The effects of salinity on the dynamics of a *Pterocarpus officinalis* forest stand in Puerto Rico

Elsie Rivera-Ocasio[1], T. Mitchell Aide and Neftalí Rios-López

University of Puerto Rico, Río Piedras Campus, San Juan, Puerto Rico 00931-3360
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Abstract: Coastal wetland plant communities are strongly structured by water depth and salinity. Rising sea level will cause changes in the hydro-period, surface water salinity and salt-water intrusion in coastal areas, which will reduce the distribution of forests in these areas. We studied the dynamics of a *Pterocarpus officinalis* stand in Puerto Rico over a 9-y period. We observed differences in plant growth, recruitment and mortality across a salinity gradient within a 1-ha plot. In areas of high salinity, recruitment, juvenile density and growth rates of juveniles and adults were lower. The detrimental effect of salinity was also observed in a growth experiment; seedlings in 5‰ and 10‰ salinity treatments had higher mortality, slower growth and less above- and below-ground biomass than control seedlings (0‰). In addition, an increase from 0 to 1‰ in salinity resulted in approximately 50% less nodulation in seedlings. Low recruitment in high salinity areas and lack of recruitment in adjacent grasslands will further reduce the distribution of this forest type. Although some ecosystems can respond to changing conditions by migration to more favourable areas, this is not the case with *P. officinalis*, and thus, restoration efforts are needed to re-establish this species where it occurred historically.

Key Words: climate change, coastal tropical wetlands, growth, mortality, nodulation, recruitment, salinity experiments, salinity gradient, sea-level rise, seedling response

INTRODUCTION

Coastal wetland plant communities are strongly structured by environmental gradients, particularly water depth and salinity (Allen *et al.* 1996, Conner *et al.* 1997, Gough & Grace 1998, Martin & Shaffer 2005). Global climate change will shift these gradients and this will change the distributions and dynamics of wetland plant species (Allen *et al.* 1996, Conner *et al.* 1997, Gough & Grace 1998). During the last 100 y the 1 °C increase in mean global temperature has increased mean sea level by 7 cm (Cabanes *et al.* 2001) resulting in an increase in wave energy, changes in the hydro-period and surface water salinity, and salt-water intrusion in the ground water. These factors have been associated with mortality and species shifts in coastal wetland plants (Allen *et al.* 1996, Gough & Grace 1998). For example, increased salinity associated with sea-level rise has caused extensive mortality in North American bald cypress (*Taxodium*

distichum) forests (Allen *et al.* 1996), and could result in the loss of millions of hectares of wetlands throughout the world (Howard & Mendelssohn 1999, Nicholls 2004, Williams *et al.* 1999). Although coastal plant species could theoretically migrate inland to areas where the effect of salt-water intrusion is reduced, agricultural and urban land-use often dominate these inland areas (López *et al.* 2000, Mitsch & Gosselink 2000, Moorhead & Brinson 1995, Nicholls 2004).

In the Caribbean Basin, forested wetlands dominated by *Pterocarpus officinalis* Jacq. (Fabaceae) are experiencing a similar scenario. Agricultural and urban expansion has reduced the distribution of *P. officinalis* to isolated patches, which often occur near the extreme of their salt tolerance (Eusse & Aide 1999). The goal of this study is to better understand the biology of *P. officinalis* and evaluate the effect of salinity on the performance of adult plants and seedlings. The major hypothesis is that *Pterocarpus officinalis* will show lower growth rates, higher mortality, and less recruitment in areas exposed to higher salinity levels. We tested this hypothesis by combining field and laboratory studies to address the following questions:

(1) What is the distribution of *P. officinalis* along a salinity gradient? (2) How does soil salinity influence the distribution, recruitment, growth and survivorship of *P. officinalis*? (3) What is the effect of salinity on the growth and survival of seedlings? Specifically, we determined the spatial distribution of *P. officinalis* along a soil salinity gradient in a 1-ha plot and we measured the growth, survivorship and recruitment over a 9-y period. We also performed two salinity experiments to determine the effect of different levels of salinity on growth and survivorship of seedlings.

METHODS

Study species

Pterocarpus officinalis is a wetland tree species that occurs along the Atlantic coast from Mexico to Brazil, the Pacific coast from Costa Rica to Ecuador, and in the Caribbean islands (Cintrón 1983, Janzen 1978). In Puerto Rico, *P. officinalis* occurs in at least 15 isolated forest stands (Alvarez-López 1990, Cintrón 1983). Although most of these sites occur along the coast, a few populations occur along streams in the Luquillo Mountains, north-eastern Puerto Rico (Alvarez-López 1990, Rivera-Ocasio *et al.* 2006) and isolated individuals have been observed along other montane streams (T. M. Aide, pers. obs.). The fruit is indehiscent with a single seed (occasionally two) and an asymmetrical wing that allows it to float. In Puerto Rico, the composition of *P. officinalis* stands vary from monospecific to mixed forest depending on the levels of salinity and duration of flooding (Alvarez-López 1990, Cintrón 1983).

Study area

The study area is located in Sabana Seca, Toa Baja (18°27′N, 66°12′W), on the northern coast of Puerto Rico (Figure 1). Aerial photographs from 1937 showed that much of the area had been converted to sugar cane plantations, but by 1951 most of the sugar cane plantations were abandoned and had been converted to cattle pastures or were dominated by herbaceous wetland species. Between 1937 and 1991, the size of the remnant patch of *P. officinalis* did not change appreciably, and in 1991, the forest covered approximately 11.9 ha, making it the third largest *Pterocarpus* forest stand in Puerto Rico (Alvarez-López 1990, Cintrón 1983).

The *Pterocarpus* forest in Sabana Seca is a coastal basin wetland, located in the Subtropical Moist Forest life zone (Ewel & Whitmore 1973), and occurs in the Martin Peña-Saladar-hydraquentes soil association (Boccheciamp 1978). In this area, the average annual
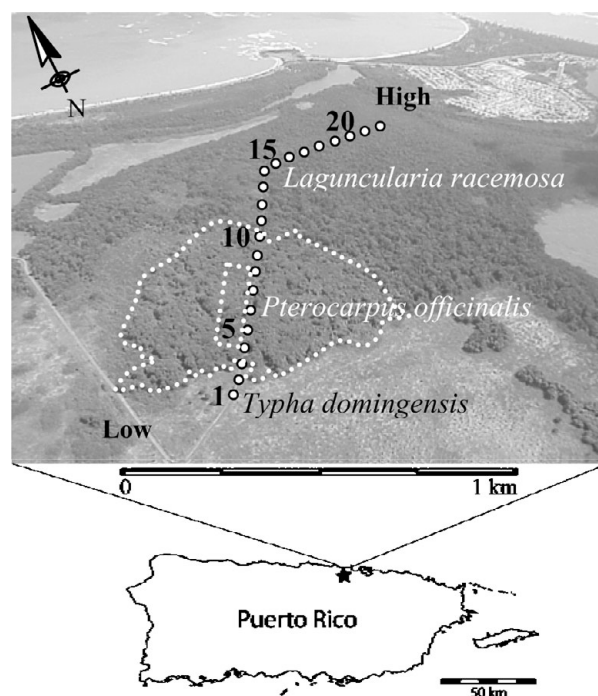

Figure 1. Aerial photograph of *Pterocarpus* study site and surrounding areas. The rectangle represents the location of the 1-ha plot in the *Pterocarpus officinalis* forest, and the 22 dots represent the approximate location of the surface water salinity measurements.

rainfall and temperature is 1693 mm y^{-1} and 27 °C, respectively (Eusse & Aide 1999). Both rainfall and temperature are mildly seasonal with most of the rain occurring from May to November, which are also the warmer months. The soils in the forested areas are characterized by having poor drainage and brackish waters, and are covered by a thick layer of peat. The *Pterocarpus* forest is surrounded by mangrove (*Laguncularia racemosa* L.) to the north-east and pastures dominated by *Typha domingensis* Pers. and patches of *Acrostichum aureum* L. to the south and west (Figure 1).

Field study: forest dynamic plot

In July 1994, a 1-ha plot (50 × 200-m) was established within the 11.9-ha *P. officinalis* stand. This plot was divided into one hundred 10 × 10-m subplots and it extended from near the pasture-forest border toward the *Pterocarpus*-mangrove ecotone (Figure 1). Between 12 July 1994 and 24 October 1994, all individuals with a diameter ≥ 1 cm dbh were identified, tagged, and the diameter was measured at 1.3 m or above buttresses. The spot where the diameter was measured was painted and the distance to the nail holding the tag was measured. The plot was re-censused between August and October in 1996, 1998, 2001 and 2003. The X and Y coordinates

of each plant in the plot were estimated by measuring the distance from two of the permanently marked 10 × 10-m corners. The distribution of hummocks and flooded areas was mapped to the nearest 50 cm between October and December 1995, a period during which the water table was high and constant. The section of the plot between the 70 and 110 m has an open canopy and a mix of *P. officinalis* and the grass *Panicum maximum* Jacq. This area was disturbed approximately 50 y ago during the construction of a power line.

Salinity and water depth measurement

Soil salinity and water level were measured at both ends of the plot (0–10 and 190–200 m) between August 1994 and January 1999. Specifically, 24 PVC tubes (1.4 m in length) were inserted in hummocks and pools to a depth of 60 cm within the 0–10 m (N = 12) and 190–200 m (N = 12) sections of the plot. Thin lines were cut along the tubes to allow water to enter for water depth and salinity measurements. Salinity at 60 cm below the soil surface was measured with a combined dissolved oxygen, salinity, conductivity and temperature meter (YSI-85 Yellow Spring Instrument Corporation, OH, USA). When the water table was above the soil surface, the depth was measured directly. When the water table was below the soil surface, a calibrated wooden dowel was inserted into the PVC tube to record the water level. We report the mean value of salinity and water level for each census in the two areas. In addition, surface water salinity was measured eight times during June–July 2003, August–December 2005 and in March 2006 to characterize the salinity gradient. These salinity measurements were done every 50 m along a 1.1-km transect from the pasture border to the mangrove forest. Five of the measurements were within the 1-ha plot (0, 50, 100, 150, 200 m) (Figures 1 and 2).

Salinity experiments

To determine the effect of increased salinity on growth and survival of *P. officinalis* seedlings, seeds and seedlings (seedling ages varied from newly germinants to 2 wk old) were collected in September 2002 from five forest stands near Luquillo, Puerto Rico. The forest stands included coastal and montane populations from the Río Espíritu Santo and Río Mameyes watersheds, and a montane population from the Río Sabana watershed. All seeds and seedlings were transported to a shade house and were planted in trays filled with unsterilized commercial peat. Seedling trays were immersed in containers filled with tap water. Most seeds germinated rapidly and the seedlings were grown in these conditions for 5 wk. The experiment was initiated by selecting three groups of
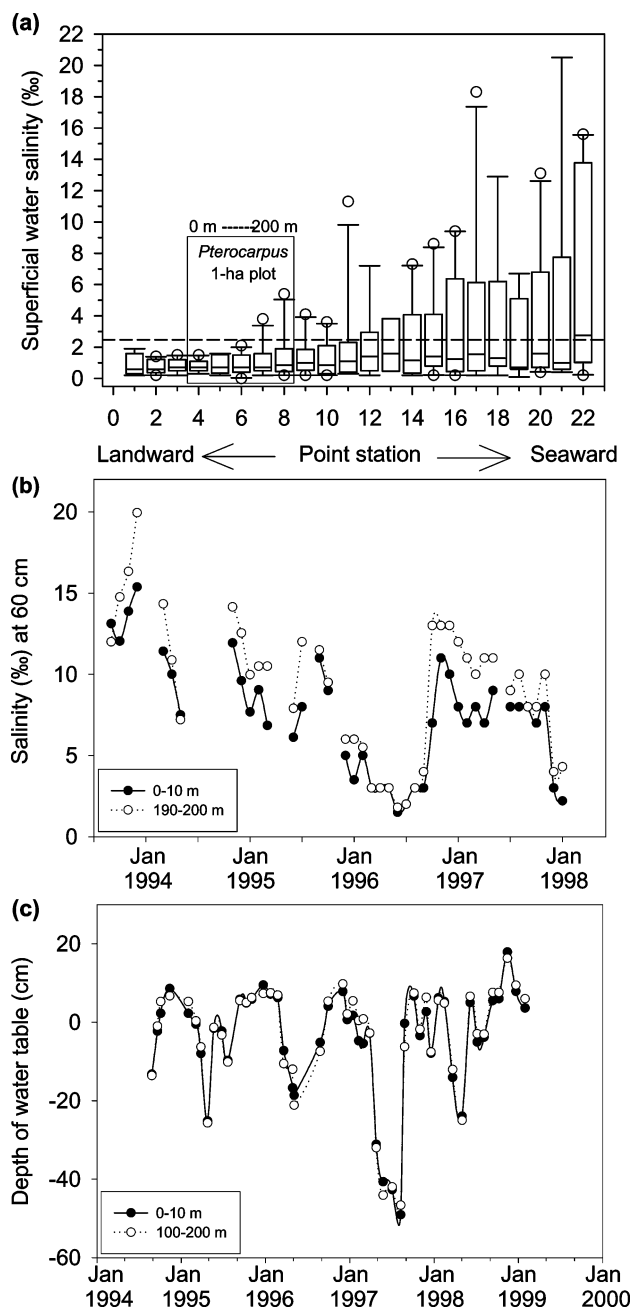

Figure 2. Salinity and water depth measurements for the study area. Variation in surface water salinity from 22 point measurements along a 1.1-km transect that crosses the 1-ha plot (a). Variation in soil salinity (b) and water table depth (c) in the 0–10-m (N = 12) and 190–200-m (N = 12) sections of the plot.

20 seedlings of similar height from each of the five populations. These seedlings were placed in trays that were randomly assigned to a salinity treatment: control (0‰), 5‰ and 10‰. Therefore, each salinity treatment (N = 3) included one tray (20 seedlings per tray) from each of the five populations. Each tray was placed into a separate plastic container filled with tap water or fresh

seawater diluted with tap water to the required salinity concentration. The initial water level in each container was marked and tap water was added to each container as needed to maintain the salinity level and to maintain all trays with the same water level (2 cm below the soil surface). In addition, salinity was measured each week using a refractometer and we changed the water every 2 mo to prevent the accumulation of algae and to avoid spoilage of water. Trays were randomly distributed within the experimental area and were randomly rotated weekly. After 6 mo (October to April), plants were harvested, and the height and diameter at 10 cm above ground were measured for all plants. At the end of the experiment, we randomly selected 10 plants per tray, and all plant parts were washed and placed in paper bags, dried at 65 °C for 4 d, and weighed.

A second salinity experiment was initiated in September 2005 to explore the effects of small changes in salinity. In this experiment the salinity treatments were: 0‰, 1‰, 2‰, 3‰, 4‰ and 5‰. For this second experiment we used seedlings that ranged in age from 1 to 2 wk and they were collected from the study site. Seedlings were grown in freshwater for 1 mo. The experiment was initiated by removing the seed if it was still attached to the seedling, counting the number of root nodules, and measuring the seedling shoot height and root length using the seed scar as the separation point between roots and shoots. The seedlings were planted in trays filled with unsterilized peat. Each tray, with three seedlings, was placed into a 3.8-litre container filled with water at the different salinity treatments. The control (0‰) and each salinity treatment had ten replicates, for a total of 60 containers and 180 seedlings. Each salinity treatment was prepared using a commercial sea salt (Instant Ocean 7, Synthetic sea salt, Aquarium Systems Inc., OH, USA), and all containers were filled with fresh water up to the same level (1 cm below the soil surface) to control for water level. Containers were randomly distributed in a 10×6 design on a table in an open-air shadehouse, which was covered with clear plastic to prevent changes in salinity due to rain. Salinity was measured weekly and water was changed once a month to prevent algal accumulation. After 5 mo, plants were harvested and shoot height, root length and number of root nodules of each seedling were recorded. All plant parts were washed and placed in paper bags, dried at 65 °C for 4 d, and weighed.

Analyses

For the analysis of the forest dynamic plot, plants were separated into juveniles ($\leq$10 cm dbh) and adults ($>$10 cm dbh). The growth analysis included all individuals except those that died during the study period or resprouts from damaged stems. In addition to *P. officinalis*, three other tree species (*Annona glabra* L., *Coccoloba venosa* L. and *Ficus citrifolia* Mill.) occurred in the plot. These species represented less than 3% of the total number of individuals, and they have been excluded from the analyses. The plot was divided into four (50 × 50 m) sections to examine the relationship between the size class distribution and position along the plot. A G-test of independence (Sokal & Rohlf 1995) was used to compare the proportion of individuals in each dbh class among the four 50-m subplots during the 1994 census. This analysis was repeated using data from the 2003 census. A nearest-neighbour analysis (Krebs 1989) was used to determine the spatial distribution of individuals in the different size classes.

To compare the number of dead individuals and recruits among the four areas of the plot we used a chi-square test for heterogeneity. Per cent annual mortality for each category (juveniles and adults) was calculated dividing the total number of dead individuals by the number of days between each census and this value was multiplied by 365.25. To determine the relationship between adult annual growth rate and the position along the salinity gradient in the plot we used a Spearman rank correlation. Annual growth rate was calculated using the difference in dbh between the first (1994) and last (2003) censuses divided by the number of years between censuses (9 y).

In the first salinity experiment using treatments of 0‰, 5‰, 10‰ the analyses were based on the mean value of the 20 seedlings within each tray, thus there were five replicates per salinity treatment. Data were not normally distributed and a non-parametric ANOVA (Kruskal–Wallis) was used to assess the difference in growth and biomass among treatments. In the second salinity experiment using treatments of 0‰, 1‰, 2‰, 3‰, 4‰ and 5‰ the analyses of growth, root to shoot ratio, and the number of nodules were based on the mean value of seedlings in each salinity treatment. Growth was calculated using the mean height for all plants in each treatment at the beginning and end of the experiment. Relative nodulation was calculated using the mean number of nodules in each treatment divided by the mean number of nodules in the control and the resulting values were then multiplied by 100. A sigmoid model was fit to these data (Figure 6). The program SigmaPlot 8 © was used to fit the model and generate the salinity response curve that best explained the data.

RESULTS

Forest plot study

Salinity condition. The forest plot occurs along a salinity gradient between freshwater wetlands and mangroves (Figure 2a). This gradient varies seasonally with rainfall and freshwater inputs from inland areas. Despite the
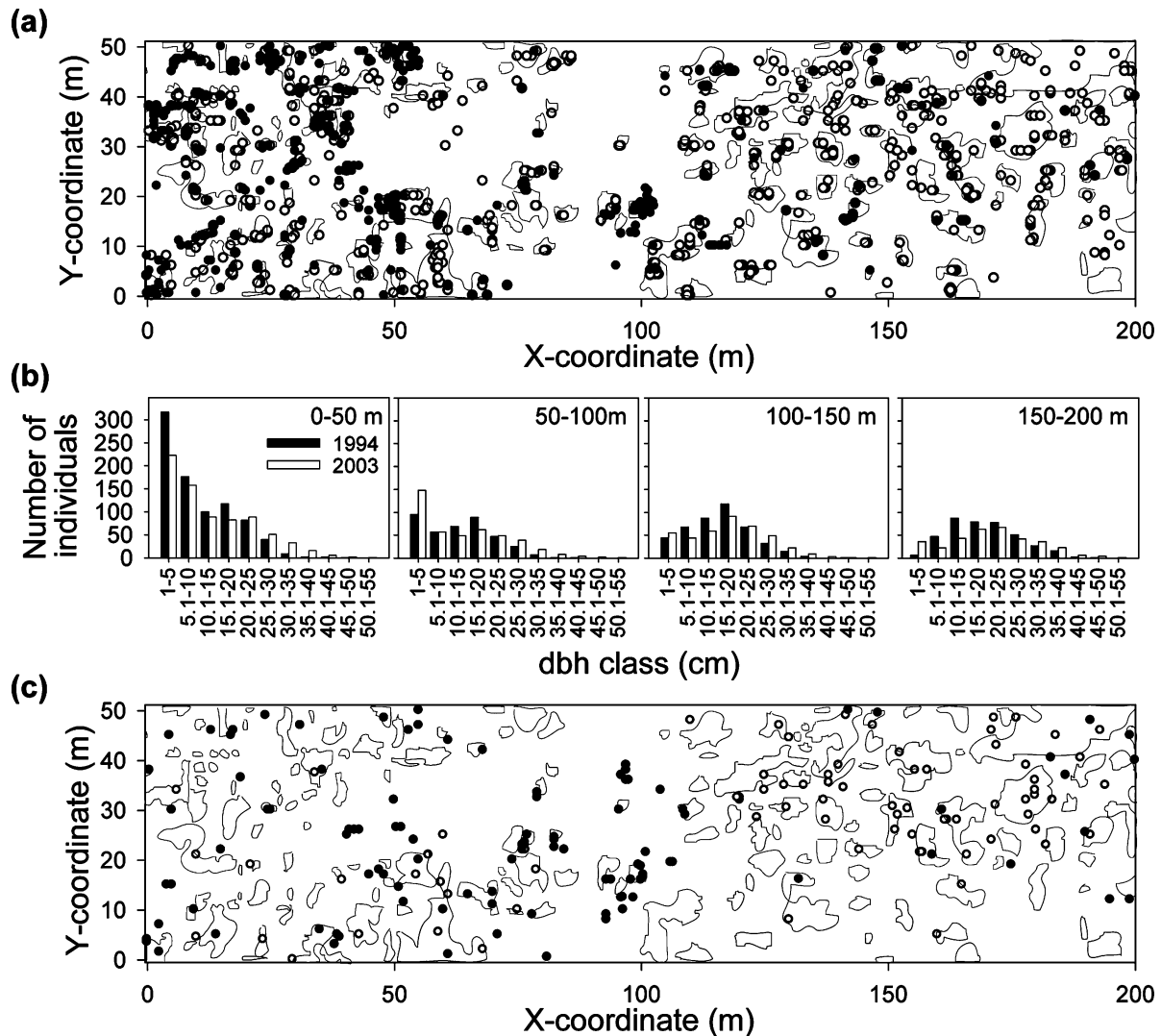
Figure 3. Size class and spatial distributions of *Pterocarpus officinalis* individuals within the 1-ha plot. Distribution of adults >10 cm dbh (open circles) and juveniles ≤10 cm dbh (closed circles) in the 1-ha *Pterocarpus* plot at the beginning of the study (a). Areas above the water level (i.e. hummocks) between October and December 1995 are represented by polygons. Size class distribution of *P. officinalis* individuals in the four 50-m sections along the plot (b). Distribution of dead adults (open circles) and recruits (closed circles) during the 9-y study period (c).

proximity with the sea (*c.* 1 km) and the low elevation of the area (1 m asl) the gradient is not affected by storm surges. Within the plot, surface water salinity averaged 1.6‰, and there was a slight, although not significant, increase in salinity near the mangrove end of the plot (Figure 2a). Between August 1994 and January 1999, water salinity at 60 cm fluctuated from 1.5 to 20‰ (Figure 2b). The 0–10-m section (forest–pasture border) consistently had lower salinity than the 190–200-m section (Pterocarpus-mangrove border), with a mean difference of 1.7‰ between sites (paired t-test, t = −8.02, df = 47, P < 0.0001, Figure 2b). The water table fluctuated approximately 70 cm between August 1994 and January 1999, and in general, was low in April and May, and high from September to February (Figure 2c).

There was no significant difference in water depth between the 0–10 and 190–200-m sections of the plot (Figure 2c, paired t-test, t = −1.94, df = 47, P > 0.05).

Forest structure. In 1994, there were 2069 individuals with dbh ≥ 1 cm; 97% of the individuals (N = 2010) were *P. officinalis*. The remaining 3% of the individuals were *Annona glabra* (N = 44), *Coccoloba venosa* (N = 24) and *Ficus citrifolia* (N = 1). *Pterocarpus* individuals showed a highly clumped distribution ($\chi^2 > 300$, P < 0.001) mainly associated with microtopography (depressions and hummocks). Although hummocks covered only 24% of the area, 76% of the individuals occurred on hummocks (Figure 3a). The median canopy height in the 1-ha plot

was 10.3 m, but ranged from 4.4 m to 13.4 m. In general, areas with low canopy height were dominated by the fern *Acrostichum aureum* and the grass *Panicum maximum* or were permanently flooded.

The distributions of size classes among the four sections of the plot were significantly different in both the 1994 and 2003 censuses (G-test 1994 = 415, df = 30, P < 0.0001, G-test 2003 = 214, df = 30, P < 0.0001) (Figure 3b). In the 1994 census the number of individuals in the 1–5-cm size class decreased from 317 in the 0–50-m section to only 6 individuals in the 150–200-m section (Figure 3b). The same pattern occurred in the 5–10-cm size class, with the number of individuals decreasing from the pasture–forest edge (0–50-m section) toward the *Pterocarpus*-mangroves ecotone (150–200-m section). The intermediate size classes were more evenly distributed along the plot and individuals in the larger size classes were more common in the high-salinity end of the plot (Figure 3b). Similar differences among the sections were observed in the 2003 census (Figure 3b).

Adult individuals (dbh > 10 cm) occurred in all sections along the salinity gradient, but there were small differences in abundance among the four sections. For example, the 0–50-m section had the highest number of adults (352 individuals), and although the abundance of individuals decreased in the 50–100-m section (239 individuals), it increased in the 100–150-m (326 individuals) and 150–200-m sections (341 individuals). In contrast, the abundance of juveniles (dbh < 10 cm) varied considerably along the plot (Figure 3a). Sixty-one per cent of the juveniles (N = 493 individuals) were located in the low-salinity section (0–50 m), while only 6% of the juveniles (N = 53 individuals) occurred in the high-salinity section (150–200 m) (Figure 3a).

Forest dynamics. Recruitment of *Pterocarpus officinalis* (individuals ≥ 1cm dbh) during the 9-y period showed a non-random distribution along the plot ($\chi^2 = 62.4$, df = 3, P < 0.0001). Most recruitment (N =102) occurred in the 0–50 and 50–100-m sections, while only 16 individuals established in the 100–150 and 150–200-m sections of the plot (Figure 3c).

Similarly, the distribution of dead adults was not random ($\chi^2 = 22.3$, df = 3, P < 0.0001). During the 9-y study period, 267 individuals of *P. officinalis* (87 adults and 180 juveniles) died in the plot, the majority (72%) occurred in the 100–150 and 150–200-m sections of the plot (Figure 3c). Adult annual mortality increased from 0.41% in the 0–50-m section to 1.31% in the 150–200-m section of the plot. The majority of dead juveniles (76%) occurred in the 0–100-m section of the plot. Nevertheless, juvenile annual per cent mortality increased from 3% in the 0–50-m section to 5.3% in 150–200-m section.
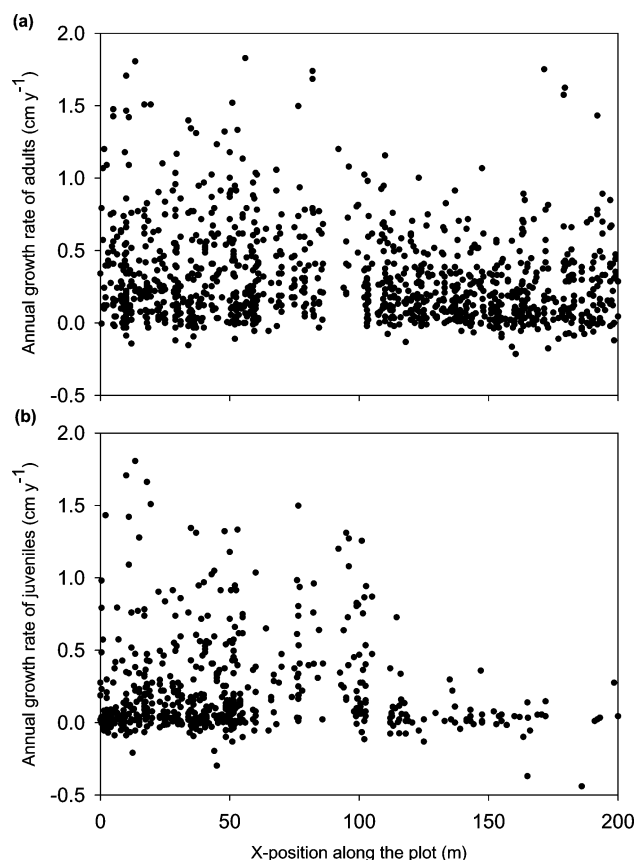

Figure 4. Annual diameter growth rate (cm y^{-1}) of adults >10 cm dbh (a) and juveniles ≤10 cm dbh (b) for the period between October 1994 to August 2003 in relation to salinity gradient.

The patterns of annual growth rate of adults and juveniles varied along the plot (Figure 4). Annual growth rate of adults decreased along the salinity gradient (Spearman $r_s = -0.163$, P < 0.0001, N =1129), but several adults had growth rates between 0.5 cm y^{-1} and 1.0 cm y^{-1} in the high-salinity section of the plot (Figure 4a). In contrast, there was not a significant correlation between juvenile growth and position along the salinity gradient (Spearman $r_s = 0.0511$, P = 0.214, N = 594). Despite the lack of significant correlation there were 81 juvenile individuals in the 0–50 and 50–100-m sections with growth rates > 0.5 cm y^{-1} in comparison with only 7 juveniles in the 100–150 and 150–200-m sections (Figure 4b).

During the 9-y study period, the overall density (1994: 2069 ha^{-1} to 2003: 1843 ha^{-1}) decreased by 10.9%. Density decreased in three of the four sections of the plot, but increased in the 50–100-m section, which initially had the lowest density and was dominated by grasses and ferns. The density of individuals in the low-salinity section (0–50 m) decreased from 845 to 744, a reduction of 11.9%. The high-salinity section (150–200 m) had the largest decrease in density (14.5%).

Basal area in the plot increased from 43.8 m² ha⁻¹ at the beginning of the study (1994) to 54.1 m² ha⁻¹ at the end of the study (2003), which represents a 25% increase. The low-salinity section of the plot (0–50 m) had the greatest increase in basal area (37%) and the high-salinity section (150–200 m) had the lowest increase (7.89%).

Salinity experiments

There was no site effect (i.e. similar response in seedlings collected from different sites), but there was a significant salinity effect on survivorship, growth and biomass of seedlings (Figure 5). Seedling mortality increased from 1% in the 0‰ treatment to 14% in the 10‰ treatment (Figure 5a). At the beginning of the study, there was no difference in plant height among treatments ($F_{12, 2} = 0.73$, $P = 0.50$), but by the end of the study, there were significant differences in plant height ($F_{12, 2} = 28.7$, $P < 0.0001$). Seedlings in the control (0‰) were taller (median plant height 56.7 cm) than seedlings in the 5‰ (median plant height 38.2 cm) and 10‰ (median plant height 35 cm) treatments (Figure 5b).

Plant biomass also differed among salinity treatments. Specifically, above-ground (shoot and leaves) and below-ground (root) biomass decreased with increased salinity ($F_{12, 2} = 28.7$, $P < 0.0001$ and $F_{12, 2} = 11.7$, $P = 0.001$, respectively) (Figure 5c, d). Seedlings in the control (0‰) had the highest above-ground biomass (median = 4.13 g) and below-ground biomass (median = 1.24 g) compared with seedlings in 5‰ and 10‰. The root:shoot ratio increased with an increase in salinity (Figure 5c, d). The decrease in root biomass with increased salinity was also accompanied by a large reduction in the number of root nodules (>25 in 0‰ to < 5 in 10‰).

In the second salinity experiment, there was no relationship between salinity treatment and mortality. In addition, there was no significant difference in growth ($F_{54, 5} = 2.34$, $P = 0.17$) or root:shoot biomass ratio ($F_{54, 5} = 2.42$, $P = 0.16$) among the salinity treatments. Nonetheless, we found a significant difference in the number of root nodules among the salinity treatments ($F_{54, 5} = 12.6$, $P < 0.0001$). The production of nodules on roots decreased with increasing salinity, from 12.6 ± 1.4 nodules per seedling (mean ± SE) in the control to 1.6 ± 0.5 nodules per seedling in the 5‰ salinity treatment. Dose-response analysis showed that a salinity level of 1.37‰ was sufficient to decrease mean nodulation by 50% of that in control plants (Figure 6).

Discussion

Increases in sea level have negatively affected many coastal wetland plant communities due to increasing soil
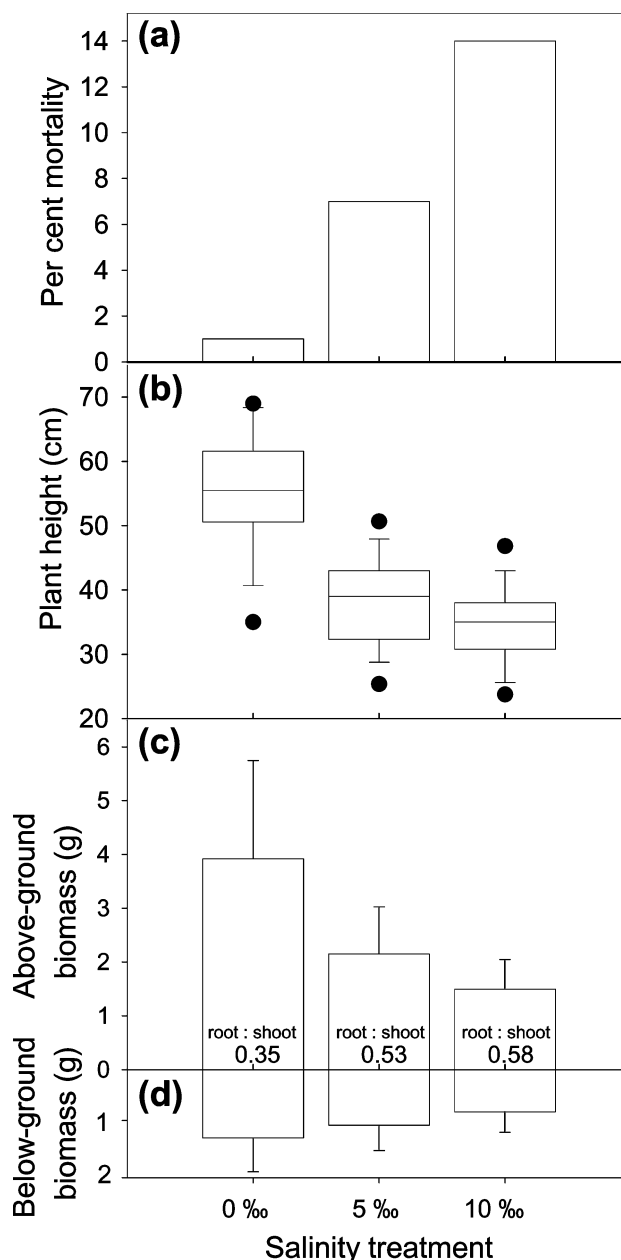

Figure 5. Response of *Pterocarpus officinalis* seedlings to salinity treatments (0, 5, 10‰) after a 6 mo period. Per cent mortality (a), plant height (b), above-ground and below-ground biomass of *P. officinalis* (c). The values inside the above-ground biomass bars represent the median root:shoot ratio for each treatment.

salinity and flooding (Allen *et al.* 1996, Conner *et al.* 1997, Gough & Grace 1998, Howard & Mendelssohn 1999). In most studies, there is a correlation between salinity and flooding, in which areas that experience greater flooding also have an increase in salinity. Although flooding can negatively affect growth in *P. officinalis* (T. M. Aide, unpubl. data), the increase in salinity in this study is independent of any flooding effect because the site is a
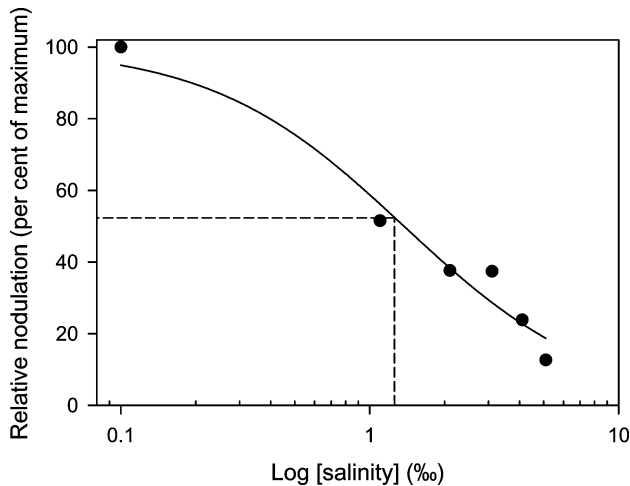
Figure 6. Salinity-nodulation response curve of *Pterocarpus officinalis* seedlings. The formula used for the model was: $y = \min + \frac{\max - \min}{1+10^{(\log EC50 - x)Hillslope}}$ where max = mean maximum response in control, min = mean minimum response among treatments, EC50 = the salinity level that produces a response halfway between minimum and maximum, and Hillslope = the steepness of the salinity-response curve. Each data point represents the mean nodulation for each salinity treatment. The solid line represents the sigmoid model and the dashed line represents the EC50 value. The values for the model are min = 2.21×10^{-8}, max = 100, EC50 = 1.37‰, and Hillslope = -1.12 ($R^2 = 0.965$, power of performed test with $\alpha = 0.05$: 0.984).

basin wetland, and there was no within-site variation in the water table level.

The dynamics of the *Pterocarpus officinalis* stand during the 9-y period suggest that small changes in salinity can have dramatic effects on this wetland species. Similar densities of adults along the salinity gradient in the plot, and the skewed distribution of juveniles towards the low-salinity areas suggest that the conditions in the high-salinity section have changed. The ages of adults in the high salinity section are 30–40 y (T. M. Aide unpubl. growth-ring data), suggesting that the conditions for juvenile recruitment have deteriorated since these adults established. High adult mortality in areas of high salinity also supports the hypothesis that salinity is a major factor affecting forest dynamics. Furthermore, although adult trees in the high-salinity section can reproduce, though at lower rates (Eusse & Aide 1999), they are unlikely to be replaced by their offspring. Along the west coast of Florida, the palm *Sabal palmetto* showed a similar pattern, with an absence of seedlings in areas where adults were abundant (Williams *et al.* 1999). The increase in groundwater salinity was believed to be the major factor limiting regeneration of the *Sabal* forests (Williams *et al.* 1999), and the authors argued that these adult palms are the final remnants of a functionally dead stand. In the present study, adult *Pterocarpus* trees in the areas of high salinity might also represent functionally dead individuals.

In the *Pterocarpus officinalis* stand, the highest annual growth rates of juveniles were in the low-salinity area (0–100 m), suggesting that these juveniles will eventually replace adults. In contrast, adult trees in areas of high salinity are unlikely to be replaced due to the low seedling establishment and low growth rates. The dramatic change in growth rates between juveniles and adults from the low- to high-salinity sections of the plot shows the sensitivity of *P. officinalis* to small changes in salinity, which was also demonstrated in the salinity experiments.

The negative effect of salinity is also supported by the low recruitment and high mortality in the high-salinity sections of the plot (100–200 m), but other factors can also influence changes in plant density. For example, the decrease in density in the 0–50-m section is probably due to self-thinning. In this area, the density of juveniles was high and basal area increased rapidly. These factors could result in density-dependent mortality and a reduction in plant density. The increase in density and basal area in the 50–100-m section could be explained by high light availability and low plant density. In this area, there is a small section that is dominated by grasses and ferns, which provided an area of high light that has favoured establishment and rapid growth, and outweighed any negative effect of salinity.

Although *P. officinalis* has the capacity to exclude sodium at the leaf level and occurs in brackish water wetlands, it is not a true halophyte (Medina *et al.* 2007). The species reduces its exposure to high-salinity conditions by extending its shallow root system laterally and by accumulating organic matter at the base of adult trees to elevate the root system. The specific mechanism by which *P. officinalis* is affected by high salinity is still unclear, but in general extended exposure to salinity reduces plant growth by creating water stress due to changes in the osmotic pressure in the root zone (Hogarth 1999). In order to survive in saline conditions plants have to retain water, which is achieved by reducing stomatal conductance, but at the cost of CO_2 acquisition and growth (Hogarth 1999). The higher rates of adult mortality and lower growth rates in the high-salinity section of the plot suggest that *P. officinalis* individuals are presently growing in conditions near the extreme of their physiological tolerance. This is further supported by the observation that individuals in this area also have lower flower, fruit and litter production in comparison to individuals in the low-salinity area (Eusse & Aide 1999).

Furthermore, changes in salinity can alter biomass allocation (Ball 1988, Munns & Termaat 1986) and symbiotic relationships (Rao *et al.* 2002, Zou *et al.* 1995). In general, plants in areas of high salinity allocate more biomass to roots than to shoots (Ball 1988, López-Hoffman *et al.* 2007). In our study, seedling root:shoot ratio increased with salinity in the first salinity experiment, and the effect was evident in the 5‰ and

10‰ salinity treatments. Similar results were observed in *Taxodium distichum* exposed to different salinity treatments (0, 2, 10‰), and the authors suggested that the increase in allocation to root biomass could be a response to maximize water extraction in the high-salinity condition (Conner *et al.* 1997). Another factor that has been associated with changes in carbon allocation to root or shoots is nitrogen availability (Agren & Franklin 2003). Most legume species can cope with nitrogen limitations due to their symbiotic relationship with nitrogen-fixing bacteria (Albrecht *et al.* 1999), but an increase in salinity can negatively affect the development of root nodules, which will reduce nitrogen fixation and plant growth (Rao *et al.* 2002, Zou *et al.* 1995).

In the second salinity experiment there was a strong negative relationship between salinity and root nodule development. The slight increase from 0 to 1‰ was sufficient to reduce nodule development by approximately 50% and when salinity was increased to 5‰ there was no formation of new nodules. Given that *P. officinalis* seedlings cannot root when water depth exceeds 3–4 cm (Alvarez-López 1990) slight changes in surface water salinity as those seen in the forest dynamics plot (Figure 2a) can affect their nodulation capacity and thus, their ability for nitrogen acquisition. Although difference in nodulation did not result in significant differences in seedling growth during the 5-mo experiment, there was a trend for higher growth in the low-salinity treatments and lower growth in the 5‰ treatment. We suggest that the slower growth rates, higher mortality and low sapling recruitment in the high-salinity section of the forest dynamics plot are related to the negative effect of salinity on nodule development. Previous studies have suggested that nodulation and symbiotic nitrogen fixation in wetland species, in particular *P. officinalis*, are adaptations to flooded conditions (Saur *et al.* 1998, 2000). These adaptations benefit plant growth because wetlands are often nitrogen depleted due to denitrification and leaching (Saur *et al.* 2000). Our results suggest that the positive effect of nodulation will be reduced by increasing salinity associated with sea-level rise. Furthermore, salinity negatively affects arbuscular mycorrhizal colonization in *P. officinalis* (Saint-Etienne *et al.* 2006), thus reducing phosphorus and micronutrient uptake (Bolan 1991, Smith *et al.* 2003). This scenario will threaten *P. officinalis* stands that are presently located near their salinity threshold, as well as other legume species that dominate tropical forested wetlands (Moreira *et al.* 1992, Saur *et al.* 2000).

This study indicates that small changes in salinity (< 2‰) can have dramatic effects on forest dynamics of *P. officinalis*. Most global climate models predict a continued increase in global temperature and sea-level rise (Nicholls 2004), which will further degrade *Pterocarpus* stands in similar conditions as well as other coastal wetland systems worldwide (Adam 2002, Allen *et al.* 1996). The fate of coastal wetlands will depend not only on the effects of climate change (i.e. increase salinity and flooding), but also on land-use practices. Some species could migrate and colonize adjacent areas with more benign conditions, however this may not be feasible if other land-use practices (e.g. urban and agriculture) occupy these areas (Alongi 2002). If wetland communities continue to degrade due to increase in salinity and flooding associated with sea-level rise, and if they cannot migrate inland, these communities will disappear unless active restoration efforts are initiated.

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