Acta Oecologica 54 (2014) 36–44

Contents lists available at SciVerse ScienceDirect

Acta Oecologica

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

Original article

Functional traits enhance invasiveness of bamboos over co-occurring tree saplings in the semideciduous Atlantic Forest

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ARTICLE INFO

Article history:
Received 18 December 2012
Accepted 9 March 2013
Available online 8 April 2013

Keywords:
Chusquea ramosissima
Chusquea tenella
Invasive species
Leaf life-span
Photosynthetic capacity
Plasticity

ABSTRACT

Many woody bamboo species are forest understory plants that become invasive after disturbance. They can grow rapidly forming a dense, nearly monospecific understory that inhibits tree regeneration. The principal aim of this study was to understand what functional traits of bamboos allow them to outcompete tree seedlings and saplings and become successful species in the semideciduous Atlantic Forests of northeastern Argentina. We studied leaf and whole-plant functional traits of two bamboo species of the genus *Chusquea* and five co-occurring saplings of common tree species growing under similar solar radiation and soil nutrient availabilities. Nutrient addition had no effect on bamboo or tree sapling survival and growth after two years. Tree species with high-light requirements had higher growth rates and developed relatively thin leaves with high photosynthetic capacity per unit leaf area and short leaf life-span when growing in gaps, but had lower survival rates in the understory. The opposite pattern was observed in shade-tolerant species that were able to survive in the understory but had lower photosynthetic capacity and growth than light-requiring species in gaps. Bamboos exhibited a high plasticity in functional traits and leaf characteristics that enabled them to grow rapidly in gaps (e.g., higher photosynthetic capacity per unit dry mass and clonal reproduction in gaps than in the understory) but at the same time to tolerate closed-canopy conditions (they had thinner leaves and a relatively longer leaf life-span in the understory compared to gaps). Photosynthetic capacity per unit dry mass was higher in bamboos than in trees. Bamboo plasticity in key functional traits, such as clonal reproduction at the plant level and leaves with a relatively low C cost and high photosynthesis rates, allows them to colonize disturbed forests with consequences at the community and ecosystem levels. Increasing disturbance in some forests worldwide will likely enhance bamboo invasion resulting in profound negative impacts on forest diversity, structure and function in the long term.

1. Introduction

Understory vegetation is often a key component of forest ecosystems that drives tree regeneration, belowground properties, and long term plant succession (Nilsson and Wardle, 2005). Bamboos are common in the understory of many forests, but some species show an invasive behavior (sensu Válery et al., 2008) after disturbance (i.e., they become overabundant and spread rapidly into new areas). When bamboos become dominant they outcompete other plant species, particularly trees, decreasing its density and species diversity (Silveira, 2005; Holz and Veblen, 2006; Lima et al., 2012), affecting seed dispersal patterns (Rother et al., 2009) and ultimately arresting forest succession (Griscom and Ashton, 2006; Campanello et al., 2007, 2009; Ito and Hino, 2007; Larpkern et al., 2010; Montti et al., 2011).

The competitive advantage of a given invasive species depends on interactions established with other species (Hayes and Holzmueller, 2012), the environment (Pyšek et al., 2010) and its functional traits (Durand and Goldstein, 2001; Leishman et al., 2007). Successful invasive plant species are associated with greater resource use efficiency, leaf traits that enable rapid growth

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http://dx.doi.org/10.1016/j.actao.2013.03.004

(e.g. high specific leaf area, high foliar N and P content and high photosynthetic rate) (Thompson et al., 1995; Pattison et al., 1998; Baruch and Goldstein, 1999; Durand and Goldstein, 2001; Leishman et al., 2007; Meiners et al., 2008) and high phenotypic plasticity (Daheler, 2003; Rejmánek et al., 2005; Pyšek and Richardson, 2007). In addition, it has been observed that invasive tree species may not conform to the general trade-offs in allocation patterns observed for tropical tree species (Martin et al., 2010), where a trade-off between high survival under low light vs. rapid growth under high light conditions occur (Kitajima, 1994; Pacala et al., 1994; Kobe et al., 1995; Wright, 2002; Díaz et al., 2004).

In undisturbed areas of the semideciduous Atlantic Forest, bamboo species of the genus *Chusquea* are a native non-dominant component of the understory. Selective logging, a common tree harvesting method in the Atlantic Forest of Northern Argentina (Giraudo et al., 2003), reduces tree density and increases the rate of large gap formation which in turn promotes bamboo growth (Campanello et al., 2007, 2009). In these disturbed forests, *Chusquea* species become dominant, particularly in areas with high solar radiation such as large canopy gaps. Here we studied functional traits that could help to explain the proliferation of *Chusquea* bamboos after canopy disturbance. We first compared survival, growth rates, photosynthetic capacity, leaf life-span, specific leaf area and leaf nutrient content of bamboos and co-occurring saplings of tree species with contrasting life history characteristics growing in natural gaps with and without nutrient addition. Then we studied the response of bamboos under low and high irradiance environments in the understory of closed canopy and in gaps, respectively. We hypothesized that *Chusquea* species have leaf functional traits and allocation patterns that enable them to grow fast when release for light limitation as well as to have high survival under shaded conditions in order to persist in the forest understory. High trait plasticity, together with clonal reproduction, would allow bamboos to outcompete co-occurring canopy tree species in gaps. Finally, we discuss the impacts of *Chusquea* spread and its consequences in the structure and dynamics of the semideciduous Atlantic Forest.

2. Methods

2.1. Study area

The research was conducted in a native forest at the Iguazú National Park (INP; 25°31′–25°43′S, 54°08′–54°32′O) that was subjected to selective logging during the 1920's (Devoto and Rothkugel, 1936; Placci and Giorgis, 1993). This forest has three strata of trees, with mature trees ranging from 20 to 45 m in height and abundant lianas, epiphytes and bamboos species in the understory. Gaps ranging between 4 and 30 m^2 are common in this forest (per. obs.). The canopy is mostly dominated by trees of the genus *Cordia* (Boraginaceae), *Ocotea* and *Nectandra* (Lauraceae), *Parapiptadenia* and *Peltophorum* (Fabaceae), *Cedrela* and *Trichilia* (Meliaceae) and *Plinia*, *Eugenia* and *Myrciaria* (Myrtaceae) (Srur et al., 2009). Precipitation (ca. 200 mm yr^{-1}) is evenly distributed throughout the year. Mean annual air temperature is 21 °C with monthly means of 25 °C in January and 15 °C in July (i.e., the warmest and coldest months of the year, respectively). Frost seldom occurs during winter (Gatti et al., 2008). Soils are mostly Alfisols and Ultisols derived from basaltic rocks containing high concentration of Fe, Al and Si (Ligier et al., 1990).

2.2. Study species

We studied the functional traits of two widely distributed woody bamboos in the semideciduous Atlantic Forest of Argentina: *Chusquea ramosissima* Lindm. and *Chusquea tenella* Nees (Poaceae). Both species are aggressive colonizers after disturbance. Although *C. ramosissima* is not invasive in some neotropical forests (Veldman et al., 2009), in semideciduous Atlantic Forest of Argentina it grows rapidly and form dense thickets that inhibit tree regeneration (Campanello et al., 2009). Both species have erect or scandent culms of approximately 15 mm diameter and 4–15 m of length that allows the plants to climb and spread onto the trees (Montti et al., 2008; Montti, 2010).

Saplings of five tree species with different life-history traits were also studied. They were (in order of decreasing shade-tolerance): *Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae), *Cordia americana* (L.) Gottschling & J.S. Mill. (Boraginaceae), *Maclura tinctoria* (L.) Steud. ssp. *tinctoria* (Moraceae), *Cordia trichotoma* (Vell.) Arrab. ex Steud (Boraginaceae) and *Peltophorum dubium* (Spreng.) Taub. (Fabaceae). These species are abundant in the semideciduous Atlantic Forest and well represent the range of ecological and physiological characteristics between light-requiring and shade-adapted species (Campanello et al., 2008, 2011). Congeneric species of *Cordia* spp. differ in leaf phenology and shade tolerance. *C. trichotoma* is a deciduous species with high light requirements that shows fast growth rates and relatively low wood density. *C. americana* is an evergreen tree with higher shade tolerance, lower growth rates and denser wood (Campanello et al., 2011). *M. tinctoria*, and *P. dubium* are deciduous species with high-light requirements and fast growth rates while *B. riedelianum* is the most shade-tolerant of the species under study and shows slow growth rates (Campanello et al., 2008, 2011; Villagra, 2012).

2.3. Experimental design

As part of a long-term study of forest dynamics we performed an experiment that included four treatments with five replicates in a complete random design. The experiment included 20 plots, 10 located in gaps (i.e., canopy opening with high irradiance, $28 \pm 0.3\%$ of full sun) and the remaining 10 plots in areas under closed-canopy (low irradiance, less than $10 \pm 0.5\%$ of full sun). Five plots of each canopy condition were randomly assigned to a nutrient addition treatment (N + P) and the other five remained as control plots. Fertilization consisted of 100 kg ha^{-1} $year^{-1}$ of Nitrogen (N) (50:50 urea and nitrate ammonium), and 100 kg ha^{-1} $year^{-1}$ of Phosphorus (P) (calcium triple superphosphate) applied (sprinkled in granular form) on the organic soil surface three times per year from 2004 to 2007. Plots size was 15 × 15 m plus a peripheral area buffer of 5 m where manipulations were also applied to reduced the edge effect. Tree species composition, soil type, slope and elevation were similar among plots (Villagra, 2012). At the beginning of the study we manually removed herbaceous non-tree vegetation (including bamboos) in all the plots in order to isolate canopy effects from any potentially confounding influence of pre-existing understory plants. Harvested biomass was stacked out of the plots and left to decompose in situ. For detailed initial microclimatic conditions at the plots see Appendix A.

During 2005, we planted between 4 and 5 saplings of similar height (22–29 cm) of each bamboo species (*C. ramosissima* and *C. tenella*) in each plot and 10–15 saplings of the five canopy tree species (*B. riedelianum*, *C. americana*, *M. tinctoria*, *C. trichotoma* and *P. dubium*) of similar height (24–49 cm). One year after planting, and during two consecutive years, we measured the functional traits described below in all these saplings. Mean values of traits measured for each species at each plot were then used in the analysis of variance (see below). As tree saplings were part of a long-term study of forest dynamics, the harvesting of whole individuals was not possible.