Forest Ecology and Management 260 (2010) 1345–1349

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Bamboo dieback and tree regeneration responses in a subtropical forest of South America

Jean Carlos Budke*, Mariângela Santin Alberti, Cleudes Zanardi, Cintia Baratto, Elisabete Maria Zanin

Plant Ecology and Systematics Lab. – ECOSSIS, Department of Biological Sciences, Universidade Regional Integrada do Alto Uruguai e das Missões–URI. Av. Sete de Setembro 1621, Erechim 99700.000, RS, Brazil

ARTICLE INFO

Article history:
Received 11 April 2010
Received in revised form 12 July 2010
Accepted 13 July 2010

Keywords:
Gap dynamics
Merostachys multiramea
Diversity indices
Rényi series
Canopy openness
Direct and diffuse light

ABSTRACT

Bamboos' vegetative growth are frequently associated to negative effects on tree recruitment and survival and despite this process, the effects of bamboo dieback after flowering events are poorly understood due the rarity of these events. 2 years after the massive flowering of the woody bamboo *Merostachys multiramea* in a southern South America subtropical forest, we compared changes in environmental conditions; tree species regeneration and production of new culms in canopy gaps resulted from bamboo dieback and areas of continuous canopy allowed by sparse bamboo cover. We observed sharp differences in environment conditions mainly resulted from differences in canopy openness and a NPMANOVA revealed differences among the stands regeneration directions (species composition and density). Average density, number of culms per sapling and total height of *M. multiramea* did not differ between stands, although slight differences were detected with increasing values toward opened sites.

Canopy gaps resulted from bamboo dieback showed higher species richness and diversity when compared to closed canopy without bamboo. After 2 years, the massive bamboo flowering and dieback resulted differences in several environmental conditions, leading to distinct regeneration directions with higher diversity toward opened areas.

1. Introduction

Forest structure is highly influenced by internal processes such as light competition, pollinators, dispersers and the interaction with exogenous disturbances, which may reflect in fine/large scale trends across time and space. The regular occurrence of some events as floods and droughts provided several insights to explain how species regulate their life cycle to avoid or tolerate these recurrent disturbance episodes (Lytle and Poff, 2004). On the other hand, large-span disturbances generated by species dynamics are less known because of long periods among events or absence of regularity. This is the case of several bamboo species which show long vegetative periods and unpredictable flowering episodes, leading to little information about the ecological impact of these phenomena on forest dynamics, particularly in the first years post-flowering (Marchesini et al., 2009). Also, because of their rapid growth, high litter production and large biomass (Christanty et al., 1996) bamboos are frequently associated to negative effect on tree recruitment, survival and growth (Campanello et al., 2007).

Woody bamboos show an unusual life cycle, which varies from 3 to 120 years and ending in a single reproductive event with massive seed production (McClure, 1993). These synchronized and widespread events involve a large fraction or even the entire population and because of such pattern, the bamboo dieback is frequently associated to disturbance of noteworthy role in structuring forests worldwide (Abe et al., 2001; Holz and Veblen, 2006; Martins et al., 2004; Taylor et al., 2004).

The woody bamboo dominance and frequency in forested areas have been greatly documented in the past few years (Campanello et al., 2007; Holz and Veblen, 2006; Marchesini et al., 2009; Rother et al., 2009) although conceptual models regarding bamboo invasion and dominance in forest stands are scarce mainly due to the absence of flowering events. A conceptual approach was designed by Griscom and Ashton (2003) which pointed out that bamboo can invade mature forests with partial opened-canopy structure resulting from wind blow-down. Furthermore, lower biomass of bamboo-dominated forests would result not only from catastrophic disturbance, but probably by combining intermediary disturbance and the capacity of an aggressive species to invade forested areas with multiple canopy gaps and exclude juvenile trees by mechanical or source competition (Griscom and Ashton, 2003). Finally, the authors suggest that the distribution of the population would contract after synchronized flowering/die-off events with trees regenerating successfully or leading to a bamboo reinvasion.

After bamboo die-off, the resulting canopy gaps may experience several changes in both environmental conditions and recruitment

---

* Corresponding author. Tel.: +55 54 35209000x9024; fax: +55 54 35209010.
E-mail address: jean@uricer.edu.br (J.C. Budke).

0378-1127/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2010.07.028

patterns. Despite the results of Guilherme and Ressel (2001) which estimated the seed production from *Merostachys riedeliana* from seasonal forests of southeastern Brazil (over 30 million seeds ha^{-1}) and González and Donoso (1999) which estimated an input of over than 195 million seeds ha^{-1} during the *Chusquea quila* flowering in a southern beech forest in Chile, the relationships among composition and density of seed rain in a tropical rainforest with occurrence of wide-sized woody bamboo *Guadua tagoara* revealed that seed rain was not altered by the occurrence of bamboos (Rother et al., 2009). In addition, Jaksic and Lima (2003) reported that the followed rodent irruptions are associated with bamboo blooming and showed that these “ratadas” differ according to the region, some of them being more associated to rainfall and others (mainly in Brazil), are related to bamboo flowering.

One may ask whether composition and regeneration of tree species would be altered after bamboo dieback. Some results from temperate forests indicate a gradational process of gaps enrichment by saplings and juveniles trees (Abe et al., 2001; Holz and Veblen, 2006) while others showed a tree establishment suppression, as in *Abies-Betula* forest in China (Taylor and Zisheng, 1988). In high diversity subtropical forests, Campanello et al. (2007) showed that bamboo inhibited tree sapling abundance and tree species richness within gaps. On this hand, Guilherme et al. (2004) revealed that in riparian forests from southeastern Brazil, both density and basal area of tree species were associated with density of *M. riedeliana* culms, which also restricted recruitment, growth and survival of trees.

In this contribution we focused on tree species establishment, 2 years after the wide and synchronized flowering and dieback event of *Merostachys multiramea* Hack., a woody bamboo of broad distribution in southern Brazil and adjacencies, in order to understand this species role in the development of a high diversity forest in the initial time after dieback. Our main questions were: (1) Do forest canopy including openness, air humidity and temperature vary across areas with presence of *M. multiramea* dieback and other of continuous canopy with sparse bamboo cover? (2) Do environmental conditions influence the new culms production, including number of culms per sapling and height of bamboo saplings after dieback? and (3) Do tree composition and diversity indices vary across these situations within the initial establishment? We hypothesized that bamboo recruitment would be greater in the gaps produced by early bamboo dieback and that tree species diversity would be higher in those areas beneath continuous canopy, followed by differences in tree species composition among areas.

2. Material and methods

2.1. Study area

M. multiramea is a monocarp bamboo species that present massive flowering each 31–33 years (Schmitt and Longhi-Wagner, 2009) with the last reproductive event registered in southern Brazil from 2006 to 2007. We conducted our study at the Horto Florestal Municipal of Erechim, a conservation unit of 68 ha located in northern Rio Grande do Sul state (central point coordinates 27°38′03″S and 52°16′26″W), with subtropical regional climate; mean annual temperature of 17.6 °C and mean annual precipitation of 1912 mm with no dry season. Typical vegetation is an Atlantic Forest Domain extension (Oliveira-Filho et al., 2006) and show a transition between seasonal semideciduous forest and Mixed *Araucaria* rain forests, which include both temperate tree species as *Araucaria angustifolia* (Araucariaceae), *Vernonia discolor* (Asteraceae) and *Piptocarpha angustifolia* (Asteraceae) as well as deciduous Fabaceae species as *Apuleia leiocarpa*, *Myrocarpus frondosus* and *Albizia edwalli*. Regional landscape shows several small remnants of such forests located in agriculture and cattle farming matrix.

Adult trees can reach over 25 m height and bamboo clumps occur as dense and abundantly patches that reach height of 6–10 m. After flowering and fruiting event, all bamboo culms died and generated several gaps of different sizes. In these areas, seeds covered all the ground and the entire remnant experienced an explosion of granivores densities (J. Marinho and E. Galiano, personal communication) also registered in several southern South America areas, according to previous and sparse descriptions which started in 1843 (Jaksic and Lima, 2003).

2.2. Field design and sampling

In order to test our predictions, we located 25 permanent sampling units of 10 m × 10 m, 2 years after bamboo flowering and dieback, in two different situations: dead bamboo gaps (13 sampling units located randomly in gaps dominated by exclusively dead bamboo beneath a semi-open tree canopy) and understory vegetation (12 sampling units randomly located in areas without dead bamboo and showing continuous canopy). Stand description included vegetation sampling of all trees with diameter at breast height $\geq$5 cm. Regeneration survey included all living saplings of tree species from 30 cm to 1 m height, including diameter at soil level and height estimation. Species were identified *in loco* or compared to vouchers of Herbário Padre Balduino Rambo - HPBR. The regeneration of *M. multiramea* was assessed by counting all young saplings, hereafter named as bamboo density (number of saplings) and identifying the number of culms and total height of each sapling. To ensure that continuous canopy areas did not have bamboo culms before our survey we also counted dead culms in each sampling unit.

To assess canopy discontinuity (hereafter named openness) we obtained a hemispherical photograph in the central point of each sampling unit, by using a Canon EOS300 digital camera with a Raynox DCR-CF true fish-eye converter lens. The camera was mounted in a self-leveling bracket, oriented north, attached to a large tripod. All photographs were taken at 1.5 m above the forest floor with 2.5 MB resolution. Canopy openness was calculated by using the Gap Light Analyzer 2.0 software (Frazer et al., 1999) and used as a reasonable percentage of open sky, then was able to describe gap size (Souza et al., 2008), because direct and indirect diffuse radiation just could be measured with more extensive field work. To avoid direct reflectance from sun rays, all photographs were taken in a completely cloudy day. Complementary lightness was obtained with a TESTO 540 luximeter. Microclimatic variables also included records of mean air temperature (°C) and mean air humidity (%), which were obtained in each sampling unit by recording four measurements with a THWD-1 therm-hygrometer while taking hemispherical photographs.

2.3. Data processing and analysis

We compared structural and environmental variables of tree density, basal area, lightness, canopy openness, humidity and air temperature, and bamboo related metrics: density, number of culms per sapling, bamboo height and dead culms, to assess environmental differences between continuous canopy and gap areas resulted from bamboo dieback. Non-parametric Mann–Whitney *U*-tests were applied when normality assumptions could not be met. This was the case of lightness, canopy openness, tree basal area, bamboo height, number of culms per sapling and dead culms.

To analyze density of tree saplings and environmental variables we applied a non-metric multidimensional scaling - NMDS based in euclidean distance matrix that included densities of all saplings of tree species with density $\geq$5 individuals. The second