Tree mortality, recruitment and growth in a bamboo dominated forest fragment in southwestern Amazonia, Brazil

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Abstract: Forest fragmentation affects the structure and dynamics of plant communities, leading to biodiversity loss in forest remnants. In this paper we show that in a bamboo (*Guadua weberbaueri* Pilger) dominated forest fragment in southwestern Amazonia edge effect may be confounded by bamboo effect, which also occur inside the forest. We measured growth, mortality and, recruitment rate of trees with DBH $\geq$ 10 cm, in a fragment of bamboo dominated open forest in southwestern Amazonia, state of Acre, Brazil, in 15 plots at the forest edge and 15 plots inside the forest fragment, 500 m away from the border. Time interval between censuses was 1.8 years. The average diameter growth rate differed significantly between edge (3.82 ± 0.10 mm a^{-1}) and interior (2.39 ± 0.18 mm a^{-1}); but there were no differences in annual mortality rate (edge = 3.8 ± 2.5 % a^{-1} CV = 65.7%; interior = 3.6 ± 2.6% a^{-1} CV = 72.2%) or in annual recruitment rate (edge = 7.1 ± 3.2% a^{-1} CV = 45%; interior = 8.9 ± 7.9% a^{-1} CV = 88.7%). Diameter growth rate, particularly of pioneer and fast-growing trees, is favored by the environmental conditions of the edge, where bamboo abundance is higher. However, the absence of an edge effect on mortality and recruitment could be due to the particular dynamics of bamboo patches, which could be mimicking forest edges and therefore masking possible edge effect in this fragment. We speculate that the mortality and recruitment patterns in fragmented forests of southwestern Amazonia is different from other areas in Amazonia and that bamboo is one of the key controllers of successional processes in these fragments.
Keywords: forest fragmentation, edge effect, open forest with bamboo, plant communities, forest succession, tropical forest dynamic.

Resumo: A fragmentação florestal afeta a estrutura e dinâmica das comunidades vegetais, levando a perda da biodiversidade nos remanescentes florestais. Neste trabalho nós mostramos que em um fragmento florestal dominado por bambu (*Guadua weberbaueri* Pilger) no sudoeste da Amazônia, o efeito de borda deve ser confundido pelo efeito efeito do bambu, que também ocorre no interior da floresta. Nós medimos as taxas de incremento diamétrico, mortalidade e recrutamento de árvores com DAP (diâmetro a altura do peito) $\geq$ 10 cm, em um fragmento dominado por floresta aberta com bambu no sudoeste da Amazônia, estado do Acre, Brasil, em 15 parcelas na borda da floresta e 15 a 500 m da borda no interior do fragmento florestal. O intervalo de tempo entre os censos foi de 1,8 anos. A taxa anual de incremento diamétrico médio diferiu significativamente entre borda ($3,82 \pm 0,10$ mm a^{-1}) e interior ($2,39 \pm 0,18$ mm a^{-1}); mas não houve diferenças na taxa anual de mortalidade (borda = 3.8 ± 2.5% a^{-1} CV = 65.7%; interior = 3.6 ± 2.6% a^{-1} CV = 72.2%) e na taxa anual de recrutamento (borda = 7.1 ± 3.2% a^{-1} CV = 45%; interior = 8.9 ± 7.9% a^{-1} CV = 88.7%). A taxa de incremento diamétrico, especialmente de espécies arbóreas de estágios iniciais de sucessão ecológica e crescimento rápido, é favorecida pelas condições ambientais da borda, onde a abundância de bambu é maior. Porém, a ausência de efeito de borda sobre a mortalidade e recrutamento, pode ser devido a própria dinâmica das manchas de bambu, que podem estar imitando as bordas das florestas, e portanto, mascarando o efeito de borda neste fragmento. Nós especulamos que os padrões de mortalidade e recrutamento em florestas fragmentadas no Sudoeste da Amazônia são diferentes de outras partes da bacia Amazônica e que o bambu nessas florestas é um dos principais atores controlando a sucessão florestal nesses fragmentos.
Palavras-chave: fragmentação florestal, efeito de borda, floresta aberta com bambu, comunidade vegetal, sucessão florestal, dinâmica de florestas tropicais.

Introduction

Because of the key role of the Amazon in maintaining the global climate and biodiversity (Malhi et al. 2008, Salati & Vose 1984, Phillips et al. 1998, Fearnside 1999, Laurance et al. 2010), it becomes more and more important to understand edge effects on plant communities and ecosystem processes, as a result of landscape fragmentation caused mainly by the expansion of agriculture, cattle ranching (Barona et al. 2010), construction and by building the infrastructure need for the production and distribution of products associated with development projects (Soares-Filho et al. 2006). Between 2001 and 2010, the Brazilian Amazon lost an average of 16.153 ± 7.500 km²/year of mature forest (Instituto… 2010), which is the equivalent of 10% of Acre State total area. As a direct consequence, the remaining forests have been gradually fragmented and isolated within a matrix dominated by pasture, annual monocultures or secondary forest patches at different successional stages.

In addition to habitat loss and changes in biological populations, changes in land cover decrease the effectively preserved area, due to edge effects (Nascimento & Laurance 2006), which include modifications in physical, chemical and biological parameters caused by the contact between the fragment and the matrix (Wiens et al. 1993, Murcia 1995, Primak & Rodrigues 2001). Fragment edges are strongly affected by external disturbances in many important ecosystem processes (Laurance et al. 2002), such as total photosynthetic rate (MacDougall & Kellman 1992), density of individuals, primary productivity and floristic diversity (Didhan & Lawton 1999).

In the Central Amazon, Laurance & Yensen (1991), Laurance et al. (1998a, b, 2000), Murcia (1995) and (Kapos 1989) observed that the edge effect changes species composition and affects diameter growth, mortality and recruitment, due to several factors, such as the reduction of water supply in the soil, increase in light penetration in the border, even after decades of the fragmentation processes (Oliveira Filho et al. 1997).

Southwestern Amazon has also undergone a process of fragmentation and vegetation loss, especially due to the expansion of cattle raising, agriculture, logging (Baitz et al. 2008) and road paving (Brown et al. 2002). Nevertheless, western Amazonia is known for the extensive cover (165,000 km²) of open forests dominated by bamboos of the genus *Guadua* (Smith & Nelson 2011). These bamboos strongly affect the structure and dynamics of these forests, causing a decrease in tree density, total basal area, floristic richness and in functional groups (Oliveira 2000, Smith 2000, Silveira 2005, Griscom & Ashton 2003, Griscom et al. 2007).

We speculate that where forests are dominated by bamboo, forest dynamics might be different, since bamboo does influence forest structure elsewhere in western Amazonia (Griscom & Ashton 2003). Due to a lack of knowledge of the impact of forest fragmentation on edge effects in southwestern Amazonia, we measured tree growth, mortality rate and recruitment on the edge and in the interior of a bamboo dominated forest fragment to address this hypothesis.

Material and Methods

1. Study area

Catuaba Experimental Farm possesses a forest fragment with ca. 1,200 ha located in Senador Guiomard, state of Acre (10°04' S and 67°37' W). It has a gently rolling topography with predominance of oxisols and to a lesser extent ultisols (Acre 2006); the A and B horizons are predominantly formed by sand (62 and 47%, respectively) and the pH is approximately 4.0 (Sousa et al. 2008). The fragment is at an average altitude of 214 m a.s.l. and is 0.8-7.4 km

away from neighboring remnants. The area is covered by bamboo dominated open rainforest, in which understory vines and culms of *Guadua weberbaueri* Pilger are very abundant. The dominant trees are *Hevea brasiliensis* (Willd. ex A. Juss.) Müll.Arg. (Euphorbiaceae), *Bertholletia excelsa* Humb. & Bonpl. (Lecythidaceae), *Tetragastris altissima* (Aubl.) Swart (Burseraceae) and *Carapa guianensis* Aubl. (Meliaceae). Canopy height is between 20 and 40 m, with emergent trees up to 45 m (Silveira 2005). Mean annual rainfall is 1,958 mm, varying from 846 mm in the wettest quarter (January to March) to 197 mm in the driest quarter (July to September). The average annual temperature is 25.3 °C, ranging from 17 to 32.7 °C (Duarte 2006).

2. Tree community sampling

We randomly selected three areas, and in each area two 500×10 m transects were set parallel to 500 m apart from each other: one at the edge, 10 m from the non-forested matrix, and one inside the forest, 500 m from the first area. On each transect five 100×10 m plots were delimited, where all live trees, as well as lianas and palms, were permanently marked with aluminum tags at 1.60 m and referenced by x/y coordinates. All individuals (DBH $\geq$ 10 cm) had their diameter measured at 1.3 m; buttressed trees were measured 50 cm above the end of the roots according RAINFOR field protocols. The RAINFOR field protocols are available at http://www.geog.leeds.ac.uk/ projects/ rainfor/rainforfield manual.doc.

The first census was carried out between October and November 2007, and a second census was carried out in September 2009; all individuals were checked for DBH on both occasions. Dead individuals were counted, and individuals that met the minimal criterion of inclusion 1.8 years after the first measurement were marked as recruits and measured.

The annual diameter growth for each individual was calculated using the formula ($DBH_1 - DBH_0$) / t, where DBH_0 represents the initial diameter, DBH_1 represents the diameter measured in the second census, and t represents the time interval between measurements. There were 191 individuals excluded (15% of total) from our analyses, due to very high buttresses or other bark characteristics which caused measuring errors (n = 58 border; n = 53 interior, not statistically different) and others because they were dead (n = 48 border; 32 interior, not statistically different). Since the differences in excluded trees were not significantly different, such exclusion was probably not a bias in our results.

Mortality (M) and Recruitment (R) rates were calculated following Sheil & May (1996), using the formulas below, where N_0 is the initial number of individuals, m is the number of dead individuals, r is the number of recruits, and t the elapsed time between censuses (Equations 1 and 2):

$$M = \{1 - [(N_0 - m)/N_0]^{1/t}\} \times 100 \tag{1}$$

$$R = \{[(N_0 + r)/N_0]^{1/t} - 1\} \times 100 \tag{2}$$

To test the influence of size on diameter growth and mortality, individuals were categorized in three DBH classes: 10-30 cm, 30.1-50 cm and over 50 cm. Data was normal and homocedastic and we used a one-way ANOVA to test differences among diameter classes.

Results

1. Diameter growth rate

Out of the 1,291 individuals sampled, the total number recorded in the edge (498.6 ind./ha) differed significantly (ANOVA: F = 7.7 p = 0.022) from the interior (362 ind. ha⁻¹). The average annual growth

rate at the edge (3.82 ± 0.10 mm.a^{-1}) was significantly (p < 0.001) higher than in the interior (2.39 ± 0.18 mm a^{-1}), Table 1.

Diameter growth at 10-30 cm DBH at the edge was significantly (ANOVA: F = 3.8 p = 0.05) higher than the forest interior. However, the difference was not significant for trees with DBH 30-50 cm (ANOVA: F = 0.03 p = 0.86) and DBH > 50 cm (ANOVA: F = 0.35 p = 0.55). Such positive relationship between DBH and growth rate was also observed separately in the edge (10-30 cm = 3.63 ± 2.07 mm a^{-1}; 30.1-50 cm = 4.6 ± 4.0 mm a^{-1}; and > 50 cm = 7.52 ± 12.44 mm a^{-1}) and in the interior (10-30 cm = 2.34 ± 1.47 mm a^{-1}; 30.1-50 cm = 3.29 ± 3.08 mm a^{-1}; and >50 cm = 6.28 ± 8.08 mm a^{-1}).

2. Mortality and Recruiting rates

Total mortality rate was 3.77 ± 2.55% a^{-1}. The number of individuals in each census and their respective mortality rates are presented in Table 1. Annual mortality rate was not difference between edge (3.89 ± 2.58 % a^{-1}) and interior forest (3.65 ± 2.60 % a^{-1}). Total average mortality rate (edge plus interior) for plants with DBH 10-30 cm (4.13 ± 3.20% a^{-1}) was significantly higher (p = 0.002, Mann-Whitney U Test) than in the class 30.1-50 cm (3.45 ± 6.38% a^{-1}). In the edge this rate differed significantly (p= 0.015 Mann-Whitney U test) between the classes of DBH 10-30 (4.09% a^{-1}) and 30.1-50 cm (3.41% a^{-1}). In the interior, although the mortality rate was higher in the class 10-30 (4.17% a^{-1}) than in the class 30.1-50 (3.48% a^{-1}), the difference was not significant. There was also no significant difference between edge and interior for the DBH classes of 10-30 cm (p = 0.945) and 30.1-50 cm (p = 0.966).

Although between 2007 and 2009 no mortality of individuals with DBH over 50 cm was recorded, 80 individuals died in the other two classes, and 176 individuals were included in the second census as recruits, which resulted in a recruitment rate of 7.22% a^{-1} (Table 1). In the edge, the recruitment rate was 7,16 ± 3,29% a^{-1} , and in the interior it was 8,98 ± 7,96% a^{-1}; nevertheless this difference was not significant (p = 0.397).

Discussion

1. Diameter growth

The average diameter growth rate observed in the present study (3.10 mm a^{-1}) is similar to the rates reported by Selhorst (2005) (3.6 mm a^{-1}) and Vieira (2003) (3.9 mm a^{-1}), in a assessments of the same area four and two years respectively. Despite the small variation, these rates are higher than the rates measured in others dense forests of Amazon basin (1.8 mm a^{-1} by Silva et al. 2002, 1.6 mm a^{-1} by Higuchi et al. 2003, 2.0 mm a^{-1} by Carvalho et al. 2004, and 1.4 mm a^{-1} by Laurance et al. 2004). Thus, trees in southwestern Amazonia grow up to twice as fast as the ones in Oriental Amazon, which could

result from variations in chemical and physical properties of the soil (Malhi et al. 2004, Quesada et al. 2009 & Quesada et al. 2010) and also by the dominant functional group – fast growing light-weighted species.

The significant difference in diameter growth rate between edge and interior probably occurs due to changes in microclimatic conditions (Camargo & Kapos 1995, Kapos et al. 1997, Laurance et al. 1998a, 2001), which are more favorable in the edge to the establishment of pioneer species, which grow faster and have a shorter life cycle (Lieberman & Lieberman 1987). Furthermore, bamboos are known to influence the structure of the forest (Silveira 2005, Oliveira 2000, Griscom & Ashton 2003, 2006). Griscom & Ashton (2006), showed that the bamboo control succession forest and thus can act as a filter, particularly for some species characteristic of early stages succession, which in general tend to exhibit rapid growth (Silveira 2005, Oliveira 2000, Griscom et al. 2007). In addition, bamboo density at the edge (3394 ± 1121 culms ha^{-1}) is two times higher than in the interior forest (1269 ± 824.49 culms ha^{-1}) (Castro et al. 2013). Thus, even without concrete evidence, we believe that the higher growth rate at the edge could be influenced by a combination of edge plus bamboo effects; which is not reported in the literature so far.

2. Mortality and tree recruitment

Not only the total mortality rates (3.77% a^{-1}) is more than three times higher than the rates observed in Central Amazon by Higuchi et al. (1997; 1.03%), Rocha (2001; 0.86%), and Teixeira et al. (2007; 1.13%), but also no edge effect was detected for this process. In Central Amazon, mortality rate is higher in the edge, and is related mainly to a combination of microclimatic conditions, wind turbulence and liana loads (Ferreira & Laurance 1997, Laurance et al. 1998a, 2000, Nascimento & Laurance 2006). Tree mortality is also higher for larger individuals (Hubell & Foster 1990, Laurance et al. 1998a, 2000).

In present study, in addition to the combination of those factors, the disturbance caused by bamboos (Silveira 2005, Griscom & Ashton, 2003) should also be considered. Tree mortality could be related more to bamboo density than to the edge effect. We suggest that the higher mortality in forests with bamboos, mainly in smaller size classes, is related to the disturbance regime imposed by *G. weberbaueri* (Silveira 2005, Griscom & Ashton 2006), favoring the establishment and growth of pioneer species that, due to their shorter life cycle, contribute more to the increase in mortality rate than the species that are characteristic of later successional stages (Silveira 1999, Swaine & Whitmore 1988). And since there is a greater bamboo abundance in edge plots, this may be the cause for our results.

Contrary to what was observed by Laurance et al. (1998a, b, 2001) and Bierregaard et al. (2001), the recruitment rate in the present study did not differ significantly between edge and interior. Again, this similarity between edge and interior might be attributed to

Table 1. Tree mortality, recruitment and diameter growth in a forest fragment in southwestern Amazon, state of Acre, Brazil. N$_0$: number of individuals in 2007 and N$_1$: number of individuals in 2009.

Variables	Edge	Interior	General
N$_0$ (ind ha^{-1})	498,6	362	430,3
N$_1$ (ind ha^{-1})	529,3	395,3	462,3
Survivors	701	510	1211
Dead	48	32	80
Recruits	93	81	174
Diameter growth (mm a^{-1})	3,82 ± 0,10	2,39 ± 0,18	3,10 ± 0,98
Annual mortality rate (% a^{-1})	3,89 ± 2,58	3,65 ± 2,60	3,77 ± 2,55
Annual recruitment rate (% a^{-1})	7,16 ± 3,29	8,98 ± 7,96	8,10 ± 6,09

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bamboo dominance, which occurs in both areas. Griscom & Ashton (2006), in an experiment with 'artificial trees', showed that in plots dominated by bamboos (*G. sarcocarpa* Londoño & P.M.Peterson and *G. weberbaueri*), the frequency of damage and weight load can be up to eight times higher than in plots without bamboos. Despite the lack of difference between interior and edge, the average recruitment rate was 40% higher than the mortality rate. This can be related to the open architecture of the canopy, which favors the recruitment of early successional plant species, such as pioneers and small gap specialists, which are tolerant to microclimatic conditions of open environments (Williams-Linera 1990, Laurance et al. 1998b).

Recruitment rate among interior forest plots varies widely (CV = 88%) and we think that bamboo can be favoring the recruitment of some species characteristic of early successional stages (Silveira 2005, Griscom & Ashton 2003, 2006, Griscom et al. 2007). Although the results shown here are not very robust in terms of replication, and that mortality and recruitment did not show the same trend as growth, bamboo is likely to be selecting pioneer and small gap specialists (sensu Denslow 1980) such as *Acacia polyphyla* DC. and *Castila ulei* Warb., which regenerate and re-sprout within bamboo patches (Griscom & Ashton 2006, Silveira 2005).

Thus, we suggest that in fragments dominated by bamboo, the edge effect may not the single major factor responsible for tree mortality and recruitment and bamboos might be masking some probable but not detectable edge effect on tree mortality and recruitment. Such results show that the area studied is still in a process of re-establishment and regeneration after the last synchronous mortality of bamboos (approximately 30 years ago). In addition, we speculate that bamboo patches of different ages might impose different effects on forest dynamics in southwestern Amazonia. Therefore, further and longer studies are important to address the influence of bamboo and edge at the same time and therefore corroborate or refute our preliminary results.

Acknowledgements

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