

## Patterns of litter production across a salinity gradient in a *Pterocarpus officinalis* tropical wetland

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### Abstract

Historically, *Pterocarpus officinalis* Jacq. (Leguminosae) dominated freshwater wetlands in the coastal plains of Puerto Rico, but deforestation has reduced its distribution to small patches adjacent to mangrove forests in areas of higher salinity. The objective of this study was to determine how a gradient in soil salinity affected litter, flower, and fruit production in a *Pterocarpus officinalis*. Three 100 m<sup>2</sup> plots were established in each of three sites along a salinity gradient: pasture/*Pterocarpus* edge (low salinity, mean salinity at 60 cm–9.7 g Kg<sup>-1</sup>), *Pterocarpus* forest (intermediate salinity, 11.5 g Kg<sup>-1</sup>) and a *Pterocarpus*/mangrove ecotone (high salinity, 15.0 g Kg<sup>-1</sup>). Across this gradient, *P. officinalis* accounted for 100% of the relative basal area in the low and intermediate sites and 43% in the high salinity site which was dominated by *Laguncularia racemosa*. The basal area of *P. officinalis* decreased along the gradient from 73.5 m<sup>2</sup> ha<sup>-1</sup> in the low salinity site to 42.0 m<sup>2</sup> ha<sup>-1</sup> in the high salinity site. Litterfall was sampled on average every 23 days in 45 0.25 m<sup>2</sup> traps (5 traps per plot) for two years. Annual litterfall for the forest was 11.9 Mg ha<sup>-1</sup> yr<sup>-1</sup>. Peaks in litterfall were associated with high precipitation in May 1995 and tropical storms in September 1995. Leaf fall of *P. officinalis* was significantly higher in the low salinity site (4.8 Mg ha<sup>-1</sup> yr<sup>-1</sup>) than the high salinity site (1.8 Mg ha<sup>-1</sup> yr<sup>-1</sup>), but total stand litterfall was greatest in the area of high salinity due to the greater contribution of *L. racemosa*. *Pterocarpus* flower and fruit production was approximately 10 times greater in low and intermediate salinity sites in comparison with the high salinity site. An increase in global temperature, will lead to higher sea level and higher soil salinity in coastal wetlands. To conserve this wetland forest type it is critical to expand the distribution into areas of lower salinity where this species occurred historically.

### Introduction

Productivity in freshwater and saltwater forested wetlands is generally higher under flowing conditions and decreases when stagnant conditions occur (Mitsch & Ewel 1979; Brown 1981; Brinson et al. 1981; Brown & Lugo 1982; Lugo et al. 1990). The interaction of hydrology and topography can affect salinity, nutrient availability, and soil anaerobiosis (Mitsch & Gosselink 1986). In particular, soil salinity can have a large effect on productivity. Saltwater wetlands with restricted tidal flow and low freshwater inputs have hypersaline soils and low productivity (Lugo & Snedaker 1974; Twilley et al. 1986). Coastal freshwater wetlands exposed to periodic saline intrusions have lower

productivity than forested wetlands that receive higher freshwater inputs as runoff, flowing water, and precipitation (Brinson et al. 1981; Brown & Lugo 1982; Alvarez-Lopez 1990).

Most studies of productivity in forested wetlands have been at the region, forest, or stand level (Pool et al. 1975; López-Portillo & Ezcurra 1985; Day et al. 1987; Alvarez-Lopez 1990; Duke 1990; Amarasinghe & Balasubramaniam 1992; Bunt 1995; Stocker et al. 1995) and have ignored variation within stands. In coastal forested wetlands, soil salinity can vary over short distances, and slight changes in microtopography, created by the accumulation of sediment and leaf litter among tree buttresses can affect hydrology (Lescuré 1980). Variation in salinity and hydrology

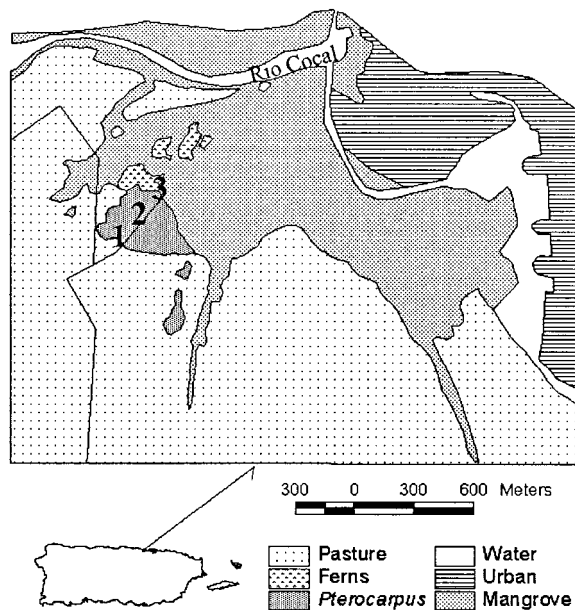


Figure 1. Location of the three study sites (1, 2, 3) on the north coast of Puerto Rico.

at small spatial scales can affect recruitment, growth, phenology, forest structure, and productivity. In particular, leaf, flower, and fruit production may respond to changes in hydrology and soil salinity at small spatial scales, but few studies have evaluated their effects within a forest stand (Twilley et al. 1986; Mackey & Smail 1995).

In the Caribbean, *Pterocarpus officinalis* Jacq. (Leguminosae) is the most important freshwater wetland tree species (Bacon 1990). Historically, the distribution of *P. officinalis* in Puerto Rico was more extensive than today (Gleason & Cooke 1926; Cintrón 1983). *Pterocarpus officinalis* covered large areas of the coastal floodplain and individual trees and small stands occurred along rivers and in the Luquillo Mountains (Cintrón 1983). During the last two centuries, the distribution of *P. officinalis* was greatly reduced when coastal plain forests were cut and drained for agriculture. Today, most of the populations of *P. officinalis* are restricted to the extreme of their physiological distribution in areas adjacent to mangroves where changes in hydrology could affect the survivorship of these stands. The goal of this study was to describe the patterns of litter production in three sites within a remnant coastal basin stand of *P. officinalis*. Specifically, we address the question: How does intrastand variation in salinity affect patterns of litter, flower, and fruit production?

## Methods

### Study site

The study was conducted on the Naval Security Group Activity Sabana Seca, Toa Baja, on the northern coastal plain of Puerto Rico ( $66^{\circ} 12' W$ ,  $18^{\circ} 27' N$ ) (Figure 1). The site is near the mouth of the Rio Cocal. Historically, the *Pterocarpus* forest extended from the mangroves inland approximately 5 km to a region of karst hills. During the last two centuries, most of this forest area was drained and converted to sugar cane plantation. Today, the forest covers 11.9 ha adjacent to mangroves (*Laguncularia racemosa* L.). Although the sugar cane plantations have been abandoned, these areas are used for cattle pastures and are dominated by *Typha domingensis* Pers. and *Cyperus* sp.. Within the *Pterocarpus* forest, the lianas, *Paullinia pinnata* L. (Sapindaceae), *Machaerium lunatum* (L. F.) Ducke (Leguminosae), *Dalbergia ecastaphylla* (L.) Taub. (Leguminosae), *Heteropteris laurifolia* (L.) A. Juss. (Malpighiaceae), and *Hippocratea volubilis* L. (Hippocrateaceae) are the other major woody species. The fern, *Acrostichum aureum* L., is common in the forest understory, and in areas of high light grows from 2 to 3 m in height.

Three sampling plots ( $10 \times 10$  m) were established in each of three sites along the salinity gradient. Three plots were located in the *Pterocarpus* forest 10 m from the pasture/*Pterocarpus* edge (Site 1: low salinity). Site 1 was dominated by *P. officinalis* (Table 1). Basal area was  $73.5 \text{ m}^2 \text{ ha}^{-1}$  and there were many *P. officinalis* saplings in the understory (Aide, unpublished data). Three plots were located 200 m to 220 m from the pasture toward the *Pterocarpus*/mangrove ecotone (Site 2: intermediate salinity). Site 2 was dominated by *P. officinalis* (Table 1). Basal area was  $68.9 \text{ m}^2 \text{ ha}^{-1}$  and there were few *P. officinalis* saplings in the understory (Aide, unpublished data). Three plots were located 410 m to 430 m from the pasture in a mixed *Pterocarpus* (43%) and *Laguncularia* (57%) forest patch (Site 3: high salinity) (Table 1). In this ecotone, the basal area of *P. officinalis* was lower ( $42.0 \text{ m}^2 \text{ ha}^{-1}$ ) in comparison with the other sites and there were few *P. officinalis* saplings in the understory (Aide, unpublished data). At each site the three  $10 \times 10$  m plots were separated by 10 m.

### Environmental factors

The mean annual rainfall for the years 1965–1973 and 1986–1993 was 1693 mm (NOAA) (Figure 2a). Rain-

Table 1. Annual litterfall (dry mass) and the description of forested wetland that included *Pterocarpus officinalis* in the Caribbean

Forest type	Country	Relative basal area (%)		Collection months	Salinity range (g kg <sup>-1</sup> )	Litterfall (Mg ha <sup>-1</sup> yr <sup>-1</sup> )	Reference
		<i>P. officinalis</i>	Other spp.				
Coastal riverine	Puerto Rico						
Mayaguez		99.6		Apr.–Aug.	1.0–9.0 <sup>a</sup>	14.1	Alvarez-Lopez 1982
Coastal basin	Puerto Rico						
Patillas		85.0	10.0 <i>L. racemosa</i>	Apr.–Sept.	0.5–2.5 <sup>a</sup>	11.9	Alvarez-Ruiz 1990
Dorado		47.6	43.0 <i>Bucida buceras</i> L.	Mar.–June	0.5–5.0 <sup>a</sup>	8.7	Alvarez-Ruiz 1990
	Guadalupe			June–June	1.5–.8 <sup>b</sup>	10.5–14.2	Febvay et al. 1981a Febvay et al. 1981b
Coastal basin	Puerto Rico						
Sabana Seca				Apr.–Apr.	7.0–24.0 <sup>c</sup>	11.9	This study
Site 1		100.0			7.0–15.0	12.0	This study
Site 2		100.0			7.0–20.0	9.8	This study
Site 3		43.0	57.0 <i>L. racemosa</i>		9.0–24.0	13.8	This study

<sup>a</sup>Salinity measured at 0.35–0.5 m.

<sup>b</sup>Salinity measured at 0.05 m.

<sup>c</sup>Salinity measured at 0.6 m.

fall is seasonal with the majority of rain occurring between April and December and a dry season between January to March. Rainfall in 1994 was 45% lower than the annual average due to a six-month drought from February to July (Figure 2a). In contrast, 1995 was 3% wetter than average. Although there was little rainfall during the first four months of 1995, the rest of the year was above average and July had the greatest rainfall (315 mm). Daily mean temperatures ranged from 23.8 °C in January to 29.4 °C in August (Parrota 1993). In September 1995, Hurricanes Luis and Marilyn passed to the northeast of Puerto Rico. These storms did not cause any tree mortality, but some branches were blown down.

Water level and salinity measurements were taken at 36 mound (i.e., hummock) and 36 depression sites (4 per plot) from August 1994 to April 1996. Water level measurements were also taken at a single mound from March to August 1994. During the rest of the study, water levels of this mound site were within the range of values for the other mound sites. PVC tubes (1.4 m in height; 6.0 cm in diameter) with thin line perforations to allow water to enter the tube were inserted to a depth of 60 cm. Monthly measurements of water level and salinity at water surface and 60 cm below soil surface were made with a YSI model 33 S-C-T meter. The study site occurs within the Martin Peña-Saladar-hydraquentes soil association (Boccheciamp 1978). The soils in the forested areas are characterized by having poor drainage, brackish waters, and are covered by a thick layer of peat.

#### Litterfall collection

Litterfall was sampled in five 0.25 m<sup>2</sup> traps in each of the nine 10 × 10 m plots for a total of 15 traps per site. The traps consisted of a metal frame with fiberglass screen bottom (mesh size 1 mm) that was held 50 cm above the ground with PVC tubes. Time intervals between litter collection varied from 14 to 76 days (median 23). The contents were oven dried at 65 °C and weighed. Litter was divided into five categories: flowers (including buds), fruits (mature and immature), leaves, wood (including stems of < 5 cm diameter, twigs, rachis, and bark), and miscellaneous. *Pterocarpus officinalis* flowers and fruits were weighed separately from the other species, but *P. officinalis* leaves were separated from other species only after April 1995. Wood and miscellaneous material were not classified by species.

#### Data analyses

Annual litter production was determined by summing the masses of each litter category for each trap during the period April 1995 to April 1996. To determine if there was an effect of salinity on *P. officinalis* leaf, flower, and fruit production it was necessary to account for among-site differences in tree densities. The basal area of all trees greater than 3 cm in diameter was determined within a radius of 5 m of each trap. There was a significant positive regression between basal area and *P. officinalis* leaf litter ( $r = 0.38$ ,  $P = 0.009$ ). The residuals of this regression were used

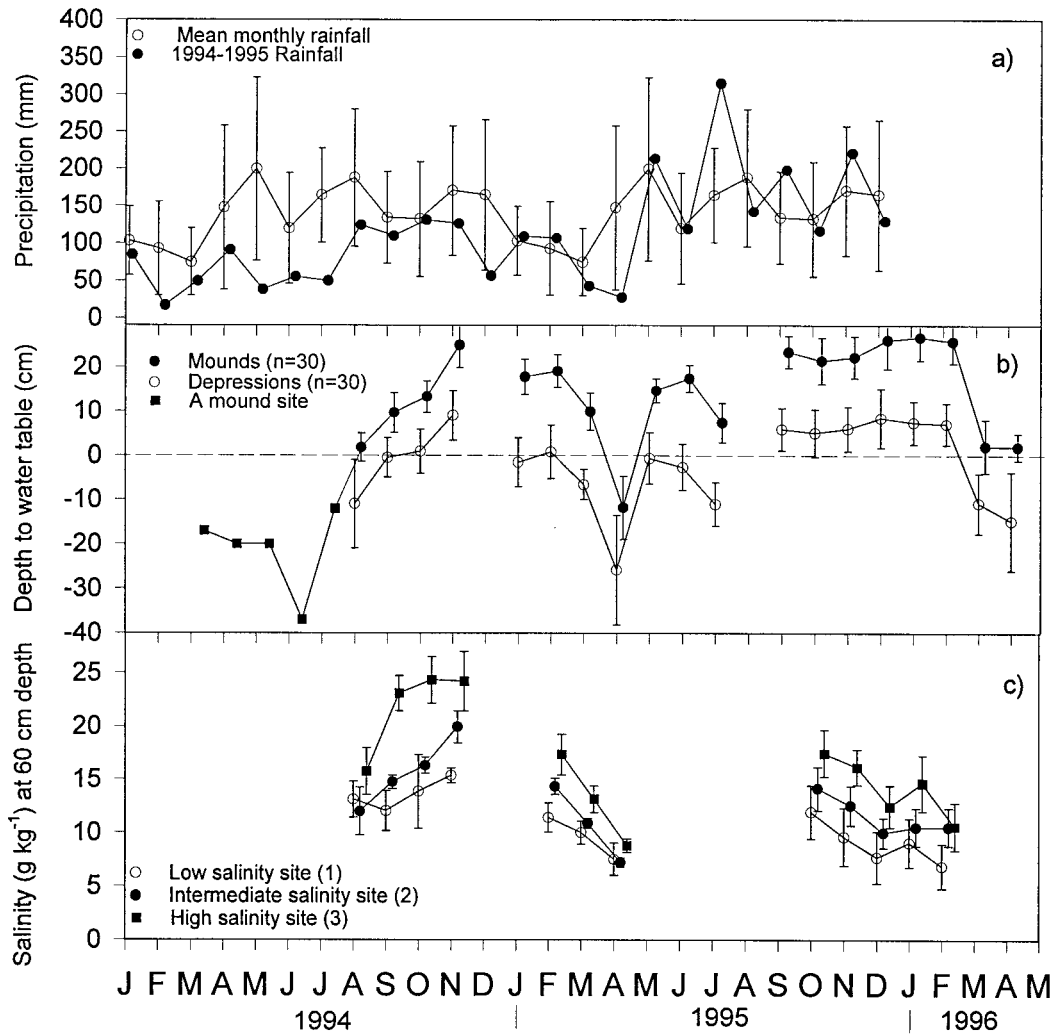


Figure 2. Precipitation, water level, and soil salinity in a *P. officinalis* forest at Sabana Seca, Puerto Rico. (a) Mean monthly rainfall (mm) for 1965–1973 and for 1986–1993 and monthly rainfall (mm) from 1994 to 1995 at three adjacent weather station. (b) Mean monthly variation in water level (cm) in mounds and depressions. For the first five water levels values (■)  $n = 1$ . (c) Mean monthly interstitial salinity at 60 cm below ground surface for the three sites. Error bars represent 1 sd. Precipitation data were obtained from NOAA for three stations (Candelaria, Dorado, and Toa Baja) in the vicinity of the study site.

in an ANOVA to determine if there was an effect of site on litter production that was independent of basal area. The regressions between basal area and *P. officinalis* flower or fruit production were not significant. An ANOVA of the ranks of each litter category was used to determine if there was significant variation among sites. If there was a significant effect, a Bonferroni Pairwise comparison was used to determine which sites were different.

**Results**

*Water level*

Between August 1994 and January 1996, water level fluctuated approximately 37 cm (Figure 2b). While there was a significant effect of time on water levels (Friedman Statistic = 62.1;  $p < 0.001$ ), there was no significant effect of site within the stand (Friedman Statistic = 3.3;  $p > 0.1$ ). Tubes in mounds registered water levels above the soil surface for 8 months, while depressions had water levels above the surface for 18 months. The water level dropped below the sur-

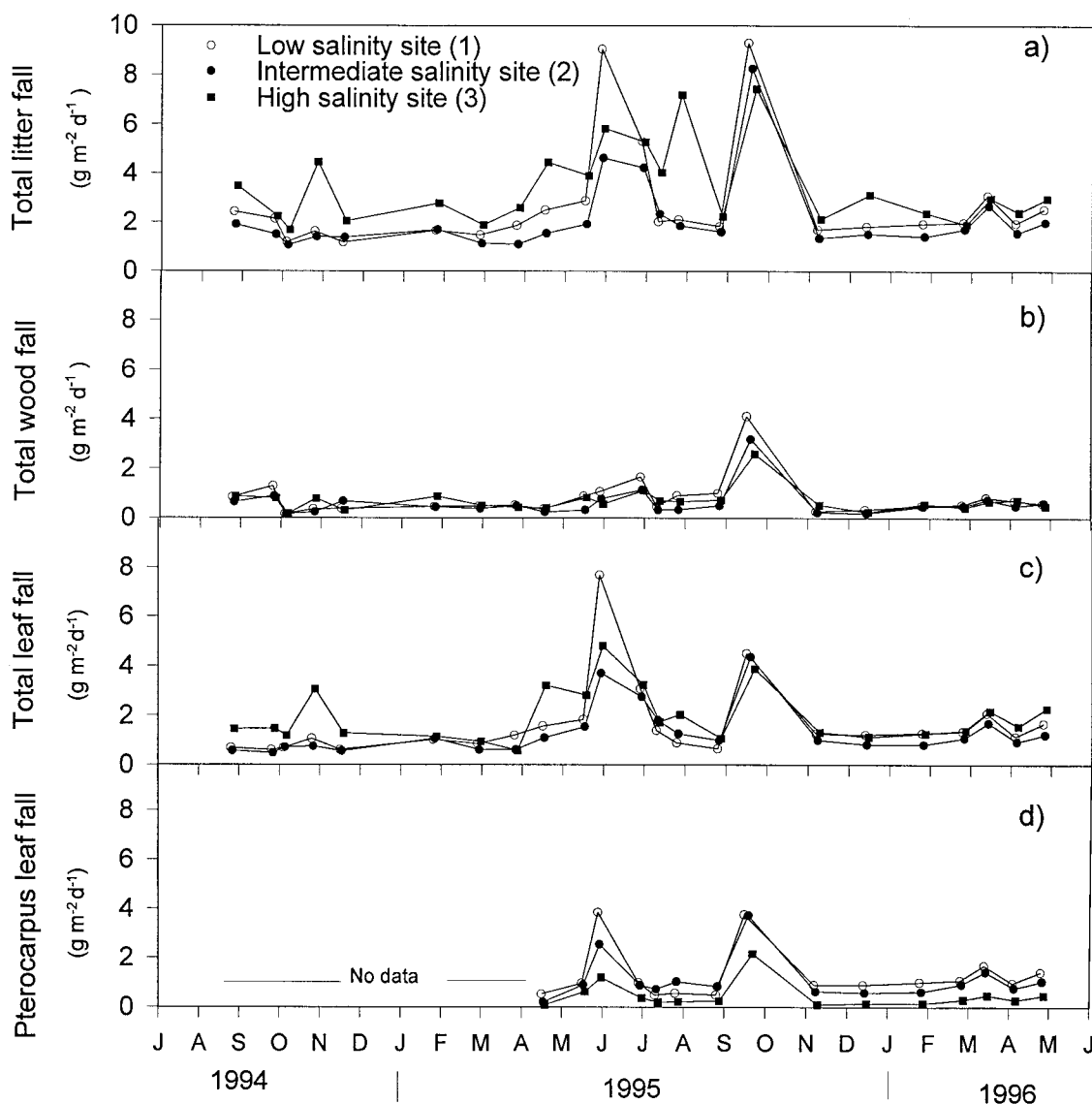


Figure 3. Seasonal patterns of litterfall at the three salinity sites in a *P. officinalis* forest. (a) Total litterfall, (b) total wood fall, (c) total leaf fall, and (d) leaf fall of *P. officinalis*. Leaves of *P. officinalis* were not separated from total leaf fall between August 1994 and April 1995.

face in depressions in June 1994 following 5 months of drought and in April 1995. Between September 1995 and February 1996, water levels stayed consistently high.

#### Salinity

From August 1994 to February 1996, there was little variation in salinity at the water surface ( $1\text{--}2\text{ g kg}^{-1}$ ) across all sites, but salinity at 60 cm fluctuated from 7 to  $24\text{ g kg}^{-1}$  (Figure 2c). Site 1 consistently had the lowest mean ( $\pm$ se) salinity ( $9.7\pm 0.5\text{ g kg}^{-1}$ ), site 2

was intermediate ( $11.5\pm 0.8\text{ g kg}^{-1}$ ), and site 3 had the highest salinity ( $15\pm 1.3\text{ g kg}^{-1}$ ). The Friedman two-way nonparametric statistic showed a significant difference between months (Friedman statistic = 31.97,  $p < 0.001$ ) and sites (Friedman statistic = 22.17,  $p < 0.001$ ) in soil salinity at 60 cm. The lowest soil salinities occurred in April 1995 during a period of low rainfall and the highest occurred with an increase in precipitation following the 1994 drought. After an increase in October 1995, soil salinities remained fairly constant until February 1996.

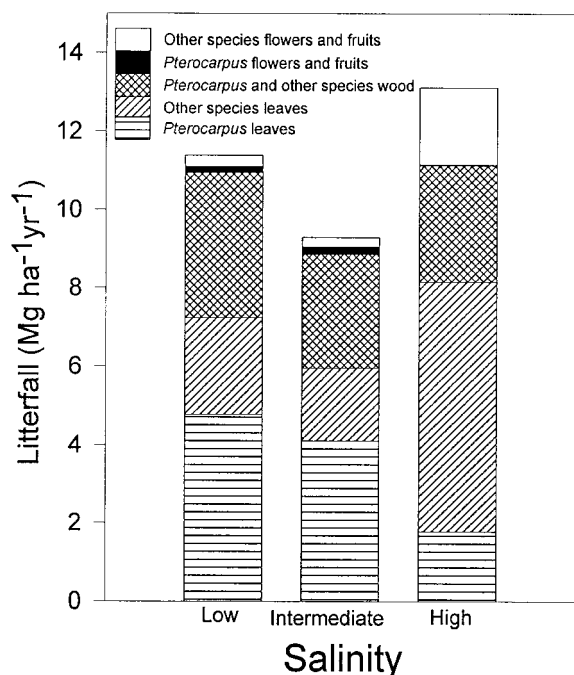


Figure 4. Components of total annual litterfall for the three salinity sites in a *P. officinalis* forest. The corrected means of *P. officinalis* leaf fall based on the basal areas regression for the three sites were: 3.69 Mg ha<sup>-1</sup> yr<sup>-1</sup> for site 1, 2.64 Mg ha<sup>-1</sup> yr<sup>-1</sup> for site 2, and 0.90 Mg ha<sup>-1</sup> yr<sup>-1</sup> for site 3.

#### Patterns of litterfall

Peaks in litterfall occurred during the beginning of the rainy season in May 1995 and during the hurricane season in September 1995 (Figure 3). Following the passage of Hurricanes Luis and Marilyn, total litterfall ranged from 7.4 g m<sup>-2</sup> d<sup>-1</sup> in the high salinity site to 9.3 g m<sup>-2</sup> d<sup>-1</sup> in the low salinity site (Figure 3). Except for periods of peak litterfall, total litterfall was generally higher in the high salinity site. During most of the year, total litterfall was <2.5 g m<sup>-2</sup> d<sup>-1</sup> in the low and intermediate salinity site and <3.5 g m<sup>-2</sup> d<sup>-1</sup> in the high salinity site (Figure 3). The major peak in wood fall also occurred during the hurricane season and ranged from 2.6 g m<sup>-2</sup> d<sup>-1</sup> in the high salinity site to 4.1 g m<sup>-2</sup> d<sup>-1</sup> in the low salinity site. In the high salinity site, peak total litterfall occurred in July 1995 when there was a large production of *L. racemosa* fruits. Daily litterfall of *P. officinalis* leaves was high in May and September, 1996 and was low during the period November 1996 to May 1997.

Annual litterfall (April 1995 to April 1996) for all species was 11.9 Mg ha<sup>-1</sup> yr<sup>-1</sup> (3.25 g m<sup>-2</sup> d<sup>-1</sup>), but litter production varied among sites (Figure 4). The

Table 2. Comparison of different litter categories among the three sites. An ANOVA was applied to the ranked data from the 45 litter baskets.

Litter Category	Source	df	ss	ms	f	p
<i>Pterocarpus</i> leaves	Between	2	5012	2506	40.8	0.001
	Within	42	2577	61		
	Total	44	7590			
Other species leaves	Between	2	2005	1002	7.5	0.001
	Within	42	5584	132		
	Total	44	7590			
<i>Pterocarpus</i> and other species wood	Between	2	1046	523	3.3	0.05
	Within	42	6543	155		
	Total	44	7590			
<i>Pterocarpus</i> flowers	Between	2	2709	1354	11.7	0.001
	Within	42	4862	115		
	Total	44	7572			
<i>Pterocarpus</i> fruits	Between	2	2090	1045	8.6	0.001
	Within	42	5090	121		
	Total	44	7181			
Other species flower	Between	2	199	99	0.5	0.56
	Within	42	7163	170		
	Total	44	7362			
Other species fruit	Between	2	2271	1135	8.9	0.001
	Within	42	5307	126		
	Total	44	7579			

high salinity site had the highest total litterfall rate (13.8 Mg ha<sup>-1</sup> yr<sup>-1</sup>), followed by the low salinity site (12.0 Mg ha<sup>-1</sup> yr<sup>-1</sup>). The intermediate salinity site had the lowest total litterfall rate (9.8 Mg ha<sup>-1</sup> yr<sup>-1</sup>). Leaf fall of 'other species' was highest in the high salinity site and was dominated *L. racemosa* (Figure 4 and Table 2). In the low and intermediate salinity sites, two liana species, *Paullinia pinnata* and *Dalbergia ecastaphylla*, produced the majority of 'other species' litter. The high salinity site also had the greatest production of 'other species' fruits and again was dominated by *L. racemosa* (Figure 4 and Table 2). The flower and wood components of litterfall were not significantly different among the sites (Table 2).

The contribution of *P. officinalis* to total litterfall decreased with increased soil salinity (Figures 3–5). There was a significant difference in *P. officinalis* leaf litter production among sites (Figure 5 and Table 2). Litterfall decreased from an average of 4.8 Mg ha<sup>-1</sup> yr<sup>-1</sup> in the low salinity site to

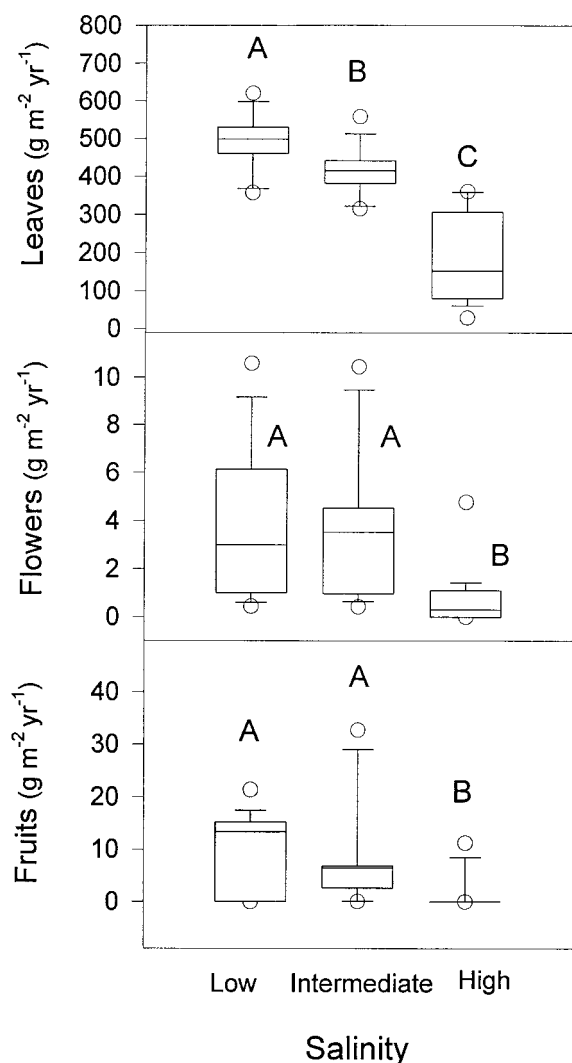


Figure 5. Rates of leaf, flower, and fruit production of *P. officinalis* in the three salinity sites. In the intermediate site, a single litter trap had one extreme value for flower production and two extreme values of fruit production that are not included in the figure, but were used in the statistical analyses. Box plots illustrate the median (horizontal line within the box), 25–75 percentiles (the box), 10–90 percentiles (T), and values greater than the 10–90 percentiles (o). The average basal area of *P. officinalis* in the low, intermediate and high salinity sites were 73.5 m<sup>2</sup> ha<sup>-1</sup>, 68.9 m<sup>2</sup> ha<sup>-1</sup>, and 42.0 m<sup>2</sup> ha<sup>-1</sup>, respectively. Sites with different letters were significantly different ( $P < 0.05$ ) using a Bonferroni Pairwise comparison of means.

1.8 Mg ha<sup>-1</sup> yr<sup>-1</sup> in the high salinity site (Figures 4 and 5). Although there was high within site variation, Bonferroni's test confirmed that the three sites (low, intermediate, and high salinity) were all significantly different.

Annual flower production of *P. officinalis* varied significantly among sites (Figure 5 and Table 2). The

low (median 3.2 g m<sup>2</sup> yr<sup>-1</sup>) and intermediate (median 3.5 g m<sup>2</sup> yr<sup>-1</sup>) sites had higher flower production in comparison with the high salinity site (0.3 g m<sup>2</sup> yr<sup>-1</sup>) (Figure 5). Annual fruit production also varied significantly among sites (Figure 5 and Table 2). The low (median 13.3 g m<sup>2</sup> yr<sup>-1</sup>) and intermediate salinity (median 6.4 g m<sup>2</sup> yr<sup>-1</sup>) sites had higher fruit production than the high salinity site (median 0 g m<sup>2</sup> yr<sup>-1</sup>) (Figure 5 and Table 2).

## Discussion

The two major peaks in leaf fall of *P. officinalis* were associated with different environmental factors. One was associated with the beginning of the wet season in May 1995 and the other with strong winds in September 1995. The leaf fall peak in May followed two months of low precipitation and the lowest water level in the previous nine months (Figure 2a). Long periods of low water level may stress wetland tree species because of a superficial root system (Boggie 1972; Montague & Day 1980). Although most adult trees occur on mounds, their roots extend into the surrounding depressions (Eusse, personal observation) where water should be available even during dry periods. It is likely that leaf fall in May/June and the immediate replacement with new leaves, during the period of greatest irradiance, is the normal phenology of *P. officinalis* and not a response to stressful conditions. 'Normal phenology patterns can be interrupted by disturbances, particularly hurricanes or tropical storms, that can defoliate trees. In September 1995, winds associated with Hurricanes Luis and Marilyn caused another major peak in leaf litter fall. Although these hurricanes did not pass directly over the study site, and there was no structural damage (e.g., uprooted trees or broken trunks), these events were important factors affecting litter production at the stand scale.

Annual litter production in the Sabana Seca forest was similar to values reported for other *Pterocarpus* forests in Puerto Rico (Alvarez-Lopez 1990) and Caribbean (Febvay et al. 1981) even though levels of salinity were higher (Table 1). This discrepancy could have been caused by measuring salinity at a deeper depth (60 cm) in comparison with the other studies or because of the increase in litter fall associated with the tropical storm winds in September 1995. More importantly, there was high within stand variation in litter fall. Although the sites were within 400 m of each other, the gradient in salinity had a strong effect on

litter production of *P. officinalis*. If we only consider *P. officinalis*, litter fall decreased along the gradient of soil salinity and was two times greater in the low salinity site than the high salinity site. Flower and fruit production were at least 10 times greater in the low salinity site than in the high salinity site. Although litter production of *P. officinalis* decreased across the salinity gradient, in the ecotone the presence of *L. racemosa* resulted in an overall higher level of litter production. These results emphasize how within stand variation in litter production can be high due to rapid changes in environmental variables (e.g., salinity) or shifts in species composition.

In this site, adults of *P. officinalis* grow in a wide range of soil salinity (0–24 g kg<sup>-1</sup>), but salinity had a negative effect on litter, flower, and fruit production. Although recruitment was not directly measured in this study, the low levels of reproduction, measured as flower and fruit production, in the high salinity site, and the lack of recruitment in the intermediate site (Aide et al. ms.) suggest that *P. officinalis* could become locally extinct. Historically, *P. officinalis* occurred in a larger range of environmental conditions, but agricultural activities during the last two centuries have reduced the majority of forest patches to areas of relatively high salinity adjacent to mangroves. An increase in sea level, associated with increased global temperature (Gornitz 1995) and groundwater pumping will increase salinity in many freshwater habitats and further threatened these remnant populations that occur near their physiological limit. To conserve this wetland forest type it is critical to expand the distribution into areas of lower salinity where this species occurred historically.

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