

# Above-ground biomass changes over an 11-year period in an Amazon monodominant forest and two other lowland forests

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**Abstract** Tropical rain forest dominated by *Peltogyne gracilipes* (Fabaceae) occurs on Maracá Island, Roraima, Brazil, on a range of soil types. Three forest types were stratified for sampling, according to the occurrence of *Peltogyne* trees: (1) *Peltogyne*-rich forest (PRF), (2) *Peltogyne*-poor forest (PPF), and (3) forest without *Peltogyne* (FWP). Biomass increment and change in total stand biomass were calculated from mortality, recruitment, and growth data for trees in the three forest types. Data were derived from permanent plots established in 1991, where all trees ( $\geq 10$  cm diameter at breast height), including palms and vines (lianas), were tagged and measured in three plots, each of 0.25 ha, in each of the three forest types. Field surveys were carried out in October 1991 and March 2003. Over a period of 11 years, the above-ground biomass in all forest types declined

slightly ( $<5\%$ ), associated with the death of large trees, especially in the monodominant forests (PRF and PPF). Within the study period, the forest on Maracá experienced two heavy droughts, related to El Niño events (1997–1998 and 2002–2003) and most mortality and loss of biomass probably occurred during these events. Therefore, as the Maracá forests appear not be increasing in above-ground biomass overall, they may not be acting as a sink for atmospheric CO<sub>2</sub>. The trees of the five most abundant species (*Ecclinusa*, *Lecythis*, *Licania*, *Peltogyne*, and *Pradosia*) accounted for about 55% of the total biomass in both FWP and PPF and for 74% in PRF. *Peltogyne gracilipes* had a stable, regenerating population in PRF, and is clearly a persistent dominant in a monodominant forest.

**Keywords** Amazonia · Biomass increment · Monodominance · *Peltogyne gracilipes*

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## Introduction

Biomass and its dynamics in tropical forests have been considered important parameters in the assessment of both the global carbon cycle and global climate change (Seiler and Crutzen 1980; Fearnside 1997; Laurance et al. 1999; Houghton et al. 2001; Nascimento and Laurance 2002; Brown 2002; Malhi and Wright 2005; Malhi et al. 2006). In this context, the Brazilian Amazon plays an important role due to

its original area of tropical forest of 4 million km<sup>2</sup>, with about 70% of which is still primary forest (Fearnside 2005). Biomass estimates for trees with diameter at breast height (dbh)  $\geq 10$  cm of different Amazonian forest types varies from 76.5% to 81.5% of the total above-ground biomass (Cummings et al. 2002). Although important, few long-term studies have been made on tree diversity and corresponding biomass, and carbon dynamics in tropical forest (Brown et al. 1995). In general, for Amazonian forests most studies are concentrated in the Central Basin (Lewis et al. 2004), reflecting typologies and dynamics distinct from those found in the peripheral regions of Amazonia, such as reported in this paper.

Tree diversity and associated biomass are related to recruitment and mortality of seedlings, saplings, and the accession of small and large trees into the canopy. The storage of carbon in a forest is related to climate, soil structure, nutrient availability, and disturbance (Brünig 1983; Chave et al. 2001; Wright 2005, Zheng et al. 2006). Small changes in the Amazonian forest structure could have global consequences for biodiversity, the carbon cycle, and the rate of climate change (Phillips and Baker 2002). Thus, differences in biomass estimates may be a result of variations in the tree and stand structures within mature forest types.

A peculiar type of rain forest, dominated by large stature *Peltogyne gracilipes* Ducke (henceforth called *Peltogyne*), a legume tree, has been described from Maracá Island and its vicinity, a protected ecological reserve with an established biological station in Roraima, Brazil (Nascimento et al. 1997). The *Peltogyne* forest has been studied since 1991, when permanent study plots were established both within the monodominant *Peltogyne* forest and in stands with no *Peltogyne* individuals. None of the permanent study plots is flooded seasonally, and *Peltogyne* is not restricted to water-saturated soils (Nascimento et al. 1997; Nascimento and Proctor 1997a; Nortcliff and Robison 1998).

The causes and processes that maintain the monodominance of *Peltogyne* are unclear, despite recent studies (Nascimento and Proctor 1997a, b; Villela and Proctor 2002). Previous research has shown that *Peltogyne* has a stable and actively regenerating population with an ability to persist in the understorey (Nascimento and Proctor 1997b). The

generally poor soils on Maracá Island differ between the *Peltogyne*-rich forest (PRF) and that without *Peltogyne* (FWP), in that the PRF soils are much richer in Mg than FWP soils (Nascimento et al. 1997; Nascimento and Proctor 1997a). It is known that Mg has unusually high concentrations in the *Peltogyne* litterfall leaves (Villela and Proctor 1999), thus contributing to the high Mg levels in PRF surface soils (Villela and Proctor 2002). However, the reasons for the elevated concentrations of MG under *Peltogyne*, and its effects on the establishment of other plant species are largely unknown.

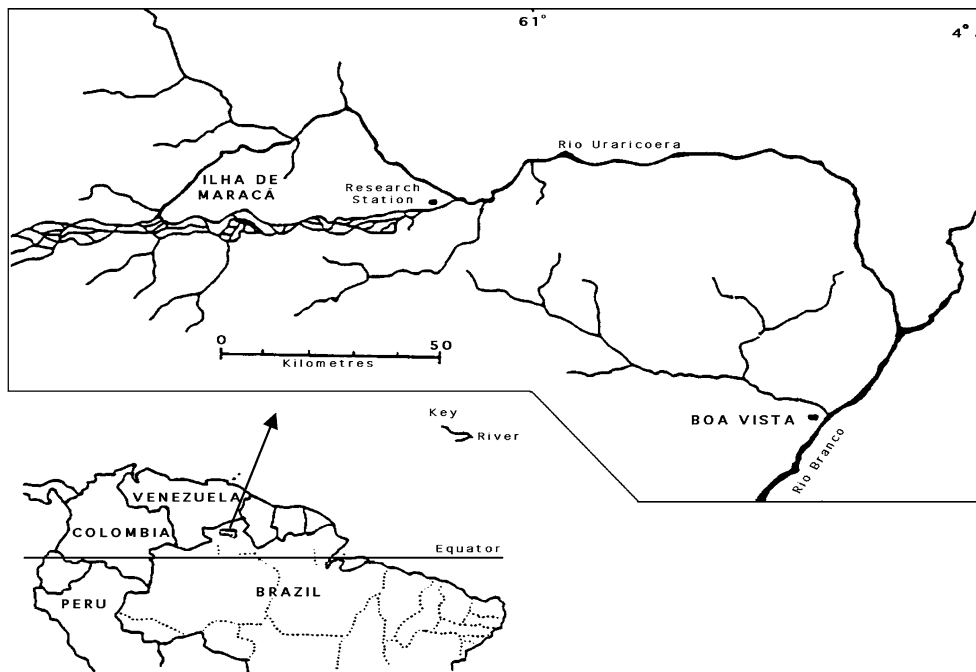
Using data from two censuses (October 1991 and March 2003) conducted on Maracá Island, in FWP, PPF, and PRF, this work reports an analysis of the growth, mortality, recruitment, and above-ground biomass change trees ( $\geq 10$  cm dbh) between the two censuses. Additionally, we test if *Peltogyne* is a persistent dominant (*sensu* Connell and Lowman 1989) as proposed by Nascimento and Proctor (1997b).

We addressed the following questions: (1) what was the temporal variation of above-ground biomass in the monodominant forest and two other low-land forests and (2) what was the biomass change related to growth, recruitment, and mortality of the main tree species found in the three different forest types defined in this study.

## Material and methods

### Study site

Maracá Island is located between 3°15' N and 3°35' N, 61°22' W and 61°58' W in Amajari municipality, Roraima State, northern Brazil, and it is formed by the splitting and rejoining of the Rio Uaricoera (Fig. 1). It has an area of 103,976 ha of which about 84% is covered by forest. About 40% (35,000 ha) is semi-deciduous closed canopy forest, which corresponds to the tropical semi-evergreen rain forest of Whitmore (1984) and 60% is dense lowland *terra firme* forest (evergreen rain forest, Furley et al. 1994; Fragozo et al. 2003). Of the three forest types chosen according to the density of *Peltogyne*, PRF, and PPF, are semi-deciduous forests and FWP is an evergreen rain forest. Most of the semi-deciduous forest on Maracá can be considered as PRF (90%) or PPF (5%), most



**Fig. 1** Location of Maracá Island (*Ilha de Maracá*) in Brazil

frequently in the central area (Milliken and Ratter 1998; Nortcliff and Robison 1998).

From 1986 to 2004 the mean annual rainfall was 2,083 mm (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, IBAMA-RR). In general, the wettest month is July and the driest is February. Mean monthly temperature maxima range from 36.1°C (June–July) to 38.6°C (October–November), with mean monthly minima from 22.3°C (August) to 23.4°C (February). The forests on the eastern part of the island are located at the climatic transition between the savanna subtype (Aw) and monsoon subtype (Am) of the tropical rain climate (A) (Eidt 1968). Further details on the soils and floristic composition of Maracá forests are in Nascimento et al. (1997) and Nascimento and Proctor (1997a).

#### Plot selection and sampling

On 8–16 July 1991, three replicate plots of 50 m × 50 m were established in each of the three forest types. All plots were within an area of 4 km<sup>2</sup>. The distances of the plots from the path were randomly chosen, except for the plots of PPF, which had to be subjectively located since this type of forest was rare.

All individual woody stems ( $\geq 10$  cm dbh), including palms and vines (lianas), in the three 50 m × 50 m replicate plots in each of PRF, PPF, and FWP were recorded, tagged, and their dbh measured between 1 and 14 October 1991. In March 2003, all tagged trees were re-measured and recruits were enumerated and measured. For a few large buttressed trees, especially for *Peltogyne*, the dbh was determined at the trunk immediately above buttresses. Five non-pioneer tree species (*cf.* Swaine and Whitmore 1988) that had a large number of individuals in at least one of the three forest types were selected: *Ecclinusa guianensis* Eyma, *Lecythis corrugata* Poit., *Licania kunthiana* Hook.f., *Peltogyne gracilipes*, and *Pradosia surinamensis* (Eyma) Penn. Henceforth, in this paper, all the species will be referred to by their generic names only.

#### Data analysis

##### *Plant mortality and recruitment*

The annual mortality rates of the individuals (with a range of unknown ages), first measured in October 1991 (recruits were not included) in each forest type were calculated as:

$$m = 1 - [(N_o - N_m)/N_o]^{1/t}$$

and recruitment as:

$$r = [(N_o - N_r)/N_o]^{1/t} - 1$$

where  $N_o$  is the number of individuals at the first measurement;  $N_m$  the number of dead trees;  $N_r$  the number of recruits at the second enumeration, after  $t$  years (Sheil and May 1996);  $t = 11.4$  years.

#### Above-ground biomass

Above-ground dry biomass of each individual was estimated from dbh using an allometric equation for trees in Central Amazonia elaborated by Chambers et al. (2001), and being suggested by Baker et al. (2004) as one of the basic equations for estimating biomass in the Amazon region:

$$AGB = \text{Exp} \left[ 0.333 \times \ln(\text{dbh}) + 0.933 \times \ln(\text{dbh})^2 - 0.122 \times \ln(\text{dbh})^3 - 0.37 \right],$$

where  $AGB$  is the above-ground dry biomass (kg);  $\text{dbh}$  the diameter at breast height (cm).

Other equations suggested by Baker et al. (2004) were not used due to lack of data for specific gravity of wood or measurements of trees >5 cm dbh. Total biomass for each plot and in each census was considered to be the sum of the biomass of all live individuals.

Change in total stand mass and above-ground biomass increment were calculated as described in Clark et al. (2001):

$$\Delta M_{\text{stand}} = AGB_{t2} - AGB_{t1},$$

$$\Delta M_t = AGB_G + AGB_R,$$

where  $AGB_{t1}$  is the above-ground biomass of individuals at time 1 (1991 census);  $AGB_{t2}$  the above-ground biomass of individuals at time 2 (2003 census);  $AGB_G$  the above-ground biomass increment of all surviving individuals between censuses;  $AGB_R$  the biomass increment of recruitment.

To calculate  $AGB_R$  it is necessary to subtract the estimated biomass of each recruit at census 2 (March 2003) from the biomass of a standard tree of 10 cm dbh, as suggested by Clark et al. (2001).

For each forest type, the allocation of AGB in different diameter classes (10 cm diameter classes starting at 10 cm dbh and continuing through to diameter class >60 cm) was considered.

For all variables, confidence intervals (95% CI) were calculated as the mean  $\pm$  ( $t_{0.05}$ )  $\times$  mean standard error (Zar 1984).

## Results

### Recruitment and tree mortality

In March 2003, after 11 years, a total of 44, 34, and 47 recruits were found in PRF, PPF, and FWP, respectively. Recruitment was similar among forests with the mean number of recruits per 0.25 ha plot being 14.7 for PRF, 11.3 for PPF, and 15.7 for FWP ( $p = 0.58$ , by one-way ANOVA,  $n = 3$ ). Recruitment rates ranged from 0.83% in PPF to 1.25% year<sup>-1</sup> in FWP (Table 1).

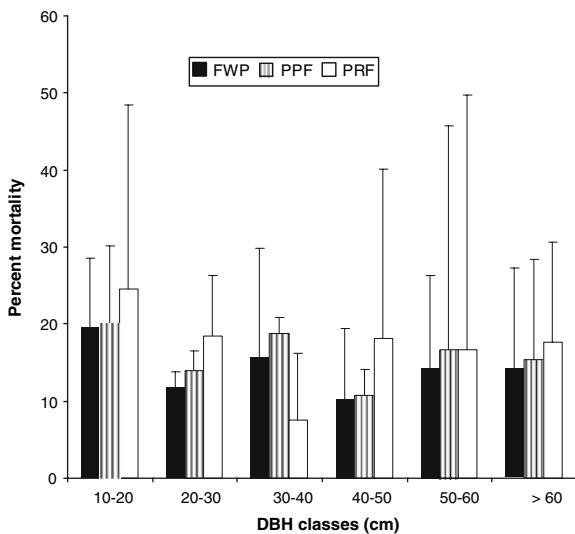
A total of 65 (mean per plot of  $21.7 \pm 4.2$  s.d., in PRF), 57 ( $19 \pm 1.7$  in PPF) and 52 trees ( $17.3 \pm 4.2$  in FWP) were found dead, representing 16.9% (PRF), 16.7% (PPF), and 16.8% (FWP) of all trees in the forest plots. As with recruitment, no difference was observed for mortality among forests ( $p = 0.38$ , by one-way ANOVA,  $n = 3$ ).

Despite the low-overall variation in mortality during 1991–2003 found for FWP and PPF, PRF showed a higher percent mortality in the 10–20 cm dbh class (Fig. 2). The biomass loss was highest in the largest class (trees >60 cm dbh), especially in PRF and PPF (Fig. 3). The annualised mortality rate for each forest type was 1.61% year<sup>-1</sup> (PRF), 1.59% year<sup>-1</sup> (PPF), and 1.61% year<sup>-1</sup> (FWP) and these values were not significantly different (Chi-square = 0.31,  $df = 1$ ,  $p < 0.05$ ). However, the mortality rates had a tendency to be higher in PRF for all species combined. Mortality was consistently higher than recruitment throughout the measurement period, with the imbalance being most pronounced in PPF (Table 1).

Annual recruitment rates of the five study species over the 11-year period in the three forest types were, in general, lower than the annual mortality rates. Only *Peltogyne* and *Pradosia* in the PRF showed recruitment higher than mortality (Table 1).

**Table 1** Annualised mortality (m) and recruitment (r) rates (% year<sup>-1</sup>) for trees ≥10 cm dbh of the five study species over the 11-year period in three forest types on Maracá Island, Roraima, Brazil. FWP, forest without *Peltogyne*; PPF, *Peltogyne*-poor forest; and PRF, *Peltogyne*-rich forest

Species	PRF		PPF		FWP	
	r	m	r	m	r	m
<i>Ecclinusa</i>	0.56	1.22	1.66	1.39	0.74	0.81
<i>Lecythis</i>	0.00	1.20	0.90	1.27	0.41	1.84
<i>Licania</i>	–	–	0.00	0.79	0.00	0.78
<i>Peltogyne</i>	1.76	0.96	0.53	1.16	–	–
<i>Pradosia</i>	0.70	0.50	0.00	1.52	0.00	0.72
All species	0.96	1.61	0.83	1.59	1.25	1.61

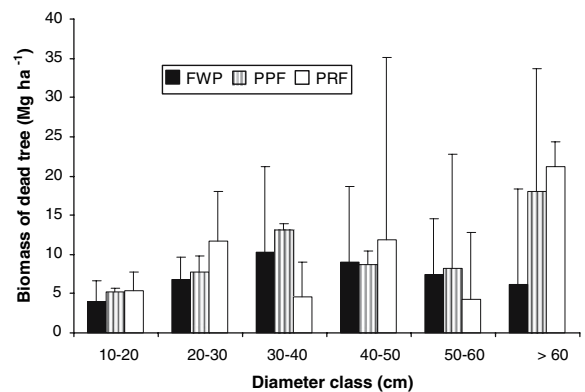


**Fig. 2** Size distribution of dead trees in different dbh classes in three forest types on Maracá Island, Roraima, Brazil. FWP, forest without *Peltogyne*; PPF, *Peltogyne*-poor forest; and PRF, *Peltogyne*-rich forest. Error bars are +95% confidence limits

All the five most abundant species showed lower mortality than the forest average. Among them, *Pradosia* had the lowest mortality rate. The highest values of tree mortality were 1.84% year<sup>-1</sup> for *Lecythis* in FWP and 1.52% year<sup>-1</sup> for *Pradosia* in PPF (Table 1).

Estimated above-ground biomass

Above-ground mean biomass across the three forest types averaged 359.6 ± 38.0 Mg ha<sup>-1</sup> (mean of nine plots ± 95% CI) at census 1 and 343.4 ± 32.7 Mg ha<sup>-1</sup> at census 2, showing a slightly decrease (4.5%) in AGB over the entire study period



**Fig. 3** Dead trees recorded in different dbh classes in three forest types on Maracá Island, Roraima, Brazil. FWP, forest without *Peltogyne*; PPF, *Peltogyne*-poor forest; and PRF, *Peltogyne*-rich forest. Error bars are +95% confidence limits

(Table 2). Thus, loss of biomass due to mortality and other losses slightly exceeded AGB gains from growth and recruitment.

Although there was a tendency of AGB to be higher in PRF and PPF at both censuses (Table 2), no significant difference was found among forests ( $p = 0.37$ , by one-way ANOVA,  $n = 3$  for the 1991 census and  $p = 0.42$ , for the 2003 census in 2003) with forests showing similar values of AGB (PPF = 384.3 ± 46.7 Mg.ha<sup>-1</sup> in 1991 and 362.9 ± 91.2 Mg ha<sup>-1</sup> in 2003, PRF = 369.1 ± 198.2 Mg ha<sup>-1</sup> and 351.4 ± 157.4 Mg ha<sup>-1</sup>, and FWP = 325.6 ± 41.2 Mg ha<sup>-1</sup> and 315.9 ± 17.1 Mg ha<sup>-1</sup>).

In all cases, the changes in total stand mass in the study period were negative: -17.8 Mg ha<sup>-1</sup> (PRF), -21.5 Mg ha<sup>-1</sup> (PPF), and -9.7 Mg ha<sup>-1</sup> (FWP), and representing a decline in AGB of 3% (FWP), 4.8% (PRF), and 5.6% (PPF).

**Table 2** Average values of stem density, total basal area, total above-ground biomass (AGB<sub>T</sub>), above-ground biomass change ( $\Delta M_{\text{stand}}$ ), above-ground biomass of survival (AGBg) and above-ground biomass of recruits over an 11-year period in Maracá forests (FWP, forest without *Peltogyne*; PPF, *Peltogyne*-poor forest; and PRF, *Peltogyne*-rich forest)

Forest	Life forms	Census 1 (Oct 1991)			Census 2 (Mar 2003)			Difference		
		Density	Basal area	AGB <sub>T</sub>	Density	Basal area	AGB <sub>T</sub>	$\Delta M_{\text{stand}}$	Increment	
		N ha <sup>-1</sup>	m <sup>2</sup> ha <sup>-1</sup>	Mg ha <sup>-1</sup>	N ha <sup>-1</sup>	m <sup>2</sup> ha <sup>-1</sup>	Mg ha <sup>-1</sup>		AGBg	AGBr
FWP	Trees	367	24.41	302.0	364	23.82	292.1	-9.9	27.4	0.9
	Palms	37	2.02	23.1	40	2.05	23.3	0.1	1.3	1.1
	Vines	4	0.06	0.5	4	0.07	0.5	0.1	0.1	0.0
	Total	408	26.49	325.6	408	25.94	315.9	-9.7	28.7	2.0
PPF	Trees	403	29.93	359.0	380	28.17	339.5	-19.5	34.6	1.5
	Palms	40	2.18	25.0	35	1.99	23.0	-1.9	0.9	0.0
	Vines	3	0.04	0.4	3	0.04	0.4	0.0	0.0	0.0
	Total	445	32.16	384.3	417	30.21	362.8	-21.5	35.6	1.5
PRF	Trees	449	29.36	344.2	443	28.34	330.2	-14.0	35.5	1.1
	Palms	39	2.16	24.7	31	1.81	21.0	-3.7	0.9	0.3
	Vines	3	0.03	0.2	1	0.02	0.2	-0.1	0.2	0.0
	Total	491	31.55	369.1	475	30.17	351.4	-17.8	36.6	1.3

Most of the total biomass was concentrated in the trees (93%); woody lianas and palms accounted for 6% and 0.1%, respectively (Table 2).

#### Biomass distribution in different dbh size-classes

Most of the tagged individual stems were in the smallest dbh classes (10–20 cm and 20–30 cm) with a reversed-J shape in all cases (Fig. 4). All forest types showed a relative AGB contribution skewed to the largest size classes, especially PRF and PPF (Fig. 4). Stems of 10–30 cm in diameter constituted more than 65% of all stems, but accounted for only 18–25% of AGB. In contrast, trees >60 cm dbh made up only 2–4.6% of stems, but totalled about 11–35% of AGB.

The pattern of distribution of the number of stems and the allocation of plant biomass to different dbh classes in the three forest types in 2003 were very similar to those in 1991 (Fig. 4), not showing much change in forest structure over the 11-year measurement period.

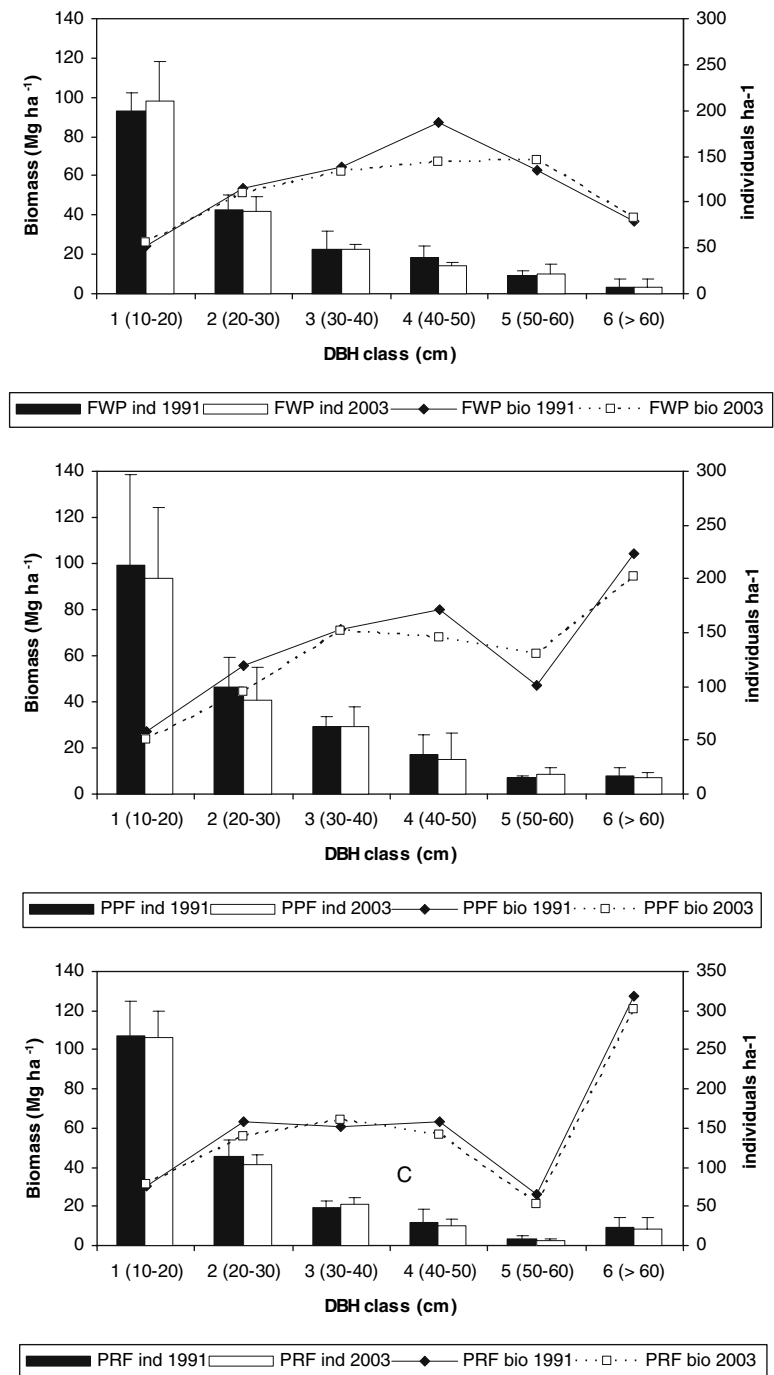
It is noteworthy that in the PRF only *Peltogyne*, of all the five selected species, occurred as large trees (>60 cm dbh) reaching a maximum dbh of 143.2 cm. For the other species, the maximum dbh in the PRF was 30.4 cm (*Licania*), 38.6 cm

(*Ecclinusa*), 39.2 cm (*Lecythis*), and 47.4 cm (*Pradosia*). In the PPF, half the *Peltogyne* trees were  $\geq 50$  cm dbh (maximum of 132.6 cm). The other species occurred in this forest mainly as small trees with few reaching >60 cm. The highest sizes of trees of the other selected species in FWP were 49.3 cm (*Ecclinusa*), 54.2 cm (*Lecythis*), 76.4 cm (*Licania*), and 77.6 cm (*Pradosia*).

#### Biomass allocation among different tree species

The biomass of the five most important species (*Ecclinusa*, *Lecythis*, *Licania*, *Peltogyne*, and *Pradosia*) accounted for about 74% of the total in the PRF and 55% in both FWP and PPF (Table 3). The average biomass among tree species in each forest type varied, ranging from 0.68 Mg ha<sup>-1</sup> for *Licania* in PRF, in 2003 to 209.26 Mg ha<sup>-1</sup> for (*Peltogyne* in PRF in 1991 (Table 3). Thus, *Peltogyne*, the dominant species in PRF and PPF, accounted for 55% and 19% of the total biomass in these forest types, respectively, while in the FWP *Licania*, the most important species, contributed only 20% to the total biomass in both censuses (1991 and 2003), followed by *Pradosia* that accounted for c. 15% of the total biomass.

**Fig. 4** Size distribution of trees, the number of stems and the allocation of aboveground biomass (AGB) in different dbh classes in three forest types on Maracá Island, Roraima, Brazil. *FWP*, forest without *Peltogyne*; *PPF*, *Peltogyne*-poor forest; and *PRF*, *Peltogyne*-rich forest. Error bars are +95% confidence limits



**Discussion**

Tree mortality and recruitment

Rates of mortality (*c.* 1.6% year<sup>-1</sup>) found for the three forest types on Maracá Island were very similar

and are within the range of 1.0–2.0% reported for tropical forest (Swaine et al. 1987; Phillips and Gentry 1994; Condit et al. 1995; Lewis et al. 2004; Rolim et al. 2005). However, as pointed out by Lewis et al. (2004), mortality, recruitment, and turnover rates decline with increasing census interval and in

**Table 3** Change in biomass allocation of plants (dbh  $\geq 10$  cm) over an 11-year period and the percentage of total above-ground biomass (AGB<sub>T</sub>) for the five most important species*(Peltogyne, Pradosia, Ecclinusa, Lecythis and Licania)* in Maracá forests. *FWP*, forest without *Peltogyne*; *PPF*, *Peltogyne*-poor forest; and *PRF*, *Peltogyne*-rich forest

Forest type	Species	Census (1991) (Mg ha <sup>-1</sup> )	% AGB <sub>T</sub>	Census (2003) (Mg ha <sup>-1</sup> )	% AGB <sub>T</sub>	Increment (Mg ha <sup>-1</sup> ) AGB <sub>g</sub> + AGB <sub>r</sub>
FWP	<i>Peltogyne gracilipes</i>	0.00	0.0	0.00	0.0	0.00
	<i>Licania kunthiana</i>	69.51	21.3	62.83	19.9	9.67
	<i>Pradosia surinamensis</i>	52.42	16.1	47.13	14.9	14.07
	<i>Ecclinusa guianensis</i>	49.38	15.2	47.57	15.1	8.27
	<i>Lecythis corrugata</i>	13.02	4.0	14.21	4.5	6.93
PPF	<i>Peltogyne gracilipes</i>	75.77	19.7	64.39	17.7	19.56
	<i>Licania kunthiana</i>	39.07	10.2	39.04	10.8	6.43
	<i>Pradosia surinamensis</i>	51.70	13.5	45.84	12.6	9.13
	<i>Ecclinusa guianensis</i>	41.06	10.7	36.20	10.0	8.10
	<i>Lecythis corrugata</i>	18.94	4.9	15.09	4.2	8.19
PRF	<i>Peltogyne gracilipes</i>	206.09	55.8	188.05	53.5	48.98
	<i>Licania kunthiana</i>	1.56	0.4	0.68	0.2	0.87
	<i>Pradosia surinamensis</i>	28.11	7.6	31.08	8.8	8.97
	<i>Ecclinusa guianensis</i>	25.01	6.8	24.31	6.9	9.87
	<i>Lecythis corrugata</i>	14.94	4.0	16.20	4.6	8.57

comparisons among rates this effect should be taken into account. Thus, considering a census interval of 11 years, Maracá forests showed rates in the upper limit found for other sites from Amazonia, such as Manaus (Brazil), Paracou (French Guiana), and Southeast Peru (*cf.* Lewis et al. 2004).

In accordance with Swaine et al. (1987) for tropical forests, mortality rate at Maracá was independent of tree size, but differed among species and forest type. *Peltogyne* had greater recruitment than mortality in PRF, suggesting that this species is a persistent dominant (*sensu* Connell and Lowman 1989).

Studies of tropical tree dynamics have shown that in the absence of extensive disturbance or environmental changes old-growth tropical forests have tree recruitment rates equal to mortality (Swaine et al. 1987; Phillips and Gentry 1994; Lewis et al. 2004; Stephenson and van Mantgem 2005). However, in the Maracá forest plots the number of recruits after 11 years was lower than the number of dead trees for the same period. Since these forests had not experienced any recent significant disturbance such as fire, high winds, extensive thinning, or selective logging, we suggest that this result might be related to environmental factors, in particular to El Niño

Southern Oscillation (ENSO) events. Several authors have reported an increase in tree mortality following a severe drought or an ENSO event (Lieberman and Liberman 1987; Condit et al. 1995; Williamson et al. 2000; Barlow and Peres 2004; Rolim et al. 2005; Meir and Grace 2005). Amazonian rain forests, especially those located at the margin of rain forest distribution, as is the case of the Roraima forests, suffered strong ENSO events in 1997–1998 and 2002–2003 (Barbosa and Fearnside 1999; Barbosa et al. 2003) which resulted in a vast area of forest being destroyed by fire (Barbosa and Fearnside 2000; Nascimento et al. 2000). Although there is a lack of detailed information on forest dynamics from pre-ENSO and ENSO periods for the Maracá forests, it is expected that most tree mortality registered for the Maracá forests should have occurred during or just after an ENSO event.

#### Maracá forest types and biomass estimates

Total above-ground biomass of Maracá forests (average about 350 Mg ha<sup>-1</sup>) is within the range found for Amazonian forests, from 200 to 400 Mg ha<sup>-1</sup> (Fearnside et al. 1993; Clark et al. 2001; Malhi et al. 2006).



Recent studies in tropical forests on changes in dynamics (Phillips and Gentry 1994; Phillips et al. 1998; Malhi and Grace 2000; Chave et al. 2001; Baker et al. 2004; Lewis et al. 2004) have shown two widespread changes: increase in tree stem turnover and increase in above-ground biomass. However, the Maracá forest data indicated a slight decrease (4.5%) in above-ground biomass during an 11-year period, suggesting that rates of recruitment and tree growth are not being sufficient to replace lost stems and basal area. Rolim et al. (2005) have also found a reduction of forest biomass in an Atlantic tropical moist forest over a 22-year period (1978–2000). They related this reduction to strong climatic disturbances caused by ENSO events. The same may well apply to Maracá forests, located in northern most Brazilian Amazonia.

Very large trees have been reported to concentrate up to a quarter of the above-ground biomass (Clark and Clark 1996). On Maracá, FWP had less of the AGB (10.7%) accumulated in the largest trees (>60 cm dbh), while PPF (27%) and PRF (35%) were over the 25% mark. Among the Maracá forest types, PRF and PPF seem to be accumulating more biomass/carbon than the FWP. This result is related to the numerous occurrences of large *Peltogyne* trees. Several studies (Brown et al. 1995; Clark and Clark 1996; Sheil et al. 2000; Nascimento and Laurence 2002) have shown the effect of large trees in the AGB estimates. Very large trees are considered as important sinks for carbon (Clark and Clark 1996).

Although our plots are towards the lower limit of size that is used for biomass estimation in tropical forests (Clark et al. 2001; Chave et al. 2005), the lack of significant differences in AGB among Maracá forest types has to be interpreted with caution due to small number of replicates ( $n = 3$  of 0.25-ha plots in each forest type).

In conclusion, a net loss of *c.* 5% of the original above-ground biomass in Maracá forests are suggesting that stands are declining in AGB because the rate of recruitment is not sufficient to replace lost stems and basal area.

Data in this paper suggest that *Peltogyne* has a stable, regenerating population in PRF and is clearly a persistent dominant in a monodominant forest (*sensu* Connell and Lowman 1989) and that Maracá forests are not increasing in above-ground biomass and therefore they may not be acting as a sink for

atmospheric CO<sub>2</sub>. To ascertain this, additional studies on coarse dead wood and below-ground biomass, are required.

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