the canopy. Similar to other studies of propagule predation in mangroves (e.g., Sousa and Mitchell 1999, Smith et al. 1989, McKee 1995), propagules were tethered using monofilament, where one end was tied around the propagule and the other end attached to a forest structure such as a seedling stem or a prop root of *R. mangle*. Each propagule was set at least 5 m away from any other propagules. After 1, 4, 7, and 15 d, I returned to check the fate of each propagule by following the tether. Many times the monofilament led down a crab burrow but the propagule could not be recovered. In these cases, the propagule was considered to be consumed and no longer viable. If the propagule was more than 50% eaten or an apical meristem was damaged, it was categorized to be unviable and consumed. If a propagule was less than 50% damaged and the shoot and root apical meristems were intact, it was considered damaged but viable.

Seedling establishment:

To assess the ability of *P. rhizophorae* and *R. mangle* seedlings to establish in different forest types, I planted propagules of both species in *P. rhizophorae*-dominated stands, *R. mangle*-dominated stands, and open canopy sites. The intent was to compare establishment success independent of crab predation, so all propagules were protected from crab predation for the first two weeks with a nylon mesh enclosure (2 mm mesh size) that surrounded the propagule but had an open top so it would not impede the propagule's growth or access to light. One hundred-fifty propagules of each species were planted in two cohorts: 70 of each species in June 2011, which is the middle of the rainy season, and 80 of each species in October 2011, which is the end of the rainy season. The June seedlings were planted in sites at Punta Galeta, Colón. The October seedlings were planted in Punta Galeta and at sites in Bocas del Toro. Propagules were soaked in water for 3 d and the outer pericarp of *P. rhizophorae* was removed before planting because propagules shed their pericarps before germinating.

Analysis:

All analyses were done in R version 3.0 (R Development Core Team 2013). Crab predation data were analyzed with a two-sample proportion test. Growth data were analyzed with an ANOVA and posthoc analysis used a Tukey HSD test. Transplanted propagule/seedling survival data were right-censored, meaning the age of death was not known for all plants, because not all plants died during the experimental period. Survival analysis, which can handle censored and time-to-event data, was used to analyze seedling survival. This type of analysis examines predictors' effects on a hazard function, which is an individual's instantaneous risk of dying. The effects of cohort, canopy type and species on the hazard function were analyzed using an extended Cox model, which allows the hazard function to change over different time periods. Two heaviside functions were defined with a cutpoint at $t = 4$ months. The model used was:

$$h(t, \mathbf{X}(t)) = h_0(t)e^{[\beta_1(\text{Canopy})+\beta_2(\text{Cohort})+\delta(\text{Species})g_1(t)+\delta(\text{Species})g_2(t)]}$$

where $g_1(t) = 1$ if $t < 4$ months

0 if $t \geq 4$ months

and $g_2(t) = \begin{cases} 1 & \text{if } t \geq 4 \text{ months} \\ 0 & \text{if } t < 4 \text{ months} \end{cases}$

$h(t)$ is the hazard function at time t and $h_0(t)$ is the baseline hazard. The treatment used for the baseline hazard was open canopy, the June cohort and *P. rhizophorae* seedlings.

One limitation of this study is that due to inherently low levels of fruit production, I was unable to collect a sufficient number of *P. rhizophorae* propagules to replicate experiments at more than one set of stand types per site. This could compromise the degree to which the results can be generalized to larger spatial scales. Nonetheless, as the first experimental study of propagule predation and seedling establishment in this rare and unusual mangrove species, the results provide novel insight to its ecology and a strong foundation for future investigations of its demography and distribution.

Results

Propagule predation:

On the Caribbean coast, crab predation was significantly lower in *P. rhizophorae* stands than in *R. mangle* stands ($\chi^2 = 28.2$, $df = 1$, $p = 1.1e^{-7}$). In the *P. rhizophorae* stand, crabs attacked 10% of propagules but completely ate less than 5% of them; in the *R. mangle* stand, 84.6% of propagules were attacked by crabs and 73% were eaten completely (Fig. 1). Of the propagules that were attacked, none were pulled down crab burrows in the *P. rhizophorae* forest and 87% were pulled into crab burrows in the *R. mangle* forest.

On the Pacific coast, crab predation was higher in the *R. mangle* stands, but the difference between *P. rhizophorae* and *R. mangle* stands was not statistically significant ($\chi^2 = 3.53$, $df = 1$, $p = 0.06$). In the *P. rhizophorae* stand, crabs ate 67% of propagules; in the *R. mangle* stand, crabs ate 90% of propagules (Fig. 1). In the *P. rhizophorae* forest, 85% of the propagules eaten were pulled into burrows and in the *R. mangle* forest, 70% were pulled into crab burrows. Overall, fewer propagules were eaten on the Caribbean coast (48%) than the Pacific coast (78%) ($N = 120$, $\chi^2 = 9.52$, $df = 1$, $p = 0.002$).

Crabs observed eating propagules were *Ucides occidentalis* and *Goniopsis pulchra* on the Pacific coast and *Ucides cordatus* and *Goniopsis cruentata* on the Caribbean coast. Small *Aratus pisonii* were observed on propagules at the Caribbean sites, but did not inflict enough damage to prevent germination. *Uca rapax* was also observed at the experimental sites, but is a detritivore and did not consume propagules.

Seedling survival and growth:

Estimated coefficients for the extended Cox model are shown in Table 1. Survival curves for each treatment are shown in Fig. 2. Canopy and cohort did not have significant effects on the hazard function. The coefficients for the two heaviside functions were significantly different from zero, indicating the hazard ratio changes over time and is different between *P. rhizophorae* and *R. mangle*.

The hazard ratio for *R. mangle* compared to *P. rhizophorae* is: 1.46 for $t < 4$ months and 3.25 for $t \geq 4$ months.

Overall, 16% of *R. mangle* propagules established as seedlings with leaves and 42% of *P. rhizophorae* propagules established as seedling with leaves. There was a significant effect of

cohort, canopy and their interaction on seedling height after 4 mo (the only point when cohorts could be compared due to sampling intervals) (Table 1, Fig. 2). Seedlings in the June cohort growing under *R. mangle* canopy grew tallest (mean height = 61.55 cm \pm 1.29), and June cohort seedlings in the open canopy were shortest (mean height = 37.37 cm \pm 1.25).

Discussion

There was a striking difference in *P. rhizophorae* propagule predation between forest types on the Caribbean coast of Panamá. The *P. rhizophorae*-dominated sites had almost no predation, and the *R. mangle*-dominated sites had very high (almost 85%) predation. In the propagule planting experiment, there was no difference in seedling survival between *P. rhizophorae* zones and *R. mangle* zones. These experiments show that if dispersed to different forest types (*P. rhizophorae* zones vs. *R. mangle* zones), the main impediment to recruitment is crab predation and not ability to survive once established. My seedling survival results agree with those of Rabinowitz (1978b), who found that *P. rhizophorae* had high survival in both *R. mangle* and *P. rhizophorae* forests. She also tested the survival of *P. rhizophorae* in *Avicennia germinans* and *Laguncularia racemosa* forests and found lower survival in those higher intertidal forest types.

Transplanted *P. rhizophorae* had higher survival than *R. mangle*, so it is unlikely that competition for resources limits *P. rhizophorae* propagules from establishing in *R. mangle* zones. *Pelliciera rhizophorae* seedlings in the early cohort grew taller in the *R. mangle* forest than in the *P. rhizophorae* forest. Other mangroves grow as well or better in zones other than their own (Rabinowitz 1978b, Chapman and Feller 2011). Since *P. rhizophorae* are often found adjacent to *R. mangle* zones (Chapter 1), they have a high likelihood of dispersing into those zone, where they would grow well if given the chance to establish. However, crabs seem to be limiting establishment of *P. rhizophorae* in *R. mangle* zones. Seed predation in many plants can be overcome by a seed bank, which contributes to population dynamics when seedlings recruit out of the seed bank rather than from seeds produced that year (Harper 1977, Crawley 1989, 1990). Seed banks do not exist for mangrove species, as their propagules have no dormancy. Because *P. rhizophorae* propagules are six times larger than those of *R. mangle*, individual trees produce fewer propagules than *R. mangle* trees do (Rabinowitz 1978a, b).

Rhizophora mangle adult trees are more abundant and produce more propagules than *P. rhizophorae*. *Rhizophora mangle* seedlings are also vulnerable to a specialist stem-boring beetle, which is responsible for a high amount of seedling mortality (Sousa et al. 2003, Devlin 2004). *Pelliciera rhizophorae* seedlings do not have any known specialist enemies. Seedling survival did not differ between cohorts, despite the fact that the two cohorts experienced different growing conditions during their first few months of life. The dry season begins in December, so the October cohort experienced dry conditions at 6 wk, while the June cohort experienced dry conditions at 6 mo. No difference in survival was detected, but there was an interaction of cohort and canopy on height after 4 mo. In the *Rhizophora* canopy, the June seedlings grew much taller than the October seedlings, but the opposite was true of the *Pelliciera* canopy. Propagules that fall and establish earlier in the rainy season (e.g., in June) grow taller in forest types other than their own, while propagules that establish later grow taller in their own canopy—this is interesting because the earlier propagules may also have more chances to disperse away into other forest types due to flooding in the rainy season. Dispersal into new habitats is thus favored earlier in the season.

McKee (1995) and Sousa and Mitchell (1999) found that crabs not only damaged propagules, but also damaged newly established seedlings--mostly the hypocotyl of *R. mangle* and the cotyledons of *Avicennia germinans*. Smith (1987) also found crabs ate the cotyledons of *A. marina*. Sousa and Mitchell (1999) found that rates of damage dropped sharply after propagules became upright seedlings. Similarly, once *P. rhizophorae* seedlings are firmly rooted, they are less vulnerable to crab predation. The width of the fully open cotyledons might be too big to fit into a crab burrow, and they might be harder to detach from the plant than the smaller, more leaf-like cotyledons of *Avicennia* species.

It is possible there is temporal variation in propagule predation that was not captured by this study. The experiment lasted two weeks, covering half of the lunar cycle from new to full moon phases and the accompanying tides. *Ucides cordatus* in Brazil stay inside their burrows for 4-5 h when the forest is inundated during spring tides (Nordhaus et al. 2009). If propagules were to fall during spring tides, they could possibly escape predation and be dispersed by the tide to a larger body of water. However, they would still be vulnerable to predation during establishment at a new site.

On the Caribbean coast, *P. rhizophorae* populations are small and fragmented (Castillo-Cardenas and Toro-Perea 2012). The variation in propagule predation between different forest zones may help explain the patchy distribution of this species on the Caribbean coast. *Pelliciera rhizophorae* is only found in areas of low salinity near a freshwater input. However, *P. rhizophorae* seedlings that escape predation survive just as well in other zones as in their own, and they can grow in higher salinities (Chapter 2), so physiological constraints do not necessarily explain the absence of *P. rhizophorae* from higher salinity sites. A possible explanation is that sites with freshwater input, and thus lower salinity, are less suitable for crabs.

In one of the only comprehensive studies of *Ucides cordatus* habitat and population structure, Diele (2000) sampled surface water of a tidal channel in mangroves where that species occurs in Brazil and found that water salinity was above 20 ppt throughout the year except during the rainy season, when it dropped to around 10 ppt. Even in the dry season, *P. rhizophorae* sites have salinity below 20 ppt. During periods of inundation, *U. cordatus* close off their burrows (Nordhaus et al. 2009); they can tolerate low salinities for some period but year-round salinity of less than 20 ppt may provide too much osmotic stress. In salinities of 15 ppt or less, *Ucides* crabs have a reduced ability to osmoregulate, causing increased mortality and less growth than in the optimal salinity of 30 ppt (Diele and Simith 2006). The fact that no propagules were pulled down burrows in the Caribbean *P. rhizophorae* forest is evidence that *U. cordatus* do not occur at high abundances in that habitat. The burrows present in that area may be used by other species, or could have been created by a previous population of crabs that was eradicated during a large inundation event.

Goniopsis spp. do not burrow, and they consume food aboveground. *Ucides* spp., on the other hand, do burrow and pull propagules into their burrows. There might be spatial variation in predation based on distribution and abundance of each predator species. Ferreira and others (2013) found that the effect of propagule predation by *Goniopsis* spp. increases in the absence of *Ucides cordatus*. *Ucides* is the larger of the two crab genera, and more likely to win antagonistic interactions. Though Lindquist and Carroll (2004) found that hermit crabs contributed to seed predation in tropical terrestrial forests, they do not eat *P. rhizophorae* propagules (Dangremond, pers. obs.), possibly because the propagules are too big, or possibly because of competition with larger crabs. *Ucides* spp. and *Goniopsis* spp. are the only crabs large enough to carry off tethered propagules (Ferreira et al. 2013). They also found that tree species that escaped crab predation

seemed to do so because of the large quantity of seeds produced. Since *P. rhizophorae* produces fewer, larger propagules than other mangroves, predation by crabs is likely to exert a much stronger effect on the demography of *P. rhizophorae* than on other species.

If crab predation limits Caribbean *P. rhizophorae* populations, how do Pacific populations persist in the face of even higher rates of predation? Propagule predation was higher on the Pacific coast, and there was not a significant difference in predation between different forest types. The answer may lie in the differing seasonality of the two coasts of Panamá. The Pacific coast has a distinct rainy season and a distinct dry season. In Pacific populations, *P. rhizophorae* produces fruit in large quantities in June or July, depending on the year. In Caribbean populations, fruit production is staggered from June until October (Chapter 1). The large quantities of fruit produced on the Pacific may exert a masting effect, swamping propagule predators. Even though many propagules are eaten, enough propagules fall at one time that some escape predation. On the Caribbean coast, the low quantities of fruits that fall throughout the rainy season likely are never enough to overwhelm the amount of predators, and a smaller number of fruits survive throughout the season.

The dominance-predation model suggests crab predation occurs in an inverse relationship to tree abundance. This experiment was not a full test of the dominance-predation hypothesis, but the results do support the idea that predation of propagules is lowest where *P. rhizophorae* dominates, and higher rates of predation are observed in areas where *P. rhizophorae* is absent. The dominance-predation model has not been generally supported for most mangrove species, but evidence still supports the model for certain species, such as *Avicennia* spp. *Pelliciera rhizophorae* may be another species that fits this model of mangrove distributions. This study provides a novel explanation for why *P. rhizophorae* occurs in low salinity sites. Sites with low water salinity provide propagules a refuge from predation by salt-dependent crabs; planted propagules survived in other canopy types just as well as in *P. rhizophorae* zones. Jimenez (1984) suggested *P. rhizophorae* cannot survive high salinity conditions, but *Pelliciera* seedlings actually can survive and grow in salinity equal to, or greater than, seawater (Chapter 2). My results support the suggestion of Lindquist and others (2009) that land crabs can exert more influence over local species composition than local abiotic factors—in the filter scheme, land crab impacts supercede those of local abiotic factors.

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Table 1. Extended Cox model for hazard function of planted seedlings.

	Coefficient	exp(coef.)	SE (coef.)	Robust SE	z	p
Canopy	-0.0761	0.927	0.0939	0.0931	-0.818	0.4100
Cohort	0.2344	1.264	0.1448	0.1450	1.617	0.1100
Species x HV1	0.3799	1.462	0.1356	0.1224	3.104	0.0019
Species x HV2	1.1791	3.251	0.4298	0.4236	2.783	0.0054

Table 2. ANOVA table for seedling height after 4 months of growth.

	Df	SS	MS	F	P
Cohort	1	651.2	651.17	4.62	0.038
Canopy	2	2321.1	1160.54	8.23	0.001
Cohort x Canopy	1	1442.8	1442.75	10.23	0.001
Residuals	41	5781.4	141.01		

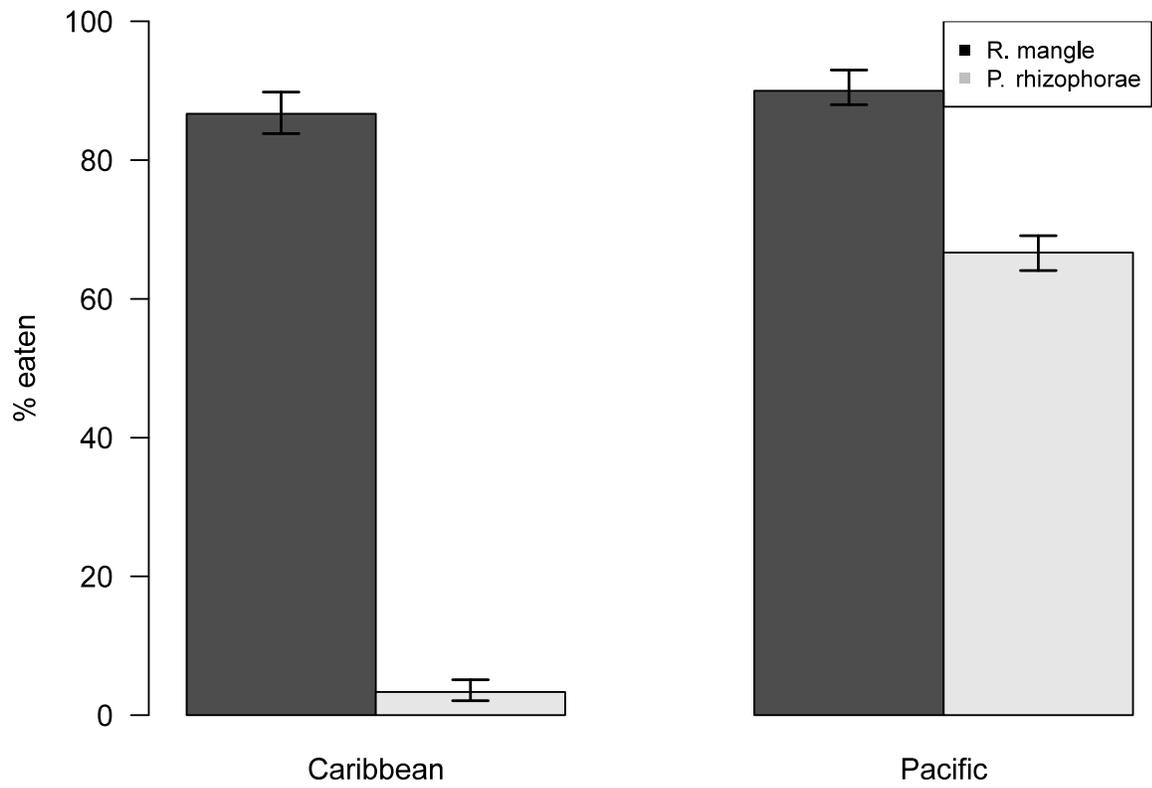


Figure 1. Percentage of *Pelliciera rhizophorae* propagules eaten by crabs in *Rhizophora mangle* and *P. rhizophorae* forests. N = 30 for all treatments.

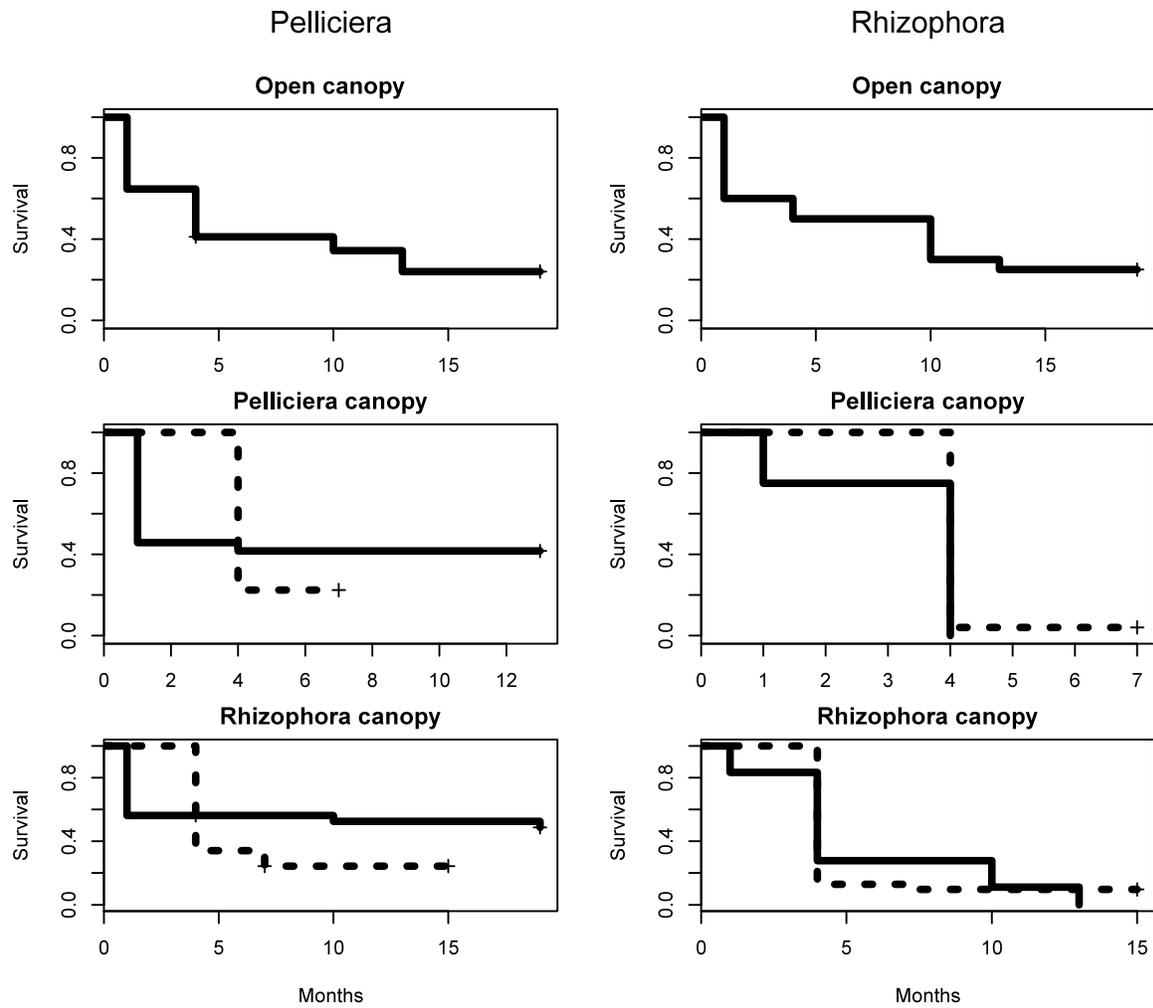


Figure 2. Seedling survival over 18 mo in three different canopy types. Solid lines are the June cohort, dashed lines are the October cohort. A cross (+) indicates censored observations.

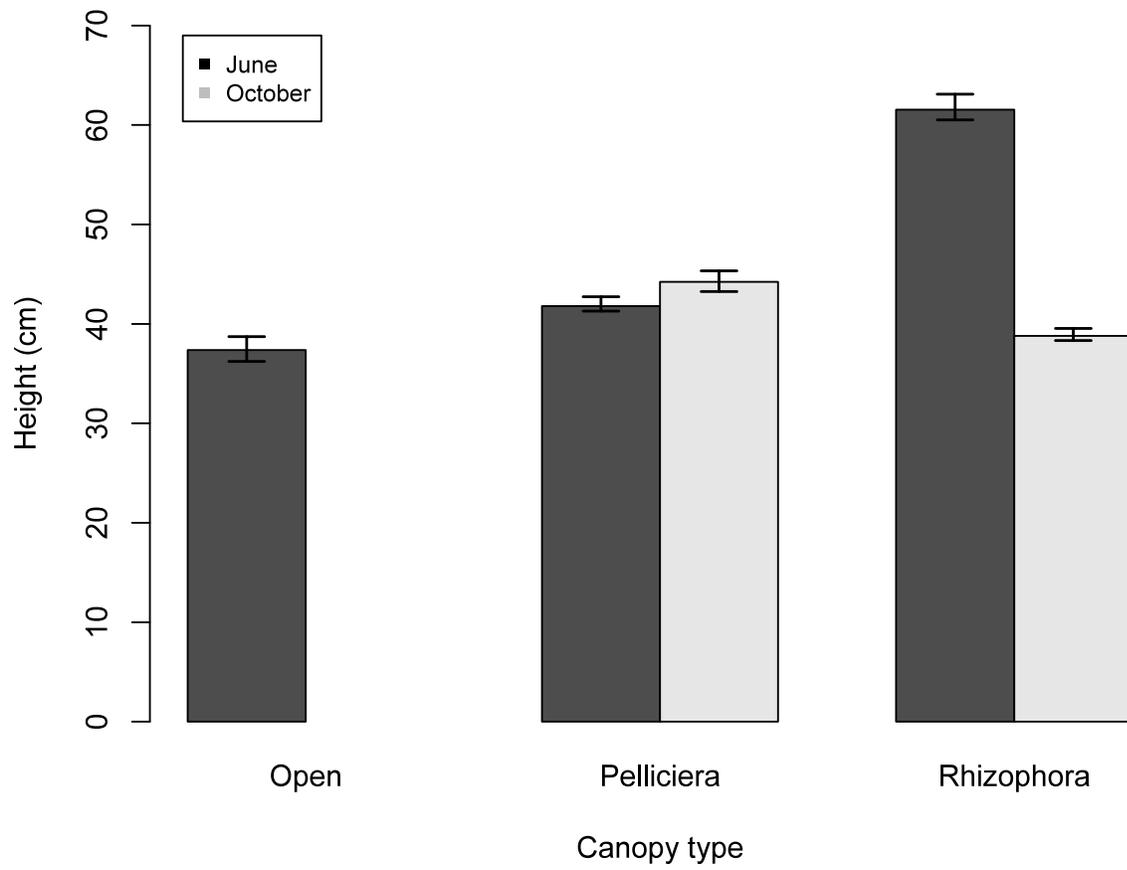


Figure 3. Mean height of established *Pelliciera rhizophorae* seedlings from two cohorts after 4 months of growth.

Chapter 4

Functional traits of the mangrove *Pelliciera rhizophorae*: a comparison of Caribbean and Pacific populations

Abstract

Functional traits reveal how plants interact with their environments, as traits can change in response to climate, soil resources, disturbance, competition, and herbivory. Nutrient limitation is a major factor structuring mangrove forests, with nitrogen (N) and phosphorus (P) limitation causing stunted growth forms around the world. This study examines how functional traits of the rare mangrove *Pelliciera rhizophorae* vary on the Pacific and Caribbean coasts of Panamá, and in dwarf compared to taller, fringe trees. Mangroves on the Pacific coast of Panamá experience increased tidal flushing, lower and more seasonal precipitation, and different geomorphology compared to mangroves on the Caribbean coast of Panamá. Functional traits were measured in Pacific and Caribbean populations of *P. rhizophorae*. Dwarf trees had lower N and P concentrations in their green leaves than fringe trees did on both coasts. Dwarf trees also differed from fringe trees in four of six biomass allocation ratios. On both coasts, dwarf trees had smaller stem length to stem biomass, leaf weight ratio, shoot weight ratio, and leaf area ratio. Specific leaf area and leaf area to stem length were not different between growth types. Caribbean trees had higher P resorption than Pacific trees, regardless of growth form.

Introduction

With climate change, invasive species, and habitat loss threatening species around the globe, it is increasingly important to understand the relationship between species and their environments. Functional traits can reveal how plants respond to their environments, with particular suites of traits predominating in certain abiotic and biotic conditions (Dyer et al. 2001, Lavorel and Garnier 2002, Westoby et al. 2002, Cornelissen et al. 2003). Growth rates, morphology and nutrient dynamics change in response to nutrient availability (Feller 1995, Craine et al. 2002, Feller et al. 2003, 2007, Lovelock et al. 2006), light levels (Dyer et al. 2001), carbon dioxide concentration (Reich et al. 2001, Klaiber et al. 2013), soil conditions (Lovelock et al. 2007a, Reef et al 2012), disturbance (Kuhner and Kleyer 2008, Carreño-Rocabado et al. 2012), competition (Violle et al. 2009) and herbivory (Diaz et al. 2007, Salgado-Luarte and Gianoli 2011).

Plants not only respond to their environments, but also influence them, and can affect nutrient cycling, CO₂ uptake, trophic webs and ecosystem functioning. Most species included in functional trait analyses are abundant (e.g. Cornelissen et al 2003, Diaz et al. 2004), as they are more easily accessible and are more likely to impact major ecosystem processes than rare species. However, rare species that are locally abundant may also impact major ecosystem processes, particularly when they comprise the majority of a habitat's biomass. For example, mangrove ecosystems are typically made up of a few species that may be globally rare but locally abundant. Though mangrove ecosystems cover only a small amount of the Earth's surface, they contribute significantly to nutrient cycling and CO₂ storage (Donato et al. 2011), and contribute to both terrestrial and marine trophic webs (Sousa and Dangremond 2011).

Nutrient limitation is a major factor structuring mangrove forests around the world. Nitrogen (N) and phosphorus (P) limitation cause stunted growth forms in mangrove trees in Florida, Belize, Panama, and Australia (Feller 1995, Feller et al. 2003, Lovelock et al. 2004, 2007b, Feller et al. 2007, 2009). Nitrogen is one of the most important elements of plant tissues, and lack of N can affect plant form and function, as well as whole ecosystem function. Evidence from many studies across multiple sites supports the idea that nutrient limitation in mangroves

depends on geomorphology (Feller 1995, McKee et al. 2002, Feller et al. 2003, 2007, 2009). In many mangrove sites, trees on or adjacent to the water form a fringing stand around an interior zone. Scrub or dwarf trees, which are less than 1.5 m in height when mature, dominate these interior zones and receive less tidal flushing and fewer nutrients than the fringe trees. Dwarf mangrove trees are common throughout the Caribbean and have been found to be nutrient limited (Feller 1995, Lovelock et al. 2004, 2006, Feller et al. 2007, 2009).

However, not all dwarf or scrub trees are found on the interior of a site—patches of dwarf trees of the rare mangrove *Pelliciera rhizophorae* can be found growing along streams, adjacent to non-stunted trees of the same species more typical of fringe zones. It is unknown if this dwarf growth form is also a plastic response to nutrient limitation or is a genetically-based phenotypic variant. *Pelliciera rhizophorae* exhibits dwarf and fringe forms on both the Pacific and Caribbean coasts of Panama. The two coasts have very different tidal regimes and environmental conditions. Pacific tides can range up to 6 m, while tides on the Caribbean coast are less than 0.5 m (Glynn 1972). Upwelling from January to April brings nutrient-rich water to the Pacific waters of Panamá, leading to increasing primary productivity throughout the year in the Pacific relative to the eastern Atlantic/Caribbean waters (Pennington et al. 2006). The Pacific coast receives less annual precipitation and has a more distinct dry season, than the Caribbean coast of Panama (Condit 1998). Soil in Caribbean mangroves is peat-based, but Pacific mangrove soil is dominated by clay. Though nutrient dynamics and functional traits of widespread mangrove species have been examined on the Caribbean coast of Panama (Lovelock et al. 2004), they have not been compared between Pacific and Caribbean sites, and very little is known about the functional traits of the less common *P. rhizophorae*.

The objectives of this study were to examine nutrient dynamics, biomass allocation and functional traits of *P. rhizophorae* in dwarf and fringe trees from Pacific and Caribbean populations. Specifically, the questions investigated were: 1) do dwarf trees of *P. rhizophorae* show nutrient limitation relative to fringe trees? 2) how do nutrient dynamics and biomass allocation vary between coasts and between growth forms?

Because the Pacific coast of Panamá has increased tidal flushing compared to the Caribbean, I hypothesized Pacific trees would have higher N and P content than Caribbean trees. Furthermore, Caribbean plants would have higher resorption efficiencies of both N and P than Pacific plants due to lower nutrient availability along that coast. I expected dwarf trees to have lower nutrient content and higher resorption efficiencies than fringe trees, and to allocate more biomass to wood than leaves.

Methods

Study system

Pelliciera rhizophorae (Tetrameristaceae) occurs from Costa Rica to northern Ecuador on the Pacific coast of Central and South America, and has Caribbean populations in Nicaragua, Panamá, and Colombia. *Pelliciera rhizophorae* is found in areas with low interstitial soil salinity, often along slow-moving streams or in estuaries. *Pelliciera rhizophorae* has been present in the Neotropics since at least the early Eocene, about 50 Mya (Graham 1995). Though the fossil record shows that *P. rhizophorae* was once widespread in the Caribbean, extant Caribbean populations in Panamá only exist in the provinces of Bocas del Toro and Cónon. Caribbean populations are relatively isolated compared to more contiguous Pacific populations. Populations on the two coasts have been separated since the closing of the isthmus ~3 mya, and

pollen flow across the isthmus of Panama is unlikely in this species (Castillo-Cardenas et al. 2012), as it is for the more abundant mangroves *Rhizophora mangle* and *Avicennia germinans* (Dodd et al. 2002, Cerón-Souza et al. 2013).

Trait measurements

Populations were sampled along streams on the Caribbean and Pacific coasts of Panamá in February 2012 (Fig. 1). Fringe trees were sampled from seven sites on the Pacific coast and five sites on the Caribbean coast, while dwarf trees were sampled at two streams on each coast (Table 1). To capture variation associated with tidal elevation, nutrients, and salinity, plants were sampled from locations close to the mouths of the streams and at the furthest upstream locations in the *P. rhizophorae*-dominated stands. Twelve individuals were sampled at each stream, and their trait values were averaged to obtain one value per stream. Fringe and dwarf trees from the same stream were treated as two different sites (e.g., “Souli dwarf” and “Souli fringe”). For each tree, I collected a sun-lit canopy branch, cutting them stem at the third branching node back from the branch terminus. Salinity of the soil porewater was measured at the leaf sampling sites following the method of McKee et al. (1988).

Leaf and branch samples were dried in a drying oven for 3 d at 60° C. Traits measured were specific leaf area (SLA), leaf length, leaf dry matter content, leaf N and P content and resorption efficiencies, and stem specific density (SSD). Sampling and measurements of traits followed the protocols described in Cornelissen and others (2003). Wood and leaf biomass for each branch was measured and used to calculate biomass allocation metrics of leaf area ratio (LAR), leaf weight ratio (LWR), stem weight ratio (SWR), stem length to biomass ratio (SL:SB), and leaf area to length ratio (LA:SL). Stem specific density (SSD) was calculated as the mass of a section of oven-dry stem divided by its volume. Leaf area, length, and standing herbivory were measured on digital photographs of fresh leaves with ImageJ64 (Rasband, NIH). We acknowledge that estimating herbivory this way is problematic, because it underestimates total herbivory because it does not include loss of yield due to damage to the leaf primordia or absence of completely eaten leaves that have been removed from the tree (Lowman 1984).

Additional leaves were collected for nutrient analyses. At least six mature green and six senescent leaves were collected at each site, with no more than one green and one senescent leaf per tree. Green leaves were the youngest fully mature leaf on a stem, taken from sunlit sections of the canopy. The senescent leaves collected had well-formed abscission layers. Tissue from green and senescent leaves was analyzed for carbon, N and P to determine nutrient content and resorption efficiencies. Concentrations of C and N were measured with a Model 440 CHN Elemental Analyzer (Exeter Analytical, North Chelmsford, Mass., USA) at the Smithsonian Environmental Research Center, Edgewater, Md. Leaf %P by mass was determined by placing a known mass (~2 mg) of dried, ground leaf material in a muffle furnace at 550°C for 2 h (Miller 1998), followed by colorimetric analysis using the ammonium molybdate method (Clesceri et al. 1998).

Resorption efficiency was calculated as:

$$([\text{X}]_{\text{green leaf}} - [\text{X}]_{\text{senescent leaf}}) / [\text{X}]_{\text{green leaf}} * 100$$
, where X is N or P (Chapin and Van Cleve 1989).

The number of leaves and flowers produced by each branch were also compared. *Pelliciera rhizophorae* flowers leave large, distinctive scars on the branch; I used these scars to

determine how many flowers each branch produced. Leaf nodes were counted to determine the number of leaves each branch produced.

Nutrient concentrations and growth measures were analyzed with a two-way analysis of variance (ANOVA) testing the effects of growth type, coast, and their interaction. When an ANOVA found significant effects, Tukey's honestly significant difference (HSD) tests were applied to examine pairwise differences within and among the treatment levels. All statistical analyses were performed in R version 2.15.2 (R Development Core Team 2012).

Results

Nutrient dynamics

Mean values of nutrients measured and ANOVA results are presented in Table 2. The N and P content of green leaves was significantly lower in dwarf trees than fringe trees (Fig. 2), but did not differ significantly between coasts and there were no interactions in nutrient measurements. Despite the fact that nutrient content of green leaves was lower in dwarf trees than fringe trees, resorption efficiencies (Fig. 3), N:P and C:P ratios (Fig. 4) did not differ significantly between the two growth types. The C:N ratios of green leaves were significantly lower in fringe trees than dwarf trees (Fig. 4).

There were a few differences in nutrient dynamics between the two coasts. Nutrients of green leaves were not significantly different between the coasts. The N content of senescent leaves was not different between coasts, but P content of senescent leaves was significantly lower in Caribbean trees. Nitrogen resorption did not differ significantly between coasts, but P resorption was higher in Caribbean trees than Pacific trees (Fig. 3). Consistent with the fact that nutrient content of green leaves did not differ between coasts, nutrient ratios (C:N, N:P, C:P) of green leaves did not differ significantly between the two coasts. However, N:P and C:P of senescent leaves were both significantly higher in Caribbean trees than Pacific trees (Fig. 4).

Salinity was very low in the Bocas del Toro populations, ranging from 5 to 10 ppt. Upstream and downstream measurements only differed by 3 ppt within a creek. The Colón populations were more saline, ranging from 11 to 29 ppt. The Pacific populations ranged from 5 to 14 ppt, with the exception of one sample at the Quebro population that was 32 ppt.

Biomass allocation

Biomass allocation ratios are presented in Table 3. Four of the six biomass allocation ratios (LAR, LWR, SWR, SL:SB) were significantly different between fringe and dwarf trees. Leaf area to stem length (LA:SL) and SLA were not different between fringe and dwarf trees, or between the two coasts. The only biomass allocation ratio that differed between the two coasts was SL:SB, which was significantly larger in Pacific fringe trees than Caribbean fringe trees. There were no significant interactions between growth type and coast.

Other growth measures

Leaf length, number of leaves and flowers, and SSD are presented in Table 2. Dwarf trees on both coasts made significantly more leaves and fewer flowers per unit of stem length than fringe trees on either coast. Stem specific density (SSD) was highest in Pacific fringe trees and lowest in Pacific dwarf trees (Fig. 5). Standing herbivory (Fig. 6) was significantly greater in fringe trees than dwarf trees. Leaves from fringe trees suffered more damage at Caribbean sites than at Pacific sites.

Discussion

Evidence of nutrient limitation was found for dwarf trees on both coasts. Dwarf trees on the Caribbean and Pacific coasts had lower N and P content in their green leaves than fringe trees did, suggesting that dwarf trees are nutrient limited on both coasts. Contrary to my prediction, the only nutrient concentration that differed significantly between coasts was P in senescent leaves, which was lower on the Caribbean coast in both fringe and dwarf trees. Caribbean trees also had higher P resorption, N:P and C:P ratios than Pacific trees, suggesting Caribbean trees are more efficient at reusing P than Pacific trees. The increased efficiency could be a plastic response to low P availability on the Caribbean, but further experimentation would be necessary to test the ability of Caribbean trees to respond to P availability. Lovelock et al. (2004) found that *R. mangle* in Caribbean Panamá responded strongly to P fertilization, suggesting other mangroves in that area are P-limited.

Four biomass allocation ratios were significantly different between fringe and dwarf trees, indicating dwarf trees are morphologically distinct from fringe trees, not only in their stature, but also in their architecture. Dwarf trees allocate much more biomass to wood than leaves, have slower shoot elongation, and branch less frequently than fringe trees. This is consistent with what is expected for nutrient-limited trees; in nutrient addition experiments, dwarf *R. mangle* trees undergo shoot elongation when treated with their limiting nutrient (Feller 1995, Lovelock et al. 2004, Feller et al. 2009). Dwarf trees also do not produce as many flowers as fringe trees. This lack of flowering in dwarf trees is an important observation, because *P. rhizophorae* trees produce a small number of very large propagules. Dwarf trees that have limited flowering further reduce the number of potential recruits for this rare species. If nutrient limitation is the reason for low flowering frequency, it could also be limiting population-level productivity and recruitment.

Nutrient resorption efficiency indicates the conservation of nutrients within an individual plant. Nutrient resorption from senescent leaves can contribute as much nutrient content to growing leaves as nutrient uptake from the soil (Chapin and Kedrowski 1983, Feller 1995, Aerts 1996, Killingbeck 1996, Wright and Westoby 2003). Phosphorus resorption is an important indicator of nutrient availability, and plants resorb a higher amount of P from senescent leaves in P-limiting conditions (Pugnaire and Chapin 1993, Feller 1995, Aerts 1996, Reich et al. 1997, Gusewell 2004, Rejmankova 2005). Phosphorus may be limiting for *P. rhizophorae* on the Caribbean coast, as P resorption was 71-75% there, but only 60% on the Pacific coast. In Bocas del Toro, Lovelock and others (2004) found P resorption efficiency of *R. mangle* to be about 80%. In their study, fertilization with P caused P resorption to decrease to 65%. The N resorption efficiency for *P. rhizophorae* of ~50% in this study was similar to what they found for *R. mangle*.

It is expected that nutrient resorption would vary among species and locations. The widely accepted values for maximal resorption in senescent leaves are N concentrations of 0.3% and P concentrations of 0.01%, though concentrations up to 0.07% for N and 0.04% for P still represent complete resorption (Killingbeck 1996). The values for *P. rhizophorae* represent incomplete resorption for N, but complete resorption for P, except in the Pacific fringe trees, whose mean P concentration in senescent leaves was 0.05%. In studies of *R. mangle* nutrient dynamics in multiple sites spanning a latitudinal gradient, Feller et al. (2009) found that fringe trees consistently had higher N resorption. In terrestrial trees in Panama, Santiago and others (2004) found higher N resorption in drier climates. Though the Pacific coast is drier than the

Caribbean, I found that N resorption was not different between the two coasts, or between fringe and dwarf trees. Lovelock and others (2007a) found that N resorption did not differ significantly between sites or vegetation type for *Avicennia marina* in New Zealand. As Killingbeck (1996) notes, resorption values fluctuate year to year, so maximal resorption may not be achieved in any given year. In Bocas del Toro, nutrient content of freshwater runoff can vary seasonally, with higher concentrations of nutrients during times of high rainfall and strong river discharge (D’Croz et al. 2005). Nutrient content of leaves and resorption may also change with seasonal variation. However, Wang and others (2003) observed that seasonal N and P fluctuations in another mangrove, *Kandelia candel*, were correlated; thus N:P ratios did not change seasonally. Nutrient ratios may therefore be better indicators of the nutrient status of these plants.

Differences between the coasts may be due to climate patterns and soil composition. Disentangling the influence of climate and soil on vegetation in Panamá is difficult, if not impossible. The Pacific coast has a distinct wet and dry season, while Caribbean precipitation peaks twice a year. The mountains along the continental divide bisect Panamá, creating different soils on the two coasts. Pacific soils are clayey with volcanic and sedimentary influences, but soils in Bocas del Toro are made of deep deposits of mangrove peat formed during the Holocene (Philips and Bustin 1996). Seasonal and yearly fluctuations in precipitation, runoff and subsequent nutrient availability may be important patterns that were not detected in this study.

With expanding development and pollution, nutrient over-enrichment is a global threat to coastal ecosystems (NRC 2000), and is increasingly a concern for undeveloped places in Panamá. Nutrient enrichment greatly affects primary productivity in mangroves (Feller 1995, Feller et al. 2003, Lovelock et al. 2004). However, the effects of nutrient enrichment sometimes, but do not always, transfer across trophic levels. Nutrient availability can alter herbivore activity in mangroves depending on site, species and type of herbivore (Feller and Chamberlain 2007). On Florida mangrove islands, insect herbivory of *R. mangle* was higher on islands with bird colonies and their guano than on islands without the extra nutrients provided by guano (Onuf et al. 1977). In a nutrient addition experiment on *R. mangle* in Belize, Feller (1995) found an increase in damage by specialized herbivores when trees were released from their P limitation through the addition of P and NPK fertilizer, but generalist herbivores did not alter their activity. In another nutrient addition experiment on *A. germinans* the damage caused by herbivores increased with addition of N fertilizer in Florida but not in Belize (Feller et al. 2007). An interesting finding of Feller and Chamberlain (2007) is that *R. mangle* leaves from dwarf trees had less than half the amount of damage over their lifespan than leaves from fringe trees. The same pattern was observed here, where dwarf *P. rhizophorae* trees had much less standing herbivory than fringe trees. The effects of nutrient enrichment on herbivory rates of *P. rhizophorae* warrants further study.

This study is the first to examine nutrient dynamics and differences between dwarf and fringe trees of *P. rhizophorae*. It is also the first study to compare nutrient dynamics and growth measures between Caribbean and Pacific populations of the same species. Future research on the nutrient dynamics of this species should include a nutrient addition experiment to determine plant and herbivore responses to increased nutrient availability.

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Table 1. Streams and growth types of *Pelliciera rhizophorae* trees in Panamá.

	Pacific	Caribbean
Fringe	Arenas Chorcha Pedregal Quebro Suay Tebario Toucan	Bahia Azul Cilico Patterson Quebrada Las Mercedes Souli
Dwarf	Chame Quebro	Bahia Las Minas Souli

Table 2. Leaf and stem traits for *Pelliciera rhizophorae* from Caribbean and Pacific populations of Panama. F = fringe trees, D = dwarf trees. Numbers in parentheses are standard errors.

Plant trait	Mean trait value		Type			Coast			Type x Coast		
	Caribbean	Pacific	df	F	p	df	F	p	df	F	p
%N green	F: 1.58 (0.02)	1.58 (0.05)	1	5.201	0.042	1	0.492	0.496	1	1.452	0.251
	D: 1.51 (0.04)	1.37 (0.04)									
%N senescent	F: 0.76 (0.03)	0.71 (0.02)	1	3.639	0.081	1	3.47	0.087	1	0.051	0.825
	D: 0.74 (0.06)	0.65 (0.01)									
%P green	F: 0.12 (0.006)	0.13 (0.004)	1	4.78	0.049	1	0.444	0.518	1	1.59	0.231
	D: 0.11 (0.01)	0.10 (0.002)									
%P senescent	F: 0.04 (0.010)	0.05 (0.004)	1	2.520	0.138	1	6.943	0.022	1	0.119	0.736
	D: 0.03 (0.006)	0.04 (0.002)									
N resorption (%)	F: 53.18 (1.87)	54.00 (1.17)	1	0.008	0.932	1	1.67	0.220	1	0.018	0.897
	D: 49.80 (2.34)	54.29 (0.72)									
P resorption (%)	F: 70.97 (4.22)	58.87 (2.03)	1	0.629	0.443	1	15.72	0.002	1	0.002	0.965
	D: 72.65 (1.85)	60.8 (4.68)									
C:N green (g g ⁻¹)	F: 29.30 (0.20)	28.85 (1.02)	1	6.700	0.024	1	0.067	0.801	1	1.420	0.256
	D: 30.89 (0.70)	33.25 (1.39)									
C:N senescent (g g ⁻¹)	F: 62.31 (2.61)	63.31 (2.20)	1	1.141	0.306	1	0.349	0.566	1	0.201	0.662
	D: 62.04 (6.60)	65.89 (3.32)									
N:P green (g g ⁻¹)	F: 13.54 (0.79)	12.36 (0.44)	1	0.471	0.505	1	1.516	0.242	1	0.073	0.792
	D: 13.85 (2.49)	13.19 (0.65)									
N:P senescent (g g ⁻¹)	F: 23.09 (2.50)	14.57 (1.21)	1	3.331	0.093	1	9.889	0.008	1	2.568	0.135
	D: 30.22 (10.1)	14.79 (0.96)									
C:P green (g g ⁻¹)	F: 395 (22.88)	351 (9.94)	1	3.675	0.079	1	1.359	0.266	1	0.763	0.399
	D: 421 (92.24)	430 (1.06)									
C:P senescent (g g ⁻¹)	F: 1441 (192)	926 (192)	1	1.726	0.214	1	7.750	0.017	1	0.814	0.385
	D: 1557 (441)	980 (110)									
Leaf length (cm)	F: 15.0 (0.26)	12.6 (0.31)	1	1.850	0.199	1	81.8	<0.001	1	0.643	0.438
	D: 16.9 (0.29)	11.9 (1.99)									
# of leaves (per cm of stem)	F: 2.03 (0.09)	3.08 (0.22)	1	13.92	0.003	1	0.376	0.551	1	0.057	0.816
	D: 3.04 (0.06)	2.19 (0.02)									
# of flowers (per cm of stem)	F: 0.047(0.017)	0.062(0.013)	1	5.856	0.032	1	0.911	0.359	1	0.015	0.905
	D: 0 (0)	0.019(0.009)									
SSD (mg/mm ³)	F: 0.62 (0.079)	0.45 (0.02)	1	4.408	0.058	1	2.56	0.136	1	5.49	0.038
	D: 0.59 (0.002)	0.72 (0.02)									

Table 3. Biomass allocation ratios for *Pelliciera rhizophorae* from Pacific and Caribbean populations in Panama. F = fringe trees, D = dwarf trees. Standard errors are in parentheses next to trait means. LAR (leaf area ratio) = leaf area (cm²)/ leaf + stem (g); SLA (specific leaf area) = leaf area (cm²)/ leaf (g); LWR (leaf weight ratio) = leaf (g)/leaf + stem (g); SWR (shoot weight ratio) = stem (g)/leaf + stem (g); SL:SB (stem length to stem biomass) = stem length (cm)/stem (g); LA:SL (leaf area to stem length) = leaf area (cm²)/stem length (cm).

Ratio	Mean trait value		Type			Coast			Type x Coast		
	Caribbean	Pacific	df	F	p	df	F	p	df	F	p
SL:SB	F: 5.96 (0.51) D: 3.77 (0.58)	8.58 (0.71) 5.18 (0.01)	1	5.221	0.041	1	7.68	0.017	1	1.796	0.211
LWR	F: 0.53 (0.02) D: 0.24 (0.04)	0.57 (0.03) 0.32 (0.04)	1	6.304	0.027	1	1.098	0.315	1	1.887	0.195
SWR	F: 0.47 (0.02) D: 0.76 (0.04)	0.43 (0.03) 0.68 (0.04)	1	6.304	0.027	1	1.098	0.315	1	1.887	0.197
LA:SL	F: 17.1 (0.33) D: 7.78 (1.75)	15.1 (1.17) 7.62 (2.25)	1	3.671	0.079	1	0.551	0.472	1	1.185	0.298
LAR	F: 40.3 (2.58) D: 21.0 (6.09)	45.9 (3.37) 23.0 (3.42)	1	5.714	0.034	1	0.716	0.414	1	2.139	0.169
SLA	F: 78.6 (4.07) D: 83.6 (9.67)	81.1 (4.46) 71.7 (2.25)	1	0.139	0.715	1	0.167	0.690	1	0.893	0.363

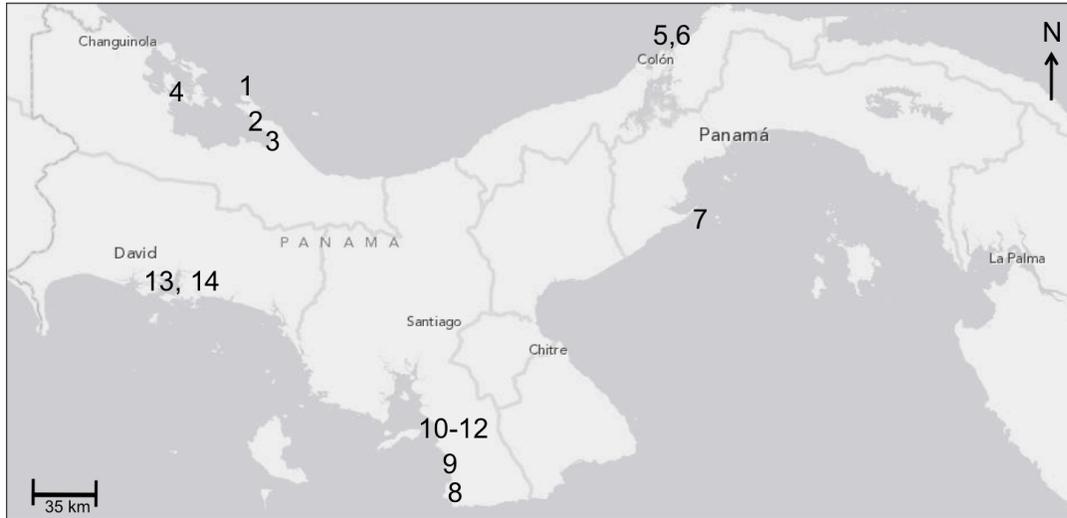


Figure 1. Locations of sampling sites in Panama. Bocas del Toro province: 1-Bahia Azul, 2-Patterson, 3-Souli Creek, 4-Cilico Creek. Colón province: 5-Bahia Las Minas, 6- Quebrada las Mercedes. Panamá province: 7-Punta Chame. Veraguas province: 8-Arenas, 9-Quebro, 10-Suay, 11-Tebario, 12-Toucan. Chiriquí province: 13-Pedregal, 14-Chorcha.

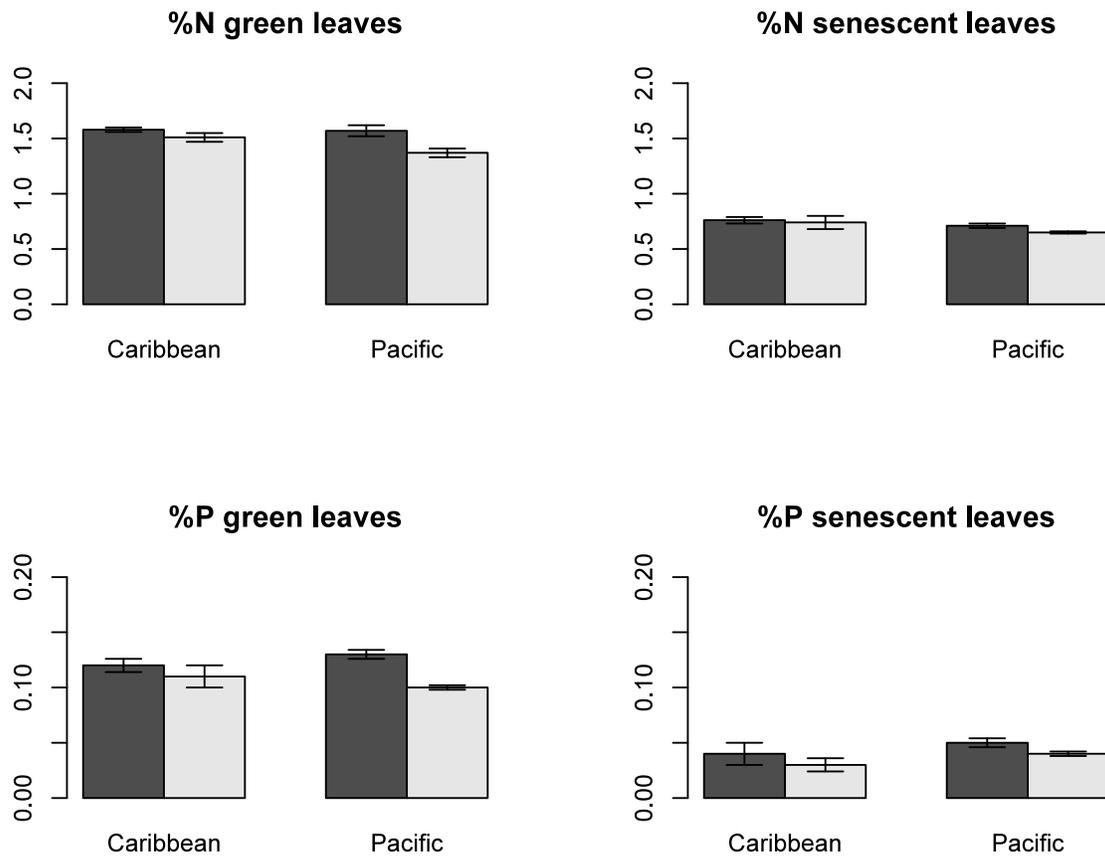


Figure 2. Nitrogen and phosphorus content in *Pelliciera rhizophorae* leaves from fringe and dwarf trees in Caribbean and Pacific populations in Panama. Dark bars are fringe trees, light bars are dwarf trees. Values are means (± 1 SE).

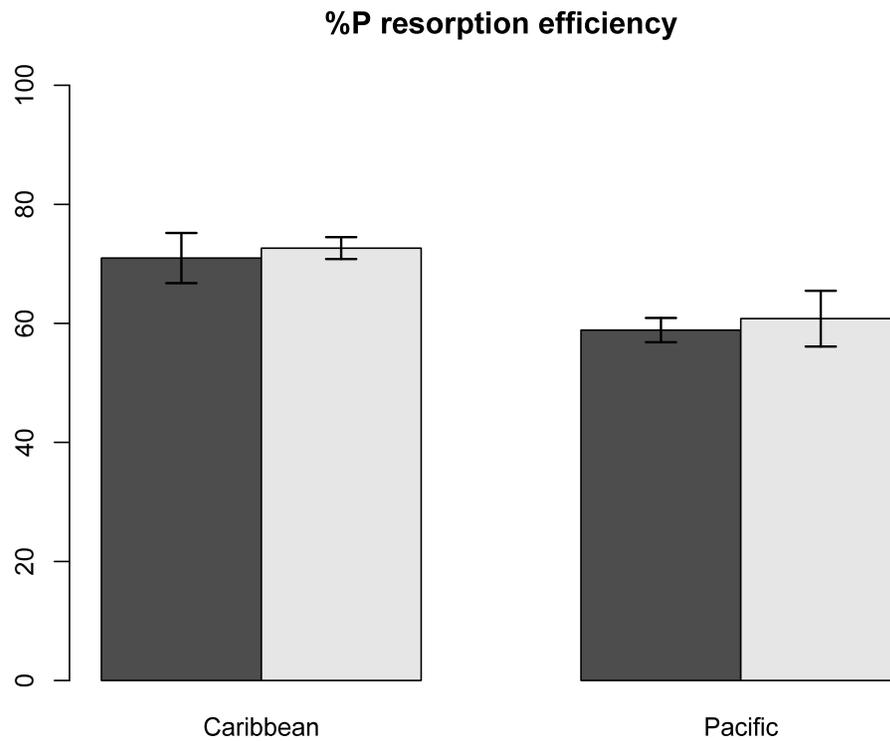
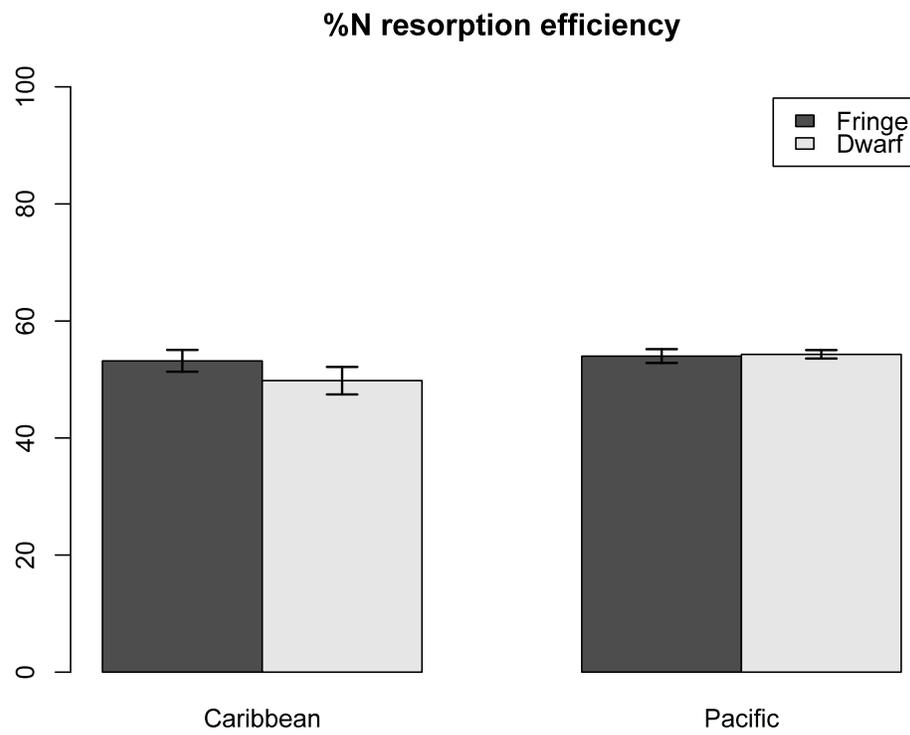


Figure 3. Nitrogen and phosphorus resorption efficiencies for fringe and dwarf *Pelliciera rhizophorae* trees from Caribbean and Pacific populations in Panama. Values are means (± 1 SE).

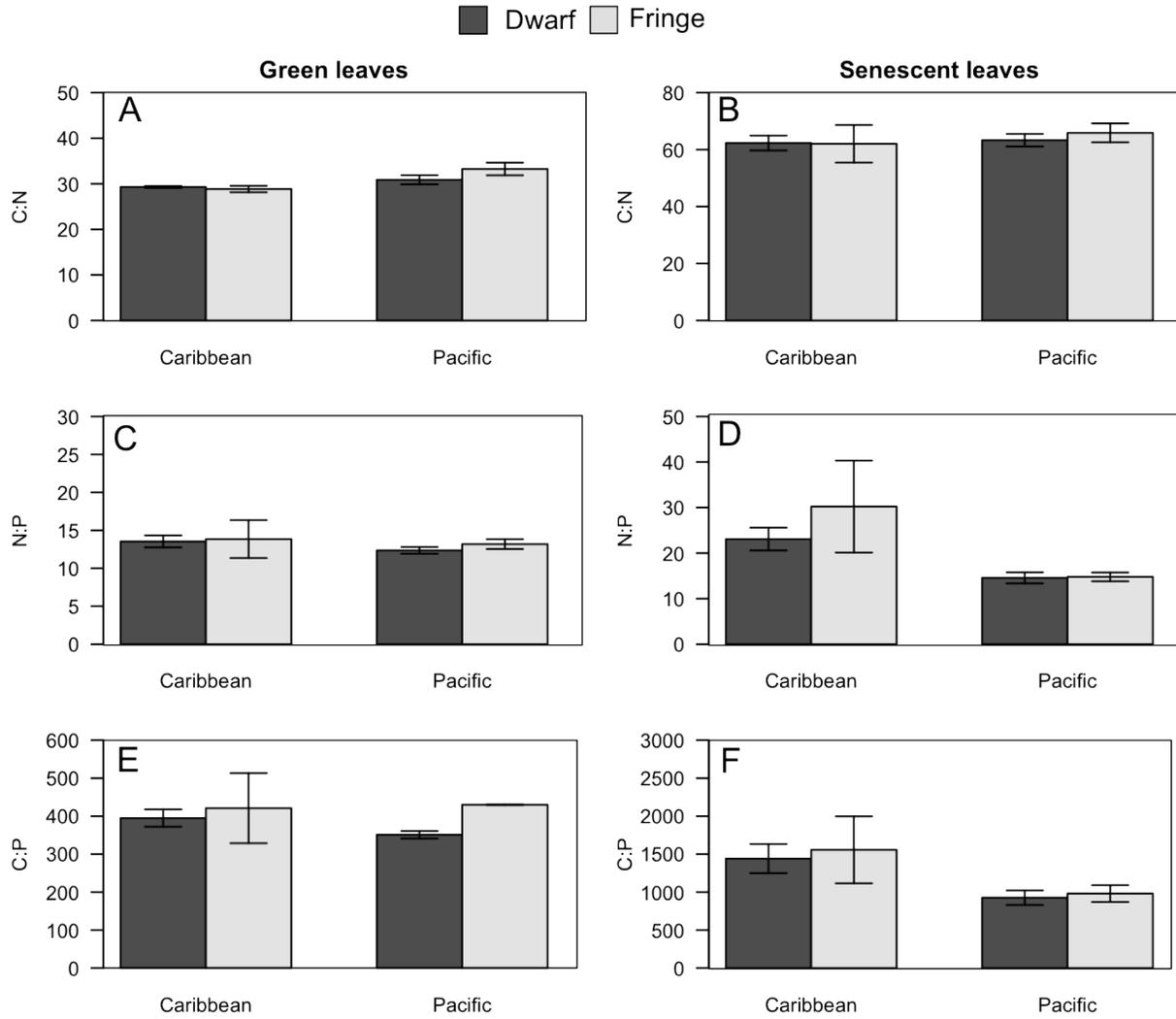


Figure 4. Leaf nutrient ratios from *Pelliciera rhizophorae* in Panama. Values are means (± 1 SE).

Stem specific density

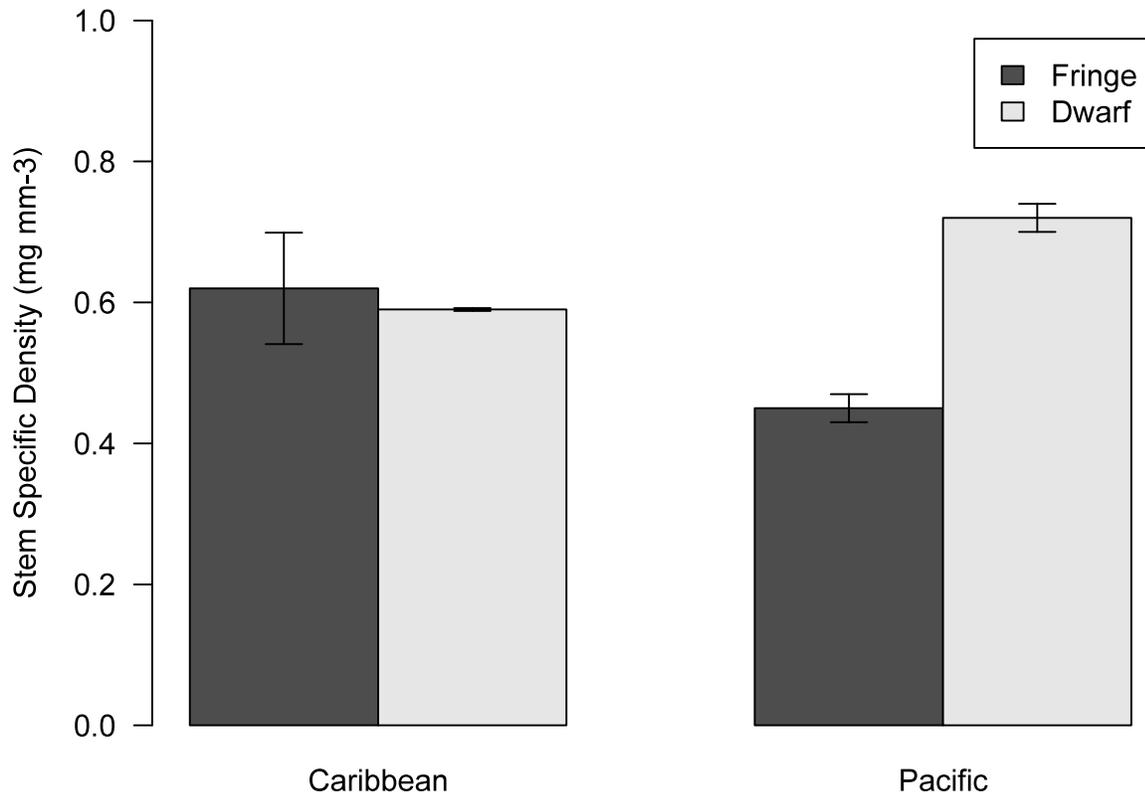


Figure 5. Stem specific density, expressed as mg/mm³. Values are means (\pm 1 SE).

Herbivory

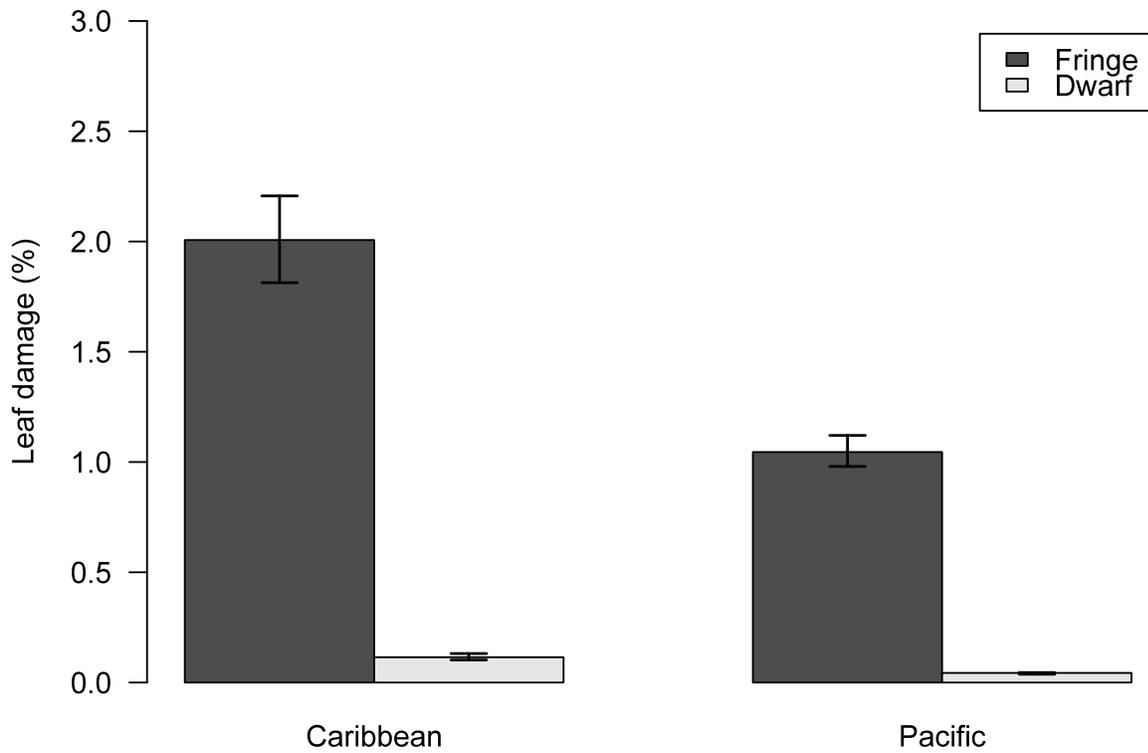


Figure 6. Standing herbivory on *Pelliciera rhizophorae* trees from populations on both coasts of Panama, calculated as cm^2 per leaf. Dark bars are fringe trees, light bars are dwarf trees. Values are means (± 1 SE).