

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Acta Oecologica

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

Original article

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

Lía Montti^{a,b,*}, Mariana Villagra^{a,c}, Paula I. Campanello^{a,c}, M. Genoveva Gatti^{a,c}, Guillermo Goldstein^{a,d}^a Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina^b Instituto de Ecología Regional (IER), Universidad Nacional de Tucumán, CC 34, 4107 Yerba Buena, Tucumán, Argentina^c Instituto de Biología Subtropical (IBS), Facultad de Ciencias Forestales, Universidad Nacional de Misiones, Bertoní 85, Puerto Iguazú, Misiones 3370, Argentina^d Laboratorio de Ecología Funcional (LEF), Universidad de Buenos Aires, Ciudad Universitaria Pab. II 2° piso, C1428EHA Buenos Aires, Argentina

ARTICLE INFO

Article history:

Received 18 December 2012

Accepted 9 March 2013

Available online xxx

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.

© 2013 Published by Elsevier Masson SAS.

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 Valéry 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 Holzmüller, 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

* Corresponding author. Instituto de Biología Subtropical, Bertoní 85, CP 3370 Puerto Iguazú, Misiones, Argentina. Tel.: +54 3757 424550; fax: +54 011 4576 3384. E-mail address: liamontti@gmail.com (L. Montti).

(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 (Giraud 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 m² 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) (Surr 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 ± 0.3% of full sun) and the remaining 10 plots in areas under closed-canopy (low irradiance, less than 10 ± 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.

2.4. Functional traits

a) Survival and growth rates

We counted all alive and dead plants per species per plot at the end of experiment in the year 2007 in order to calculate percentages of survival. Relative growth rate was estimated as annual leaf area increments (LA RGR). Leaf area is a driving variable for relative growth rates of whole-plants (Lambers et al., 1998), and was considered here as a representative measure of aboveground colonization and radiation interception during the earliest stages in the life-cycle of both bamboos and trees. In the case of bamboos relative growth rate was also estimated in terms of dry mass (DM RGR). LA RGR was estimated as the difference between the final (2006) and initial (2005) total leaf area (LA), divided it by its initial value (LA RGR is a dimensionless variable). Plant total LA was estimated based on the mean area per leaf multiplied by the number of fully expanded leaves per plant. To calculate the mean LA, we collected eight leaves per plant that were scanned and their areas measured using Scion Image Software (National Institute of Health, Bethesda, MD, USA). Additional traits were measured in harvested bamboo plants. One bamboo plant per plot was randomly collected to calculate DM RGR. Plant material was divided in leaf, culms and rhizome, dried at 60 °C for 5 days, and weighted. DM RGR was calculated as: $DM\ RGR = (\ln SM_{t_1} - \ln SM_{t_0}) / (t_1 - t_0)$ where SM is seedling mass. Five bamboo seedlings of each species were randomly selected, dried and weighted at the beginning of the study to calculate the initial mass of seedlings (SM at t_0). We estimated clonal reproduction by counting the number of culms and shoots produced per plant during two consecutive years. Clonal production was expressed as the increment in this variable divided by its initial value.

Comparisons among tree species and bamboos (except survival) were only made in gaps because most of the trees of high-light requirement species growing under closed-canopy did not survive or produced enough leaves for measuring.

b) Leaf traits and leaf life-span

Different leaf traits were measured in tree and bamboo saplings. Specific leaf area, N and P foliar content and photosynthetic capacities were studied both in gap and closed-canopy conditions for bamboos and only in gaps for tree. For specific leaf area (SLA) samples of fresh leaves (five per plant, and four to five plants per plot) were collected in the field. Leaves were scanned to estimate leaf area and then dried at 60 °C for five days and weighted to obtain dry weight. To determine foliar N and P concentrations (% of dry weight) we collected 2 g of fully expanded leaves per plant growing in each treatment (in gaps, sun-exposed leaves were selected). The foliar N and P content were determined by the micro Kjeldahl technique and flame photometry.

To estimate leaf photosynthetic capacity we selected four to five individuals per species per plot, using leaves with similar sun exposure and size. A chlorophyll fluorescence analyzer with a pulse-amplitude modulated yield (Mini-PAM, Waltz, Effeltrich, Germany) was used. Steady-state light–response curves were generated for a single, young fully expanded leaf per plant using the external halogen light unit of the Mini-PAM. Leaves were allowed to adjust to light conditions for at least 10 min at each of five irradiances before a saturation pulse was applied for 0.8 s at 3500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Dark-adapted quantum yields (Fv/Fm) of photosystem II (PSII) were recorded before dawn and corresponded to the initial points of the light curves. Values of Fv/Fm below 0.8 were considered an indicator of permanent photoinhibition (see Lüttge et al., 1998; Franco et al., 1999; Krause et al., 2001;

Campanello et al., 2008). Electron transport rates (ETR) through PSII were calculated from light-adapted quantum yield ($\Delta\text{F}/\Delta\text{Fm}$) as:

$$ETR = 0.5\alpha(\Delta\text{F}/\Delta\text{Fm})(PPF)$$

where α is leaf absorbance and the 0.5 factor assumes an even distribution of absorbed quanta between PSII and PSI so that two photons are required for each electron passed through PSII. The ETR correction factor α takes into account that a fraction of the incident light that is absorbed by the two photosystems. A value of $\alpha = 0.84$ was used for calculations (Björkman and Demmig, 1987; Ehleringer, 1981). Photosynthetic capacity, expressed as the maximum electron transport rate (ETR_{max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), was calculated from the light curves as described by Rascher et al. (2000):

$$y = (ETR_{\text{max}})(1 - e^{-bx})$$

where y is photosynthetic rate, x is irradiance and b is the instantaneous fractional growth rate of the exponential function. In addition we expressed ETR_{max} per unit leaf mass ($\mu\text{mol g}^{-1} \text{s}^{-1}$).

To measure leaf life-span (LL) we marked all emergent leaf buds in all plants at the different treatments. Each leaf bud represented a cohort of leaves of the same age. Leaves were checked monthly until all of the originally marked leaves had abscised.

Leaf life-span was estimated via survival analysis using the Kaplan–Meier method, the sample sizes for leaf demography ranged from 125 to 285 leaves per species.

All leaf traits were measured in both bamboo species in gaps and under closed-canopy conditions and in both nutrient treatments (control and N + P), which allows the calculation of a plasticity index (PI), which spans from 0 (no-plasticity) to 1 (maximal plasticity). The PI for each trait was calculated as the difference between the mean minimum and maximum values of the trait in the treatments considered divided by the mean maximum value (Valladares et al., 2000).

2.5. Data analysis

Differences in morphological and physiological traits between bamboo species were analyzed by mean of three-way ANOVA, with species, canopy condition, and nutrient treatments as main factors. For comparisons among tree species and bamboos growing with different nutrient availability in gaps we performed a two-way ANOVA. Data were transformed when was necessary to satisfy the assumptions of the statistical analysis. Post-hoc comparisons were performed with a Tukey Honest Significant Difference (HSD) test. To compare leaf life-span among treatments and species we performed a log-rank test (Kleinbaum and Klein, 2005). A significance level of 5% was used in all cases. All ANOVA analyses were performed with InfoStat 2009 (Di Rienzo et al., 2009).

3. Results

3.1. Survival and growth rates

The effect of canopy condition on survival rate after two years varied depending on the species in question (i.e., the interaction species \times canopy condition was significant: $df = 6$, $F = 10.67$, $p < 0.0001$). All the species showed low mortality rates in gaps (less than 20% after two years) (Fig. 1c and d). Bamboo species also have high survival rate under closed-canopy (Fig. 1a and c), but tree species responded differently to canopy condition according to their shade-tolerance. Saplings of the most shade tolerant tree

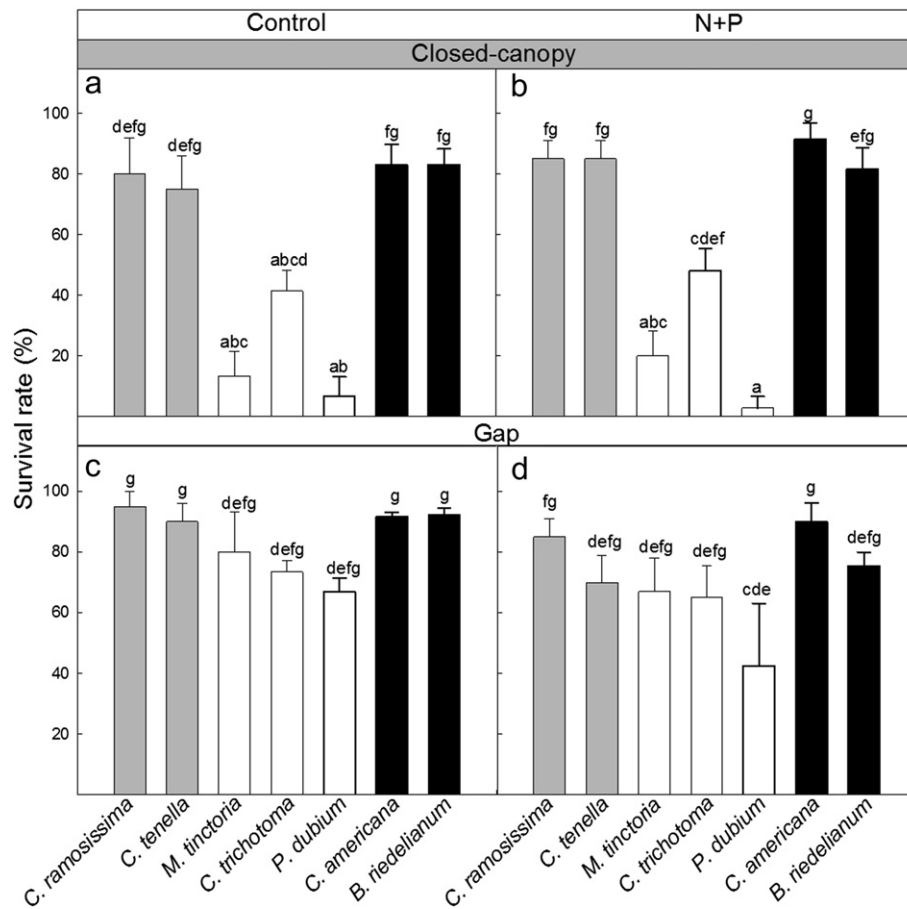


Fig. 1. Survival rate (%) for bamboo and tree sapling after two years under different canopy conditions (gap and closed) and nutrient treatments (control and N + P addition). Data are means \pm (SE) for all variables. Different letters indicate significant differences ($p < 0.05$) between species and treatment.

Table 1
Foliar nutrient concentration (N and P), Total leaf area (LA), relative increment of LA (LA RGR) and mean leaf life-span (LL), for saplings of two bamboo and five tree species growing under different canopy conditions (gap and closed) and soil nutrient treatments (control and N + P addition). Data are means \pm SE.

Species	Canopy condition	Nutrient treatment	N %	P %	LA ($\text{m}^2 \text{kg}^{-1}$)	LA RGR	LL (days)
<i>C. ramosissima</i>	Closed	Control	2.7 \pm 0.1	0.10 \pm 0.01	0.09 \pm 0.03	1.12 \pm 0.3	147 \pm 8
		N + P	2.8 \pm 0.1	0.14 \pm 0.01	0.04 \pm 0.01	0.59 \pm 0.2	148 \pm 7
	Gap	Control	2.2 \pm 0.2 ^a	0.12 \pm 0.01 ^{ab}	1 \pm 0.2 ^{ab}	4 \pm 1 ^{abcd}	144 \pm 4
		N + P	2.4 \pm 0.1 ^{ab}	0.14 \pm 0.01 ^{abcd}	2 \pm 0.4 ^{abc}	6 \pm 2 ^{bcd}	129 \pm 4
<i>C. tenella</i>	Closed	Control	2.7 \pm 0.0	0.12 \pm 0.00	0.2 \pm 0.05	1.23 \pm 0.6	163 \pm 7
		N + P	2.9 \pm 0.1	0.18 \pm 0.01	0.1 \pm 0.02	0.19 \pm 0.1	156 \pm 6
	Gap	Control	2.5 \pm 0.1 ^{ab}	0.11 \pm 0.01 ^a	3 \pm 3 ^{abcd}	11 \pm 3 ^d	163 \pm 5
		N + P	2.7 \pm 0.2 ^{abc}	0.17 \pm 0.00 ^{de}	4 \pm 2 ^{abcd}	13 \pm 5 ^d	142 \pm 5
<i>C. trichotoma</i>	Gap	Control	3.5 \pm 0.1 ^d	0.13 \pm 0.00 ^{abc}	4 \pm 0.3 ^{bcd}	4 \pm 0.3 ^{abcd}	138 \pm 6
		N + P	3.6 \pm 0.1 ^d	0.15 \pm 0.00 ^{bcd}	4 \pm 1 ^{bcd}	6 \pm 1 ^{bcd}	132 \pm 4
	Gap	Control	3.1 \pm 0.0 ^{cd}	0.14 \pm 0.00 ^{abcde}	15 \pm 5 ^{ef}	6 \pm 1 ^{bcd}	125 \pm 3
		N + P	3.2 \pm 0.1 ^{cd}	0.19 \pm 0.01 ^{ef}	36 \pm 8 ^f	10 \pm 1 ^d	116 \pm 3
<i>M. tinctoria</i>	Gap	Control	2.7 \pm 0.0 ^{bc}	0.12 \pm 0.00 ^{ab}	1 \pm 0.3 ^a	9 \pm 1 ^{cd}	146 \pm 5
		N + P	2.8 \pm 0.1 ^{bc}	0.15 \pm 0.00 ^{abcd}	2 \pm 0.3 ^{abcde}	11 \pm 1 ^d	133 \pm 6
	Gap	Control	2.6 \pm 0.1 ^{ab}	0.12 \pm 0.00 ^{ab}	3 \pm 0.6 ^{abcd}	2 \pm 1 ^a	213 \pm 4
		N + P	2.7 \pm 0.1 ^{ab}	0.15 \pm 0.00 ^{bcd}	8 \pm 3 ^{ef}	3 \pm 1 ^{abc}	207 \pm 4
<i>B. riedelianum</i>	Gap	Control	3.2 \pm 0.1 ^{cd}	0.16 \pm 0.01 ^{cde}	3 \pm 0.4 ^{abcd}	2 \pm 0.4 ^{ab}	183 \pm 4
		N + P	3.3 \pm 0.1 ^d	0.21 \pm 0.01 ^f	5 \pm 1 ^{cde}	6 \pm 1 ^{bcd}	167 \pm 4
<i>F</i> (df = 6)	Sp		33.6**	15.09**	25.18**	11.36**	
<i>F</i> (df = 1)	N		3.34	90.14**	12.42**	12.92**	
<i>F</i> (df = 6)	Sp \times N		0.36	2.61	0.98	0.96	

Different superscript letters indicate differences between treatments ($p < 0.05$) for bamboos and trees growing in gaps. Differences were evaluated with two-way ANOVA with species (Sp) and nutrient treatments (N) as main factors ($*p < 0.05$; $**p < 0.001$). Post-hoc comparisons were performed with a Tukey Honest Significant Difference (HSD) test. Differences between bamboo species under closed-canopy and gap were tested by means of three-way ANOVA. LL obtained by survival curves of Kaplan–Meier were compared by a log-rank test. Results of those analysis are shown in the text.

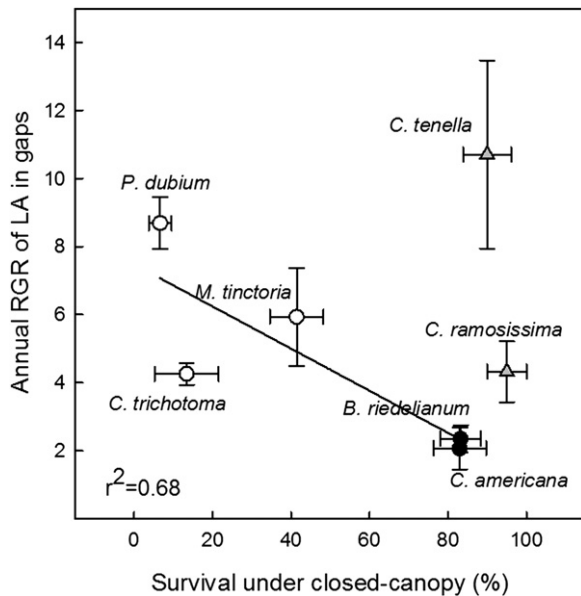


Fig. 2. Relationship between the annual increment in total leaf area (LA RGR) in gaps and survival in closed-canopy after two years for bamboo and tree species. r^2 corresponds to tree saplings data.

species (*C. americana* and *B. riedelianum*) exhibited low mortality under closed-canopy (Fig. 1a and c). The species with high-light requirements (*M. tinctoria*, *C. trichotoma* and *P. dubium*) showed relatively high mortality rates under closed-canopy (Fig. 1a; Tukey

test $p < 0.05$). Nutrient addition had no effect on bamboo and tree saplings survival (Fig. 1b and d; Tukey test $p > 0.05$).

Total leaf area (LA) differed among species at the end of the experiment and increased with nutrient addition in all cases (Table 1). In general, trees and bamboos had similar total LA but *M. tinctoria* (species with high-light requirements) had three times higher values of total LA than other tree species. The relative increment in LA (LA RGR) was as fast in bamboos (particularly in *C. tenella*) as it was in tree species with high-light requirements. Nutrient addition increased LA RGR in all species (approximately by a factor of 1.5) but no statistical differences were found between species (Tukey test $p > 0.05$).

The survival rate of tree species under low light in the understory (i.e. closed-canopy condition) was negatively correlated with their growth in gaps (Fig. 2). In contrast, both bamboo species had high growth in gaps and high survival under closed-canopy, and thus departing from the negative relationship between growth and survival observed for tree species (Fig. 2).

Clonal reproduction was a very plastic trait (Table 3). Bamboos in gaps developed a larger number of culms (Table 2) than bamboos in the understory. As a consequence, gap condition favored bamboo growth rates at plant level resulting in 20 times more final biomass in gap plants than in shaded plants (Table 2). Bamboos biomass was mainly allocated to culms (50–60%), followed by leaves (25–30%) and finally to rhizomes (15–20%) (Table 4). Nutrient addition did not substantially enhanced bamboo growth but plants in fertilized gaps tended to be bigger than control plants. Although, some differences were observed between both *Chusquea* species (e.g., clonal reproduction, LA RGR, or total LA), their response to different treatments was similar.

Table 2

Bamboo growth rates under different canopy conditions (gap and closed) and nutrient treatments (control and N + P addition). Data are means per plant \pm SE.

Species	Canopy condition	Nutrient treatment	Dry mass (g)	Annual clonal reproduction (culms year ⁻¹)	Final total culms (number of culms per plant)
<i>C. ramosissima</i>	Closed	Control	14 \pm 5 ^a	0.07 \pm 0.1 ^a	3.0 \pm 0.6 ^a
		N + P	5 \pm 0.4 ^a	0.05 \pm 0.1 ^a	2.3 \pm 0.7 ^a
	Gap	Control	177 \pm 29 ^b	0.80 \pm 0.2 ^{abc}	7.8 \pm 1.3 ^{bc}
<i>C. tenella</i>	Closed	N + P	345 \pm 117 ^b	1.67 \pm 0.5 ^{abc}	13 \pm 2.3 ^c
		Control	28 \pm 9 ^a	0.50 \pm 0.1 ^{abc}	4.0 \pm 0.5 ^{ab}
	Gap	N + P	14 \pm 4 ^a	0.35 \pm 0.1 ^{ab}	3.4 \pm 0.5 ^{ab}
	Closed	Control	471 \pm 92 ^b	2.80 \pm 0.3 ^c	13 \pm 2.4 ^c
		N + P	798 \pm 351 ^b	2.90 \pm 0.7 ^{bc}	14 \pm 2.7 ^c
	Gap	Control	11.11 [*]	5.37 [*]	6.35 [*]
<i>F</i> (df = 1)	Sp		0.40	0.90	2.9 ⁻⁰³
<i>F</i> (df = 1)	N		200.1 ^{**}	24.37 ^{**}	90.8 ^{**}
<i>F</i> (df = 1)	Cc		0.13	2.40	0.24
<i>F</i> (df = 1)	Sp \times N		3.82	1.95	3.92
<i>F</i> (df = 1)	N \times Cc		0.03	1.50	0.27
<i>F</i> (df = 1)	Sp \times Cc		0.14	1.21	1.42
<i>F</i> (df = 1)	Sp \times N \times Cc				

Different superscript letters indicate differences between treatments ($p < 0.05$). The differences were tested by mean of tree-way ANOVA with species (Sp), canopy condition (Cc) and nutrient treatment (N) as main factors (* $p < 0.05$; ** $p < 0.001$). Post-hoc comparisons were performed with a Tukey Honest Significant Difference (HSD) test.

Table 3

Plasticity index (PI) for both *Chusquea* species in response to canopy conditions (gap and closed) and nutrient treatments (control and N + P addition) considering nine functional traits.

Trait	Canopy condition		Nutrient treatment		Mean PI of trait
	<i>C. ramosissima</i>	<i>C. tenella</i>	<i>C. ramosissima</i>	<i>C. tenella</i>	
Total biomass	0.88	0.94	0.49	0.41	0.68
Annual clonal reproduction	0.91	0.82	0.52	0.03	0.67
Leaf area	0.91	0.93	0.50	0.25	0.65
ETR _{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.41	0.48	0.29	0.01	0.30
ETR _{max} ($\mu\text{mol g}^{-1} \text{s}^{-1}$)	0.19	0.22	0.24	0.24	0.22
Specific leaf area	0.23	0.25	0.32	0.16	0.24
Foliar N content	0.19	0.07	0.08	0.07	0.10
Foliar P content	0.17	0.08	0.14	0.35	0.19
Leaf life-span	0.06	0.07	0.07	0.01	0.05
Species' mean PI	0.44	0.43	0.30	0.17	

Table 4

Mean biomass allocation (%) in the different organs of two bamboo species when growing under different canopy condition (gap and closed) and nutrient treatment (control and N + P addition). Data are means for all variables.

Species	Canopy condition	Nutrient treatment	Leaf	Culms	Rhizome
<i>C. ramosissima</i>	Closed	Control	27	55	18
		N + P	24	48	28
	Gap	Control	24	61	15
		N + P	29	55	16
<i>C. tenella</i>	Closed	Control	29	54	16
		N + P	33	50	17
	Gap	Control	23	59	18
		N + P	24	58	18

3.2. Leaf traits and leaf life-span

Bamboos had thinner leaves than trees (the highest values of SLA) (Fig. 3b; $df = 6$, $F = 51.51$, $p < 0.001$). Nutrient addition tended to increase this trait between 5 and 10% but differences were not significant (Fig. 3b; $df = 1$, $F < 0.01$, $p = 0.98$). Foliar N content was different between species (Table 1). Bamboos exhibited lower N content than tree species, and tree species with high-light requirements (e.g. *C. trichotoma*) tended to have the highest values of foliar N content. Fertilization had no effect on this trait. Foliar P content increased with fertilization and tended to be lower in bamboo compared to tree species. *B. riedelianum* had the highest value of foliar P (Table 1).

ETR_{max} estimated on a leaf area basis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was different among species and nutrient treatments (i.e., the interaction species \times nutrient was significant: $df = 6$, $F = 4.81$, $p < 0.001$). Trees (except *B. riedelianum* in control plots) showed higher

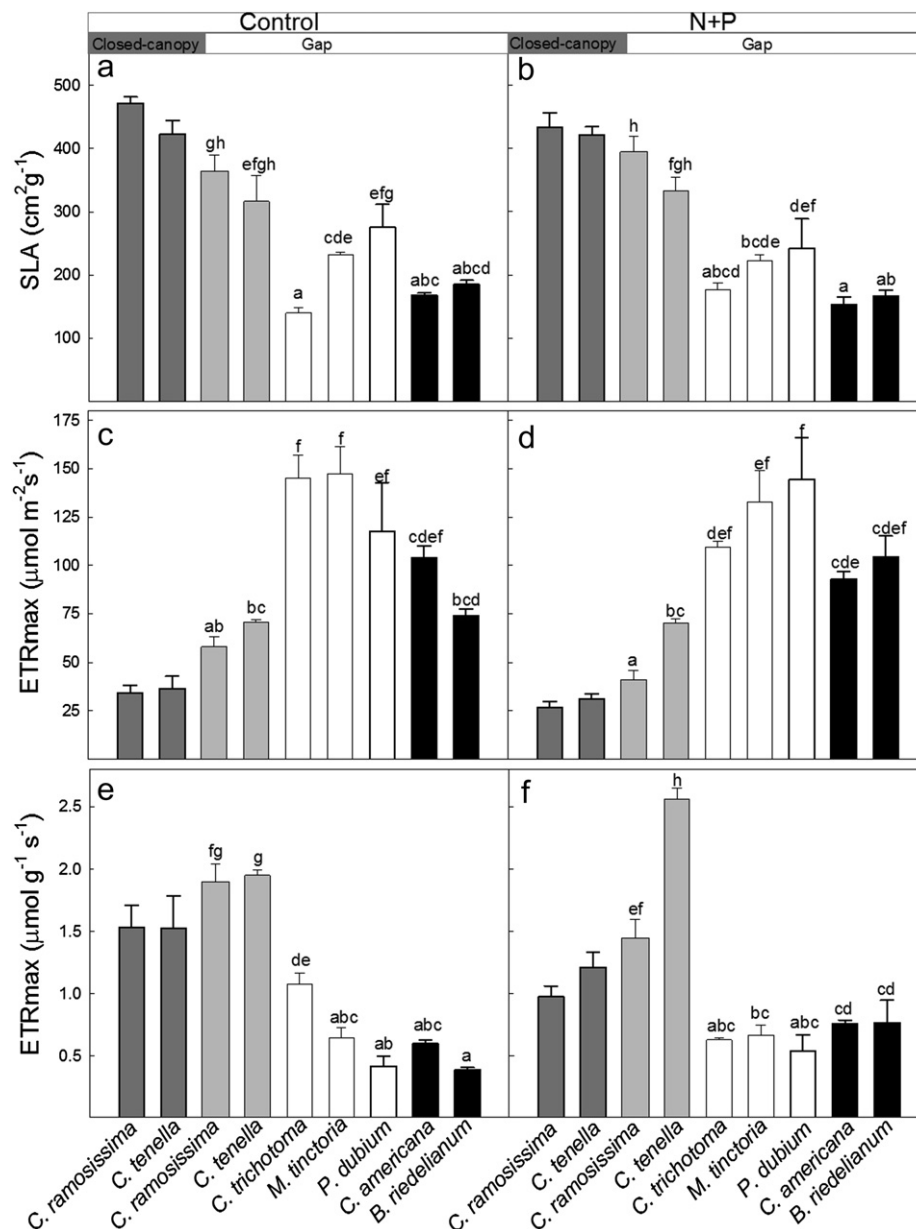


Fig. 3. Mean (SE) specific leaf area (SLA) and maximum electron transport rate (ETR_{max}) for saplings of two bamboo and five tree species under different canopy conditions (gap and closed) and nutrient treatments (control and N + P addition).

photosynthetic capacity than both bamboo species (Fig. 3c and d). Among the trees, ETR_{max} values decreased with decreasing light requirements (Tukey test, $p < 0.05$). Nutrient addition tended to have a negative effect on the ETR_{max} of most species (Fig. 3d). However, bamboos showed the higher ETR_{max} values when expressed per unit leaf mass ($\mu\text{mol g}^{-1} \text{s}^{-1}$) (Fig. 3e and f; Tukey test, $p < 0.05$) even when they were growing under low irradiance (i.e., closed-canopy). Nutrient addition did not affect this trait (Fig. 3f), except in the cases of *C. tenella* and *C. trichotoma* that positive and negative effect on ETR_{max} , respectively were observed.

Leaf traits of bamboo species differed between two canopy conditions. SLA and foliar N content decreased 20% for both species in gaps (Fig. 2a; $df = 1$, $F = 24.4$, $p < 0.001$ and Table 1; $df = 1$, $F = 14.92$, $p < 0.001$, respectively). In contrast, total LA increased five times (Table 1; $df = 1$, $F = 236$, $p < 0.001$) and ETR_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was two times higher for plants in gaps than those growing under the closed-canopy (Fig. 3c and d; $df = 1$, $F = 9.64$, $p < 0.05$).

Leaf life-span was different between species for plants growing in gaps (Table 1; $X^2_6 = 564.24$, $p < 0.05$). The evergreen tree species *C. americana*, had the longest LL (100 days longer than all the other species). The most shade-tolerant semi-deciduous tree species (*B. riedelianum*) and both bamboo species showed intermediate leaf half-life (140–160 days). Deciduous or semi-deciduous species with high-light requirements (*M. tinctoria*, *P. dubium* and *C. trichotoma*) showed a shorter LL (about 125 days). The N + P addition tended to decrease leaf life-span, particularly in *B. riedelianum* and *M. tinctoria* (Table 1; $X^2_1 = 7.33$ and $X^2_1 = 4.52$, $p < 0.05$ respectively). In the case of bamboos, LL showed a significant decrease with fertilization in gaps (Table 1; $X^2_1 = 3.61$ for *C. ramosissima* and $X^2_1 = 8.86$ for *C. tenella*, $p < 0.05$) but not under canopy (Table 1; $X^2_1 = 0.12$ for *C. ramosissima* and $X^2_1 = 0.14$ for *C. tenella*).

The PI values of most traits for bamboos growing under contrasting canopy conditions were high, but plasticity in response to fertilization was low (Table 3). The most plastic traits were biomass accumulation, clonal reproduction and total LA, as well as ETR and SLA. In most cases both species had similar PI values under the different treatments.

4. Discussion

Bamboo species are an important component of forests that can change its original structure and dynamics when spreading rapidly after disturbances (Veblen, 1982; Griscom and Ashton, 2006; Campanello et al., 2007; Montti et al., 2011). In this work we identified functional traits that enhance bamboo invasiveness over saplings of co-occurring trees in forests.

Bamboo species growing in gaps had more biomass and clonal reproduction (increased culms and rhizome production) and leaf area per plant than bamboos in the understory of the closed-canopy. Also, *C. ramosissima* and *C. tenella* improved their photosynthetic capacity in gaps, as observed in other bamboo species (Agata et al., 1985; Lei and Koike, 1998; Kumar et al., 2002). Previous studies reported low values of photosynthetic capacity for bamboos compared to trees (Lei and Koike, 1998; Motomura et al., 2008; Ely, 2009; Saha et al., 2009). In this study we found that bamboos had twice the photosynthetic capacity of trees (including some with high-light requirements) when values are expressed per unit leaf mass. In the forest understory, thin leaves (high SLA) can improve CO_2 assimilation with a relatively low C cost, thus conferring bamboos a significant competitive advantage over tree saplings. Other traits of bamboos, such as long leaf life-span, may also confer them competitive advantages over trees (Kikuzawa, 1995; Givnish, 2002). Bamboos, as well as evergreen plants (e.g., *C. americana*), are

favored over deciduous competitors because of its ability to photosynthesize during longer periods of time (Lei and Koike, 1998). In the semideciduous Atlantic Forest, where 25–50% of the canopy tree species drop their leaves during winter (Leite and Klein, 1990), bamboos in the understory would have a competitive advantage over other species. Also, both bamboo species in this study allocated a high percentage of biomass to the culms and leaves, which enabled them to reach the canopy and increase light interception.

Both bamboo species showed leaf traits that enabled them to grow rapidly with high solar radiation (i.e., a high photosynthetic capacity in gaps) and to tolerate and survive under low irradiance (i.e., very thin leaves and a relatively long leaf-life span in the understory). Differences in minimum light requirements for the survival of co-occurring species are central for the understanding of community and ecosystem dynamics (Bazzaz, 1979; Canham et al., 1999; Zavala et al., 2007). A trade-off between growth rates in gaps and survival in the understory was recognized for light-requiring and shade-tolerant tree species (see Wright, 2002). Bamboos in our study did not conform to this pattern. Plasticity in leaf traits allows them both to tolerate low irradiances in the understory and grow fast in gaps, thus taking advantage over tree saplings.

Identifying the traits that determine plant invasibility is crucial to develop management strategies for the conservation of forest ecosystems. Connections between the physiological responses of individual species and processes at the community and ecosystem-level are important for our understanding of forest dynamics. Our results highlight bamboos as a key functional group in the semideciduous Atlantic Forest, and probably in other ecosystems where they are abundant. A model describing physiological traits to

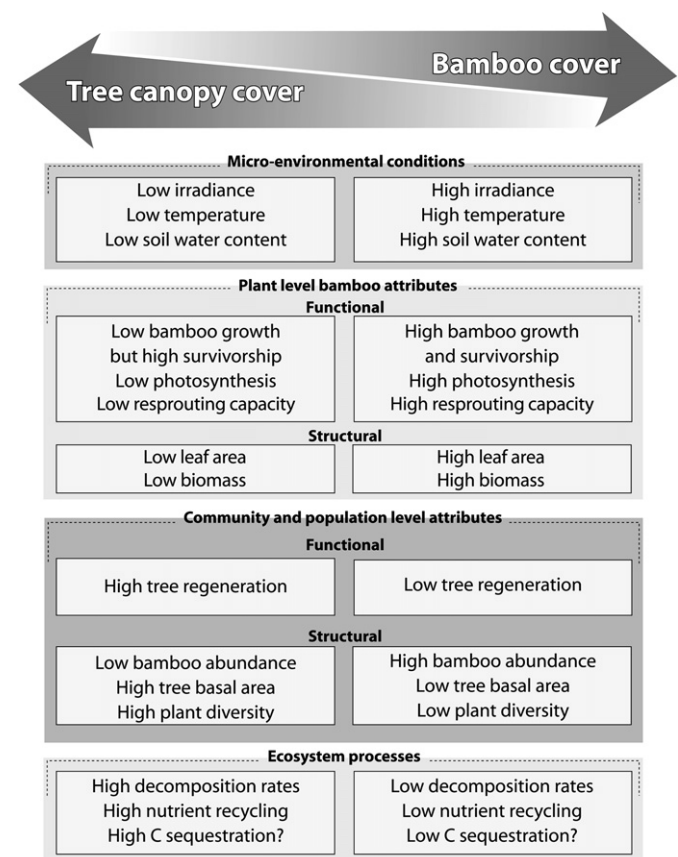


Fig. 4. Summary of bamboo impacts in the semideciduous Atlantic Forest based on Campanello et al. (2007, 2009); Montti et al. (2011) and this study.

ecosystem-level processes impacted by bamboo abundance is depicted in Fig. 4. In degraded forests with relatively low tree canopy cover, bamboos rapidly colonize open areas and limit co-occurring native tree saplings. This occurs because of a combination of traits typical of early (high photosynthesis capacity, fast growth rate) and late successional species (shade-tolerance, long leaf life-span) that enhance bamboo invasiveness in disturbed environments. Bamboo abundance as a result of forest degradation affects tree regeneration (germination, survival and growth of tree saplings), tree basal area, and the physical characteristics of the environment (e.g., radiation at soil level, soil humidity, air temperature), thereby impacting ecosystem processes such as litter decomposition rates, nutrient cycling (Campanello et al., 2007, 2009; Montti, 2010; Montti et al., 2011) and, probably the carbon sequestration capacity of native forests. If forest disturbance continues to increase, we would expect further invasive spreading of bamboos, with concomitant impacts on forest diversity, structure and function.

Acknowledgments

This research was supported by the Agencia Nacional de Promoción Científica y Tecnológica (FONCYT), Rufford Small Grants, and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). We would like to thank to Administración de Parques Nacionales de Argentina and to M. Camposano, D. Larraburu, A. Paviolo, M. Gonzalez, F. and A. Foletto for their field assistance. This manuscript benefited from useful comments of Jorge Gutiérrez and two anonymous reviewers.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2013.03.004>.

References

- Agata, W., Hakoshima, S., Kawamitsu, Y., 1985. Influence of light intensity, temperature, and humidity on photosynthesis and transpiration of *Sasa nipponica* and *Arundinaria pygmaea*. Bot. Mag. Tokio. 98, 125–135.
- Baruch, Z., Goldstein, G., 1999. Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawaii. Oecologia 121, 183–192.
- Bazzaz, F.A., 1979. The physiological ecology of plant succession. Annu. Rev. Ecol. Syst. 10, 351–371.
- Björkman, O., Demmig, B., 1987. Photon yield of O₂ evolution and chlorophyll fluorescence characteristics at K among vascular plants of diverse origins. Planta 170, 489–504.
- Campanello, P.I., Gatti, M.G., Ares, A., Montti, L., Goldstein, G., 2007. Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. For. Ecol. Manag. 252, 108–117.
- Campanello, P.I., Gatti, M.G., Goldstein, G., 2008. Coordination between water-transport efficiency and photosynthetic capacity in canopy tree species at different growth irradiances. Tree Physiol. 28, 85–94.
- Campanello, P.I., Montti, L., Goldstein, G., Mac Donagh, P., 2009. Reduced Impact Logging and Post-harvesting Forest Management in the Atlantic Forest: Alternative Approaches to Enhance Canopy Tree Growth and Regeneration and to Reduce the Impact of Invasive Species. In: Grossberg, S.P. (Ed.), Forest Management. Nova Science, New York, pp. 39–59.
- Campanello, P.I., Gatti, M.G., Montti, L.F., Villagra, M., Goldstein, G., 2011. Ser o no ser tolerante a la sombra: economía de agua y carbono en especies arbóreas del Bosque Atlántico (Misiones, Argentina). Ecol. Austral 21, 285–300.
- Canham, C.D., Kobe, R.K., Latty, E.F., Chazdon, R.L., 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia 121, 1–11.
- Daheler, C.C., 2003. Performance comparisons of co-occurring native and alien invasive plants: implication for conservation and restoration. Annu. Rev. Ecol. Syst. 34, 183–211.
- Devoto, F., Rothkugel, M., 1936. Informe sobre los bosques del Parque Nacional Iguazú. Ext. Bol. del Ministerio de Agricultura de la Nación 37 (1–4), 1–99.
- Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehe, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., Zak, M.R., 2004. The plant traits that drive ecosystems: evidence from three continents. J. Veg. Sci. 15, 295–304.
- Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., González, L., Tablada, M., Robledo, C.W., 2009. InfoStat Versión 2009. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.
- Durand, L.Z., Goldstein, G., 2001. Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. Oecologia 126, 345–354.
- Ehleringer, J., 1981. Leaf absorptances of Mohave and Sonoran desert plants. Oecologia 49, 366–370.
- Ely, F., 2009. Respuesta ecofisiológica y diversidad genética en *Chusquea* (Bambusoideae, Poaceae) de la Cordillera de Mérida. Tesis Doctoral. Universidad de Los Andes, Mérida, Venezuela.
- Franco, A.C., Herzog, B., Hübner, C., de Mattos, E.A., Scarano, F.R., Ball, E., Lüttge, U., 1999. Diurnal changes in chlorophyll a fluorescence, CO₂-exchange and organic acid decarboxylation in the tropical CAM tree *Clusia hilariana*. Tree Physiol. 19, 635–644.
- Giraud, A.R., Povedano, H., Belgrano, M.J., Krauczuk, E.R., Pardiñas, U., Miquelarena, A., Ligier, D., Baldo, D., Castilino, M., 2003. Biodiversity status of the interior Atlantic Forest of Argentina. In: Galindo-Leal, C., Gusmão Câmara, I. (Eds.), The Atlantic Forest of South America: Biodiversity Status, Threats and Outlook, first ed. Island Press, Washington, USA, pp. 160–180.
- Gatti, M.G., Campanello, P.I., Montti, L., Goldstein, G., 2008. Frost resistance in the tropical palm *Euterpe edulis* and its pattern of distribution in the Atlantic Forest of Northeast Argentina. For. Ecol. Manag. 256, 633–640.
- Givnish, T.J., 2002. On the adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. Sil. Fennica 36, 703–743.
- Griscom, B.W., Ashton, P.M.S., 2006. A self-perpetuating bamboo disturbance cycle in a neotropical forest. J. Trop. Ecol. 22, 587–597.
- Hayes, S.J., Holzmüller, E.J., 2012. Relationship between invasive plant species and forest fauna in eastern North America. Forest 3, 80–852.
- Holz, A., Veblen, T.T., 2006. Tree regeneration responses to *Chusquea montana* bamboo die-off in a subalpine *Nothofagus* forest in the southern Andes. J. Veg. Sci. 17, 19–28.
- Ito, H., Hino, T., 2007. Dwarf bamboo as an ecological filter for forest regeneration. Ecol. Res. 22, 706–711.
- Kikuzawa, K., 1995. Leaf phenology as an optimal strategy for carbon gain in plants. Can. J. Bot. 73, 158–163.
- Kitajima, K., 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98, 419–428.
- Kleinbaum, D.G., Klein, M., 2005. Survival Analysis, a Self-learning Text, second ed. Springer, United States, pp. 1–596.
- Kobe, R.K., Pacala, S.W., Silander Jr., J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. 5, 517–532.
- Krause, G.H., Koroleva, O.Y., Dalling, J.W., Winter, K., 2001. Acclimation of tropical tree seedlings to excessive light in simulated tree-fall gaps. Plant Cell Environ. 24, 1345–1352.
- Kumar, R., Pal, M., Teotia, U.V.S., 2002. Diurnal changes in chlorophyll fluorescence in four species of bamboo. J. Bamboo Rattan 1, 341–349.
- Lambers, H., Chapin III, F.S., Pons, T.L., 1998. Plant Physiological Ecology. Springer-Verlag, New York, pp. 299–300.
- Larppern, P., Moe, S.R., Totland, O., 2010. Bamboo dominance reduces tree regeneration in a disturbed tropical forest. Oecologia 165, 161–168.
- Lei, T., Koike, T., 1998. Functional leaf phenotypes for shaded and open environments of a dominant dwarf bamboo (*Sasa senanensis*) in northern Japan. Int. J. Plant Sci. 159, 812–820.
- Leishman, M.R., Haslehurst, T., Ares, A., Baruch, Z., 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparison. New Phytol. 176, 635–643.
- Leite, P.F., Klein, R.M., 1990. Geografia do Brasil-Região Sul. Rio de Janeiro. Instituto Brasileiro de Geografia e Estatística-IBGE, Brasil, pp. 113–150.
- Lima, R.A.F., Rother, D.C., Muler, A.E., Lepsh, I.F., Rodrigues, R.R., 2012. Bamboo overabundance alters forest structure and dynamics in the Atlantic Forest hotspot. Biol. Conserv. 147, 32–39.
- Ligier, H.D., Matteio, H.R., Polo, H.L., Rosso, J.R., 1990. Provincia 622 de Misiones. In: I.S.D.A.G. y P. Centro de Investigaciones de Recursos Naturales, INTA (Ed.), 1990. Atlas de suelos de la República Argentina. Tomo II, pp. 109–154. Argentina.
- Lüttge, U., Haridasan, M., Fernandes, G.W., de Mattos, E.A., Trimborn, P., Franco, A.C., Caldas, L.S., Ziegler, H., 1998. Photosynthesis of mistletoes in relation to their hosts at various sites in tropical Brazil. Trees 12, 167–174.
- Martin, P.H., Canham, D., Kobe, R.K., 2010. Divergence from the growth–survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. J. Ecol. 98, 778–789.
- Meiners, S.J., Timothy, A., Klass, J.R., 2008. On a level field: the utility of studying native and non-native species in successional systems. App. Veg. Sci. 12, 45–53.
- Montti, L., Graciano Riveiro, D., Goldstein, G., 2008. Anatomical traits of woody bamboos useful for taxonomic identification: a case of study in Neotropical species. J. Bamboo Rattan 7 (1&2), 1–20.
- Montti, L., 2010. Ecología y fisiología de *C. ramosissima*, una especie de bambú monocárpico y los efectos de su floración en la dinámica y funcionamiento del

- Bosque Atlántico semideciduo. PhD Dissertation, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina.
- Montti, L., Campanello, P.I., Gatti, M.G., Blundo, C., Austin, A.T., Sala, O., Goldstein, G., 2011. Understory bamboo flowering provides a very narrow light window of opportunity for canopy tree recruitment in a neotropical forest of Misiones, Argentina. *For. Ecol. Manag.* 262, 1360–1369.
- Motomura, H., Hikosaka, K., Suzuki, M., 2008. Relationships between photosynthetic activity and silica accumulation with ages of leaf in *Sasa veitchii* (Poaceae, Bambusoideae). *Ann. Bot.* 101, 463–468.
- Nilsson, M.C., Wardle, D.A., 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Front. Ecol. Environ.* 3 (8), 421–428.
- Pacala, S.W., Canham, C.D., Silander Jr., J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. For. Res.* 24, 2172–2183.
- Pattison, R.R., Goldstein, G., Ares, A., 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117, 449–459.
- Placci, G., Giorgis, P., 1993. Estructura y diversidad de la selva del Parque Nacional Iguazú, Argentina. Eldorado, Misiones: VII Jornadas Técnicas sobre Ecosistemas Forestales Nativos: Uso, Manejo y Conservación.
- Pyšek, P., Richardson, D.M., 2007. Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig, W. (Ed.), *Biological Invasions, Ecological Studies*. Springer-Verlag, Berlin, pp. 97–126.
- Pyšek, P., Chytrý, M., Jarošík, V., 2010. Habitats and land use as determinants of plant invasions in the temperate zone of Europe. In: Perrings, C., Mooney, H., Williamson, M. (Eds.), *Bioinvasions and Globalization*. Oxford University Press, New York, pp. 1–12.
- Rascher, U., Liebig, M., Lüttge, U., 2000. Evaluation of instant light-response curves of chlorophyll fluorescence parameter obtained with portable chlorophyll fluorometer on site in the field. *Plant Cell Environ.* 23, 1397–1405.
- Rejmánek, M., Richardson, D.M., Higgins, S.L., Pitcairn, M.J., Grotkopp, E., 2005. Ecology of invasive plants: state of the art. In: Mooney, H.A., Mack, R.N., McNeely, J.A., Neville, L.E., Schei, P.J., Waage, J.K. (Eds.), *Invasive Alien Species: a New Synthesis*. Island Press, Washington DC, USA, pp. 104–161.
- Rother, D.C., Rodrigues, R.R., Pizo, M.A., 2009. Effects of bamboo stands on seed rain and seed limitation in a rainforest. *For. Ecol. Manag.* 257, 885–892.
- Saha, S., Holbrook, M.N., Montti, L., Goldstein, G., Cardinot, G.K., 2009. Water relations of *Chusquea ramossissima* and *Merostachys clausenii* in Iguazú National Park. *Plant Physiol.* 149, 1992–1999.
- Silveira, M., 2005. A floresta aberta com bambu no sudoeste da Amazônia: padrões e processos em múltiplas escalas. EDIUFAC, Rio Branco.
- Srur, M., Gatti, F., Benesovsky, V., Herrera, J., Melzew, R., Camposano, M., 2009. Los tipos de vegetación y ambientes del Parque Nacional Iguazú y su distribución en el paisaje. In: Carpinetti, C., et al. (Eds.), *Parque Nacional Iguazú, Conservación y desarrollo en la Selva Paranaense de Argentina*. Administración de Parques Nacionales, Buenos Aires, Argentina, pp. 99–118.
- Thompson, K., Hodgson, J.G., Rich, T.C.G., 1995. Native and alien invasive plants: more of the same? *Ecography* 18, 390–402.
- Valéry, L., Fritz, H., Lefeuvre, Simberloff, D., 2008. In search of a real definition of the biological invasion phenomenon itself. *Biol. Invasions* 10, 1345–1351.
- Valladares, F., Wright, S.J., Lasso, E., Kitajima, K., Pearcy, R.W., 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology* 81, 1925–1936.
- Veblen, T.T., 1982. Growth patterns of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forests and their influences in forest dynamics. *Bull. Torrey Bot. Club* 109, 474–487.
- Veldman, J.W., Mostacedo, B., Peña-Claros, M., Putz, F.E., 2009. Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest. *For. Ecol. Manag.* 258, 1643–1649.
- Villagra, M., 2012. Plasticidad morfológica y fisiológica de especies arbóreas del Bosque Atlántico en respuesta a la disponibilidad de luz y nutrientes. PhD Dissertation, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina.
- Wright, S.J., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130, 1–14.
- Zavala, M.A., Angulo, O., de la Parra, R.B., Lopez-Mareos, J.C., 2007. An analytical model of stand dynamics as a function of tree growth, mortality and recruitment: the shade tolerance-stand structure hypothesis revisited. *J. Theor. Biol.* 244, 440–450.