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Effects of fire on above-ground forest biomass in the northern Brazilian Amazon

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Abstract: Fires can significantly affect the structure, floristic composition and biomass content of tropical forests, which are not adapted to this disturbance. To assess the impact of understorey fires on above-ground biomass, this study was conducted in the northern Brazilian Amazon (Roraima state), where uncontrolled forest fires are recurrent. Fifty plots (0.25 ha each) distributed across five fire disturbance classes were inventoried. Losses in biomass stocks were significant (–57% and –63%) for forests that suffered from recurrent fires and progressively occurred until some point between 3 and 7 y after the last fire, as deduced from previous studies. Twelve years after a fire event, biomass stocks were reconstituted, although differences in the floristic composition were associated with greater fire severity, particularly driven by the dominance of the *Cecropia* spp. In thrice-burned forests, live biomass reached levels of secondary forests of the same region. For large trees (> 50 cm dbh), the reduction (–54%) in biomass was significant in thrice-burned areas. These findings highlight the threat that fires represent for tropical rain forests and emphasise the need for long-term surveys in order to distinguish between the effects of fire severity, fire frequency and time-since-fire artefact.

Key Words: above-ground biomass, Amazon, carbon emissions, forest fire, tropical rain forest

INTRODUCTION

Fire occurrence generally increases after large-scale droughts in the Amazon (Alencar *et al.* 2006, 2011; Aragão *et al.* 2007, Bush *et al.* 2008, Yang *et al.* 2011). In 1997–1998, the region suffered from the influence of the El Niño–Southern Oscillation (ENSO), which contributed to one of the most important mega-fires in the world with 3.9 million ha of burned forests and up to 0.329 Pg of biomass loss (Alencar *et al.* 2006). In the state of Roraima (northern Amazon), up to 1.4 million ha of primary forest were affected (Barbosa & Fearnside 1999), which highlights the prominence of fires as a threat to these forests that should not normally burn (Cochrane & Laurance 2002).

Uncontrolled fire incidents results in a wide diversity of ecological effects (Bowman *et al.* 2009), altering forest structure and floristic composition. Amazonian studies have demonstrated the higher mortality of small-diameter trees in recently burned areas (Barlow *et al.*

2003, Cochrane & Schulze 1999), whereas an increase in mortality of larger trees (≥ 50 cm dbh) has been reported 1–3 y after a fire (Barlow *et al.* 2003). A positive relationship was found between tree mortality and char height, which can be used as a proxy of fire intensity (Balch *et al.* 2011, Barlow *et al.* 2003).

Fire can dramatically reduce living biomass in tropical forests (Haugaasen *et al.* 2003, Slik *et al.* 2008), even to the same degree as logging activities (Gerwing 2002). In Amazonian forests, Cochrane & Schulze (1999) estimated average biomass losses of 80%, 50% and 10% in heavily, moderately and lightly burned areas, respectively. Three years after the fire, the biomass had recovered to 49% of that of a neighbouring unburned forest and the loss of 107 Mg ha^{–1} was attributed to the delay in mortality of trees ≥ 50 cm in stem diameter (Barlow *et al.* 2003). Balch *et al.* (2011) reported losses of 32% and 21% with respect to the initial above-ground live biomass in once- and thrice-burned forests, respectively, with trees < 30 cm dbh significantly contributing to the total dead biomass. Thus, fire may be a critical factor for determining carbon balance in tropical forests (Balch *et al.* 2008, Zarin *et al.* 2005).

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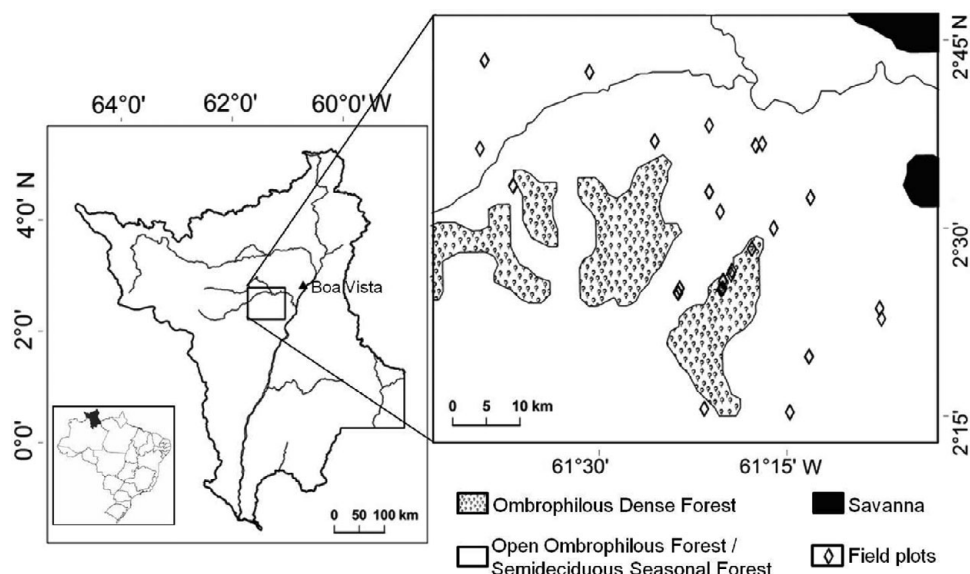


Figure 1. Location of the study area in northern Brazilian Amazon (state of Roraima) and of the sample plots used in data analysis. The 50 inventoried plots are not all distinguishable due to their proximity.

Tree species composition may have a considerable impact on the response of a forest to fire, as the probability of mortality is species-dependent (Balch *et al.* 2011, Brando *et al.* 2012, Slik *et al.* 2010). Fire tends to favour species that can tolerate heat stress and to increase the abundance of pioneer species (Barlow & Peres 2008, Slik *et al.* 2010), at least in the short term (Cochrane & Schulze 1999).

Ecosystems can normally recover from disturbances. However, frequent and severe fires can offset this balance. As a result, the ecosystem may lose the ability to recover, which could lead to its collapse with the loss of their major ecological functions. We hypothesize that fire disturbances of increasing frequency and severity, associated with shorter recovery times, may lead to declines in biomass and in species diversity. In this study, we examined the impact of single and repeated forest fires of different intensities on the above-ground live biomass.

STUDY SITE

This study was conducted in the Apiaú and Roxinho region in the central part of the state of Roraima, northern Brazilian Amazon (Figure 1). This region contains many rural land grants concentrated along the roads. Fires, which occur more frequently during the dry season, have historically been used for forest conversion and pasture maintenance, occasionally causing accidental fires in primary forests. Thus, in the study area, these fires are mainly understorey fires that escape from neighbouring pastures and reach the forest. The region was identified as the centre of the Great Fire of Roraima (Fearnside

et al. 2007), which occurred in 1998 and was strongly influenced by ENSO.

The average annual precipitation is approximately 2000 mm (Barbosa & Fearnside 1996), and the dry season extends from December to March. The topography is gently undulating to hilly predominantly 100–180 m asl (Fearnside *et al.* 2007). Soils are acidic and poor in nutrients (Barbosa & Fearnside 1996). The natural vegetation mosaic is composed of tropical rain forests, tropical open forests and tropical semideciduous forests, which are located close to savannas (IBGE 1992).

METHODS

Field sampling and data collection

Field work was conducted in January and February of 2010. Plots (25 × 100 m) were set up in unburned primary forests and across different classes of fire-damaged primary forests (Table 1). The level of fire disturbance was defined in terms of the times of recurrence (fire frequency). The level of burn damage (severity) was also characterized for the areas that burned in 1998. Severity classes were defined based on historical information from remote-sensing data, locally obtained from landowner interviews and especially from results of IBAMA (1998) on post-fire mortality of trees, fuel quantity, scorch height and damage levels. Based on IBAMA (1998), 50% of the area where plots are located was affected only at the understorey level (lightly burned), whereas 30% was affected by stronger fires that reached the understorey and canopy levels (heavily burned). The

Table 1. Plot characterization and distribution across fire disturbance classes in northern Brazilian Amazon. *N* is the number of plots.

Fire disturbances classes (code)	Year(s) of fire occurrence(s)	<i>N</i>	Area (ha)
Unburned forest (UF)	–	8	2
Once lightly burned forest (BF1L)	1998	8	2
Once heavily burned forest (BF1H)	1998	10	2.5
Twice-burned forest (BF2)	1998, 2003	14	3.5
Thrice-burned forest (BF3)	1998, 2003, 2007	10	2.5
Total		50	12.5

rest of the area (20%) was not affected by fire. In addition, field work observations on tree density and the general aspect of understorey supported the classification of the areas affected in 1998 in terms of severity. There were no signs of logging activities or history of other degradation type in the inventoried area.

Within each georeferenced plot, dbh and height were obtained for all individuals (trees, palms, bamboos and pseudostems of *Phenakospermum guyannense* with dbh ≥ 10 cm. Tree heights were estimated visually by one of us (J. R. dos Santos) and then each tree height was modelled according to Gonçalves & Santos (2008). The identification of morphospecies was performed from dendrological characteristics. Species nomenclature and family classification were adjusted to the Tropicos database (cite URL Tropicos.org 2012).

Above-ground biomass estimation

Five allometric equations were used to estimate individual above-ground living dry biomass (Table 2), hereafter simply called biomass. For tree species (other than *Cecropia* spp.), we compared estimates from the allometric equations developed by Brown *et al.* (1989) and Chave *et al.* (2005), which are frequently employed in the Amazon Basin. Because there was no significant difference between them (ANOVA; $\alpha = 0.05$), we decided to use the biomass values resulting from the allometric equation presented by Chave *et al.* (2005).

Above-ground biomass (AGB) was defined as the cumulative tree biomass whereas the total above-ground biomass (TAGB) was defined as the sum of the biomass of all individual trees, palms and *P. guyannense* pseudostems

(dbh ≥ 10 cm). Bamboos, which occurred in just one plot, were not included in the estimation of TAGB. Carbon content of biomass was assumed to be 50% (Fearnside 1997).

Analysis of fire impacts on forest above-ground live biomass, structure and diversity

Comparisons of the mean AGB and TAGB among the five fire disturbance classes were based on one-way analyses of variance (ANOVA) after checking each treatment for normality with Shapiro–Wilk's test (Shapiro & Wilk 1965) and for homoscedasticity with Bartlett's test (Snedecor & Cochran 1989). The Tukey's multiple comparison test was then used to identify significant differences ($\alpha = 0.05$) among the groups. This method was also used to assess changes in the contributions of each diameter size class to AGB, with or without considering individuals of the *Cecropia* spp. It is important to note that differences in AGB and TAGB between unburned and burned forests are indicative of direct reductions by fire as well as delayed mortality. Biomass gains incorporate growth of surviving trees in addition to the establishment of new individuals.

Floristic composition across plots was compared based on the species and families with the highest contributions to AGB. Shannon's diversity index (H') and the importance value index (IVI), determined only for tree species, were assessed in relation to AGB. Finally, a principal coordinate analysis (PCO) was performed using the Bray–Curtis similarity measure and species abundance in order to identify floristic composition gradients within the classes.

RESULTS

General characteristics

A total of 5593 individuals were measured across all plots (12.5 ha). The sample was composed of 177 species (83 identified only to the generic level and 19 unidentified) distributed across 122 genera and 53 families. For the unburned forest plots, the mean (\pm SD) density of trees, mean (\pm SD) dbh and mean (\pm SD) basal area were $310 \pm$

Table 2. Allometric equations used to estimate above-ground live biomass (*Y*) per individual (kg) in each species group in northern Brazilian Amazon. ρ is the specific gravity (g cm^{-3}), *Ht* is total height (m) and dbh is diameter at breast height (cm).

Species group	Allometric equation	Equation source	ρ
Generic trees	$\ln Y = -2.98 + \ln(\rho \times \text{dbh}^2 \times \text{Ht})$	Chave <i>et al.</i> (2005)	0.69 (Fearnside 1997)
Generic trees	$\ln Y = -3.11 + (0.97 \times \ln(\text{dbh}^2 \times \text{Ht}))$	Brown <i>et al.</i> (1989)	
Urticaceae (<i>Cecropia</i> spp.)	$\ln Y = -2.51 + 2.43 \times \ln(\text{dbh})$	Nelson <i>et al.</i> (1999)	
Palms	$\ln Y = -6.38 - 0.88 \ln(1/\text{dbh}^2) + 2.15 \ln(\text{Ht})$	Saldarriaga <i>et al.</i> (1988)	
<i>P. guyannense</i> (pseudostems)	$\ln Y = -2.98 + \ln(\rho \times \text{dbh}^2 \times \text{Ht})$	Chave <i>et al.</i> (2005)	0.31 (Baker <i>et al.</i> 2004)

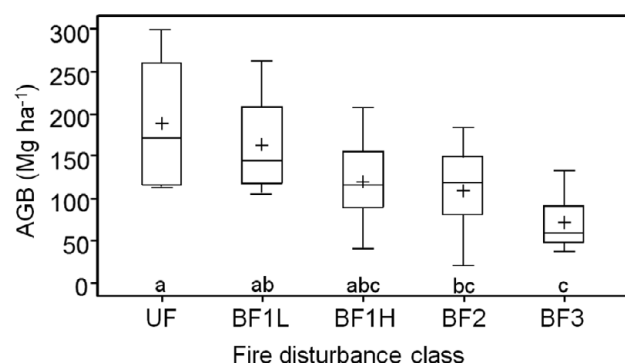


Figure 2. Boxplots showing the gradual effect of fire frequency and severity on mean above-ground living biomass (AGB in Mg ha^{-1}) in northern Brazilian Amazon. UF = unburned forest; BF1L = once lightly burned forest; BF1H = once heavily burned forest; BF2 = twice-burned forest and BF3 = thrice-burned forest. Different letters (a, b and c) associated with the fire disturbance classes indicate significant differences according to the Tukey's test ($\alpha = 0.05$).

28 ind. ha^{-1} , 23 ± 15 cm and 18 ± 5 $\text{m}^2 \text{ha}^{-1}$, respectively. A Shannon index (H') of 4.02 was obtained for the UF plots considering only the tree species.

Effects of fire on above-ground live biomass

Significant differences in AGB were found between the fire disturbance classes, indicating a gradual effect of successive fires on biomass (Figure 2). The mean AGB ranged from 70 ± 32 Mg ha^{-1} in thrice-burned forest (BF3) to 188 ± 78 Mg ha^{-1} in unburned forest (UF). According to the Tukey's test, the mean AGB was not significantly different among the UF, the once lightly (BF1L) (163 ± 57 Mg ha^{-1}) and the once heavily (BF1H) (119 ± 52 Mg ha^{-1}) burned forest plots. UF plots had significantly higher levels of AGB than twice- (BF2) (108 ± 48 Mg ha^{-1}) and thrice- (BF3) (70 ± 32 Mg ha^{-1}) burned forest plots, which showed mean reductions of biomass stocks of 57% and 63%, respectively.

The loss of biomass between UF and BF1H (37%) was about three times greater than the difference between UF and BF1L (13%). BF1H presented an intermediate degree of degradation, as its mean biomass was not significantly different from either the two less-disturbed classes (UF and BF1L) or the most disturbed classes (BF2 and BF3). The presence or absence of *Cecropia* spp. from the analysis did not change the results.

In UF plots, carbon storage in the living AGB was estimated at 94 Mg C ha^{-1} . After a single fire event, this stock was reduced to 81 Mg C ha^{-1} in BF1L and to 59 Mg C ha^{-1} in BF1H. The latter value is close to the 54 Mg C ha^{-1} found in BF2. In BF3, 35 Mg C ha^{-1} remained stored in living AGB, indicating a difference of 59 Mg C ha^{-1} of carbon in relation to UF plots.

The mean contribution of palms and *P. guyannense* pseudostems to the TAGB reached approximately 5%

Table 3. Variation in biomass values for fire disturbance classes (UF = unburned forest; BF1L = once lightly burned forest; BF1H = once heavily burned forest; BF2 = twice-burned forest and BF3 = thrice-burned forest) in northern Brazilian Amazon. AGB = above-ground live biomass (mean \pm SD); TAGB = total above-ground live biomass (mean \pm SD). The values of AGB and TAGB were not significantly different, considering each class, according to the Tukey's test ($\alpha = 0.05$).

Class	AGB (Mg ha^{-1})	TAGB (Mg ha^{-1})
UF	188 ± 78	195 ± 74
BF1L	163 ± 57	171 ± 58
BF1H	119 ± 52	127 ± 50
BF2	108 ± 48	111 ± 48
BF3	70 ± 32	74 ± 33

(Table 3) considering the five classes, while the palms alone contributed 3.2% (4.2 Mg ha^{-1}). The low biomass contributions of palms and *P. guyannense* explained the similar results of the ANOVA and Tukey's test between AGB and TAGB (Table 3). In UF plots, the mean contribution of palms to TAGB was estimated at $6.81 \pm 6.94 \text{ Mg ha}^{-1}$ or 3%. Palm contributions to TAGB were substantial in UF and BF1L (4%) plots, whereas *P. guyannense* pseudostems were most important in BF1H plots (4%).

Effects of fire on biomass in relation to tree size distribution

The distribution of mean AGB values in dbh sizes ≤ 50 cm did not show a clear pattern with respect to fire disturbance classes, except for the BF3, in which the mean AGB decreased when compared with the other ones (Figure 3a). However, mean AGB was significantly lower in UF3 than in UF or BF1L. For the dbh class greater than 50 cm, the AGB differences were more evident and progressively decreased as the level of fire disturbance increased (Figure 3a). However, the only significant difference was observed between UF and BF3 plots. For these large trees, AGB from the BF1L to BF3 fire disturbance classes was reduced by 21%, 45%, 50% and 54% relatively to the UF. We also noted that the mean contribution of ≤ 50 cm dbh trees was similar to that of > 50 cm dbh trees in unburned plots. In these plots, differences in tree density of small (293 ind. ha^{-1}) and large (17 ind. ha^{-1}) trees highlighted the major contributions made by a few large trees to the AGB in primary undisturbed forests. The only gain in biomass observed in burned forests, in relation to UF, occurred in the BF1L among the < 50 cm dbh trees.

Because the individuals of *Cecropia* spp. (pioneer species that are common in burned areas) had generally less than 30 cm in diameter, the removal of this genus only altered the biomass in the smaller size classes (Figure 3b). For example, in the fire disturbance classes BF1H, BF2 and

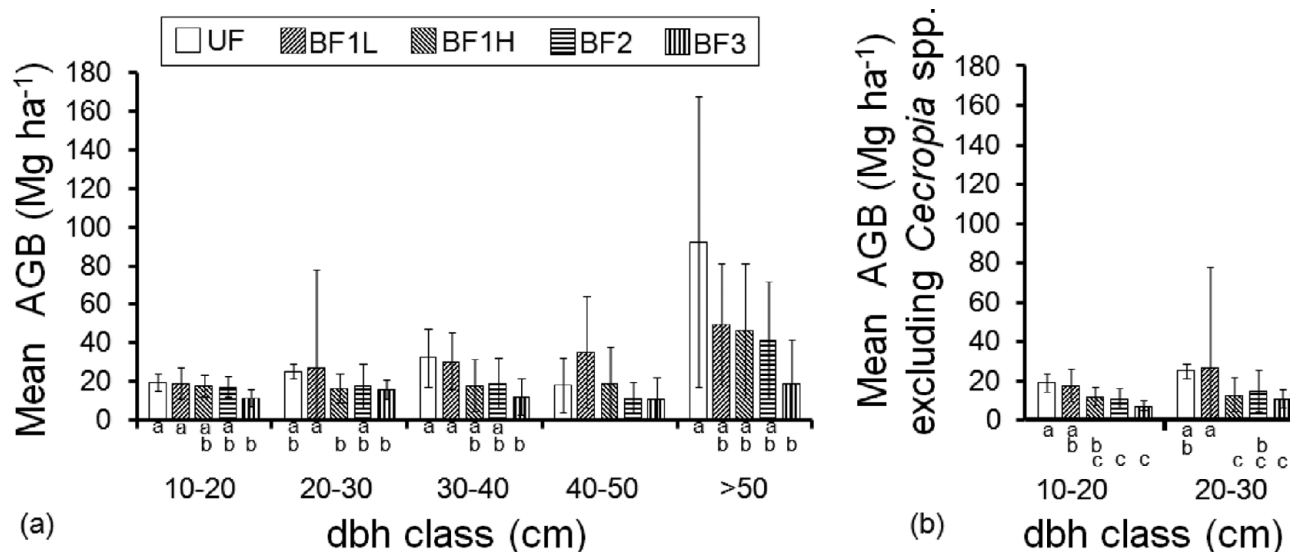


Figure 3. Fire effects on the above-ground biomass content by tree size classes in northern Brazilian Amazon. Mean values considering all tree species, merging large (> 50 dbh cm) individuals (a) and considering only small individuals (dbh ≤ 30 cm) other than the *Cecropia* spp. (b), by fire disturbance classes: UF = unburned forest; BF1L = once lightly burned forest; BF1H = once heavily burned forest; BF2 = twice-burned forest and BF3 = thrice-burned forest. Different letters (a, b and c) associated with the fire disturbance classes indicate significant differences by dbh class according to Tukey's test ($\alpha = 0.05$). For the 40–50 dbh class, the data did not fulfil the requirements for ANOVA.

BF3, removal of these species from the 10–20-cm dbh class resulted in biomass losses of 32%, 36% and 34%, respectively. As a result, differences in biomass between these heavily disturbed forests and unburned or lightly burned forests were accentuated.

Species contributions to biomass

For the five species with the highest contributions to AGB, mean dbh generally decreased and mean density increased with fire disturbance (Appendix 1). These trends were partially driven by individuals of *Cecropia leucocoma* Miq., which made notable contributions to AGB in the BF1H as well as in the more heavily burned classes, also with increasing IVI. Similar results were found for *Pouteria* sp., whereas *Protium* sp. made major contributions to AGB in the UF, BF1L, BF1H and BF2 plots (approximately 9%) and it was not an important species in BF3 plots. These selected tree species were mainly classified as non-pioneer species, except in the thrice-burned forest. *Vochysia* sp. and *Manilkara huberi* (Ducke) A. Chev., two species of economic interest, had the highest AGB values in BF1L.

Concerning palm species, *Oenocarpus bacaba* Mart. was present with highest abundance in UF and BF1L plots, while *Maximiliana martiana* H. Karst. was more frequent in BF2 and BF3 plots. However, *Maximiliana martiana* made the highest contribution to biomass among all palms in every fire disturbance class except BF1L.

The contribution of Leguminosae to AGB decreased with increasing fire disturbance and reached 5% in BF3 (Appendix 1). The contribution of Vochysiaceae showed

values close to 1% in BF1H, BF2 and BF3. The Sapotaceae made high contributions to AGB in all classes and no clear trend in relation to fire damage was detected. The Burseraceae, another predominant family, contributed to AGB up to BF3, where the contribution fell to 4%. The Apocynaceae made a substantial contribution to AGB in BF1H plots (16%) but only accounted for 2% in the other classes. The AGB contribution of Urticaceae, represented by two species of *Cecropia*, increased with fire damage. The contribution of Sapindaceae to AGB increased slightly in the most damaged plots (Appendix 1).

Relationships between plant diversity, biomass and fire disturbance

The highest mean diversity of tree species (H') was found in the UF class (4.02). BF1L and BF1H plots, which only differed in fire severity, exhibited the greatest difference in diversity between two successive classes (3.95 and 3.14, respectively, or -22%). A significant reduction in diversity was observed in BF1H in relation to UF plots (-28%), even 12 y after the fire. Conversely, BF1L plots showed only minor reductions in diversity after the same recovery time. Similar and lower values of H' were found for BF2 and BF3 (2.90 and 2.89, respectively).

H' was positively related to AGB (Figure 4). An outlier plot was removed from the regression (in BF1H, $\text{AGB} = 207 \text{ Mg ha}^{-1}$; $H' = 1.81$) because the abnormal biomass value could be mostly explained by two trees. For the BF1H and BF2, there was a positive relationship between AGB and H' . For the UF, BF1L and BF3 classes, no

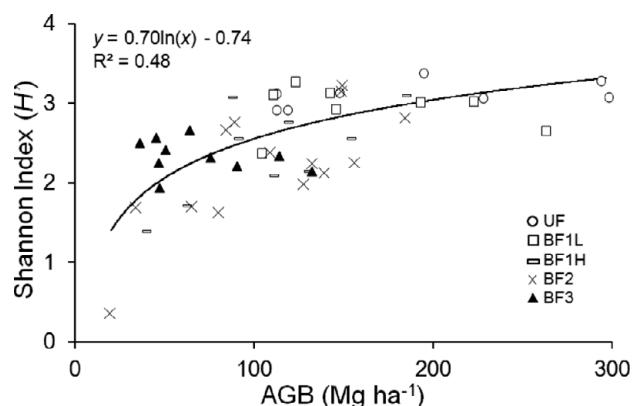


Figure 4. Logarithmic relationship between AGB and H' for the full set of plots inventoried in the northern Brazilian Amazon and their relationships with each fire disturbance class (UF = unburned forest; BF1L = once lightly burned forest; BF1H = once heavily burned forest; BF2 = twice-burned forest and BF3 = thrice-burned forest).

significant relationships were found because the diversity was constant across the biomass range.

The first two ordination axes of the PCO explained 21.1% and 13.4% of the total variability of the floristic composition (Figure 5). The plots were gradually distributed along the first axis according to the fire-damage classes, with a clear discrimination between UF and BF3 plots. The second axis showed a detachment of a set of plots mainly associated with the BF1H class.

DISCUSSION

Above-ground biomass content of unburned primary forests in Apiaú region

The mean AGB recorded in unburned primary forests, $188 \pm 78 \text{ Mg ha}^{-1}$, was consistent with results of previous

studies in the same region by Xaud (1998) and Barbosa *et al.* (2010). Our results agreed with earlier findings showing that these Amazon forests located close to savannas had lower biomass than the dense rain forest of the central Amazon (Malhi *et al.* 2006, Saatchi *et al.* 2007). In these tropical forests, the effect of large trees on biomass was exemplified by individuals of *Dinizia excelsa*, which strongly increased the AGB in the UF and BF1H classes. *Dinizia excelsa* is an emergent species that occurs at low densities and has a high specific gravity (EMBRAPA 2004).

Losses and post-fire biomass recovery

As expected, our results showed a gradual reduction in biomass stocks after more frequent/severe fires on the studied time scale. By comparing BF1L and BF1H, the impact of fire severity to produce higher reductions in biomass was demonstrated, as also reported by Gerwing (2002). Thus, the dynamics of biomass recovery was reduced by fire severity.

The range of AGB values in the BF3 class ($36\text{--}114 \text{ Mg ha}^{-1}$) revealed that some plots that experimented recurrent fire events reached similar levels of live above-ground biomass to those of secondary forests estimated in the same region by Xaud (1998) and Araújo (1999) with values ranging from 33 to 57 Mg ha^{-1} and from 14 to 79 Mg ha^{-1} , respectively. The gain in biomass observed for the BF1L in relation to UF class, regarding $\leq 50 \text{ cm dbh}$ trees, showed forest recovery and establishment of intermediate-diameter and non-pioneer trees after 12 y from the fire. For the dbh class $> 50 \text{ cm}$, differences in AGB were more pronounced revealing the impact of fire on the AGB of large trees.

Figure 6 summarizes some of the major post-fire biomass studies performed in the Amazon basin and

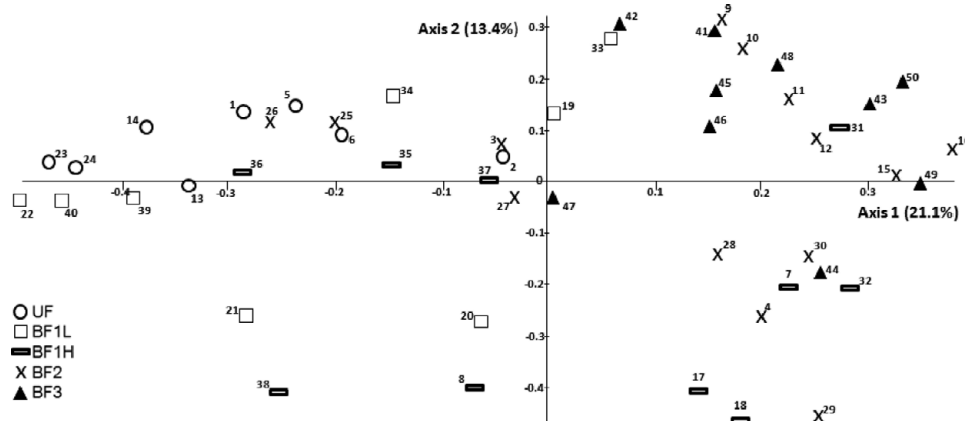


Figure 5. Scatter plot showing the first and second axis of the principal coordinate analysis (PCO) considering the 50 inventoried forest plots in northern Brazilian Amazon, based on Bray-Curtis similarity measure and floristic abundance data. UF = unburned forest; BF1L = once lightly burned forest; BF1H = once heavily burned forest; BF2 = twice-burned forest and BF3 = thrice-burned forest.

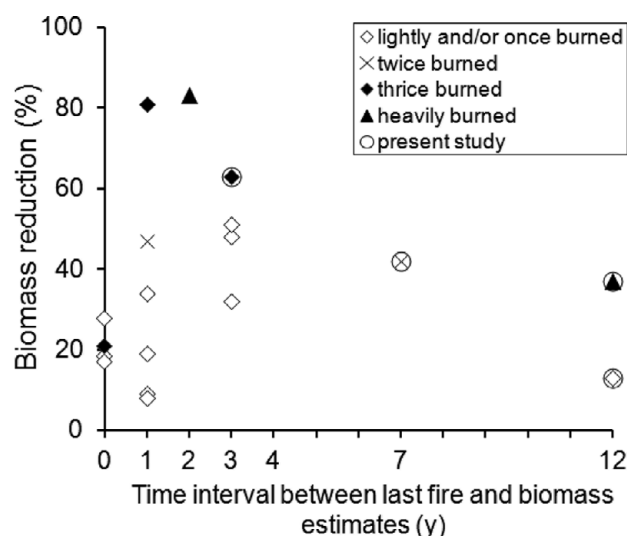


Figure 6. Synthesis of results in terms of living above-ground biomass reduction (or difference) with respect to the time interval between the last fire and AGB data collection (y) based on nine studies in the Brazilian Amazon (Balch *et al.* 2011, Barbosa & Fearnside 1999, Barlow *et al.* 2003, Cochrane *et al.* 1999, Fearnside *et al.* 2001, 2007; Gerwing 2002, Graça *et al.* 1999, Haugaasen *et al.* 2003) as well as the present study.

illustrates the temporal dynamics of biomass levels after a fire event. Time intervals between fires, the number of fire occurrences, fire severity and remaining biomass estimates have been reported. The biomass estimates from the present study were associated with the longest post-fire time interval (12 y), complementing the results of the previous ones. The values formed a hump-shaped distribution, with an increase in biomass loss within the first 3 y after the fire.

Previous studies reported a reduction in biomass of approximately 20% immediately after a fire (Balch *et al.* 2011, Fearnside *et al.* 2001, 2007; Graça *et al.* 1999), with an average loss of approximately 50% 3 y later (Balch *et al.* 2011, Barlow *et al.* 2003, Gerwing 2002). This delay in biomass loss was likely the result of the higher resistance of large trees to fire, which expanded the mortality distribution over several years (Barlow *et al.* 2003). The loss of biomass was less severe 7 and 12 y after the fire, similar to the biomass values estimated immediately after the fire. Although the precise point at which biomass stops decreasing after a fire remains unclear, our analysis suggested that it may be between 3 and 7 y after the fire, assuming no additional disturbances. Twelve years after the fire occurrence, the biomass was not significantly different from the initial level, illustrating the resilience of these forests in term of biomass recovery, at least for areas burned only once.

Our results confirmed that forest resilience in terms of biomass depends on the fire history, which includes not only the elapsed time after the fire but also the fire

frequency and severity (Numata *et al.* 2011). Both fire frequency and severity increased the loss of biomass and delayed its recovery. The exception was for the thrice-burned forests in which biomass was measured less than 1 y after the last fire, and because the intervals between the three fires were abnormally short (Balch *et al.* 2011). Thrice-burned and heavily burned forests, observed 1 and 2 y after the last fire, respectively, had experienced the greatest loss of biomass. For these two cases, only one of the two critical variables (severity and frequency) was available.

Relationships between biomass, diversity and fire

The Shannon index (H') of 4.02 obtained in our UF plots was slightly those obtained in the Roraima state by Alarcón & Peixoto (2007), 4.66, or in the National Forest of Tapajós (Pará state), by Gonçalves & Santos (2008), 4.22. In the central Amazon, high levels of diversity were found by Oliveira *et al.* (2008) (H' of 5.1).

Tree diversity decreased with fire disturbance in the Amazon, as demonstrated by Barlow *et al.* (2003) and Cochrane & Schulze (1999). In the case of BF1L, a post-fire recovery time of 12 y allowed tree diversity (H') to return to initial levels with a floristic composition very similar to the unburned forests, as shown by our PCO analysis. However, severely, recently and/or recurrently burned areas (BF1H, BF2 and BF3) showed lower diversity than lightly burned or unburned forests (BF1L, UF). The difference between H' values of BF1H and BF1L likely stems from the fact that this type of disturbance favoured the regeneration of *P. guyanense* pseudostems. This was confirmed by our PCO results, where the second axis clearly discriminated plots with high pseudostem densities, reaching 237 pseudostems ha^{-1} in plot 8. Thus, fire severity seems to be one of the most important factors for determining post-fire forest resilience, at least in terms of diversity.

In cases of increased fire recurrence and decreased recovery time (BF2), the positive relation between biomass and diversity illustrates the similar responses of the two proxies to fire disturbance. In plots exhibiting increased fire recurrence and reduced post-fire intervals (BF3), no relationship between biomass and diversity was observed. We hypothesize that in these recurrently disturbed forests, the time after each fire was not sufficient for the biomass to recover, as large tree mortality continues for several years after a fire event (Barlow *et al.* 2003). BF3 also had the lowest mean values for biomass but not for diversity. This pattern suggests that the characteristics of BF3 fires favoured the installation of evenly distributed pioneer species and that these changes in vegetation composition did not alter the Shannon diversity index. Such recurrent disturbances thereby

negated the relationship between biomass and diversity. As neither biomass nor diversity values were estimated before the second or third fires, and as no long-term studies on post-fire biomass dynamics have been performed in this region, we were not able to dissociate the effects of fire recurrence, severity and elapsed time after fire on biomass and vegetation diversity.

When pioneer individuals of *Cecropia* spp. were removed from the analysis of tree size distribution, differences in AGB and the significance of these differences were enhanced only for small trees. This result can be explained by the observation that *Cecropia* spp. diameters were always < 40 cm in our sample. Indeed, Cochrane & Schulze (1999) and Barlow & Peres (2008) described the dense post-fire establishment of pioneer species, which compensates for the loss of Amazonian primary forest trees.

Despite a few reports of low mortality of *Cecropia* spp. after low or mild fire severity (d'Oliveira *et al.* 2011, Uhl *et al.* 1981), Barlow & Peres (2008) found that the density of these pioneer species and their contributions to AGB decreased relative to other species after recurrent fires. In other words, these pioneers were more sensitive to fire recurrence. However, we found that pioneer IVI, density and contributions to AGB increased in sites where fires have occurred two or three times since 1998, especially for *Cecropia* spp. and *Jacaranda copaia* (Aubl.) D. Don. Except for lightly burned forests, *Cecropia* spp. made the highest contributions to AGB 3, 7 and 12 y after the fire incident. Cochrane & Schulze (1999) also reported an increase in pioneer density with increasing fire intensity and frequency. Moreover, not all individuals of *Cecropia* spp. in these forests were recently established, as their mean diameter was higher in the most disturbed plots. Therefore, the sensitivity of pioneer species to fire recurrence does not necessarily modify the vegetation structure through middle-term reductions in biomass or density contributions of such species, because non-pioneer species are progressively excluded from forest as fires occur. Fire recurrence might thus favour pioneer species renewal. The time elapsed between or after fires must be considered as a key factor in determining the biomass contribution patterns of pioneer species.

To some extent, our results agreed with those of Balch *et al.* (2011), who found that *Protium guianense* and *Vochysia vismiifolia* had high fire-induced mortality rates. Indeed, the biomass contribution of *Protium* sp. decreased with increasing fire frequency and for *Vochysia* sp. this contribution was the highest where the forest was only lightly burned (BF1L). The latter species was also recorded in UF plots. *Pouteria* spp. showed similar behaviours in the two studies, as its fire-induced mortality rate was low in Balch *et al.* (2011) and its biomass contribution increased with fire incidence. Fire-induced tree mortality may be influenced not only by cambium insulation but also by

species traits that reduce the indirect effects of fire (Brando *et al.* 2012).

In the same region, Fearnside *et al.* (2007) found a palm biomass reduction of 79% (2.09 Mg ha⁻¹ to 0.44 Mg ha⁻¹) immediately after a fire event. Less severe reductions were found in the present study (–65% in BF2, –56% in BF1H and –52% in BF3). Both results illustrate the major impact of fire on palm species, which represent less than 50% of the initial biomass, even 12 y after a fire. These studies showed greater reductions in palm biomass compared with results by Graça *et al.* (1999) in open forests (8.6 to 7.1 Mg ha⁻¹ or 17%), or by Fearnside *et al.* (2001), in palms of central Amazon (1.3 to 1.1 Mg ha⁻¹ or 15%).

Carbon emissions

Assessing changes in carbon stocks of the AGB is difficult because they are related not only to immediate fire impacts but also to delayed mortality and biomass recovery. Therefore, this balance integrates many sources and sinks and carbon estimates become more difficult with increasing time after a fire. However, for thrice-burned areas measured 3 y after the last fire (maximum biomass losses according to findings of this work), we expected more precise estimations of carbon losses.

The need for long-term, precise surveys of burned sites in the Amazon is immediate, particularly given the present and future fire scenarios for the region. According to Cochrane & Barber (2009), the future fire regime will be a product of climate change and human land practices. For example, the predicted warmer and drier climate (Salazar *et al.* 2007) may result in an increase in hazards related to natural fire ignition and propagation. Fires may therefore become more frequent and intense, increasing the vulnerability of the forest and imparting high risks of biodiversity erosion and biomass loss.

In conclusion, the biomass stocks in the studied area were drastically affected by fire, and important shifts in tree size distribution and species contributions to biomass occurred after each additional fire event. Losses in biomass stocks were significant after fire recurrence. Twelve years after the fire, biomass stocks had recovered in once-burned forests, although differences in floristic composition were still observed in higher fire severity classes. For large trees (> 50 cm dbh), there was a notable reduction in biomass after one or two fire events, whereas this reduction was significant in thrice-burned areas. In terms of species contribution, we observed that *Cecropia* spp. dominated the biomass composition, even 12 y after a severe fire incident. Our results, in combination with those of previous studies, showed that forest recovery of biomass depends on fire history (e.g. elapsed time,

fire frequency and severity) and that losses progressively occur until some point between 3 and 7 y after the last fire, assuming no additional disturbances. Both fire frequency and severity exacerbated biomass losses and delayed biomass recovery. Overall, the present study confirms the high vulnerability of these tropical forests (located close to savannas) to fire. It remains difficult to distinguish between the effects of fire frequency, fire severity and time since last fire artefact on vegetation. Long-term surveys are therefore essential for assessing the diversity of ecological impacts of fire on Amazon forests.

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Appendix 1. Summarized floristic statistics for fire disturbance classes (UF = unburned forest; BF1L = once lightly burned forest; BF1H = once heavily burned forest; BF2 = twice-burned forest and BF3 = thrice-burned forest) in northern Brazilian Amazon; Dens. = density of the listed species (ind. ha⁻¹); dbh = species diameter at breast height (mean \pm SD); IVI = importance value index (%) of species considering only tree species. An asterisk (*) indicates the pioneer species.

Class	Species with highest contribution to AGB (%)	Dens. (ind. ha ⁻¹)	dbh (cm)	IVI (%)	Families with highest contribution to AGB (%)
UF	<i>Dinizia excelsa</i> (15)	2	94 \pm 73	4.4	Leguminosae (32)
	<i>Protium</i> sp. (9)	14	40 \pm 17	5.7	Sapotaceae (13)
	<i>Pouteria</i> sp. 2 (9)	5	56 \pm 21	3.6	Burseraceae (12)
	<i>Qualea paraensis</i> (6)	12	27 \pm 20	3.5	Vochysiaceae (8)
	<i>Sclerolobium</i> sp.* (4)	7	30 \pm 19	2.5	Lecythidaceae (5)
BF1L	<i>Vochysia</i> sp. (17)	38	27 \pm 14	9.3	Vochysiaceae (22)
	<i>Manilkara huberi</i> (10)	9	43 \pm 16	4.2	Leguminosae (19)
	<i>Protium</i> sp. (6)	10	36 \pm 14	3.8	Sapotaceae (15)
	<i>Vitex</i> sp.* (5)	12	29 \pm 15	3.3	Burseraceae (13)
	<i>Protium</i> sp. (4)	21	20 \pm 10	4.7	Lamiaceae (5)
BF1H	<i>Dinizia excelsa</i> (16)	2	86 \pm 19	4.1	Leguminosae (26)
	<i>Geissospermum sericeum</i> (12)	27	30 \pm 10	8.3	Apocynaceae (16)
	<i>Cecropia leucocoma</i> * (7)	110	16 \pm 4	18.2	Sapotaceae (9)
	<i>Pouteria</i> sp. (5)	12	22 \pm 14	3.8	Burseraceae (9)
	<i>Protium</i> sp. (5)	4	38 \pm 19	2.6	Urticaceae (8)
BF2	<i>Talisia</i> sp. (8)	6	37 \pm 24	3.5	Leguminosae (14)
	<i>Cecropia leucocoma</i> * (8)	137	15 \pm 4	21.1	Sapotaceae (13)
	<i>Pouteria</i> sp. (7)	18	23 \pm 11	5.3	Burseraceae (10)
	<i>Protium</i> sp. (6)	5	41 \pm 15	3.1	Urticaceae (8)
	<i>Spondias mombin</i> (5)	3	35 \pm 30	1.8	Sapindaceae (8)
BF3	<i>Cecropia leucocoma</i> * (13)	95	18 \pm 5	22.8	Sapotaceae (16)
	<i>Pouteria</i> sp. (11)	20	24 \pm 11	7.9	Urticaceae (14)
	<i>Talisia</i> sp. (9)	8	30 \pm 13	4.2	Sapindaceae (9)
	<i>Jacaranda copaia</i> * (6)	2	45 \pm 30	2.0	Lamiaceae (9)
	<i>Vitex</i> sp.* (4)	9	24 \pm 11	3.9	Lecythidaceae (7)