Bamboo abundance, edge effects, and tree mortality in a forest fragment in Southwestern Amazonia

Densidade de bambu, efeito de borda e mortalidade arbórea em um fragmento florestal no Sudoeste da Amazônia

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Abstract

We show that in a bamboo-dominated forest in Southwestern Amazonia the tree mortality rate does not differ between the forest edge and the interior, even though bamboo abundance is higher closer to the edge. We tested whether bamboo abundance affects mortality rate in three areas within a forest fragment of ca. 1,166 ha. We estimated mortality rate for trees with > 10 cm dbh during 1.8 years. Bamboo abundance was approximately three times higher on the edge (3394 ± 1121 culms ha⁻¹) than in the interior of the forest (1123 ± 754 stems ha⁻¹). The annual mortality rate did not differ significantly between edge (3.8 ± 2.6 % y⁻¹) and interior (3.6 ± 2.6 % y⁻¹), but the main modes of tree mortality, ‘dead standing’ and ‘broken,’ differed significantly between edge and interior. Tree mortality was higher for smaller trees (10-30 dbh) and did not differ between forest edge and interior. However, bamboo abundance explained 23% of tree mortality rate at the edge, even though edge effects may have been masked by advanced edge age. Bamboo dominated forests impose a faster turnover time in forests of western Amazonia, which may be reflected in mortality rates being similar between edge and forest interior.

Keywords: diameter classes, forest dynamics, mortality mode, mortality rate, Guadua weberbaueri

INTRODUCTION

In Southwestern Amazonia, forests dominated by arborescent bamboos (Guadua spp.) cover approximately 165,000 km² (SMITH; NELSON, 2011). In the state of Acre, especially in the eastern part of the state, approximately 50% of the area originally covered by forest has been deforested, and the remaining forest is highly fragmented (SALIMON; BROWN, 2009). However, there are no published studies about fragmentation effects on tree mortality in bamboo-dominated forests, or about the effects of the disturbance regime imposed by the bamboos (GRISCOM; ASHTON, 2006; SILVEIRA, 2005).

In fragmented forests, the area and shape of the fragments, type of matrix, and edge effects (LAURANCE et al., 2002; MURCIA, 1995) are

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the main factors responsible for alterations in forest structure and dynamics. The edge effect comprises a combination of factors, such as microclimatic stress and increase in wind turbulence, and it is considered the main cause of increased tree mortality (D'ANGELO et al., 2004; LAURANCE et al., 1998, 2000). Several studies in bamboo-dominated forests in southwestern Amazon have pointed out that the disturbance regime imposed by bamboos can decrease tree density, basal area, species richness, and biomass (GRISCOM; ASHTON, 2003; 2006; GRISCOM et al., 2007; SILVEIRA, 2005; TOREZAN; SILVEIRA, 1999). The dynamics of bamboo-dominated forests are considered to be unique, as mortality rates are approximately twice as high in these environments compared to other areas of the Amazon (SILVEIRA, 2005). The bamboo’s influence on tree mortality can be related to its sarmentose habit and its tendency to lean on trees between 10 and 30 cm dbh, resulting in breaking or death of trees due to overloading and physical damage (GRISCOM; ASHTON, 2003; SILVEIRA, 2005).

Based on the above statements and findings, we expect to find greater tree mortality and also higher abundance of bamboos in forest edges. However, there are no studies on edge effects in bamboo-dominated forests, or on the relationship between edge effects and bamboo abundance. Hence, we investigated whether forest edge and interior differ in abundance of Guadua weberbaueri Pilg. (Poaceae); whether bamboo abundance influences trees mortality rate and also if different tree size classes are influenced by bamboo abundance and of mortality mode.

MATERIAL AND METHODS

The study was carried out at the Catuaba Experimental Farm (Fazenda Experimental Catuaba, hereafter called Catuaba) (67°37’W, 10°04’S), located in Senador Guiomard, Acre State, northern Brazil (Figure 1). Catuaba is a forest fragment of approximately 1,200 ha that belongs to the Federal University of Acre (Universidade Federal do Acre). The original vegetation consisted of mainly Terra Firme forest (upland) with patches of open forest dominated by arborescent bamboo (Guadua weberbaueri). There are some secondary forests 15-30 y old and pastures on the edges of the forest fragment. The understory is closed, with a predominance of vines and culms of the bamboo G. weberbaueri. The canopy is open and 20-45 m high. The most abundant canopy trees are Hevea brasiliensis (Willd. ex Adr. Juss.) Müll. Arg. (Euphorbiaceae), Bertholletia excelsa Bonpl. (Lecythidaceae), Tetragastris altissima (Aubl.) Swart (Burseraceae), and Carapa guianensis Aubl. (Meliaceae). The relief is gently rolling, and latosols (Oxisols or Ferralsols) predominate in the area (ACRE, 2006). The A- and B- horizons are formed predominantly by sand (62 and 47%, respectively) and the pH is approximately 4.0 (SOUZA et al., 2008). The annual rainfall in the region is around 1958 mm y⁻¹, varying from 846 mm in the rainiest quarter (January to March) to 197 mm in the driest quarter (July to September). The average temperature is 25.3 °C, ranging from 20.3 to 31.4 °C (DUARTE, 2006).

Between October and November 2007, three modules were set up in different parts of Catuaba. Each module consisted of two parallel 500 m transects within 500 m of each other, one parallel to the edge of the forest (starting at 5 m from pasture) and the other inside (hereafter referred to as edge and interior, respectively). On each transect, five plots of 10 x 100 m were established; the diameter of all trees ≥ 10 cm dbh (i.e. 1.3 m above the ground) was measured. When buttress roots were present, diameter was taken 50 cm above the buttress. All individuals were tagged, and their positions in the plot were georeferenced.

Between November 2007 and September 2009 the plots were visited five times to evaluate dead trees and record mortality modes. Mortality modes were classified as dead standing, broken, uprooted, and other causes CHAO et al., 2009). The annual mortality rate was calculated following Sheil and May (1996), with the formula:

\[ M = \left\{1 - [\{(N0 - m)/N0\}^{1/3}] \right\} \times 100 \]

where \(N0\) is the initial number of individuals, \(m\) is the number of dead individuals, and \(t\) is the time between censuses.

The effect of spatial autocorrelation on mortality rate and abundance of bamboo culms was tested with the I index of Moran in R (R DEVELOPMENT CORE TEAM, 2011). The values of the index were estimated for six distance classes (347, 952, 1556, 2161, 2766 and 3379 m, computed the R package [R Development Core Team, 2011]). No spatial autocorrelation was detected for any distance class and any variable, except for bamboo abundance in the smallest
distance class (347 m, I = 0.43, p < 0.001). As spatial autocorrelation affects the inferential analyses only if it is detected in both dependent and independent variables (LEGENDRE et al., 2002), it was not necessary to include spatial variables in the analysis.

We counted all bamboo culms with height > 3 m in all plots, even those that had no branches and leaves. As bamboo patches persist for over 20 years (SILVEIRA 2005), we considered that bamboo abundance during our two-year study was constant. We measured dbh of 200 bamboo culms chosen randomly on the transects, in order to estimate the average diameter of culms per plot.

For both abundance of bamboo culms and tree mortality rate, we tested data normality with a Kolmogorov-Smirnov test and differences between categories (edge and interior) with a t test. To test for the relationship between bamboo abundance and mortality rate on the edge and in the interior, we used a simple linear regression estimated with the command “lm” of R. All analyses were performed in R (R DEVELOPMENT CORE TEAM, 2011). All measures of uncertainty associated with averages are on standard deviation of the mean.

RESULTS AND DISCUSSION

Bamboo abundance was 2309 ± 1149 culms ha⁻¹ (CV= 33%), and the average diameter was 4.4 ± 0.6 cm (CV= 13.9%). Culm abundance differed significantly (p= 0.000001) between edge (3394 ± 1121 culms ha⁻¹, CV=33%) and interior (1123 ± 754 culms ha⁻¹, CV= 62%), and it was over twice greater at the edge (Figure 2). Even though the edges in this fragment were not recently created, there is still a greater penetration of light in the first 5-10 m from the pasture and G. weberbaueri, which is clearly a pioneer species, which takes advantage of this increase in light availability.

We sampled 1291 trees with dbh ≥ 10 cm (430 ± 166 tree ha⁻¹), of which 76 died during the observation period. The average annual mortality rate did not differ significantly (p= 0.89) between edge (3.8 ± 2.6 % y⁻¹) and interior (3.6 ± 2.6 % y⁻¹).

From the total 76 trees that died during the study period, 46 were in the edge and 30 in the interior. The most common mode of death was “standing dead” (50 individuals in total). Separately, both edge and interior also had “standing dead” as the most common mode of death.

Figura 1. Área de estudo, Fazenda Experimental Catuaba, Senador Guiomard, Acre, Brasil. Figure 1. Study site, Catuaba Experimental Farm, Senador Guiomard, Acre state, Brazil.
(33 in the edge and 17 in the interior). Mortality modes differed between edge and interior (ANOVA: $F = 4.4, p < 0.01$) and were higher on the edge than in the interior (dead standing = 44% vs. 21% and broken = 13% vs. 9%, respectively). The most common mortality modes were ‘dead standing’ (65%) and ‘broken’ (22%), which together represented over 80% of tree mortality. The modes ‘dead standing’ and ‘broken’ were higher on the edge (44% and 13%, respectively) than in the interior (21% and 9%, respectively).

In the present study, contrary to what was found in other fragmented forests in the Amazon (LAURANCE et al., 1998, 2000), an edge effect on overall tree mortality was not detected. Such difference could be explained in part because of the difference in time since edge formation, where in central Amazonia the studies were conducted in recently fragmented forests (FERREIRA; LAURANCE, 1997), whereas in our study site, fragmentation occurred more than 10 years ago and therefore some of the tree mortality related to edge formation may have already happened before our sampling. In our study, the tree mortality rate in the interior of fragment (3.6 ± 2.6 % y$^{-1}$) is approximately 2.5 times higher than those estimated in interior plots in Central Amazonia (FERREIRA; LAURANCE, 1997; LAURANCE et al., 2009, 1998 NASCIMENTO; LAURANCE, 2004) and similar to that estimated on the edge (3.85 ± 0.72% y$^{-1}$; FERREIRA; LAURANCE, 1997). Nevertheless, our results do not refute the current knowledge of edge effects, especially because our study covers a short period of time in a single fragment, and did not examine a recently created edge.

Disturbance by bamboo in the interior of the forest causes a high and probably constant level of mortality, comparable to that caused by edge creation in newly isolated forest fragments of the Central Amazon. Also, keeping in mind that edge creation time was quite different from other studies, we suggest that the mortality rates in southwestern Amazonia could be higher and vary in time and space, specially where forests are dominated by bamboo and also occur in more fertile soils, where forest turnover rates are known to be faster than Central and Eastern Amazonia (QUESADA et al., 2009).

The predominant modes of mortality were ‘dead standing’ and ‘broken’, with higher incidences in the class 10-30 cm of dbh, and both differed between edge and interior, being higher in edge plots. Most dead standing and broken trees served as a support for bamboo. Griscom and Ashton (2003), in an experiment with ‘artificial trees’ concluded that the frequency of physical damage and amount of weight in plots dominated by bamboo (G. sarcocarpa and G. weberbaueri) can be eight times higher than in areas without bamboo. G. weberbaueri has an advantage in relation to tree species, considering its sarmentose habit that uses trees for anchors and support, and its mechanisms of vegetative propagation. Nevertheless, dead standing and broken trees are also associated with fire penetration and death of short-lived pioneer species, therefore bamboo higher abundance in the edge is not the only neither necessarily the main driver of these mortalities; this could be associated with fire penetration or the just the heat of pasture fires along the edge, or the presence of more short-lived pioneer trees at the border.

The fact that we only observed relationship between bamboo abundance and tree mortality...
in the edge, could be in part due to an experimental design that did not include control plots with no bamboo, either in the edge or in the interior. However, since G. weberbaueri is a pioneer species, its abundance in the edge was almost twice that of interior. Such higher abundance imposes more weight in tree branches and could be the cause of the relationship found between dead standing trees and bamboo on the edge plots.

CONCLUSIONS

Although our sampling time span was short and edge age is different from other fragment studies, we believe that bamboo dominated forests impose a faster turnover time in forests of western Amazonia, which may be reflected in mortality rates being similar between edge and forest interior, even though bamboo abundance was higher in edge plots. Also, bamboo seems to play a weak role in modes of tree mortality in the edge of the forest, even after a decade of edge creation.

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