Post-fire recovery of a dense ombrophylous forest in Amazon

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How to cite: DE ANDRADE DFC, GAMA JRV, RUSCHEL AR, MELO LO, DE AVILA AL AND CARVALHO JOP. 2019. Post-fire recovery of a dense ombrophylous forest in Amazon . An Acad Bras Cienc 91: e20170840. DOI 10.1590/0001-3765201920170840.

Abstract: The fires that occur in the Amazon are as damaging as the deforestation is. There is a need for further long-term studies on dynamics of tree communities in forests affected by fires. In the present study we evaluated the dynamics of tree species, before and after an accidental fire that occurred in 1997 in an experimental area of *terra firme* forest in the Floresta Nacional do Tapajós, in western Pará State, Brazil. Approximately 3500 trees with diameter measured at 1.30 m above ground (DBH) $\geq$ 5 cm were botanically identified and measured in 12 permanent plots of 0.25 ha (50 m x 50 m), in 1983, 1987, 1989, 1995, 2008 and 2012. Analyses of survival, mortality and recruitment of trees were performed. The results showed that although the fire has increased the mortality and recruitment rates after 15 years, the highest mortality occurred on trees with smaller diameters (DBH < 30 cm), so the fire did not affect the survival of large trees in the long term, explaining why the reduction in density of living trees has not greatly influenced the decrease in basal area in the burned forest.

Key words: primary forest, tree mortality, post-fire dynamics, tree recruitment, resilience.

INTRODUCTION

The Amazon forest is a source of fascination for scientists (Correia et al. 2016), among them there is consensus that as greater is the knowledge of the dynamics and biological diversity as more efficient will be management, conservation and restoration actions of this biome (Silva et al. 2015). At the same time, the Amazon diversity also is the target of economic interests that, in recent decades, have contributed significantly to changes in the landscape of this territory (Nepstad et al. 2013). In addition to the deforestation that has led to the

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loss of environmental services (Fearnside 2006), recent studies have shown that degradation caused by selective logging without technical criteria, fires and others inappropriate anthropogenic uses are as damaging as deforestation, although only deforestation is monitored by the government (Barlow et al. 2016).

Moreover, it is likely that in this century, the Amazon will experience an increase in temperature, frequency and extent of drought events (Betts et al. 2016). Thus, forest fires may be increasingly recurrent (Barlow et al. 2016), considering that the leakage fire agricultural areas surrounding forests is threatening synergy between deforestation and climate change (Aragão et al. 2008), while little knowledge is available on the resilience of these forests to fire. The monitoring of burned forests is the best way to know the mechanisms of resilience after fire (Betts et al. 2016) and to describe the recovery path (Sato et al. 2016). The impact of forest fire is directly associated with tree mortality (Sato et al. 2016). The existing knowledge infers that, in fire-affected forests, mortality is directly proportional to the severity of the fire and after initial light burning, is higher in trees with smaller stems (Xaud et al. 2013).

However, most studies dealing with mortality after burning are based on short-term assessments - less than 2 years (Barlow et al. 2003). In the medium and long term, it is important to evaluate the survival of large and coarse-grained trees, considering that trees with more than 70 cm in diameter (Clark and Clark 1996), are resistant in the first years to fire impacts (Barlow et al. 2003).

The survival of large trees does not persist after severe fires, where all trees appear to become equally vulnerable (Barlow and Peres 2004). In addition to these questions about tree mortality after fire events, long-term studies for recruitment processes, including the survival of early recruits remain unknown (Bentos et al. 2017).

In this study, forest dynamics, considering survival, mortality and recruitment of trees, was monitored over 29 years (1983 - 2012), 14 years before and 15 years after fire. The monitoring was carried out in the Floresta Nacional do Tapajós. Permanent sample plots were installed - in a forest area with no history of selective timber extraction. In the present study it was intended to answer the following questions: (1) What was the effect of fire on mortality and recruitment of trees over 15 years after an accidental fire? (2) Was there any significant loss of basal area and density of trees due to fire? (3) What was the class of tree size most affected by fire?

Based on previous studies (Araujo et al. 2013, Barlow et al. 2003, Avila et al. 2017, Xaud et al. 2013), the first hypothesis of this study is that (1) the rates of mortality and recruitment of forest affected by fire were higher when compared to non-burned forest and (2) after 15 years, only the small trees were affected by the fire and the time elapsed after the fire was sufficient to have the losses in basal area and density of trees recovered.

MATERIALS AND METHODS

AREA OF STUDY

Approximately 527 thousand hectares are part of the Floresta Nacional do Tapajós, Federal Conservation Unit, located in the west of the State of Pará (Lat. 3°19'S, Long: 54°57'W, DATUM WGS 84), along the BR-163 (Andrade et al. 2015, Avila et al. 2017). The climate of the region, based on the data collected at the Belterra station (35 km north of Floresta Nacional do Tapajós), is hot and humid, with an annual average temperature of 26º C, relative humidity of 87.30% and average of accumulated annual precipitation of 1780 mm (INMET 2017).

The study area is located in the plateau region of Floresta Nacional do Tapajós, near Km 114 of the BR-163. There are 36 hectares of forest,

where 3 (three) plots were installed in 1983 in four continuous blocks of 9 (nine) hectares, totaling 12 sample units of 0.25 hectares (50 m x 50 m), subdivided into 25 subplots of 10 m x 10 m, numbered from 1 to 25 to facilitate the location of the trees and control of the actions in the continuous sample inventories (Fig. 1).

The experimental area represents a typical dense ombrophylous forest of the region, with no history of forest exploitation (Carvalho 2002, Oliveira et al. 2005), characterized by the dominance of large arboreal individuals and by the abundance of woody lianas, palms and epiphytes, with a uniform canopy or with emergent trees (Gonçalves and Santos 2008).

The topography varies from flat to slightly undulating, with an approximate altitude of 175 m above sea level. The predominant soil is of the dystrophic yellow latosol type, medium to very clayey texture (Rodrigues et al. 2001, Vieira 1975).

The sampling area corresponds to the minimum number recommended to capture the heterogeneity of the site in research on the diversity and abundance of species in the forest (Bonar et al. 2011).

All trees DBH ≥ 5 cm were measured in 1983, 1987, 1989, 1995, 2008 and 2012, once each year, according to the methodology described in Silva et al. (2005). All trees were identified with numbered platelets (plot, subplot and tree number) to allow monitoring of their growth and survival rates over the years.

The species were identified in the forest with their vernacular names by parataxonomists. Those trees not identified in the forest had botanical material collected for later identification in the Embrapa Amazônia Oriental herbarium. The research was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), according to SISBIO Authorization No. 57419/2017.
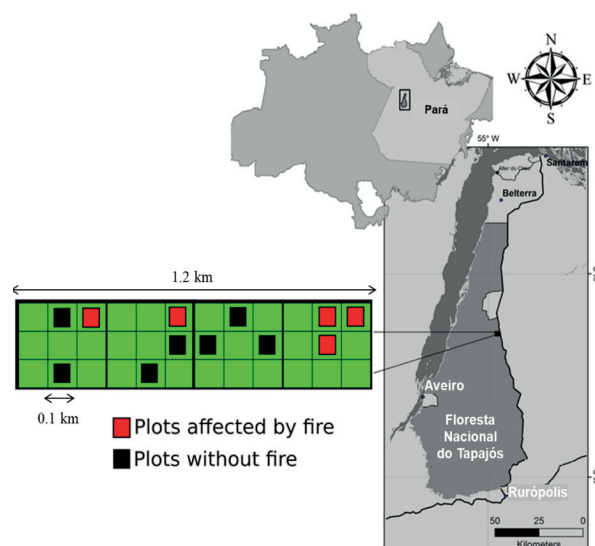

Figure 1 - Location of the T0 plots (black squares) and T1 (plots affected by fire), installed in an area of 36 hectares of dense ombrophylous forest, with no history of logging, in the Floresta Nacional do Tapajós, Pará State, Brazil.

Forest Fire

From December 9 to 13, 1997, an accidental fire burned a 1200-meter stretch of the Floresta Nacional do Tapajós, in the vicinity of Km 114 of the BR-163 Highway. The fire hit the vegetation very quickly and affected part of the permanent plots but it was put out by the Embrapa regional staff that worked during two days for minimizing the damage.

DATA ANALYSIS

The monitoring history of the area including the identification of the plots potentially affected by the fire (Avila et al. 2015, 2017, Oliveira et al. 2005, Sousa 1997) and data obtained in the measurements carried out in 1995 (before fire) and 2008 (after fire) were used for a quantitative analysis (descriptive statistics) with the mortality data (mean and standard deviation) and qualitative analysis of the species that entered in the tree community in that period, allowing the identification of a common pattern among the plots affected by fire. After this

analysis, five fire-affected plots were, termed "T1" and seven "fire-free" plots were termed "T0".

The grouping of the plots made it possible to analyze the interaction between the ecological characteristics (recruitment rates - RR, mortality rates - MR, percentage of survival of remaining trees - SR, those recorded in the first measurement performed in 1983, basal area - BA - and density of trees - DA - and the explanatory variables (time and fire occurrence in 1997), comparing data from the different measurements performed in the plots, before and after fire, using the impact study method (Sit and Taylor 1998).

Those trees that reached or exceeded the minimum inclusion diameter of 5 cm (DBH $\geq$ 5 cm) were considered "recruited" in each subsequent measurement. This value was divided by the number of years of the interval between measurements to obtain the number of recruits per hectare per year. From this value the annual percentage of recruits was calculated by the relation between the number of new trees in each measurement and the number of trees present in the previous measurement (Colpini et al. 2010).

"Dead" trees were considered those with DBH $\geq$ 5 cm found dead in each measurement. The number of trees recorded as dead in each measurement was converted to the equivalent in hectares and divided by the number of years of the interval between the surveys to obtain the number of deaths in the period and then expressed hectare per year. From this value, as in the case of recruitments, the annual percentage of mortality was calculated by the ratio between the number of dead trees in each measurement and the total number of trees present in the previous measurement (Colpini et al. 2010).

The "remaining" trees were all trees recorded in the first measurement (1983) that remained alive in subsequent measurements. SR was calculated by the ratio between the number of remaining trees in each measurement and the total trees present in the

first measurement. Graphical methods were used for evaluating the mortality of remaining trees, trees recruited and mortality by diameter class.

The BA was calculated by summing the sectional areas of each tree in each plot and then expressed in hectares according to the area sampled. The density of trees was calculated by the total number of trees per unit area, in this case, in hectares (Mueller-Dombois and Ellenberg 1974).

Statistical Analysis

The variables BA and DA were tabulated, considering T0 and T1 plots, for the seven measurements performed, as well as mortality and recruitment rates, among the five monitored periods (1983 - 1987, 1987 - 1989, 1989 - 1995, 1995 - 2008). In order to evaluate if the fire significantly affected the dynamics and structure of the forest, an ANOVA for repeated samples was applied, considering time as subdivided plots, due to the dependence between the multiple observations in the same sample units (Von Ende 1993).

To test the assumptions of the parametric analysis, the tests of normality of Shapiro-Wilk and homogeneity of variance of Bartlett were applied. The value of F was corrected using the Greenhouse-Geisser (G-G) or Huynh-Feldt (H-F) correction factors to infer on each variation source (Von Ende 1993).

We used the lowest factor (GG or HF) instead of the "F" value to test the hypotheses: null hypothesis (H0) $\mu 1 = \mu 2 = \mu 3$: that is, there is no significant difference between the variables analyzed (BA, Density, RR and MR) between the measurements or periods; Alternative hypothesis (H1) $\mu 1 \neq \mu 2 \neq \mu 3$: there is at least one mean of the observed variables (BA, Density, MR and RR) different between measurements or periods.

All data were processed by the Tropical Forest Monitoring – MFT (software produced by Embrapa

Amazônia Oriental) and later exported to Microsoft Office Excel 2016 for analysis.

RESULTS

In the year 1983, 3360 trees were inventoried, in a three hectare sample area. Over the 29 years of monitoring, 1588 trees were recorded as dead and 1495 new trees as recruited. In the 29-year period, in T1 plots 49.41% of the 1230 trees ha^{-1} existing in 1983 died in 2012, corresponding to a mortality of 21.03 trees ha^{-1} year^{-1}, while in the T0 plots 32.33% of 1041 ha^{-1} trees died (11.64 trees ha^{-1} year^{-1}).

Only in the period from 1995 (2 years before fire) to 2008 (11 years after fire), in the T1 plots 27.50% of the remaining trees died, corresponding to 25.86 trees ha^{-1} year^{-1}, while in T0 this percentage was 14.27% (11.36 trees ha^{-1} year^{-1}), in the same period. Before fire, the average mortality of remaining trees was 13.14 trees ha^{-1} year^{-1}, in T0, and 19.00 trees ha^{-1} year^{-1} in T1, so there was a difference of 5.86 trees ha^{-1} year^{-1} which made the number of trees increased to 11.86 trees ha^{-1} year^{-1} after fire (Fig. 2a).

The percentage of survival of remaining trees (SR) in the last measurement in 2012 was 50.59% for T1 and 67.67% for T0, indicating a natural tendency for gradual replacement of older trees in both areas, intensified in the area affected by fire.

In the whole sample area, 239 trees that had been recruited after the first measurement were found died in the last measurement (29 years of monitoring), representing the number of 2.76 trees ha^{-1} year^{-1}, corresponding to 15.05% of the total trees dead in the study area. Before fire, the average mortality of recruited trees was 0.94 trees ha^{-1} year^{1} for T0 and 1.13 trees ha^{-1} year^{-1} for T1, but the difference increased to 4.54 trees ha^{-1} year^{-1}, after fire (Fig. 2b).

In T1 the increase in tree mortality after fire was compensated by the increase in the recruitment of new individuals (Fig. 2c) and, in the same way as it occurred with mortality rates, the recruitment rates of T0 and T1 distanced themselves after fire, indicating the role of the fire as an agent of changes in the forest dynamics, considering trees mortality and recruitment (Fig. 2d).

In the burned area (T1), there was a significant increase in mortality rates from 1995 to 2008 (F = 3.27, P value = 0.05, Table I) and a significant increase in recruitment rates from 2008 to 2012 (F = 5.01, P value = 0.03, Table I). These were above the 2.5% range in the 29 years studied, being 2.77% and 2.99%, respectively (Fig. 3a, b).

Before the fire (1983 - 1995), 92.54% of the dead trees in T1 and 89.58% in T0 had diameters smaller than 30 cm (Fig. 4a). After fire, mortality rates of dead trees with DBH < 30 cm increased to 94.58% in T1 and to 94.12% in T0 in the 1995 - 2008 period and remained high with 91.95% in T1 and 90.91% in T0 in the 2008 - 2012 period (Fig. 4b, c).

All the trees recruited and recorded as dead had a DBH ≤ 20 cm, so the period of 29 years was not enough to evaluate the mortality of trees recruited with larger diameters. Regarding the losses in basal area, in T1 plots there was an increase of 63.16% in loss of basal area for trees with DBH < 30 cm in the period from 1995 to 2008 (Fig. 4e), when it was compared to the period prior to the fire (1983 - 1995) (Fig. 4d), while in T0 there was a reduction of 7.14%.

In the 2008 - 2012 period (Fig. 4f) there was a greater loss of large trees (DBH > 60 cm) in unburned plots (T0) (Fig. 4h), unlike T1 where few large trees died (Fig. 4c), indicating that, after 15 years, the fire had mainly affected trees of smaller size. In the period prior to the fire, the difference between the number of trees smaller than 30 cm that died in T1 and T0 was only 5.96 trees ha^{-1} year^{1} and became 12.24 trees ha^{-1} year^{-1}, which raised losses in basal area for trees smaller than 30 cm (Fig. 4g, h).
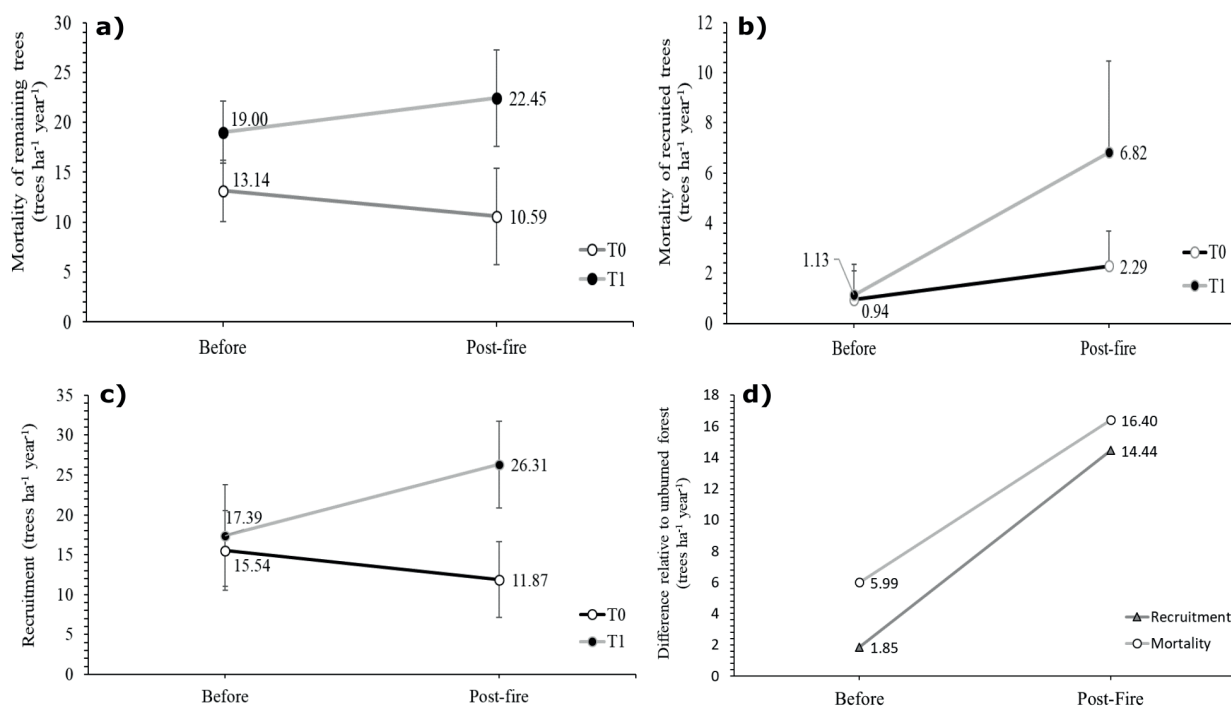
Figure 2 - Annual mortality rate (trees ha^{-1} year^{-1}) for remaining trees (**a**) and trees recruited (**b**), annual recruitment rate (trees ha^{-1} year^{-1}) and (**c**) the difference between the mortality and recruitment rates recorded for T0 (1.75 ha) and T1 (1.25 ha), before and after fire (**d**), considering trees with DBH ≥ 5 cm, monitored during 29 years in an area of dense ombrophylous forest with no logging history in the Floresta Nacional do Tapajós, Pará State, Brazil.

TABLE I
Analysis of Variance (ANOVA) of repeated measurements of historical records (1983-2012) of density (trees ha^{-1}), basal area (m² ha^{-1}), mortality rate (% year^{-1}) and recruitment rate (% year^{-1}) in T0 (no fire) and T1 (affected by fire, in 1997) plots, in an dense ombrophylous forest, with no history of logging, in the Floresta Nacional do Tapajós, Pará State, Brazil.

	Source of variation	Density (trees ha^{-1})					BA (m² ha^{-1})				
		GL	F	*P* value	G-G	H-F	GL	F	*P* value	G-G	H-F
T0	Time	5	0.13	0.99	0.84	0.89	5	3.43	0.01	0.04	0.04
	Error	20					20				
T1	Time	5	4.59	0.01	0.04	0.05	5	1.85	0.15	0.24	0.23
	Error	20					20				

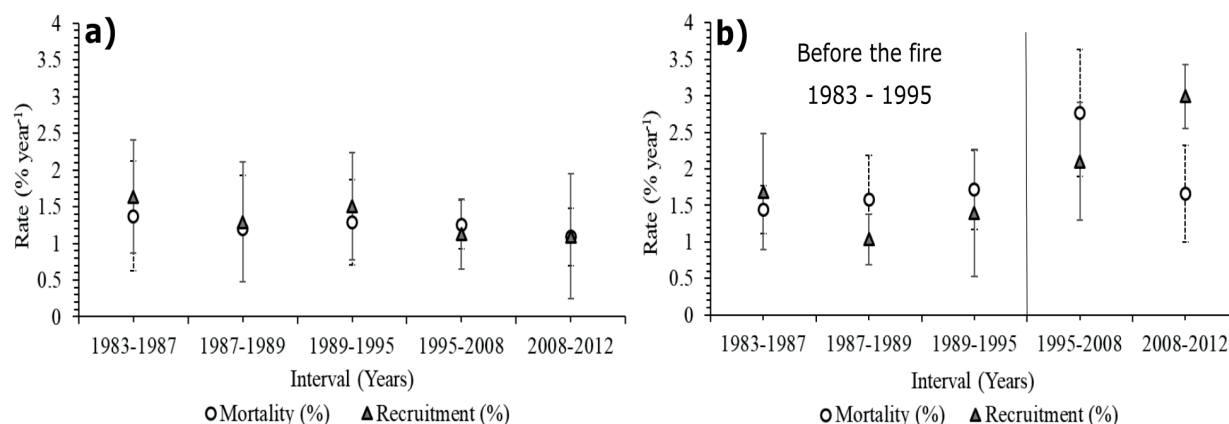|	Source of variation	MR (%)					RR (%)				
		GL	F	*P* value	G-G	H-F	GL	F	*P* value	G-G	H-F
T0	Time	4	0.28	0.89	0.73	0.80	4	0.78	0.55	0.53	0.55
	Error	24					24				
T1	Time	4	3.27	0.04	0.05	0.04	4	5.01	0.01	0.03	0.01
	Error	16					16				

Figure 3 - Annual mortality and recruitment rates - percentage of recruited or killed trees compared to alive trees in the previous measurement, plus the respective standard deviation, for trees ≥ 5 cm DBH, in the T0 plots (1.75 ha), in **a**, and in the T1 plots (1.25 ha), in **b**, during 29 years of monitoring, in an dense ombrophylous forest, with no history of logging, in the Floresta Nacional do Tapajós, Pará State, Brazil.

The relationships between mortality and recruitment (Figs. 2 and 3) in the monitored periods were responsible for the positive or negative balances of tree abundance and basal area in the forest, before and after fire (Fig. 5).

In 29 years, there was little variation in the tree density (trees ha^{-1}) for the T0 plots while in T1 plots a reduction, in density was observed after the fire (F = 4.59, P value = 0.05, Table I; Fig. 5a, b). In relation to basal area (m² ha^{-1}), the values obtained from the last measurement were the highest of the whole study period, in both T1 and T0, and there was therefore no fire effect in the reduction of basal area (Table I), although in T0 the forest stored more biomass in the 29 years of study (F = 3.43, P value = 0.04, Table I, Fig. 5c, d).

DISCUSSION

MORTALITY AND RECRUITMENT

The annual mortality and recruitment rates (Fig. 3), presented a characteristic pattern of native tropical forests, with no history of selective logging, with rates of 1 to 2% per year (Fernandes et al. 2017, Souza et al. 2012), exception to recruitment rates recorded from 2008 to 2012 and mortality rates from 1995 to 2008 in T1 plots, where the mortality

rate was similar to the standard found in a logged area in Floresta Nacional do Tapajós – 2.6%, 2.4% and 2.2% per year for five, six and eleven years after harvesting, respectively (Silva et al. 1995).

Mortality and recruitment should decrease with increasing census interval when obtained from censuses of non-homogeneous populations (Lewis et al. 2004). There is a tendency in the areas not affected by fire to decrease the mortality of the remaining trees, correlated to the monitoring period (Fig. 2), a pattern that diverged from the burned plots, where after the fire (2008) occurred the highest mortality (Table I, Figs. 2 and 3).

The stabilization in mortality rates and continued recruitment rates 15 years after fire is probably associated with the canopy opening caused by the mortality of remaining trees (Chazdon 2008), but it was expected that the effects of the changes that caused the increase in recruitment rates would be temporary and short-lived as observed in the studies of Avila et al. (2017).

After fire the mortality and recruitment rates recorded for T1 plots were relatively higher than in T0 plots (Fig. 3), and significantly higher when compared to the rates recorded in the same plots, in pre-fire years (Table I). In relation to the total number of dead trees in the entire community,
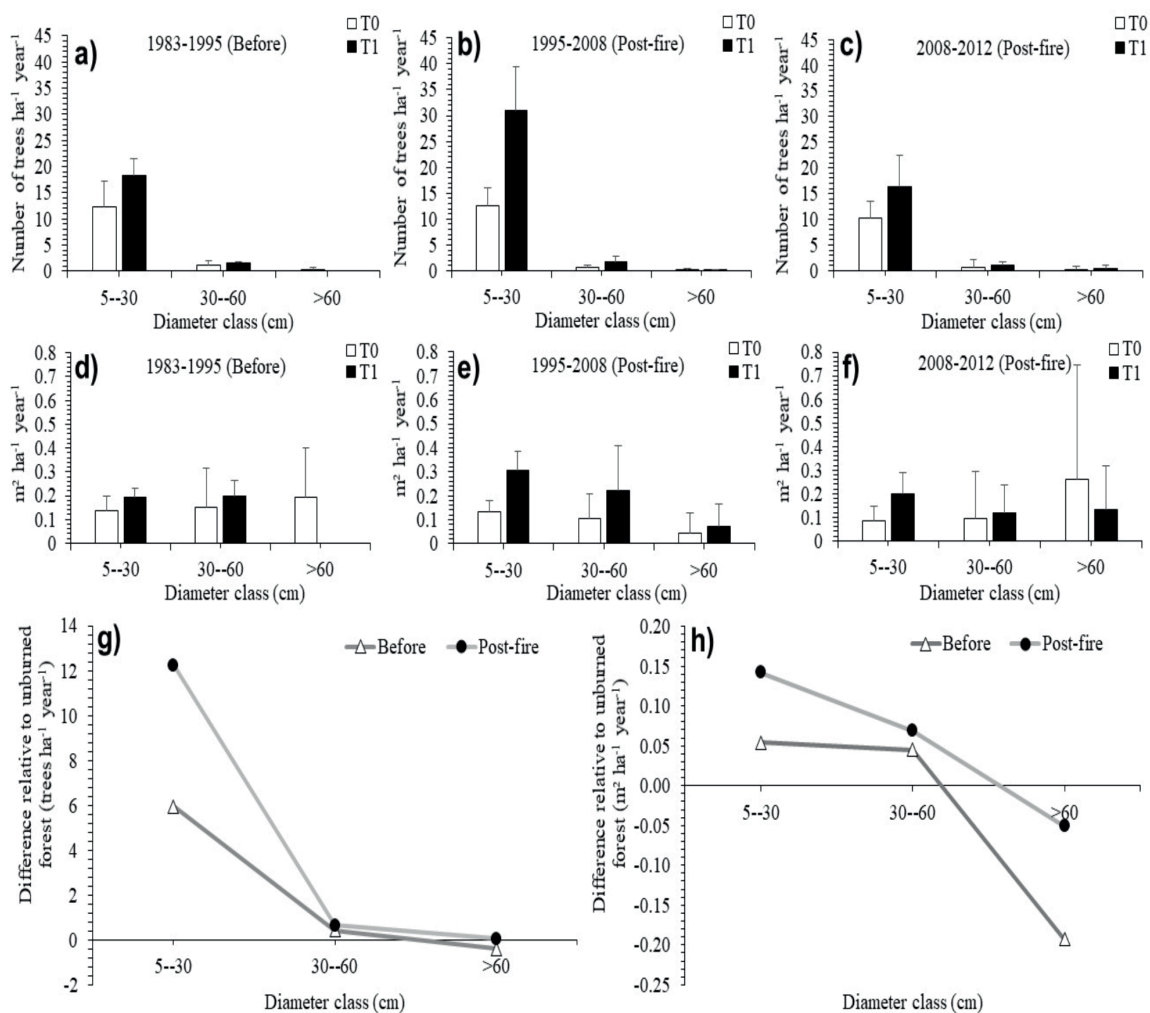
Figure 4 - Annual Mortality (trees ha^{-1} year^{-1}) by diameter classes (cm), from 1983 to 1995 (**a**), 1995 to 2008 (**b**), 2008 to 2012 (**c**) and losses in basal area (m^2 ha^{-1} year^{-1}), caused by tree mortality from 1983 to 1995 (**d**), 1995 to 2008 (**e**) and 2008 to 2012 (**f**), for burnt (T1) and unburned (T0) plots, and the difference between the mortality rates (**g**) and losses in basal area (**h**), by diameter class, recorded for the forest affected by fire in comparison to the forest not affected, before and after fire, in an dense ombrophylous forest, with no history of logging, in the Floresta Nacional do Tapajós, Pará State, Brazil.

the percentage of dead trees recruited was only 15.05%, below the percentage of trees that had been recorded at the first measurement and that were dying over time (remaining) (Fig. 2).

In relation to the increase of the mortality of trees recruited in the T1 and T0 plots after fire, it is expected that as more are the trees registered as recruits, the greater will be the probability of death records for these trees. This type of monitoring should be carried out in the long term so that

information on the survival of recruited trees should be known in longer time.

Recruit mortality (DBH < 20 cm) information plus the higher mortality of small remaining trees (DBH < 30 cm) may be a result, besides the direct effect of fire, of a greater competition caused by recruitment / densification of individuals, especially in canopy gaps generated by fire.

After fire, there was, therefore, a reduction in the abundance of trees (*P* value = 0.05, Table I),
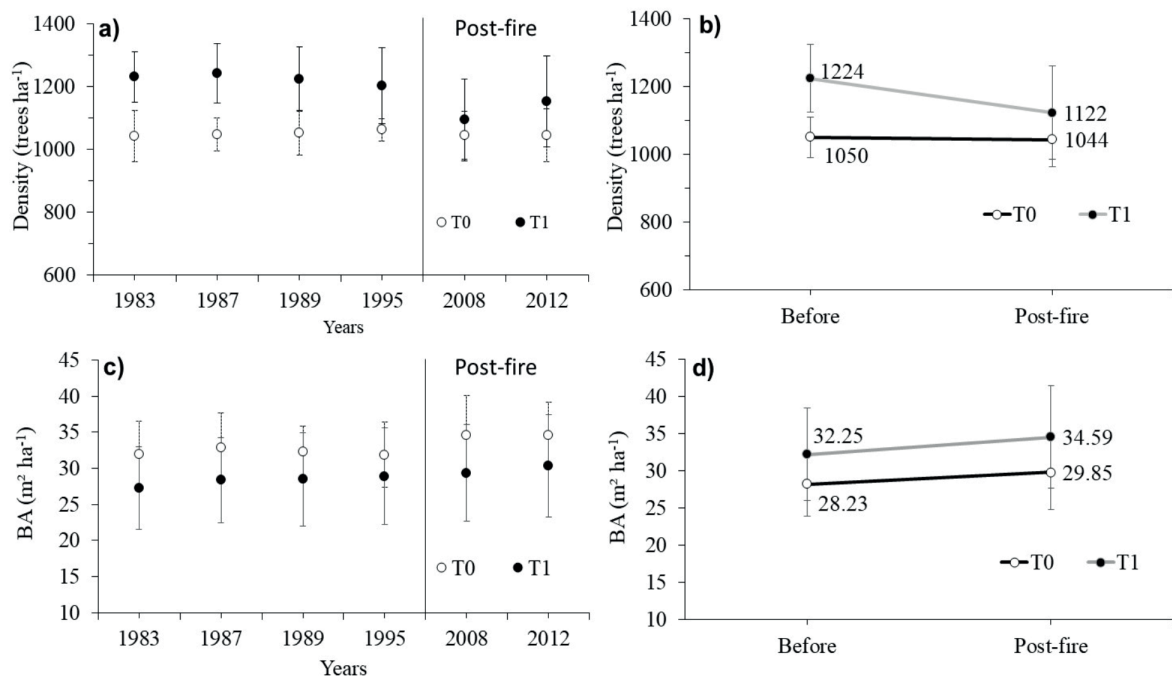
Figure 5 - Medium values of density (**a**) and difference between the means of density of before and after fire (**b**) and mean values of basal area (**c**) and difference between basal area averages before and after fire (**d**) in all measurements, in the 29 years of monitoring, for affected by fire (T1) and not affected by fire (T0) plots, in an dense ombrophylous forest, with no history of logging, in the Floresta Nacional do Tapajós, Pará State, Brazil.

mainly due to the higher mortality rates recorded for smaller trees (DBH < 30 cm), in which the competition was intensified.

The SR values recorded for both areas have shown that there is a gradual replacement of the remaining individuals in the forest strata over time, and fire seems to have accelerated this process, a characteristic that needs to be monitored in longer time intervals.

FOREST RECOVERY

The successional dynamics is driven by high mortality rates (Chazdon 2008) and the canopy opening caused by the death of large trees can play a fundamental role in the processes of changes in forest dynamics and structure (Clark and Clark 1996), a condition that was expected to be observed, after the occurrence of the fire (Barlow et al. 2003, Clark and Clark 1996).

However, in this study, before and after the occurrence of fire, the highest mortality occurred among trees with smaller diameters (DBH < 30 cm) (Xaud et al. 2013) and the fire in the study area did not impact the survival of large trees (Sato et al. 2016), explaining why the reduction in the density of living trees (Barlow et al. 2003) did not strongly affect the decrease of the basal area in the burned forest.

The approach adopted here to investigate forest recovery was limited to mortality and recruitment rates as well as to changes in forest structural components - tree density and basal area. Among the observed variables, mortality and recruitment rates were useful to characterize the effects of fire on the dynamics of tree vegetation and were extremely sensitive to assess a stage of non-equilibrium in the forest.

Forests are dynamic ecosystems (Chazdon 2012) and complexes that after disturbances have

ecologically organized processes of recovery to states prior to changes (Ghazoul et al. 2015). Post-fire measurements showed a rapid forest recovery with high mortality rates shortly after fire, which were offset by high recruitment rates in the first post-fire decade and by the gradual decrease in mortality rates over time.

CONCLUSIONS

Fifteen years after fire, the forest affected by fire recovered in terms of mortality rate and still show high recruitment rates. The highest mortality occurred on trees with smaller diameters (DBH < 30 cm) and the fire in the studied area did not impact the survival of large trees, explaining why the reduction in the density of living trees did not have a strong negative effect on the basal area in the forest burned.

ACKNOWLEDGMENTS

AUTHOR CONTRIBUTIONS

DFC Andrade, JRV Gama and AR Ruschel are responsible for the study conception and sampling design and also contributed to the data analysis and to the writing of the manuscript. JOP Carvalho, LCO Melo and AL Avila are responsible to the writing of the manuscript with input from the other authors. All authors contributed to the interpretation of the results and provided critical feedback and contributed to the final version of the manuscript.

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