Changes in Forest Structure and Biomass over Ten Years in a Lowland Amazonian Forest

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Abstract

The topographic effects on biomass and its increment were evaluated for a *terra-firme* forest near Manaus, Brazil. We established three plots (60×60 m) on a plateau and at the bottom of a valley (namely *baixio*), and measured stem diameter at breast height D (> 10 cm) for tree and palm species in 2002 and 2012. Small trees (10 cm $> D > 5$ cm) were measured in subplots (20×60 m) within each plot. We also estimated tree height with the D – tree height H relationship model based on a hundred samples of the tree species in each topography. The aboveground biomass AGB was estimated as 315.4 $\pm$ 33.2 (average $\pm$ SE) Mg ha^{-1} on the plateau, which was higher than 224.2 $\pm$ 20.3 Mg ha^{-1} in *baixio* though the difference was statistically marginal ($p = 0.09$). The difference in AGB was partly ascribed to the decrease of H for large trees and a lack of large trees whose $D > 80$ cm at the *baixio* site. The AGB of palm species in *baixio* was 2.7 $\pm$ 0.87 Mg ha^{-1}, which was higher than 0.24 $\pm$ 0.08 Mg ha^{-1} on the plateau though the difference was statistically insignificant ($p = 0.11$). On the other hand, the increment of AGB did not differ significantly between the two sites ($p > 0.05$), and the variation of AGB increment among the plots was mainly ascribed to the variation of biomass loss caused by mortality.

Discipline: Forestry and forest products
Additional key words: biomass increment, topography, Amazon

Introduction

An assessment of forest biomass in tropical forests is essential for studies on ecosystem productivity, which is crucial for a better understanding of global climate change (Fearnside 2003). There are large variations of biomass in the Amazon, such as the aboveground biomass (AGB) reportedly ranging from 155 to 492 Mg ha^{-1} (Houghton et al. 2001). In a lowland Amazonian forest, namely the *terra-firme* forest, the topographic effects on the edaphic factors are distinct, and the plateau and bottom of the valley (here-inafter referred to as *baixio*) are generally characterized by clayish and sandy soils, respectively (Ferraz et al. 1998). The relatively infertile sandy soil in *baixio* as compared to the clayish soil on the plateau could result in higher biomass on the plateau than in *baixio* (Castilho et al. 2006). On the other hand, studies on the topographic effects on biomass increment are apparently scarce except for the short-term research (at two-year intervals) by Castilho et al. (2010).

In the present study, we conducted repeated measurements of biomass for two types of topographic features (plateau and *baixio*) that included tree and palm species, in

order to elucidate the effects of topography on biomass and its temporal change (at 10-year intervals) for a *terra-firme* forest in the central Amazon. To estimate the biomass, we considered differences in the diameter relative to the breast height D – tree height H relationship between the two topographic types, as a previous study found that the $D-H$ relationship changed according to a topographic gradient in an Amazonian forest (Suwa et al. 2013).

Materials and Methods

1. Study sites
This study was conducted in the ZF-2 experimental forest of the National Institute for Amazon Research (INPA) near Manaus, Brazil. The annual precipitation there is 2,547 mm on average. Rainfall is more or less evenly distributed throughout the year with some dryer months (< 100 mm per month) from July to October. The annual mean temperature is 25.8°C and shows no distinct seasonal change. The main type of vegetation is evergreen tropical moist lowland forest defined as *terra-firme* forest, which grows on clay rich Oxisols on plateaus, and on spodosols at *baixio* (Ferraz et al. 1998). The study plots were established within an 18 ha inventory plot (300 m × 600 m) called "Quadradão" (2°36′S, 60°08′E), where both plateau and *baixio* were involved. In each topography, three study plots (60 m × 60 m) were set with at least 20-m intervals between the plots. The distance between the selected plateau and *baixio* sites is about 200 m, and the difference in altitude between both sites is about 25 m, where the *baixio* areas are seasonally inundated.

2. Tree census
A tree census was carried out in 2002 and later in 2012. The stem diameter at breast height (hereafter "D") was measured for all individual trees whose $D > 10$ cm. In addition, D was measured for small trees ($5 < D < 10$ cm) in a sub plot (20 m × 60 m) established in each plot. In 2012, tree height (hereafter "H") was measured for at least 30 trees in each plot using a laser range finder (TruPulse 220, Laser Technology, Inc., USA). The sample trees were selected to cover a wide range of D regardless of species. For palm species, H was measured for all individual trees in 2012.

3. Models and Statistics
stem diameter D – tree height H model

The $D-H$ relationship was fitted to the following hyperbolic model (cf. Suwa et al. 2013):

$$H = \left(\frac{1}{aD} + \frac{1}{H_{max}} \right)^{-1} \tag{1}$$

where a and H_{max} denote a coefficient and an asymptotic tree height, respectively. The model was fitted to the dataset obtained for each topographic type (plateau and *baixio*). To examine the difference in the fitted $D-H$ relationship models between both topographic types, one-way ANOVA was conducted based on the residual sum of squares (RSS) when the pooled data were regressed, and on the sum of RSS when data for each site were regressed separately (Aiba and Kohyama 1997). Nonlinear regression analyses were conducted using the nls function of statistical software R ver. 3.2.1 (R Core Team 2015).

4. Estimation of biomass stock increment
For estimating aboveground biomass in Mg ha^{-1} (AGB), the aboveground mass (hereafter "*AGM*") of tree species in kilograms was estimated with the following model (Silva 2007):

$$AGM = 0.0323 \, (D^2H)^{0.991} \tag{2}$$

where the dimensions of D and H are indicated in units of centimetres and meters, respectively. This model was developed in a *terra-firme* forest near the present study site. H was estimated from the established $D-H$ relationship models in each topography. To estimate the *AGM* of palm species, the following allometric model was applied (Saldarriaga et al. 1988):

$$AGM = 0.001697D^{1.754}H^{2.151} \tag{3}$$

where H was assumed as being constant for each palm species according to a previous study (Castilho et al. 2006), the mean value of H for each species was used (as the palm species dataset showed very poor fitting to the $D-H$ model), and the average H values (13.2 m for *Euterpe precatoria*, 12.3 m for *Oenocarpus bacaba*, 13.2 m for *Oenocarpus minor*, 8.3 m *Mauritiella armata*, and 15.2 m for *Oenocarpus bataua*) were applied.

The aboveground biomass increment in Mg ha^{-1} 10-yr^{-1} (hereafter "Δ*AGB*") was estimated as the differences in *AGB* (Mg ha^{-1}) between the two tree censuses in 2002 and 2012. Δ*AGB* can be reduced to the following three components: Δ*AGB* = $G + RC - M$, where G denotes the sum of individual tree growth, RC the sum of biomass of recruited individual trees, and M the sum of biomass loss caused by tree mortality. To test the difference in biomass or its related components between the two topographic types, the student's *t*-test was applied. To evaluate the relationships between the biomass components, Pearson's correlation coefficient r was also calculated.

Results and Discussion

1. Forest structure and biomass
In total, 935 individual trees including seven palm trees were measured on the plateau, and 953 individual

trees including 75 palm trees were measured at *baixio* in 2002 (Table 1). In total, 177 tree species and six palm species were identified. A total of 121 individual trees were identified at the genus level, but 36 individual trees were not identified. According to the number of individual trees, the top five dominant trees in ascending order were *Eschweilera coriacea*, *Protium hebetatum*, *Pouteria guianensis*, *Goupia glabra*, and *Nectandra cuspidata* for the plateau, and *Mabea paniculata*, *E. coriacea*, *P hebetatum*, *E. precatoria*, and *Mabea taquari* for *baixio*. The maximum *D* values were 101 cm and 74 cm for the plateau and *baixio*, respectively.

A total of 100 trees were measured in *H* in each topographic type. The maximum *H* values were recorded as 38 m and 33 m for the plateau and *baixio*, respectively. The $D - H$ relationships were well fitted to Eq. 1 in each topographic type (Fig. 1, $R^2 = 0.93$ and 0.85 for plateau and *baixio*, respectively), and differed significantly between the two topographic types (ANOVA, $p < 0.001$). Coefficient *a* did not show any significant difference between the two topographic types, while H_{max} was significantly higher on the plateau than at *baixio* (Table 2) due to the differences in *H* for large trees ($D >$ ca. 30 cm). Similarly, Suwa et al. (2013) also found that H_{max} decreased at *baixio* in a *terra-firme* forest near the present study site. The plateau and *baixio* sites in the present study are characterized by clayish and sandy soils, respectively, and *baixio* areas are seasonally inundated. Duivenvoorden (1996) reported that the canopy height was higher at well-drained sites than at poorly drained sites in an upper Amazonian region. Aiba and Kitayama (2002) suggested that the high allocation of biomass to height growth was related to productive

Table1. **Structural parameters for *plateau* and *baixio* are shown. Values regarding the number of individual trees, number of species, and maximum diameter at breast height (*D*) and aboveground biomass (*AGB*) were summarized based on the tree census in 2002. The number of species means the recorded number of species except for some unidentified individual trees (see the body text for details). Maximum *H* was measured directly in 2012. Parenthesized values denote standard error.**

Structural attributes	*Plateau*	*Baixio*
Number of individual trees (ha⁻¹)		
Tree species ($5 < D < 10$ cm)	650.0 (58.3)	733 (134.1)
Tree species (10 cm $< D$)	642.6 (21.8)	589.8 (25.9)
Palm species ($5 < D < 10$ cm)	2.8 (2.8)	44.4 (15.5)
Palm species (10 cm $< D$)	5.6 (1.6)	33.3 (11.6)
Total	1300.9 (46.8)	1400.9 (112.3)
Number of species		
Tree species	143	139
Palm species	3	4
Total	146	143
Maximum *D* (cm)		
Tree species	101	74
Palm species	18	23
Maximum *H* (m)		
Tree species	38	33
Palm species	17	21
AGB (Mg ha⁻¹)		
Tree species ($5 < D < 10$ cm)	11.7 (1.0)	12.2 (2.6)
Tree species (10 cm $< D$)	303.5 (33.7)	209.3 (22.2)
Palm species ($5 < D < 10$ cm)	0.03 (0.03)	0.60 (0.15)
Palm species (10 cm $< D$)	0.21 (0.07)	2.06 (0.88)
Total	315.4 (33.2)	224.2 (20.3)

environments in a tropical Malaysian rainforest. Accordingly, such stressful conditions as sandy and nutrient-poor soils with seasonal inundation could explain the decrease in canopy height at *baixio*. Although we also measured H for palm species, Eq. 1 showed a very poor fitting to the $D - H$ relationship ($R^2 = 0.07$). Similarly, Goodman et al. (2013) reported that the $D - H$ relationship was weak for a dataset involving different palm species in the Amazon. This is because the $D - H$ relationships varied among species, though some species reportedly showed an apparently positive $D - H$ relationship, such as *Euterpe precatoria* (Silva et al. 2015) and *Iriartea deltoidea* (Goodman et al. 2013).

For tree species, AGB on the plateau was estimated as 315 ± 33 (SE) Mg ha^{-1}, which was higher than $224 \pm$ 17 Mg ha^{-1} in *baixio* though the difference was statistically weak (*t*-test, $p = 0.09$). Similarly, several previous studies reported that *terra-firme* forests showed higher AGB on a plateau than in *baixio* (Laurance et al. 1999, Castilho et al. 2006, Suwa et al. 2010). The palm biomass was estimated in *baixio* as 2.66 ± 0.87 Mg ha^{-1}, which was approximately ten times higher than 0.24 ± 0.08 Mg ha^{-1} on the plateau though the difference was insignificant (*t*-test, $p = 0.11$). Castilho et al. (2006) suggested that palm biomass was higher on the plateau than in *baixio* for a *terra-firme* forest.

In each topographic type, the number of stems decreased in line with a higher D-class and the *baixio* showed a lack of large trees whose $D > 80$ cm (Table 3). As a result, AGB showed two maximum peaks in the 30-40 cm and
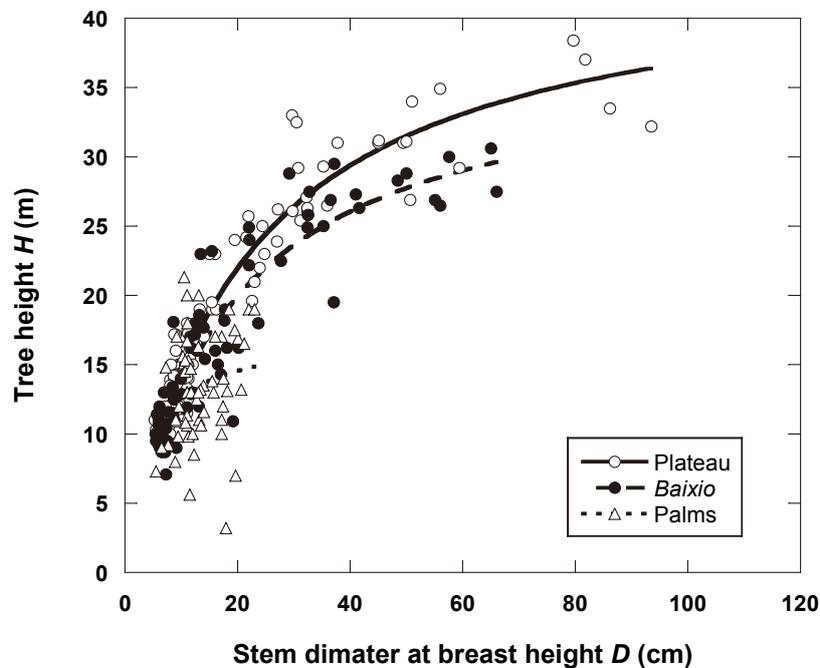

Fig. 1. Stem diameter at breast height (***D***) and tree height (***H***) relationships for tree species on the plateau (open circles and a solid line, ***n*** = 100) and in ***baixio*** (closed circles and a dashed line, ***n*** = 100), and palm species (open triangles and a dotted line, ***n*** = 60). The ***D*** – ***H*** relationships were fitted to Eq. 1 (***R***² = 0.931, 0.849 and 0.067 for ***plateau, baixio*** and palm species, respectively).

Table 2. The estimated coefficients of a (m cm^{-1}) and H_{max} (m) in Eq. 1 for tree species in *plateau* and *baixio*, and palm species are shown with the coefficient of determination R^2. Parenthesized values denote the 95% confidence interval *CI*.

Types	n	a	H_{max}	R^2
Plateau	100	2.18 (2.03-2.33)	44.3 (41.8-46.8)	0.93
Baixio	100	2.12 (1.87-2.37)	37.6 (34.1-41.1)	0.85
Palm	60	4.61 (-0.31-9.53)	17.3 (11.8-22.8)	0.07

80-90 cm classes on the plateau, while *AGB* showed one maximum peak in the 20-30 cm class in *baixio* (Fig. 2). Thus, the existing large trees (*D* > 80 cm) partly explained the relatively high *AGB* on the plateau. Silk et al. (2013) suggested that the number of large trees (*D* > 70 cm) tends to explain the variation of *AGB* among different tropical forests on the basis of a large dataset involving South America, South East Asia, and Africa. The small number of large trees in *baixio* may be explained by the stressful environments characterized by seasonal inundation and infertile sandy soils, though Castilho et al. (2006) reported that the number of large trees (*D* > 70 cm) was not explained by topographic parameters alone.

2. Forest dynamics and aboveground biomass increment

During the study period from 2002 to 2012, 85 trees (including two palm trees) and 193 trees (including 35 palm trees) were recruited into the plateau and *baixio* sites, respectively. On the other hand, 156 trees (including two palm trees) and 227 trees (including 14 palm trees) were recorded as being dead on the plateau and *baixio*, respectively (Table 4). The resultant mortality by *D*-class differed insignificantly between the two topographic types (Fig. 3, ANOVA, $F_{1, 34} = 2.905$, $p = 0.10$), and the size-related mortality rate showed a similar pattern ($r = 0.812$, $p = 0.03$), where the mortality rate decreased to a minimum peak in the middle-sized class (about 20-40 cm in *D*), increased to a maximum peak in the 40-50 cm *D*-class, and dropped slightly in the largest *D*-class. The size-related mortality is generally explained by multiple factors including species-specific characteristics, age, recent growth, environmental conditions, and the competitive effects of neighboring trees and their interactions (e.g. Shimatani et al. 2008). When the datasets of different species were pooled as done in the present study, different patterns of size-related mortality have been reported. For instance, Condit et al. (1995) found that the mortality of smaller trees (*D* < 10 cm) was higher than that of larger trees on Barro Colorado Island, Panama. Conversely, Chao et al. (2008) reported a constant mortality rate regardless of size class in northwestern Amazonia. In the present study, both the plateau and *baixio* sites interestingly showed the same ladle-shaped pattern of mortality, suggesting that a similar mortality event had controlled the forest dynamics of both sites during the study period from 2002-2012, regardless of different floristic compositions and environmental conditions resulting from different topographies. Although confirming whether such mortality event actually occurred at the present study site is rather difficult, several disturbance events such as blowdown (Nelson et al. 1994) and severe drought (Lewis et al. 2011) have been reported as the candidate factors causing mass mortality in the Amazon region.

ΔAGB was estimated as -1.78 ± 14.96 and 7.51 ± 5.75 Mg ha^{-1} 10 yr^{-1} on the plateau and *baixio*, respectively. The growth of surviving individual trees (*G*) was estimated as 45.46 ± 1.71 and 45.57 ± 3.16 Mg ha^{-1} 10 yr^{-1} on the plateau and *baixio*, respectively. The biomass of recruitment *RC* was estimated as 5.18 ± 1.85 and 9.06 ± 2.77 Mg ha^{-1} 10 yr^{-1} on the plateau and *baixio*, respectively. The biomass loss caused by mortality (*M*) or dead trees was estimated as 52.42 ± 14.68 and 47.11 ± 8.43 Mg ha^{-1} 10 yr^{-1} on the plateau and *baixio*, respectively. However, ΔAGB, *G*, *RC* and *M* did not differ significantly between the two topographic

Table 3. Number of individual trees (ha^{-1}) and aboveground biomass (*AGB*) (Mg ha^{-1}) for each stem diameter *D*-class of tree and palm species in 2002.

| Plateau	No. of individual trees	%	*AGB*	%
D-classes				
5 - 10 cm	650	50	11.7	3.7
10 - 20 cm	406.5	31.2	43.3	13.7
20 - 30 cm	122.2	9.4	50.9	16.2
30 - 40 cm	67.6	5.2	62.6	19.8
40 - 50 cm	23.1	1.8	41.5	13.1
50 - 60 cm	9.3	0.7	24.2	7.7
60 - 70 cm	6.5	0.5	24.3	7.7
70 - 80 cm	2.8	0.2	17.2	5.4
80 - 90 cm	2.8	0.2	21.1	6.7
90 - 100 cm	0.9	0.1	8.4	2.7
100 cm <	0.9	0.1	10	3.2
Palm species	8.3	0.6	0.2	0.1
Baixio	No. of individual trees	%	*AGB*	%
D-classes				
5 - 10 cm	733.3	52.3	12.2	5.4
10 - 20 cm	377.8	27	39.3	17.6
20 - 30 cm	128.7	9.2	49.8	22.2
30 - 40 cm	44.4	3.2	39	17.4
40 - 50 cm	21.3	1.5	32.4	14.5
50 - 60 cm	11.1	0.8	25.5	11.4
60 - 70 cm	5.6	0.4	18.8	8.4
70 - 80 cm	0.9	0.1	4.5	2
80 - 90 cm	0	0	0	0
90 - 100 cm	0	0	0	0
100 cm <	0	0	0	0
Palm species	77.8	5.6	2.7	1.2
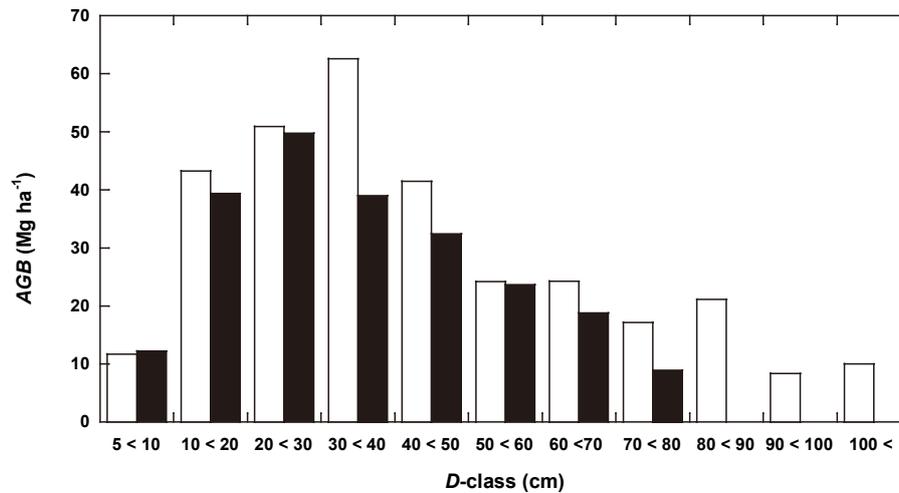
Fig. 2. Distribution pattern of aboveground biomass *AGB* according to the size class of stem diameter at breast height (*D*) in two topographic types (open and closed bars mean *plateau* and *baixio*, respectively).

Table 4. Number of recruited individual trees n_r (ha⁻¹ 10-yr⁻¹) and dead individual trees n_d (ha⁻¹ 10-yr⁻¹) for each stem diameter *D*-class of tree and palm species.

Plateau

D-classes	n_r	%	n_d	%
5 - 10 cm	42	48.3	46	29.5
10 - 20 cm	38	43.7	64	41
20 - 30 cm	2	2.3	17	10.9
30 - 40 cm			16	10.3
40 - 50 cm			7	4.5
50 - 60 cm			1	0.6
60 cm <			3	1.9
Palm species	5	5.7	2	1.3

Baixio

D-classes	n_r	%	n_d	%
5 - 10 cm	87	45.1	76	33.5
10 - 20 cm	71	36.8	95	41.9
20 - 30 cm			24	10.6
30 - 40 cm			8	3.5
40 - 50 cm			7	3.1
50 - 60 cm			1	0.4
60 cm <			2	0.9
Palm species	35	18.1	14	6.2

types (*t*-test, p = 0.61, 0.98, 0.32 and 0.77 for ΔAGB, G, RC and M, respectively). Similarly, Castilho et al. (2010) reported that the relationship of ΔAGB to topographic or edaphic factors was unclear in a *terra-firme* forest based on a large dataset covering 72 ha. As a result of correlation analysis (Fig. 4), G and RC showed an insignificant correlation to ΔAGB (G, r = 0.463, p = 0.355; RC, r = -0.357, p = 0.487), while ΔAGB showed an apparent negative correlation to M (r = -0.956, p = 2.80 × 10⁻²). Thus, the biomass loss caused by mortality (M) was the most important factor in determining ΔAGB in the present study. In particular, larger trees were more important for estimating ΔAGB than smaller trees, as the large trees whose D > 30 cm showed contributions of 74% and 56% to M on the plateau and *baixio*, respectively (Table 5). In contrast, Castilho et al. (2010) reported that ΔAGB was mainly explained by G in a *terra-firme* forest. In Amazonian forests, ΔAGB generally changes spatiotemporally and could be related to multiple factors including disturbance regimes, species composition, and soil fertility (Phillips et al. 2004). In the present study, M was detected as being the most influential component in determining ΔAGB, which suggests that the forests being studied might experience such disturbance events as blow-down (Nelson et al. 1994) and severe drought (Lewis et al. 2011) during the interval between censuses (2002-2012).
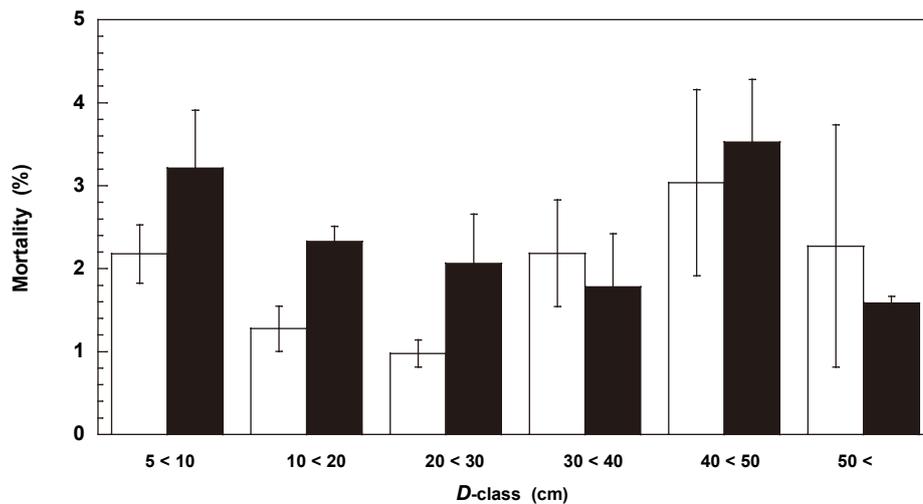
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Fig. 3. Distribution of mortality according to size class of stem diameter at breast height (*D*) in two topographic types (open and closed bars mean *plateau* and *baixio*, respectively). Error bars mean standard error.
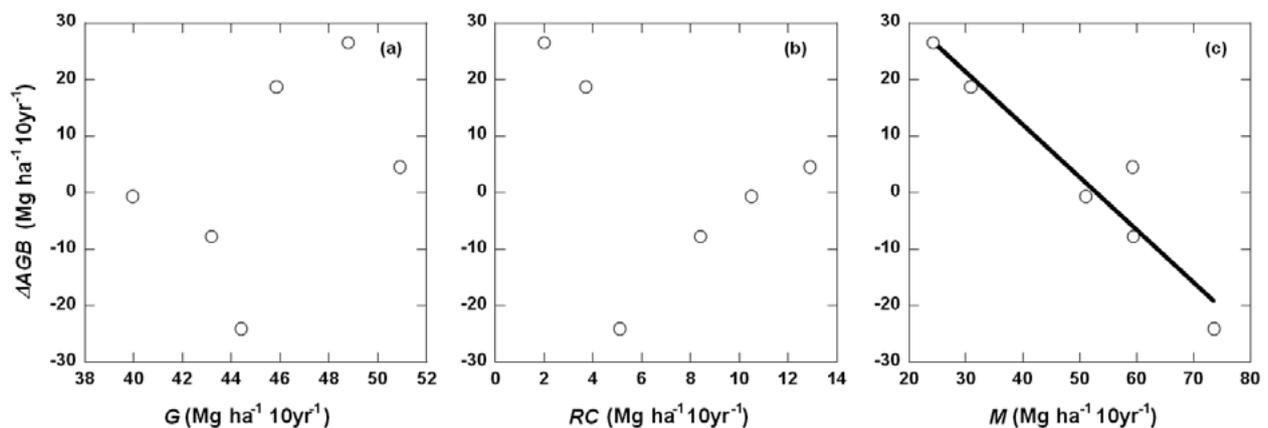

Fig. 4. Relationships of aboveground biomass increment (Δ*AGB*) to (a) growth (*G*) of surviving individual trees, (b) biomass of recruitment (*RC*), and (c) biomass loss caused by mortality (*M*), respectively. The solid line denotes a significant negative linear relationship between Δ*AGB* and *M*.

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Table 5. Aboveground biomass increment (ΔAGB) (Mg ha^{-1} 10-yr^{-1}), growth of surviving individual trees (G) (Mg ha^{-1} 10-yr^{-1}), biomass of recruitment (RC) (Mg ha^{-1} 10-yr^{-1}), and biomass loss caused by mortality (M) (Mg ha^{-1} 10-yr^{-1}) for each stem diameter D-class of tree and palm species.

Plateau

D-classes	ΔAGB	G	R_c	M
5 - 10 cm	2.85	3.05	1.55	1.76
10 - 20 cm	8.16	12.21	2.35	6.4
20 - 30 cm	4.38	9.46	0.53	5.61
30 - 40 cm	-4.67	9.37	0.66	14.71
40 - 50 cm	-8.19	2.93	0	11.12
50 - 60 cm	0.41	2.54	0	2.13
60 - 70 cm	-9.84	0.79	0	10.64
70 - 80 cm	1.96	1.96	0	0
80 - 90 cm	2.96	2.96	0	0
90 - 100 cm	0.1	0.1	0	0
100 cm <	0.04	0.04	0	0
Palm species	0.07	0.04	0.08	0.05

Baixio

D-classes	ΔAGB	G	R_c	M
5 - 10 cm	5	5.11	3.13	3.24
10 - 20 cm	8.51	12.47	4.83	8.79
20 - 30 cm	2.77	10.87	0	8.1
30 - 40 cm	-0.45	6.34	0	6.79
40 - 50 cm	-5.55	4.11	0	9.65
50 - 60 cm	2.75	4.71	0	1.96
60 - 70 cm	-1.76	1.71	0	3.47
70 - 80 cm	-4.46	0	0	4.46
80 - 90 cm	0	0	0	0
90 - 100 cm	0	0	0	0
100 cm <	0	0	0	0
Palm species	0.7	0.25	1.1	0.64

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