

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

Wendeson Castro¹, Cleber Ibraim Salimon¹, Herison Medeiros¹, Izaías Brasil da Silva¹ and Marcos Silveira¹**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*

Resumo

Nós mostramos que em uma floresta dominada por bambu no Sudoeste da Amazônia a taxa de mortalidade arbórea não difere entre a borda e o interior da floresta, apesar da abundância de bambu ser maior na borda. Nós testamos se a densidade de bambu afeta a taxa de mortalidade em três áreas de um fragmento florestal com cerca de 1166 ha. Estimamos a taxa de mortalidade para árvores com DAP > 10 cm em um intervalo de 1,8 anos. A densidade de bambu foi cerca de três vezes maior na borda (3394 ± 1121 colmos ha^{-1}) que no interior (1123 ± 754 colmos ha^{-1}) da floresta. A taxa anual de mortalidade não diferiu significativamente entre borda ($3.8 \pm 2,6$ % y^{-1}) e interior (3.6 ± 2.6 % y^{-1}), mas os principais modos de mortalidade 'morta em pé' e 'quebrada' diferiram significativamente entre borda e interior da floresta. A mortalidade arbórea foi maior para árvores menores (10-30 DAP) e não diferiu entre borda e interior da floresta. No entanto, a densidade de bambu explicou 23% da variabilidade na taxa de mortalidade na borda. Estes resultados mostram que os padrões de mortalidade em florestas com bambu podem ser diferentes daqueles observados em outras florestas da Amazônia, porém o efeito de borda pode ter sido mascarado pela idade avançada da borda. Florestas com bambu dominante implicam numa taxa de reposição mais rápida na Amazônia ocidental, o que pode estar refletido no fato de as taxas de mortalidade serem semelhantes entre a borda e o interior.

Palavras-chave: classe de diâmetro, dinâmica florestal, modo de mortalidade, taxa de mortalidade, *Guadua weberbaueri*

INTRODUCTION

In Southwestern Amazonia, forests dominated by arborescent bamboos (*Guadua* spp.) cover approximately 165,000 km^2 (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

¹Botany and Plant Ecology Laboratory, Natural Science and Biology Center, Universidade Federal do Acre, BR 364 km 4, Distrito Industrial, Rio Branco, AC 69900-000, Brazil. E-mail: wendesoncastro@gmail.com

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 Guimard, 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 Ferrasols) 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 (SOUSA 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:

$$M = \{1 - [(N0 - m)/N0]^{1/t}\} \times 100$$

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

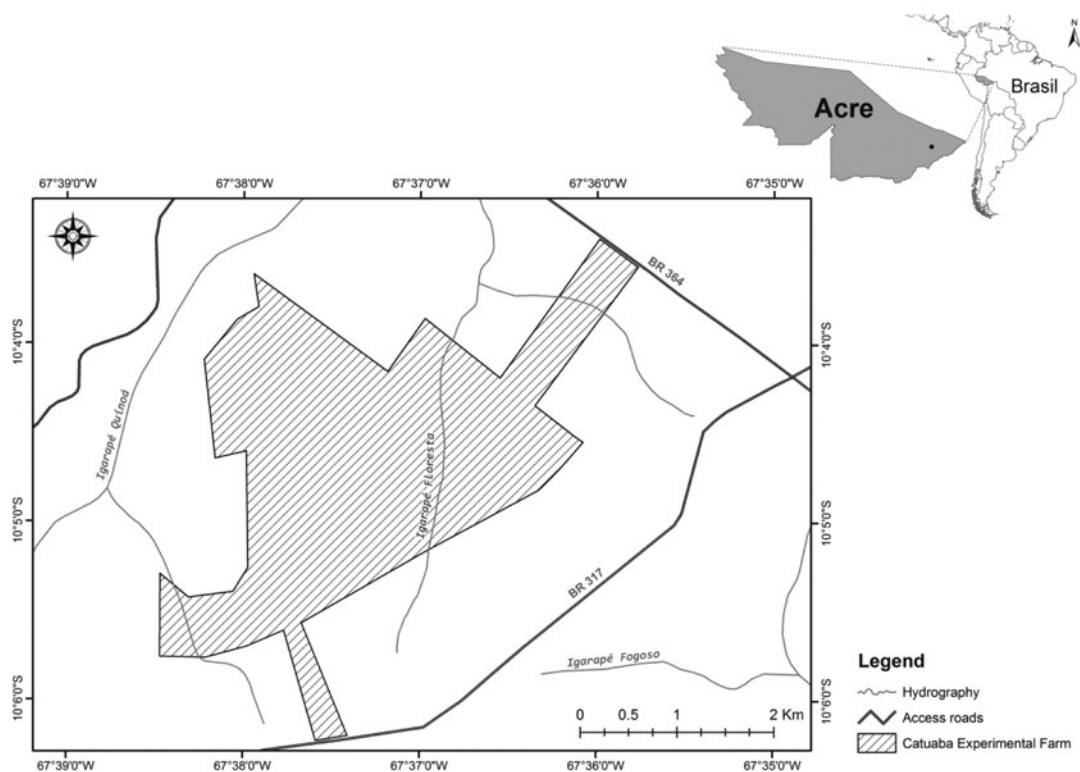


Figura 1. Área de estudo, Fazenda Experimental Catuaba, Senador Guiomard, Acre, Brasil.
Figure 1. Study site, Catuaba Experimental Farm, Senador Guiomard, Acre state, Brazil.

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} ($\text{CV} = 33\%$), and the average diameter was 4.4 ± 0.6 cm ($\text{CV} = 13.9\%$). Culm abundance differed significantly ($p = 0.000001$) between edge (3394 ± 1121 culms ha^{-1} , $\text{CV} = 33\%$) and interior (1123 ± 754 culms ha^{-1} , $\text{CV} = 62\%$), 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 ($3.8 \pm 2.6\% \text{ y}^{-1}$) and interior ($3.6 \pm 2.6\% \text{ y}^{-1}$).

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

(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).

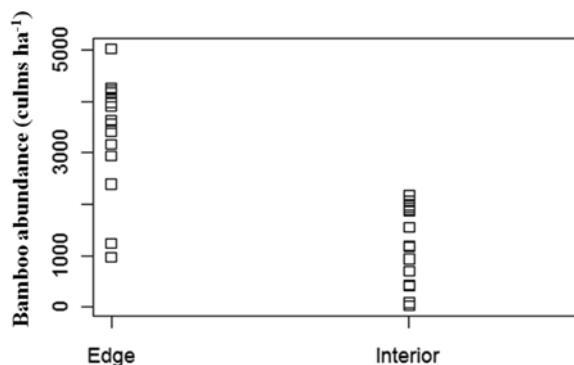


Figura 2. Densidade de bambu (colmos ha^{-1}) na borda e no interior da floresta em Catuaba.

Figure 2. Bamboo abundance (culms ha^{-1}) on the edge and in the interior of the forest of the forest at Catuaba.

There was no significant difference in mortality ($t = 1.30$, $p = 0.15$) between edge and interior for all dbh classes combined. However, mortality in the dbh class 10-30 cm (89%) was higher than that observed in the class 30-50 cm (11%) (ANOVA: $F = 30.50$ $p < 0.001$) considering edge and interior together. We did not record mortality in the class dbh > 50 cm during the study period. Bamboo abundance did not explain the overall mortality rate ($p = 0.12$, $r^2 = 0.08$, $n = 30$). Mortality rate was not associated with bamboo abundance on the edge ($p = 0.09$, $r^2 = 0.20$, $n = 15$) and in the interior ($p = 0.19$, $r^2 = 0.12$, $n = 15$). However, on the edge, bamboo abundance explained 23% of the variation in mortality of dead standing trees ($p = 0.03$, $r^2 = 0.23$, $n = 15$).

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 $\% \text{ y}^{-1}$) 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 ($3.85 \pm 0.72\% \text{ y}^{-1}$; 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.

ACKNOWLEDGEMENTS

We thank The Brazilian Research Council (CNPq; project no. 620236/2006-0; scholarships n. 128855/2009-06 and 137587/2011-2); the Large Scale Biosphere- Atmosphere Experiment in Amazonia (LBA) for logistic support. We thank Edilson Consuelo, Flávio Obermuller and Lívia Souza for help during field work, Lucas Souza for the study area map and Douglas Daly for final revision of manuscript. This study was written as a product of a writing workshop supported by PROCAD No. 108/2007 of CAPES, INCT-CENBAM and PPBio.

REFERENCES

ACRE. Secretaria de Meio Ambiente do Acre. **Zoneamento ecológico-econômico do Acre fase II**. Rio Branco: Governo do Estado do Acre, 2006. 356 p.

CHAO K-J, PHILLIPS; O. L., MONTEAGUDO A.; TORRES-LEZAMA, A.; VÁSQUEZ-MARTÍNEZ, R. How do trees die? Mode of death in northern Amazonia. **Journal of Vegetation Science**, Oxford, v. 20, n. 1, p. 260-268, 2009.

D'ANGELO, S. A.; ANDRADE, A. C. S.; LAURANCE, S. G.; LAURANCE, W. F.; MESQUITA, R. C. G. Inferred causes of tree mortality in fragmented and intact Amazonian Forests. **Journal of Tropical Ecology**, Cambridge, v. 20, n. 2, p. 243-246, 2004.

DUARTE, A. F. Aspectos da climatologia do Acre, Brasil, com base no intervalo 1971 – 2000. **Revista Brasileira de Meteorologia**, São José dos Campos, v. 21, n. 3b, p. 308-317, 2006.

FERREIRA, L. V.; LAURANCE, W. F. Effects of Forest Fragmentation on mortality and Damage of Selected Trees in Central Amazonia. **Conservation Biology**, Barking, v. 11, n. 3, p. 797-801, 1997.

GRISCOM, B.W.; ASHTON, P. M. S. A self-perpetuating bamboo disturbance cycle in a neotropical forest. **Journal of Tropical Ecology**, Cambridge, v. 22, n. 5, p.587-597, 2006.

GRISCOM, B. W.; ASHTON, P. M. S. Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru. **Forest Ecology and Management**, Amsterdam, v. 175, n.1 – 3, p.445-454, 2003.

GRISCOM, B. W.; DALY, D. C.; ASHTON, P. M. Floristics of bamboodominated stands in lowland terra-firma forests of southwestern Amazonia. **Journal of the Torrey Botanical Society**. Lawrence, v. 134, n. 1, p.108-125, 2007.

LAURANCE, W. F.; DELAMONICA, P.; LAURANCE, S. G.; VASCONCELOS, H. L.; LOVEJOY, T. E. Rainforest fragmentation kills big trees. **Nature**, London, v. 404, p. 836, 2000.

LAURANCE, W. F., FERREIRA, L. V., RANKIN-DEMERONA, J. M.; LAURANCE, S. G. Rain forest fragmentation and the dynamics of Amazonian tree communities. **Ecology**, Washington, v. 79, n. 6, p. 2032-2040, 1998

LAURANCE, S. G. W.; LAURANCE, W. F.; NASCIMENTO, E. M.; ANDRADE, A.F. P. M.; REBELLO, E. R. G; CONDIT, R. Long-term variation in Amazon forest dynamics. **Journal of Vegetation Science**, Oxford, v. 20, n. 2, p. 323–333, 2009.

LAURANCE, W. F.; LOVEJOY, T. E.; VASCONCELOS, H. L.; BRUNA, E. M.; DIDHAM, R. F.; STOUFFER, P. C.; GASCON, C.; BIERREGAARD, R. O.; LAURANCE, S. G.; SAMPAIO, E. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. **Conservation biology**, Barking, v. 16, n. 3, p. 605-618, 2002.

MURCIA, C. Edge effects in fragmented forests: implications for conservation. **Trends in Ecology and Evolution**, Amsterdam, v. 10, n. 2, p. 58-62, 1995.

- QUESADA, C. A., LLOYD, J., SCHWARZ, M., BAKER, T. R., PHILLIPS, O. L., PATIÑO, S., CZIMCZIK, C., HODNETT, M. G., HERRERA, R., ARNETH, A., LLOYD, G., MALHI, Y., DEZZEO, N., LUIZÃO, F. J., SANTOS, A. J. B., SCHMERLER, J., ARROYO, L., SILVEIRA, M., PRIANTE FILHO, N., JIMENEZ, E. M., PAIVA, R., VIEIRA, I., NEILL, D. A., SILVA, N., PEÑUELA, M. C., MONTEAGUDO, A., VÁSQUEZ, R., PRIETO, A., RUDAS, A., ALMEIDA, S., HIGUCHI, N., LEZAMA, A. T., LÓPEZ-GONZÁLEZ, G., PEACOCK, J., FYLLAS, N. M., ALVAREZ DÁVILA, E., ERWIN, T., DI FIORE, A., CHAO, K. J., HONORIO, E., KILLEEN, T., PEÑA CRUZ, A., PITMAN, N., NÚÑEZ VARGAS, P., SALOMÃO, R., TERBORGH, J., AND RAMÍREZ, H. Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties. *Biogeosciences Discussions*, Göttingen, v. 6, n. 2, p. 3993–4057, 2009.
- R DEVELOPMENT CORE TEAM. **R**: A language and environment for statistical computing. Viena: R Foundation for Statistical Computing, 2011.
- SALIMON, C. I.; BROWN, I. F. Desmatamento, Fogo e Emissões de carbono no Estado do Acre. In: BUENAUENTE, S. M. (Org.). *Amazônia: dinâmica do carbono e impactos sócioeconômicos e ambientais*. Bela vista: EdUFRR Editora da Universidade Federal de Roraima, 2009. p. 141-152
- SHEIL, D.; MAY, R. M. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology*, Oxford, v. 84, n. 1, p. 91-100, 1996.
- SILVEIRA, M. *A floresta aberta com bambu no sudoeste da Amazônia: padrões e processos em múltiplas escalas*. Rio Branco: EDUFAC, 2005. 157 p.
- SMITH, M.; NELSON, B. W. Fire favours expansion of bamboo-dominated forests in the south-west Amazon. *Journal of Tropical Ecology*, Cambridge, v. 27, n. 1, p. 59–64, 2011.
- SOUSA, E. S.; SALIMON, C. I.; VICTORIA, R. L.; KRUSCHE, A. V.; ALIN, S. R.; LEITE, N. K.; 2008. Dissolved inorganic carbon and pCO₂ in two small streams draining different soil types in Southwestern Amazonia, Brazil. *Revista Ambiente e Água*, Taubaté, v. 3, n. 2, p. 37-50, 2008.
- TOREZAN, D. M. T.; SILVEIRA, M. The biomass of bamboo (*Guadua weberbaueri* Pilger) in open forest of the southwestern Amazon. *Ecotropica*, Bonn, v. 6, n. 1, p. 71-76, 2000.

Recebido em 16/02/2012
Aceito para publicação em 30/01/2013