



# Stand Structure and Aboveground Biomass of a *Pelliciera rhizophorae* Mangrove Forest, Gulf of Montijo Ramsar Site, Pacific Coast, Panama

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**Abstract** Mangroves provide several ecosystems services including carbon storage. Aboveground biomass as a proxy for carbon storage and stand structure were investigated in nine plots located in a riverine *Pelliciera rhizophorae* forest, Gulf of Montijo Ramsar Site, Pacific Coast, Panama. Aboveground biomass for all trees above 2 cm was estimated using common pantropical mangrove biomass regression models. Despite a comparatively low tree species diversity there was a considerable variation in stand structure and biomass among the plots. *P. rhizophorae* dominated the river and center plots with tree densities between 1,275 and

10,075 trees ha<sup>-1</sup>. Further inland, species composition shifted towards a *Rhizophora racemosa* dominated forest. Lower density of larger trees in the inland plots may be due to small-scale cutting of trees at the forest margin. Across all plots, *P. rhizophorae* was smaller in diameter and height than *R. racemosa*. Aboveground biomass ranged from 76 Mg ha<sup>-1</sup> to 335 Mg ha<sup>-1</sup> (average: 176 Mg ha<sup>-1</sup>) and was closely related to stem density and basal area. Compared to other neotropical mangrove forests this riverine *P. rhizophorae* forest stores substantial amounts of biomass. Conservation strategies have to be put in place to maintain the threatened *P. rhizophorae* forest in Central America.

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**Keywords** Allometric equations · Diameter-height-relationships · Disturbance · Riverine mangroves · Species composition · Wood density

## Introduction

Mangroves, occurring at the land ocean interface in the tropics and subtropics, provide important ecosystem services such as raw material, coastal protection and carbon sequestration (Polidoro et al. 2010; Barbier et al. 2011). The role of coastal vegetation in carbon uptake and storage has become of specific interest in relation to mitigating atmospheric carbon dioxide concentrations (McLeod et al. 2011). The amount of carbon captured and stored in mangrove biomass and sediments is highly variable (Saenger and Snedaker 1993; Bouillon et al. 2008; Komiyama et al. 2008) and influenced by plant productivity, species composition, physical and chemical site conditions, decomposition rates, and human disturbances (Brown and Lugo 1982; Day et al. 1987; Chen

and Twilley 1999; Sherman et al. 2003; Walters 2005). Thus, it is important to assess all mangrove forest types in order to obtain reliable global mangrove biomass estimates (Lovelock et al. 2005).

Despite the value and importance of mangroves and other coastal habitats, these ecosystems are subject to degradation and destruction worldwide (Alongi 2002; Spalding et al. 2010). For example, in Panama where this study was conducted, the mangrove-covered area decreased from 250,000 to 170,000 ha between 1980 and 2005 (FAO 2007). Around 40 % of mangrove species along the Atlantic and Pacific coasts of Central America are threatened with extinction (Polidoro et al. 2010). Increasing pressure on mangrove forests in Panama resulted in new legal regulations that among others impose high fines for illegal logging (ARAP 2008a, b).

The Convention on Wetlands of International Importance (Ramsar Convention) highlights in their resolution on ‘Climate Change and Wetlands’ (Resolution X.24) that the protection of remaining wetlands and the restoration of degraded ones is crucial since destruction and degradation of mangrove results in the loss of stored biomass and carbon into the atmosphere (Ramsar 2008). This resolution also encourages contracting parties to assess the role of wetlands in carbon storage and sequestration (Ramsar 2008). Biomass is a useful indicator for the productivity of a stand. It provides information on the storage of carbon and nutrients, and is a measure of stand conditions (i.e. age, structure, silvicultural practices, disturbance) (Soares and Schaeffer-Novelli 2005).

Aboveground biomass and carbon storage are commonly derived from tree inventory data (such as diameter and height) and species-specific allometric equations (Clough and Scott 1989; Fromard et al. 1998; Komiyama et al. 2005). For sites where species-specific allometric equations are lacking, the pan-tropical mixed species biomass regression models (model I and model II) developed by Chave et al. (2005) are often applied. Biomass regression model I includes trunk diameter, total tree height and wood density whereas model II only includes trunk diameter and wood density (Chave et al. 2005).

Mangrove biomass estimates have been reported from only a few sites in Panama (Golley et al. 1969; Lovelock et al. 2005) and to the best of our knowledge the present study is the first assessment of aboveground biomass stocks for *Pelliciera rhizophorae* (Triana and Planchon) mangrove forests located in the western part of the Pacific Coast of Panama.

*P. rhizophorae* (common Spanish name: *Mangle piñuelo*) was a widely distributed mangrove species along the Caribbean and Pacific Coast of Central America and

northern South America during the Holocene (Jaramillo and Bayona 2000). The area of *P. rhizophorae* declined since the Holocene and *P. rhizophorae* is considered to be one of the rarest ‘true’ mangrove species (Condit et al. 2001). The distribution of *P. rhizophorae* is mainly restricted to the wetter regions along the Pacific Coast between the Gulf of Nicoya in Costa Rica and the Esmeraldas River in Ecuador and a few locations on the Caribbean Coast (Winograd 1983; Jimenez 1984; Lacerda et al. 1993; Jimenez 1999). Due to its small geographic range, specific habitat requirements (low salinity) and ongoing habitat loss, *P. rhizophorae* is classified as vulnerable under the International Union for Conservation of Nature Red List (Ellison et al. 2010a, b; Polidoro et al. 2010).

*P. rhizophorae* stands are still found in the Gulf of Montijo Ramsar Site on the western Pacific Coast of Panama (CREHO 2010). However, there is no information about the structure and aboveground biomass in this mangrove forest. The objectives of our study were: (1) to assess the forest structure of riverine *P. rhizophorae* stands, (2) to quantify the aboveground biomass combining forest structure data and published allometric equations, and (3) to investigate the relationship between aboveground biomass and structural parameters.

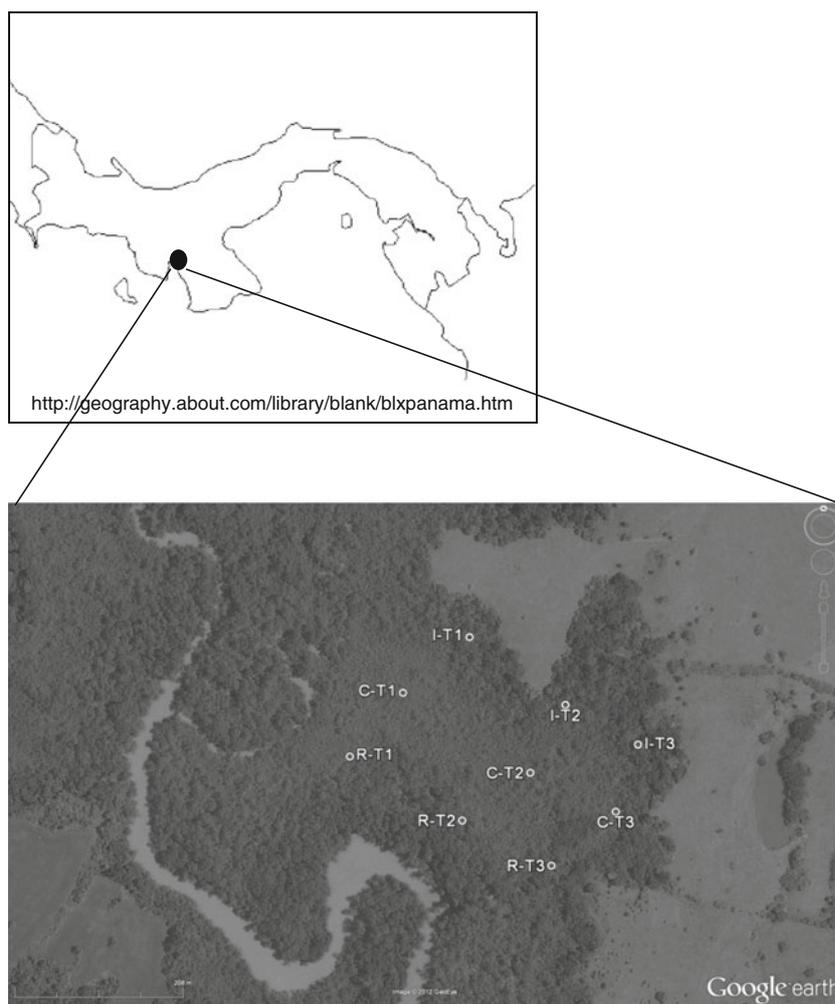
## Materials and Methods

### Study Area

The study was conducted in the vicinity of the river Rio de Jesus within the Gulf of Montijo Ramsar Site No. 510 (Fig. 1). The Ramsar Site (7° 46′ 19″ N, 81° 7′ 51″ W) covers an area of 80,765 ha and is located in the southern part of the Veraguas province on the Pacific Coast of Panama. The elevation of the area ranges from 0 m to 250 m above sea level (CREHO 2010). Average annual precipitation is around 2,800 mm with a pronounced dry season from December to April (CREHO 2010). Average annual temperature is 27 °C (CREHO 2010). Salinity in the Gulf of Montijo area varies between 8.2 ‰ in the wet season (May to November) and 33.8 ‰ in the dry season (December to April) (CREHO 2010).

Different vegetation types such as woodlands, mangroves, swamps and marsh areas are found within the Gulf of Montijo. Mangroves (approximately 6,310 ha) grow on flat alluvial sediments along the coastline and rivers and extend up to 300 m inland in some parts, meanwhile cropland and pastures form the inland border with the mangrove forest (CREHO 2010). The dominating tree species found in the study area are *Pelliciera rhizophorae* (Triana and Planchon) and *Rhizophora racemosa* (G. Meyer).

**Fig. 1** Location of the nine study plots, river Rio de Jesus, Gulf of Montitjo Ramsar Site, Panama



### Plot Selection and Forest Inventory

Three parallel transects of approximately 200 m in length were laid out extending from the river Rio de Jesus inland in the direction 40° N-E (Fig. 1). The distance between each transect was around 100 m. Along each transect, three 20 m×20 m sample plots were established (nine plots in total). Subplots (5 m×5 m) were established at the center of each plot. Geographic coordinates were recorded with a GPS (eTrex Venture Cx, Garmin Ltd., New Taipei City, Taiwan) at each plot center.

The stand inventory was conducted between May and July 2009 using the methods described in Cintron and Schaeffer-Novelli (1984). Within the 20×20 m plot all trees ≥10 cm diameter (dbh class II) were identified and labeled with aluminum tags. The diameter at breast height (dbh; 1.3 m above ground level) was measured with a diameter tape. If the prop-roots (*R. racemosa*) or buttresses (*P. rhizophorae*) were higher than 1.3 m the

measurements were made 50 cm above the highest prop root and the point of measurement (pom) was recorded. The measurement was still referred to as dbh. The height of trees was measured with an extendable pole for trees below 5 m. The height of trees above 5 m was estimated visually. The dbh and height of trees/saplings (2 cm < dbh < 10 cm; dbh class I) were measured in the 5×5 m subplots. Sediment properties such as salinity and redox potential were not determined due to the lack of suitable equipment.

### Structural Characteristics

Stand basal area ( $G$ ,  $\text{m}^2 \text{ha}^{-1}$ ) is the sum of all individual tree basal areas per unit ground area and was calculated following Cintron and Schaeffer-Novelli (1984) (Eq. 1):

$$G = \sum_{i=1}^N g_i \times 25 \quad (400) \quad (1)$$

where  $g_i$  ( $m^2$ ) is the basal area of a single tree (Eq. 2) and 25 (400) are the conversion factors to upscale from the plot size ( $400 m^2$ ) and subplot ( $25 m^2$ ) to 1 ha.

$$g_i = \pi \times \left( \frac{dbh_i}{2} \right)^2 \quad (2)$$

The importance value index ( $I_v$ ) is a quantitative parameter which is used to characterize the importance

of each species in a stand in terms of density, basal area and frequency. The  $I_v$  index was calculated following Cintron and Schaeffer-Novelli (1984):

$$I_v = \text{Relative Density} + \text{Relative Frequency} + \text{Relative Dominance} \quad (3)$$

where

$$\text{Relative Density (\%)} = \frac{\text{number of individuals of a species (n ha}^{-1}\text{)}}{\text{total number of individuals (N ha}^{-1}\text{)}} \times 100 \quad (4)$$

$$\text{Relative Frequency (\%)} = \frac{\text{frequency of species (n)}}{\text{total number of species (N)}} \times 100 \quad (5)$$

$$\text{Relative Dominance (\%)} = \frac{\text{total basal area of a species}}{\text{basal area of all species (G)}} \times 100 \quad (6)$$

### Aboveground Biomass

The development of site and species-specific allometric equations was not possible as tree harvesting is not permitted within the Ramsar Site. Thus, aboveground biomass was estimated using the model I (diameter-height-wood density) mangrove biomass regression model developed by Chave et al. (2005). This regression model is based on datasets collected from old-growth mangrove forests composed of *Avicennia germinans* (L.) Stearn, *Laguncularia racemosa* Gaertn., and *R. racemosa* in French Guiana (Fromard et al. 1998) and Guadeloupe (Imbert and Rollet 1989).

$$\text{Plot aboveground biomass (AGB, Mg ha}^{-1}\text{)} = \sum_{i=1}^N agb_i \times 25(400) \quad (7)$$

where

$$agb_i \text{ (kg)} = 0.0509 \times \rho \times dbh^2 \times \text{tree height} \quad (8)$$

Where  $\rho$  is the wood specific gravity ( $g cm^{-3}$ ). The wood specific density for *A. germinans* ( $0.9 g cm^{-3}$ ) and *R. racemosa* ( $0.88 g cm^{-3}$ ) were taken from the Global Wood Density Database (Chave et al. 2009; Zanne et al. 2009). The wood density of *P. rhizophorae* ( $0.75 g cm^{-3}$ ) was obtained from Southwell and Bultman (1971). The wood density of *M. oleifera* was  $0.74 g cm^{-3}$  according to Cordero (1971).

Nonparametric tests (Mann–Whitney U Test, Spearman Rank correlation) were used to compare forest structural

characteristics and biomass among plots, sites, and parameters. Statistical analyses were conducted using SPSS/PASW Statistics 18 (18.0.2, SPSS Inc., Chicago, IL, USA). The values presented in the text, tables and figures are mean values  $\pm$  standard deviation ( $n=3$  plots).

## Results

### Species Composition and Stand Structure

The species composition and stand structure varied among the nine plots (Table 1, see Online Resource 1). *P. rhizophorae* was the dominant species in the river and center plots with up to 10,000 *P. rhizophorae* trees (dbh class I and II) per ha (Table 1). High  $I_v$  indices also highlight the dominance of *P. rhizophorae* in these plots (Table 1). The density of *R. racemosa* in the river and inland plots was considerable lower and ranged from 25 to 1,050 trees  $ha^{-1}$  (Table 1). In two of the six river and center plots the mangrove associate *Mora oleifera* (Triana ex Hemsl.) Ducke was also present (Table 1). A characteristic feature of the center plots was the high density of *Acrostichum aureum* (L.), a large (up to 3 m high) understory fern. The species composition changed with distance from the river. Inland plots were dominated by *R. racemosa* (dbh class I and II) with an importance value of up to 300 (Table 1). Besides *P. rhizophorae*, the black mangrove *Avicennia germinans* (L.) and *M. oleifera* were found in the inland plots (Table 1).

Stem density of dbh class I trees ( $8,267 \pm 1,617$  stems  $ha^{-1}$ ) and dbh class II trees ( $708 \pm 450$  stems  $ha^{-1}$ ) was highest in center plots (Table 1). However, differences in stem density among plots were statistically not significant (Mann–Whitney U Test,  $p=0.246$ ). Tree height of dbh class II trees averaged  $14.4 \pm 5.0$  m across all species and plots. Averaged across all plots, *P. rhizophorae* (dbh class II) had smaller diameters ( $13.3 \pm 0.9$  cm) and lower heights ( $10.1 \pm 1.3$  m) compared with *R. racemosa* (diameter:  $24.3 \pm 5.6$  cm; height:  $18.2 \pm 3.9$  m;

**Table 1** Structural characteristics, importance value (Iv) and aboveground biomass (AGB). The values for dbh and height are means  $\pm$  standard deviation ( $n=3$  plots). The amount of biomass per plot is given in italics. dbh I = trees >2 cm and <10 cm dbh; dbh II = trees  $\geq$ 10 cm dbh

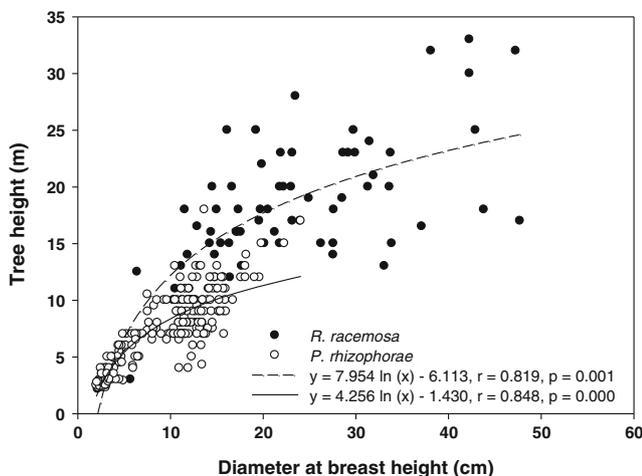
Site	Plot	UTM X UTM Y	Species	Stem density (n ha <sup>-1</sup> )		dbh (cm)		Height (m)		Basal area (m <sup>2</sup> ha <sup>-1</sup> )		Iv		AGB (Mg ha <sup>-1</sup> )			
				dbh I	dbh II	dbh I	dbh II	dbh I	dbh II	dbh I	dbh II	dbh I	dbh II	dbh I	dbh II		
River	R-T1	876654 491312	<i>P. rhizophorae</i> <i>R. racemosa</i> <i>M. oleifera</i>	6400	525	4.5 $\pm$ 2.5	12.5 $\pm$ 1.8	4.9 $\pm$ 2.4	8.3 $\pm$ 1.1	13.2	6.5	204	191	45.4	27.0		
				400	200	6.4	13.6 $\pm$ 2.6	12.5	12.4 $\pm$ 3.3	1.3	3.0	47	109	9.2	22.5		
				800		3.6 $\pm$ 0.2		4.5 $\pm$ 0.5		0.8		49				1.6	
	R-T2	876575 491453	<i>P. rhizophorae</i> <i>R. racemosa</i>	2400	225	4.8 $\pm$ 2.3	12.4 $\pm$ 1.2	5.4 $\pm$ 2.1	11.7 $\pm$ 2.8	5.3	2.7	300	110	18.1	15.8		
				800	250	29.2 $\pm$ 12.4	23.5 $\pm$ 6.4	19.5	19.0	5.3	22.2					18.1	317.2
				800	475	8.1 $\pm$ 2.2	14.4 $\pm$ 3.5	5.7 $\pm$ 0.7	10.9 $\pm$ 2.6	4.2	8.1	300	194	12.4	46.8		
R-T3	876519 491563	<i>P. rhizophorae</i> <i>R. racemosa</i>	800	125	20.7 $\pm$ 5.4		19.8 $\pm$ 2.0		4.2	12.5		106		12.4	98.4		
			6400	1200	4.8 $\pm$ 2.4	13.1 $\pm$ 1.7	4.3 $\pm$ 2	8.9 $\pm$ 2.0	14.4	16.4	241	236	40.9	72.0			
			400	25	3.6	33.9	2.4	15.0	0.4	2.3	59	64	0.5	19.3			
Center	C-T1	876733 491380	<i>P. rhizophorae</i> <i>R. racemosa</i> <i>M. oleifera</i>	6400	50	4.5 $\pm$ 2.2	13.5 $\pm$ 1.9	4.7 $\pm$ 2.4	11.0 $\pm$ 1.4	15.9	0.7	300	69	53.3	3.9		
				8000	350	24.3 $\pm$ 21.2	15.9 $\pm$ 4.8									231	107.0
				400	475	4.2 $\pm$ 1.2	14.2 $\pm$ 2.4	4.3 $\pm$ 1.3	8.9 $\pm$ 2.6	14.2	7.3	239	236	33.5	33.7		
	C-T2	876586 491642	<i>P. rhizophorae</i> <i>R. racemosa</i>	9600	25	5.7	19.6	3.0	17.0	1.0	0.8	61	64	1.7	7.3		
				400	475	3.4 $\pm$ 1.5	3.7 $\pm$ 2.1			15.2	8.1					35.2	41.0
				400	350	3.1 $\pm$ 0.8	27.5 $\pm$ 9.5	4.9 $\pm$ 0.7	17.5 $\pm$ 4.1	1.9	23.2	141	300	3.7	234.9		
Inland	I-T1	876802 491462	<i>P. rhizophorae</i> <i>R. racemosa</i> <i>A. germinans</i>	800	25	7.7	7.1					86		8.5			
				2400	400	6.7 $\pm$ 2.8	13.6 $\pm$ 5.9	7.1 $\pm$ 3.1	11.4 $\pm$ 3.3	4.5	23.2					13.8	234.9
				400	275	2.9	24.4 $\pm$ 9.0	3.0	18.1 $\pm$ 2.8	0.3	14.4	169	62	40.4	14.0		
	I-T2	876718 491580	<i>P. rhizophorae</i> <i>R. racemosa</i> <i>A. germinans</i> <i>M. oleifera</i>	2400	50	5.2 $\pm$ 2.0	26.3 $\pm$ 20.2	6.2 $\pm$ 2.6	14.0 $\pm$ 7.1	2.8	3.5	85	53	12.3	37.4		
				400	25	16.7	10.0									33	2.6
				400	75	3.1	12.0 $\pm$ 0.9	4.0	10.0	12.8	20.6					53.2	214.0
I-T3	876669 491669	<i>P. rhizophorae</i> <i>R. racemosa</i> <i>A. germinans</i>	400	125	3.8	25.2 $\pm$ 10.7	5.0	24.2 $\pm$ 7.0	0.5	7.1	160	144	1.3	109.7			
			400	100	17.3 $\pm$ 6.4	13.9 $\pm$ 4.9			0.8	10.3					24.7	137.2	
			400	100	17.3 $\pm$ 6.4	13.9 $\pm$ 4.9			0.8	10.3					24.7	137.2	

Mann–Whitney U,  $p=0.001$  for diameter and height, respectively) (Fig. 2). The basal area (dbh class II) ranged from  $8.1 \text{ m}^2 \text{ ha}^{-1}$  (C-T3) to  $23.2 \text{ m}^2 \text{ ha}^{-1}$  (I-T1), averaging  $15.0 \pm 6.9 \text{ m}^2 \text{ ha}^{-1}$  across all plots (Table 1). Basal area of dbh class I trees varied greatly also among plots ( $0.8\text{--}15.9 \text{ m}^2 \text{ ha}^{-1}$ ), averaging  $9.9 \text{ m}^2 \text{ ha}^{-1}$  across all plots (Table 1).

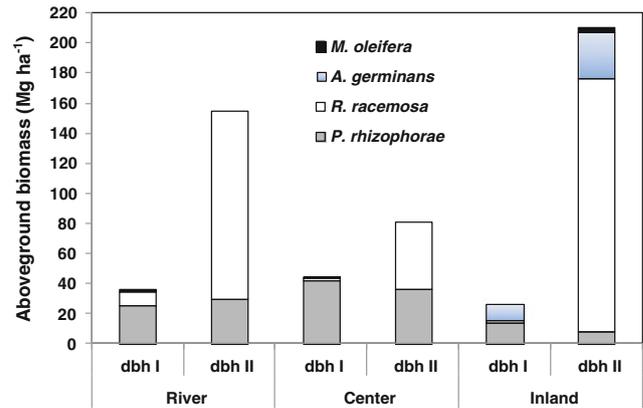
### Aboveground Biomass

The aboveground biomass varied considerably among species and plots (Table 1, Fig. 3). The aboveground biomass of dbh class I trees ranged from 2 to  $56 \text{ Mg ha}^{-1}$  with an average of  $31 \pm 21 \text{ Mg ha}^{-1}$  across plots (Table 1). *P. rhizophorae* comprised between 80 and 100 % of the total plot biomass except for the inland plots C-T1 (11 %) and C-T3 (31 %). The contribution of dbh class I trees to total plot biomass ranged from 2 to 53 %. Aboveground biomass for the larger trees (dbh class II) varied between  $41 \text{ Mg ha}^{-1}$  and  $317 \text{ Mg ha}^{-1}$  with an average value across all plots of  $144 \pm 93 \text{ Mg C ha}^{-1}$  (Table 1). On a species level *R. racemosa* ( $112 \text{ Mg ha}^{-1}$ ) had on average a higher biomass than *P. rhizophorae* ( $27 \text{ Mg ha}^{-1}$ ; Mann–Whitney U,  $p=0.046$ ). The contribution of *P. rhizophorae* to the total aboveground biomass of a given plot varied between 0 % in inland plot C-T1 and 97 % in center plot C-T2 (Table 1). The amount of biomass stored in the center plots was lower compared to inland plots (Mann–Whitney U,  $p=0.05$ , Fig. 3). No statistically significant differences were found between the river and inland plots (Mann–Whitney U,  $p=0.513$ ) and the river and center plot (Mann–Whitney U,  $p=0.513$ ).

Aboveground biomass increased linearly with increasing stem density for both, *P. rhizophorae* (Spearman's  $\rho=0.898$ , slope= $0.560$ ,  $p=0.002$ ) and *R. racemosa* (Spearman's  $\rho=0.742$ , slope= $0.059$ ,  $p=0.027$ ) (Fig. 4a). Biomass of *P. rhizophorae* (Spearman's  $\rho=0.985$ , slope= $4.377$ ,  $p=0.000$ ) and *R. racemosa* (Spearman's  $\rho=0.967$ ,

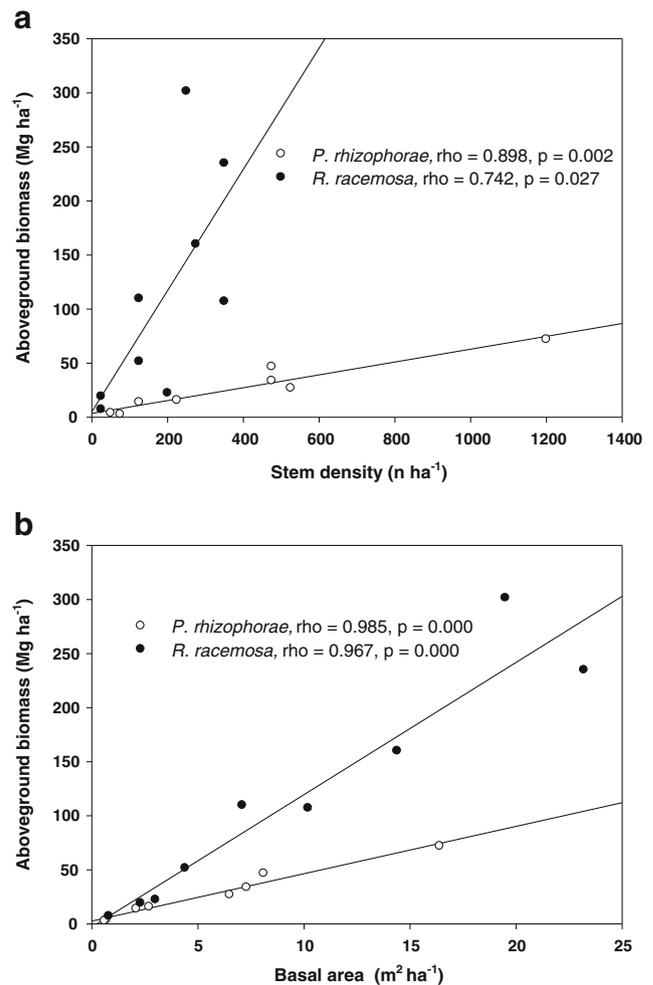


**Fig. 2** Height-diameter relationships for *R. racemosa* and *P. rhizophorae*



**Fig. 3** Aboveground biomass of all trees (dbh class I = trees  $< 10 \text{ cm dbh}$ ; dbh class II = trees  $\geq 10 \text{ cm dbh}$ ) in river, center and inland sites. Values represent means ( $n=3$  plots)

slope= $12.230$ ,  $p=0.000$ ) was also closely related to the species basal area (Fig. 4b). In contrast, no significant correlations were found between *P. rhizophorae* and *R. racemosa* biomass and the diameter and height of these species.



**Fig. 4** Relationships between aboveground biomass and a) stem density and b) basal area for dbh class II trees

## Discussion

### Stand Structure

The main tree species found in our study plots were *P. rhizophorae* and *R. racemosa* (Table 1). This is in line with an earlier vegetation survey done in the Gulf of Montijo (ANAM and AECI 2004). The low number of species present in our study area is common for Latin and Central American mangrove forests which are characterized as species poor (Tomlinson 1986; FAO 2007). The Neotropic mangrove flora evolved from species of the Indo-Pacific and only 11 out of 70 true mangrove species occurring in the Indo-Pacific reached the Neotropics during the Eocene Period (Lacerda et al. 1993).

Despite considerable variability among the study plots, a shift in species composition and an increase in species number were observed with distance from the river. *P. rhizophorae* was the dominant species in most plots located within 150 m from the river bank, while *R. racemosa* was the prevailing species in the inland plots. Species shifts with distance from the coast or rivers are a common feature and these so-called zonation patterns have been described for different geographic regions (Jimenez and Sauter 1991; Smith 1992; Satyanarayana et al. 2002). Biological (e.g. propagule abundance and dispersal characteristics) and environmental factors (e.g. salinity) influence mangrove establishment and thus are important drivers in determining species composition along an inundation gradient (Saenger 2002). *P. rhizophorae* is predominantly found in medium to high intertidal or intermediate and upstream estuarine zones whereas *A. germinans*, *L. racemosa* and *R. racemosa* are found primarily in the intermediate and lower intertidal or estuarine positions (Polidoro et al. 2010). According to Calderon-Saenz (1984) *P. rhizophorae* is often found where fresh water is available. The genera *Pelliciera* is more sensitive to high soil salinities compared with other neotropical mangroves and is not found in sediments with salinities higher than 37 ‰ (Winograd 1983; Jimenez 1984). In summary, *P. rhizophorae*'s distribution is associated with alluvial, estuarine and interchannel areas with a regular supply of fresh water (Fuchs 1970 as cited in Jimenez 1984); conditions which are likely to exist along the river banks of Rio de Jesus. Lower abundance of *P. rhizophorae* in the inland plots may also reflect the impact of selective harvesting of *P. rhizophorae*. Selective logging was suggested to have led to the local extinction of *P. rhizophorae* in the Uraba Gulf, Colombian Caribbean (Blanco et al. 2012).

The high abundance and importance values of *P. rhizophorae* saplings and small trees in all plots suggest that the physical and chemical site conditions are favorable for the establishment of this species. *P. rhizophorae* saplings and small trees were also found in high numbers in all center plots despite a considerable coverage (up to 40 %) of *A. aureum*. *A. aureum* can colonize cleared mangrove areas (Blanco et al. 2012) and its presence

often indicates habitat disturbance (Ellison et al. 2010a, b; Sharpe 2010). *A. aureum* is difficult to eradicate and is reported to be a major barrier for the regeneration of mangroves (Dahdouh-Guebas et al. 2005; Blanco et al. 2012).

We did not find a correlation between the stem density of dbh class I and II trees suggesting that the presence of larger trees did not impede the establishment and survival of *P. rhizophorae*. Thus, light conditions may have been favorable for *P. rhizophorae* regeneration as was reported for other mangrove species (Smith 1987; Ellison and Farnsworth 1993; Duke 2001). *P. rhizophorae* dominated the sapling layer under high light conditions as well as under dense forest canopy at Rio de Jesus. In conclusion, the establishment appears to depend both on light availability and the complex and variable changes in the soil environment as reported by Sherman et al. (2000). However, these variables were not measured in the present study and other natural and anthropogenic factors may influence the distribution of *P. rhizophorae* in the vicinity of the river Rio de Jesus.

The *P. rhizophorae* sapling and small trees abundance (dbh class I) reflect the composition of trees  $\geq 10$  cm (dbh class II). In contrast, *R. racemosa* saplings and small trees (dbh class I) were only found in two out of the six river and center plots although *R. racemosa* trees with  $\text{dbh} \geq 10$  cm were present in all plots. The low number of *R. racemosa* trees belonging to dbh class II in the river and center plots may explain the lack of regeneration as higher chances of successful dispersal has been associated with high adult stem density and distance to parent trees (Delgado et al. 2001). *R. racemosa* regeneration might also be negatively influenced by the presence of the root-boring isopod *Sphaeroma peruvianum* Richardson in the Gulf of Montijo (Seixas 2011). The organism is mainly found in *R. mangle* roots but may affect other species too (Seixas 2011). The presence of the root-boring isopod *Sphaeroma terebrans* in an East African *Rhizophora mucronata* forest caused extensive damage on aerial roots, especially in the lower intertidal zone (Svavarsson et al. 2002). The failure of roots reaching the ground may result in decreased productivity (Cannicci et al. 2008) and may influence mangrove regeneration and forest structure by creating light gaps (Feller 2002). Further studies are required to assess whether the presence of isopods explains the lack of *R. racemosa* regeneration in our study area.

The stem density of dbh class II trees at Rio de Jesus is similar to the values reported for mature coastal and adult riverine *Laguncularia-Avicennia-Rhizophora* stands in French Guiana (Fromard et al. 1998) and other riverine mangroves in the Neotropics (Lacerda et al. 1993). The IV of dbh class II *P. rhizophorae* trees in the river and center plots ( $185 \pm 53$ ) exceeded the value of 153 reported for a mature *P. rhizophorae* forest in Costa Rica (Pool et al. 1977). The existence of *P. rhizophorae* dominated stands in the Gulf of Montijo is of great importance given the limited distribution and restricted genetic variation of *P. rhizophorae* (Castillo-Cardenas and Toro-Perea 2011).

The lower stem density of dbh class II trees in the inland plots (375 stems  $\text{ha}^{-1}$ ) compared to the river and center plots (600 and 710 stems  $\text{ha}^{-1}$ , respectively) may be the result of selective logging. Small-scale mangrove cutting in the Philippines resulted in lower stem density (Walters 2005). However, harvesting may also have an impact on the stem density of smaller sized trees as in some regions mangroves are exploited for poles (Lopez-Hoffman et al. 2006; Blanco et al. 2012). It is likely that logging occurred throughout the Gulf of Montijo before the establishment of the Ramsar Site in 1990. Small-scale tree cutting may still take place especially at the inland margin which is more accessible (Carlos Seixas, personal communication). The set-up of extensive buffer zone around the protected area should be considered to minimize human impacts on the core areas. Based on our dataset it remains unknown if *P. rhizophorae* was harvested to a larger extent than *R. racemosa*. *Rhizophora* spp. is the most commonly harvested mangrove species in Central America but the use of other species such as *P. rhizophorae* has been suggested to minimize the pressure on *Rhizophora* spp. (Windevoxlhel-Lora and Imbach 1999).

Mean stand diameter, height, and basal area measured at Rio de Jesus are within the range reported for a *Pelliciera* dominated stand of Las Perlas Archipelago, Gulf of Panama (McGowan et al. 2010) and a *Rhizophora mangle* dominated forests in Bocas del Toro, Caribbean Coast, Panama (Lovelock et al. 2005). However, our results are at the lower end of the range reported for *Rhizophora-Pelliciera* forests from Costa Rica (Pool et al. 1977), mature and adult *Laguncularia-Avicennia-Rhizophora* stands in French Guiana (Fromard et al. 1998) and *Rhizophora-Laguncularia* dominated stands in the Dominican Republic (Sherman et al. 2003).

Given the uniform climate within the study area the considerable variation in stand structure among plots is likely to be attributed to differences in physical and chemical site conditions such as salinity and nutrient conditions (McKee 1995; Sherman et al. 2003; Lovelock et al. 2005) and disturbance (Walters 2005). The inland plots may have been subjected to small-scale tree cutting lowering stem density and basal area. In contrast, tree growth in the inland plots may have benefited from nutrient inputs through runoff from adjacent agricultural fields and roaming cattle. However, we are unable to disentangle the potential impact of natural and anthropogenic drivers on stand development and structure due to the lack of data on the physical and chemical site conditions and detailed information on tree harvesting for our study plots.

#### Aboveground Biomass

Total aboveground biomass, including dbh class I and II trees, at Rio de Jesus ranged from 76 to 335  $\text{Mg ha}^{-1}$  (average: 176  $\text{Mg ha}^{-1}$ ). Mangrove biomass in this study area was higher than the aboveground biomass (range: 8.3 to

194.3  $\text{Mg ha}^{-1}$ ) estimated in *R. mangle* dominated forests in the Bocas del Toro Archipelago in western Panama (Lovelock et al. 2005). Aboveground biomass in *Rhizophora-Laguncularia-Avicennia germinans-Pelliciera* forests in the Uraba Gulf, Colombia, varied between 31  $\text{Mg ha}^{-1}$  and 188  $\text{Mg ha}^{-1}$  (Blanco et al. 2012). At the southern coast of Costa Rica and several areas of the Panamanian coast, where seasonality is less pronounced and annual rainfall ranges from 2,100 to 6,400 mm, mangrove biomass of up to 280  $\text{Mg ha}^{-1}$  has been measured (Jimenez 1992). In a mature *Rhizophora brevistyla* forest in the vicinity of La Palma, Darien, Eastern Panama, 279  $\text{Mg ha}^{-1}$  were estimated by harvesting 0.25 ha of forest (Golley et al. 1969). Our values are at the upper end of values reported for mangroves in the Neotropics (range: 8 to 394  $\text{Mg ha}^{-1}$ , average: 118  $\text{Mg ha}^{-1}$ ) (Fromard et al. 1998; Sherman et al. 2003; Komiyama et al. 2008) suggesting that this riverine *P. rhizophorae* forest has a high biomass reservoir.

Biomass estimates are strongly influenced by the allometric equation applied and researchers have emphasized that errors will be introduced by applying regressions obtained for mangroves other than the site one is working on (e.g., Day et al. 1987). Our biomass estimates were calculated using the mangrove biomass regression model I (diameter-height-wood density) developed by Chave et al. (2005). The Chave et al. (2005) regression models were established using mangrove biomass and inventory data from locations in the in the Caribbean (Imbert and Rollet 1989; Fromard et al. 1998), where environmental and climatic conditions may differ considerably from the Panamanian Pacific coast. Height measurements impose considerable uncertainties as shown by the wide range in height for a given diameter class (Fig. 2). Thus, we compared Chave et al. (2005) model I with model II (using diameter and wood density only). The average plot biomass calculated across the nine plots did not differ between model I and model II. However, model I underestimated the biomass of *P. rhizophorae* (up to 40 %). The small stature of *P. rhizophorae* (maximum height of 20 m, Tomlinson 1986) and lower wood density may partly explain the difference in biomass compared to *R. racemosa*. Furthermore, *P. rhizophorae* trees were considerably younger (around 30 years) than *R. racemosa* trees (around 80 years) which may explain the observed differences in diameter and height between *R. racemosa* and *P. rhizophorae*.

The use of alternative equations revealed that the Chave et al. (2005) model I and II underestimate biomass by 13 and 25 % compared to species-specific diameter based functions by Fromard et al. (1998) and parabolic volume based function by Sherman et al. (2003), respectively. Direct tree harvest data are not available for the Gulf of Montijo as tree removal within the Ramar site is prohibited. Therefore, it was impossible to assess the quality of the applied allometric regression models. Especially the biomass values for *P. rhizophorae* should be interpreted with care due to *Pelliciera's* specific growth form, low stature and low wood density. Despite its limitation, the

application of Chave et al. (2005) regression model I is a viable option to estimate aboveground biomass in areas where site- and species-specific allometric equations cannot be established.

Our average total biomass estimate ( $176 \text{ Mg ha}^{-1}$ ) matches the biomass value ( $172 \text{ Mg ha}^{-1}$ ) calculated using the pan-tropical linear regression of biomass against the log-transformed ratio of latitude/height (Saenger and Snedaker 1993). This confirms that both structural characteristics and latitude as a surrogate for solar insolation and temperature are good indicators of mangrove stand biomass on a global scale assuming that growth is not limited by unfavourable site conditions (Saenger and Snedaker 1993). The great variability in biomass among the investigated plots cannot be explained by the geographic location and macroclimate. A relevant parameter for describing differences in stand biomass among plots was basal area. The significant positive correlation between biomass and stem density as well as basal area suggests that stand structure is closely related to biomass as has been reported elsewhere (e.g., Fromard et al. 1998). However, the slope of the curves for both stem density and basal area differed between the two dominant species reflecting the distinct characteristics such as stature and wood density. Despite species-specific differences basal area is a good surrogate for aboveground biomass.

## Conclusions

Overall, the stand characteristics of the *P. rhizophorae* were similar to other stands in Central America. The number of saplings and small trees suggests that regeneration is not impeded which is of importance given the threatened status and restricted genetic variation of *P. rhizophorae*. The amount of aboveground biomass in our study plots is substantial and was closely related to the stand structural characteristics. Thus, the protection of these sites is crucial since exploitation of the mangroves would result in the loss of considerable amounts of carbon. Our study also addressed the limitations of non-species specific allometric equations. Due to its specific growth characteristics it is recommended to establish an allometric equation for *P. rhizophorae* in order to improve the biomass estimates for the still existing *P. rhizophorae* mangrove forest in Central America and the Caribbean. Despite its limitations, combining forest structure data with published allometric equations is a viable option in providing a basis for the carbon storage in conservation areas.

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