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Understory bamboo flowering provides a very narrow light window of opportunity for canopy-tree recruitment in a neotropical forest of Misiones, Argentina

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ABSTRACT

Chusquea ramosissima is a native monocarpic bamboo species growing in subtropical forests of northeastern Argentina, which can dominate gaps and open forests in the region, particularly after human disturbance. This bamboo species started to flower in different areas of northeastern Argentina in 2001, with the flowering peak during 2002 and 2003 and small isolated flowering events still occurring until 2010. We studied the effects of *C. ramosissima* flowering and die-back on microclimate, litter decomposition, nutrient availability, sapling growth, abundance and regeneration of tree canopy species. We wanted to know how environmental conditions and ecosystem processes change through time after bamboo flowering and if bamboo die-back would favor regeneration of canopy trees. Twenty 50 × 50 m plots of flowering and non-flowering bamboo were permanently marked and vegetation dynamics as well as nutrient cycling and microclimate studies were performed. *C. ramosissima* die-back enhanced growth and reduced mortality rate of tree saplings during the first year after flowering. Only growth of tree saplings previously established was enhanced by the flowering event and tree-species richness and saplings abundance of canopy trees did not change as expected due to bamboo flowering. The short-term effect of tree saplings growth was likely due to incident solar radiation at the forest floor which doubled in the first year after the bamboo flowering event. Increased light availability at the forest floor simultaneously promoted the growth of other understory plants such as ferns, lianas and *Piper* spp. that rapidly colonized gaps and intercepted a percentage of the incident solar radiation after the first year, which together with an increased litter layer due to the senescence of the bamboo, may have inhibited establishment of new tree individuals and affected tree growth. Contrary to predictions, soil water, litter decomposition and soil nutrients were not significantly affected by bamboo flowering. Thus, successful tree regeneration in gaps following bamboo flowering appears to be restricted to a very narrow window of increased light availability (i.e., 1 year) before growth of other understory plants and rapid re-colonization of bamboo. Changes in resource availability, and the opportunity for overstory regeneration after bamboo flowering events appears to depend on climatic and community characteristics of the ecosystem where the flowering event occurs and also, on the flowering patterns and their synchronicity.

1. Introduction

Ecological studies in forests have been mostly focused on trees, however understory vegetation can have a significant effect on forest dynamics by inhibiting tree sapling recruitment and ultimately impacting forest productivity (Maguire and Forman, 1983; George

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Abbreviations: FRT, fraction of solar radiation transmitted; INP, Iguazú National Park.

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and Bazzaz, 1999; Abe et al., 2002; Nilsson and Wardle, 2005; Holz and Veblen, 2006; Tsvuura et al., 2010). Bamboos are very abundant in the understory of some tropical and temperate forests, and some species are well adapted to colonize areas affected by natural and anthropogenic disturbances because of their fast growth rates and clonal reproduction (Judziewicz et al., 1999). Also, bamboos play a key role in tree diversity, abundance and growth (Tabarelli and Mantovani, 2000; González et al., 2002; Griscom and Ashton, 2003, 2006; Wang et al., 2006; Campanello et al., 2007a). Griscom et al. (2007) found that bamboo-dominated forests had a distinctive floristic community and less tree species diversity compared to non-bamboo forests in the Amazon. Recently, Larpkern et al. (2010) showed that seedling abundance and species richness are reduced by bamboo canopy in a disturbed tropical forest in Thailand. In addition, bamboos can influence environmental conditions, nutrient turnover, soil water availability and litter decomposition rates (Rao and Ramakrishnan, 1989; Tripathi and Singh, 1994; Singh and Singh, 1999; Takahashi et al., 2003; Embaye et al., 2005; Tripathi et al., 2005).

Some monocarpic bamboo species have long intervals of vegetative growth between successive generally unpredictable synchronized flowering events followed by the death of all plants (Janzen, 1976). Several studies have revealed that bamboo die-back results in substantial changes in environmental conditions that may enhance overstory tree germination (Giordano et al., 2009), regeneration (Nakashisuka, 1987; Taylor and Qin, 1992; Taylor et al., 1996; Abe et al., 2001; González et al., 2002; Marchesini et al., 2009; Budke et al., 2010) and synchronized tree seedling establishment (Nakashizuva and Numata, 1982; Makita et al., 1995; Taylor et al., 1995). The colonization process in gaps as a result of bamboo death could be similar to that occurring after a tree fall (Martins et al., 2004). Nevertheless, the integrated response of forest ecosystems to bamboo reproductive events is not well understood, due in part to their infrequent nature and to the complex interactions among multiple ecosystem processes. The dynamics of non-tree vegetation in the understory have been undervalued, and in the Neotropics, monocarpic bamboo flowering has received comparatively little attention. We studied how environmental conditions and ecosystem processes changed through time after bamboo flowering and die-back and if this event favored regeneration of canopy trees.

In the semi-deciduous Atlantic Forest, species of the genus *Chusquea* are especially abundant in large gaps created by natural or anthropogenic disturbances where they can form impenetrable thickets (Tabarelli and Mantovani, 2000). *Chusquea ramosissima* Lindm. is a native monocarpic woody bamboo and a dominant understory species in the southern portion of this forest (Campanello et al., 2007a; Montti et al., 2009). The culms of this rhizomatous species can be either erect or scandent with solid internodes (Montti et al., 2008). These culms have a diameter of approximately 15 mm and a length of 4–15 m (Montti, 2010). In Argentina, the Semi-deciduous Atlantic Forest was historically subjected to selective logging (Giraudo et al., 2003). This activity reduced the diversity of timber species, increased the rate of large gap formation and enhanced bamboo growth (Campanello et al., 2009). In these logged forests, *C. ramosissima* is very abundant (e.g., 23,000 culms per hectare depending on the stand history of management and environmental characteristics) and forms a dense stratum 2–3 m in height (Campanello et al., 2007a), which represents an aerial biomass of 4000–5500 kg ha^{-1} (unpublished results) that significantly reduces transmitted solar radiation and inhibits canopy tree regeneration (Campanello et al., 2009).

In 2001, *C. ramosissima* started to flower in different areas of northeastern Argentina. The flowering peak in the studied area occurred during 2002 and 2003, but isolated flowering events were observed until 2010 (Montti et al., 2011). Due to the abundance of this understory species, we predicted that after die-back: (1) solar radiation, air temperature and water availability in the understory would increase, (2) nutrient availability would rise due to of higher rates of litter decomposition and nutrient turnover and (3) these environmental changes substantially would increase sapling abundance and growth, that would be reflected on higher species richness and diversity of canopy trees in the understory. We studied the effects of *C. ramosissima* die-back on light levels and water availability, air temperature, soil nutrient pool and litter decomposition, and monitored changes in forest dynamics; particularly the understory vegetation cover and composition, and tree sapling growth, damage, mortality rate, abundance and richness in flowered and non-flowered sites.

2. Methods

2.1. Study area

The research was conducted in a native bamboo-dominated forest inside the Iguazú National Park (INP; 25°31′–25°43′S, 54°08′–54°32′O; 58,600 ha) between 2002 and 2005. This forest was subjected to selective logging before the creation of National Park in 1934, since this time not logging activities occurred. Natural catastrophes like wildfires or landslides do not occur in this area; however wind-storms are common. Mean annual precipitation in the area is about 2000 mm, evenly distributed throughout the year but with several short dry spells. The mean annual air temperature is 21 °C with monthly means of 25 °C in January and 15 °C in July (Servicio Meteorológico Nacional, 2006). The soils in the study area are mostly Ultisols derived from basaltic rocks containing high concentration of Fe, Al and Si (Ligier et al., 1990).

This semi-deciduous subtropical forest constitutes the lower portion of the Atlantic Forest that extends along the coast of Brazil. It is also included as part of a broad group of neotropical seasonally dry forests (Prado and Gibbs, 1993; Pennington et al., 2000, 2009). Some of the dominant canopy tree species are *Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae), *Nectandra megapotamica* (Spreng.) Mez (Lauraceae), *Bastardiopsis densiflora* (Hook. and Arn.) Hassler (Malvaceae), *Cedrela fissilis* Vell. (Meliaceae), *Cordia americana* L. (Boraginaceae) and *Lonchocarpus leucanthus* Burkart (Fabaceae). Common subdominant tree species are *Trichilia catigua* Adr. Juss., *Trichilia elegans* A. Juss. and *Sorocea bonplandii* (Bailon) Burg. Lianas are abundant particularly in disturbed sites (Campanello et al., 2007b).

2.2. Experimental design

In 2002, we installed a total of 20 50 × 50 m plots in the same study area: 10 in *C. ramosissima* flowering sites (flowered plots); and 10 in non-flowering nearby sites that were used as control plots. All plots had similar tree cover, canopy species composition and understory vegetation. The plots were located along both sides of a small dirt road with a border of at least 100 m from the road edges. Inside each 50 × 50 m plot, we established one 5 × 5 m subplot to study soil nutrient dynamics, soil water availability and litter decomposition and 24 1 × 2 m subplots to study tree sapling growth and abundance of non-bamboo understory species.

2.3. Environmental conditions

During December 2002 and January 2003 (summer 2002–2003), August 2003 (winter 2003), and December 2003 and January 2004 (summer 2003–2004), we obtained hemispherical photographs in all the control and flowered plots to estimate the fraction of solar radiation transmitted (FRT) through the canopy into the understory. Photographs were taken with a digital camera Nikon Coolpix 950 with a Nikkor 8-mm lens on a self-leveling platform (Delta-T Devices, Cambridge, UK). We obtained four photographs per plot located at the corners of a 20 m-side square centered on the 50 × 50 m plot. Measurement locations were marked with stakes for repeat measurements at the same sites. Distance among locations was 20 m to assure independence among contiguous photographs (Clark et al., 1995). In each site, two photographs were taken, one at 0.7 and the other at 2 m height. Measurement heights were selected based on the average height (0.7–2 m) of *C. ramosissima* clumps.

In three random plots per treatment and in the same sites where the hemispherical photographs were taken, we measured air temperature 10 cm above-ground during the beginning of summer (November–December 2003). Data were recorded simultaneously in the six plots every 5 min for 32 continuous days with copper-constantan temperature data loggers (HOBO Type T, Onset Corporation, MA, USA).

During a short dry spell (i.e., 20 days without rainfall) in March 2003, we collected soil samples at 0–5 cm depth in each one of the 50 × 50 m plots and soil water potential was estimated using the filter-paper technique (Deka et al., 1995). Two soil pits of 30 cm of depth were made in 7 plots per treatments to measure the depth of the organic horizon and the litter layer. In the same plots we also collected litter in 1 × 1 m subplots that was dried at 70 °C until constant weight. Biomass was separated and the litter corresponding to *C. ramosissima* weighted.

2.4. Nutrient dynamics

Every month from May 2003 until April 2004 inside the 5 × 5 m subplots, we collected soil samples to measure N and water content. Soil samples of the top 10 cm of mineral soil were obtained using a PVC tube. Soil samples were stored during a short time period under refrigerated conditions until they were processed in the laboratory. We sieved fresh soils through a 2-mm mesh to remove roots, leaves and rocks. In each case, a subsample of 5 g of soil was used to extract inorganic nitrogen (NH_4–N and NO_3–N) with 25 ml 2 N KCl. We placed each subsample in the oven at 105 °C for 48 h for determination of gravimetric soil water content. Soil nitrogen concentrations were corrected for soil water content (Robertson et al., 1999).

Nitrogen mineralization was also measured inside the 5 × 5 m subplots in all the plots using the buried bag technique (Stark, 2000). An intact sample of forest soil was collected and incubated in a polyethylene bag (40 μ) buried into the soil for 30 days. After incubation, the buried samples were collected and transported inside a cooler to the laboratory where NH_4–N and NO_3–N were extracted as previously described. All soil extracts were analyzed using an Alpkem®autoanalyzer (O-I Corporation, College Station, Texas, USA), which is a colorimetric analysis of inorganic nitrogen in liquid extracts. The detection limit from the manufacturer is 0.09 ppm for NO_3–N and 0.15 ppm for NH_4–N, although due to some adjustments in the specifications of the autoanalyzer, the working limits of detection in the laboratory were 0.03 ppm for NO_3–N and 0.12 ppm for NH_4–N (Austin and Tagliazucchi, pers. comm.). In March 2003, also we determined P availability (PO_4–P) at 0–5 cm depth soil by the anion-exchange resins method (Sibbesen, 1978).

2.5. Litter decomposition

Senescent leaves, branches and culms of *C. ramosissima* and senescent leaves of *S. bonplandii* (a common subdominant tree species) were collected and rates of mass loss and litter quality determined by decomposition studies. The decomposition experiment was carried out using 1-mm mesh fiberglass litterbags of 15 × 15 cm with 2 g of leaves and branches that were placed in separate bags. Culms were placed separately in the field close to the litterbags. A total of 100 litterbags with *C. ramosissima* leaves and branches and 50 culms were placed in the field in five control plots and in five flowered plots randomly selected in May 2003 (five bags per plot). Collections of litterbags were completed at 1, 3, 6, 9 and 12 month(s) at all sites, selecting randomly one bag and culm of each type per plot at each harvest. After collection, any external material (such as mineral soil or debris) was carefully removed from the litter, and samples were dried at 70 °C until constant mass and then weighted. Mass loss over time was described by the equation of Olson (1963):

$$\ln(Mt/Mo) = y - kt$$

where "*M*" is the initial organic matter mass, "*Mt*" the organic matter mass at time "*t*", "*y*" the intercept of the fitted function to the *Y* axes, and "*k*" the exponential decomposition constant. This constant was used to compare decomposition rates among the four litter types and to calculate the time required for 95% (*t*95) decay of the original litter mass (Singh and Singh, 1999). Initial litter quality measurement for percent moisture, carbon, sugar, hemicellulose and lignin were made with subsample of initial litter pool for each vegetal material ($n = 5$ for moisture and carbon, and $n = 3$ for other variables, except for culms that $n = 1 - 2$). Carbon content was calculated as 50% of ash-free dry mass and lignin and hemicellulose by fiber detergent analysis (Van Soest, 1963).

2.6. Tree sapling diversity and growth

We studied the growth of tree saplings already established at the time of bamboo die-back. On July 2003 we identified, tagged and measured the height and diameter of all tree saplings (>30 cm of height and <10 cm dbh) inside the 24 1 × 2 m subplots per plot. All saplings were re-measured in June and July 2004 and 2005; and also we counted and identified all new tree saplings that got more than 30 cm of height in these years. A total of 480 subplots were surveyed (240 plots per treatment). Only the growth rates of healthy tree saplings (i.e., undamaged individuals) at the end of the study period (June 2005) were analyzed. Also, physical damage and mortality were registered in all the tagged individuals.

Physical damage was included as a dichotomic variable (yes: damaged individuals, no: healthy individuals). For physical damage we considered the visual evidence of broken branches or stems, stems wound without shed bark and saplings tip over.

2.7. Understory species abundance

To quantify understory vegetation cover and composition, including bamboo abundance we used the "point intercept" method (Mostacedo and Fredericksen, 2000). Inside each 1 × 2 m subplot, we counted the "hits" of bamboo and other species from the soil to 2 m height on a vertical stick in three points along a 2 m transect located in the middle of the subplot. A total of 72 points were measured per plot (three points in 24 subplots). Species were grouped in eight classes: flowered bamboo, dead not flowered bamboo, live bamboo, herbs, ferns, *Piper* spp., lianas and "others" (i.e., shrubs, tree canopy saplings, woody and not determined spp.). For each vegetation class, the percentage cover (%C) in each plot was calculated as total hits of one class divided by total hits of all classes in the plot and multiplied by 100.

2.8. Data analysis

The hemispherical photographs were analyzed using the Hemiview software (Delta-T Devices Ltd., Cambridge, UK). The fraction of solar radiation transmitted (FRT) was calculated as the proportion of the solar radiation reaching the measurement site point relative to the solar radiation at the top of the forest canopy. *t*-Test for independent samples was used to compare FRT between control and flowered plots. Paired measurements of minimum and maximum temperatures obtained in summer were compared with the Wilcoxon test (Wilcoxon, 1945). The soil water content (gravimetric water content) and nutrient availability between control and flowered plots were compared using a repeated measure ANOVA considering as main effects the treatment (control or flowered plots) and time (dates). The statistical differences of soil water potential, P availability, litter layer and organic horizon depths were evaluated by the Mann Whitney *U*-test (Mann and Whitney, 1947). Statistics for differences in litter quality were conducted using a one-way ANOVA. The effect of the flowering event on the exponential decomposition constant (k) in flowered and control plots was evaluated using a two-way ANOVA considering as main effects the treatment and the litter type. Post-hoc comparisons were performed with a Tukey Honest Significant Difference (HSD) test. Flowering effect on saplings density and growth rates were analyzed comparing means by a *t*-test for independent samples. The difference between the amount of dead and damaged seedlings in both situations was compared using statistical Mann–Whitney (*U* test). Alpha diversity was measured with the following indices: (1) species richness (counting all species in control vs. flowered plots) and (2) Shannon diversity index $H' = -\Sigma\ pi\ \ln pi$, where pi = proportion of individuals in the ith species. The H′index was calculated for combined all plots for each treatment (control vs. flowered) because considered individually plot were small for a meaningful estimate of this index. We used a non-parametric Wilcoxon test ($n = 10$) to compare richness between control and flowered plots and the Hutcheson test (Hutcheson, 1970) for H′. The tree sapling species composition between control and flowered plots was compared by a non-metric multidimensional scaling ordination method (NMDS, Kruskal and Wish, 1978) based on the similarity index of Sørensen (also known as Bray–Curtis index) and using abundance data (individuals per species). To explore environmental variables (FRT, soil humidity, NO_3–N, NH_4–N and PO_4–P soil content) and understory composition (% of understory species contribution cover: ferns, herbs, *Piper* spp., bamboos and lianas to total biomass) to differentiation across plots, we first made a NP-MANOVA (Anderson, 2001) applied to the sequential surveys (2003–2004 and 2004–2005) among treatments and within years in order to verify if the same treatment vary among surveys. Then we computed a species similarity matrix using the Bray–Curtis index, a general measure of proximity that can detect underlying ecological gradients. Finally we performed a principal coordinate analysis (PCoA) on this similarity matrix using R packages. PCoA is a general form of principal component analysis (PCA) that allows the use of a wide array of distance measures (Legendre and Legendre, 1998). The result of this analysis was equivalent to those of a PCA with variables previously transformed to correct for skewed distributions. The significance of the extracted axes was tested using broken-stick model distribution which predicts the partition of the total variance among the axes if it is made at random; observed ordination axes are considered interpretable when they explain more variation than expected from this model distribution (Legendre and Legendre, 1998). To explore in detail the correlations between environmental and understory composition variables and ordination axes (not provided in PCoA) we used Kendall rank correlations because many of the variables did not fit normal distributions and some of them had natural outliers. For analyses PC-ORD program (McCune and Mefford, 1999) and R packages (2011) were used. A heterogeneity χ^2 analysis was used to compare height frequency distribution of saplings between control and flowered plots. The effect of flowering on the understory vegetation was compared by repeated measures analysis and Mann–Whitney (*U* test). A significance level of 5% was used in all cases.

3. Results

3.1. Environmental conditions, nutrient cycling and litter decomposition

During the first year after bamboo flowering and die-back, the understory of flowered plots at 0.7 and at 2 m above the forest floor had two times more solar radiation than the understory of control plots (Fig. 1). The amount of solar radiation reaching the understory was higher during the winter than in summer. Significant differences in FTR (fraction of solar radiation transmitted) between control and flowered plots were found in the summer of 2002–2003 and in the winter 2003 (for summer 2002–2003 at 0.7 m: d.f. 18, $t = 2.57$, $p = 0.0097$; at 2 m: d.f. 18, $t = -4.08$, $p < 0.0004$; for winter at 0.7 m: d.f. 18, $t = 2.45$, $p = 0.01$; 2 m: d.f. 18, $t = 2.94$, $p = 0.004$). In the following summer (2003–2004), the differences in FRT between control and flowered plots became non-significant.

Maximum temperatures during summer 2003 were significantly different between control and flowered plots, having control plots the highest values (Wilcoxon Matched Pairs Test, $n = 32$ days, $Z = 4.72$, $p < 0.001$). The mean maximum air temperatures were 28.9 and 27.3 °C in control and flowered plots, respectively (Table 1) and absolute maximum temperatures were 35 and

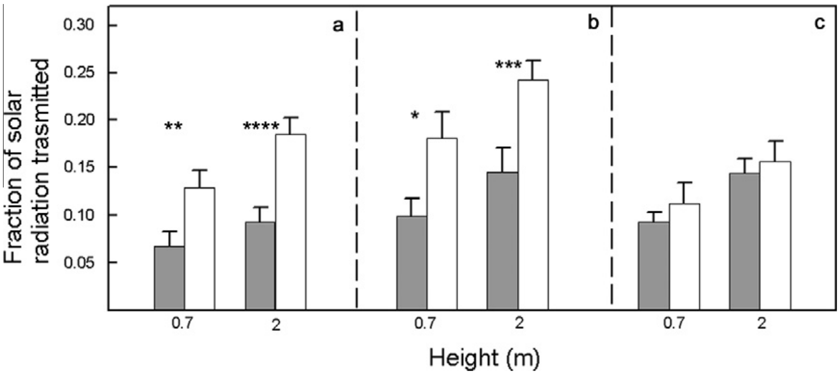

Fig. 1. Average fraction of solar radiation transmitted (FRT) for (a) summer 2002–2003, (b) winter 2003 and (c) summer 2003–2004 seasons at 0.7 and 2 m above-ground in control (solid bars) and flowered (open bars) plots. Bars indicate FRT means + SE. Statistical significant differences (*t*-test for independent samples, $n = 10$) were observed between control and flowered plots at 0.7 m and at 2 m height ($^{****}p < 0.001$, $^{***}p < 0.005$ and $^{**}p < 0.01$ and $^{*}p < 0.05$) during the summer 2002–2003 and winter 2003. No significant differences were found during the summer 2003–2004. Flowering was first seen at the end of 2001.

Table 1
Daily mean maximum summer air temperatures, soil water potential, depth of litter layer, litter biomass, soil phosphorous and nitrogen concentration, and annual rate of ammonification, nitrification and net N mineralization in control (CP) and flowered (FP) plots.

Variable	CP	FP	Test result
Air temperature (°C)	28.9	27.3	$Z = 4.72$, $p < 0.001$, $n = 32$
Soil water potential (MPa)	−0.57 (−0.63; −0.54)	−0.73 (−0.85; −0.55)	$U = 8$, $p = 0.34$, $n = 5$
Litter layer thickness (cm)	4.25(4.12; 6.25)	3.81 (3.28; 4.18)	$U = 9.5$, $p = 0.06$, $n = 7$
Bamboo litter biomass (g/m^2)	127 (84; 198)	137 (102; 186)	$U = 23$, $p = 0.84$, $n = 7$
PO_4–P (μg/g dry soil)	0.37 (0.04; 0.54)	0.53 (0.30; 1.56)	$U = 39$, $p = 0.41$, $n = 10$
Mineral N (μg N g dry soil^{-1} month^{-1})	28.32 (22.5; 30.4)	25.23 (22.3; 27.9)	$U = 120$, $p = 0.26$, $n = 10$
Ammonification (μg NH_4–N g dry soil^{-1} year^{-1})	1.33 ± 0.60	1.02 ± 1.02	$F = 0.06$, $p = 0.79$ g.l. 18, $n = 10$
Nitrification (μg NO_3–N g dry soil^{-1} year^{-1})	10.62 ± 0.91	11.29 ± 1.00	$F = 0.24$, $p = 0.62$ g.l. 18, $n = 10$
Net N mineralization (μg N g dry soil^{-1} year^{-1})	13.18 ± 1.04	13.89 ± 1.05	$F = 0.22$, $p = 0.63$ g.l. 18, $n = 10$

Values are median (lower; upper quartile) or media (±) SE. Samples or measurements were obtained in March 2003. *P*-values from Mann Whitney *U*-test, Wilcoxon Matched Pairs Test; one-way ANOVA and sample size (*n*) are shown.

Table 2
Water content (moisture) and chemical composition of litter (% dry weight). Average annual decomposition rates (*K*, yr^{-1}) and calculated turnover rates for 95% (T_{95}%) of the initial biomass in the litter decomposition bags for different litter types of bamboo and *Sorocea bonplandii* leaves in control (CP) and flowered (FP) plots.

		Litter Type			
		Bamboo leaves	Bamboo branches	Bamboo culms	*S. bonplandii*
Litter quality variable	Moisture	10 ± 0.001^a	9.7 ± 0.002^a	11 ± 0.003^a	9.5 ± 0.007^a
	Carbon	32 ± 0.009^a	41 ± 0.003^b	47 ± 0.007^c	38 ± 0.009^b
	Sugar	53.4 ± 1.7^a	46.35 ± 1.9^b	32.1	58.0 ± 1.0^a
	Hemicell	26.0 ± 2.3^a	32.43 ± 1.4^b	54.1	26.5 ± 0.4^{a,b}
	Lignin	15.0 ± 0.5^a	18.3 ± 0.7^b	13.6	13.1 ± 0.4^a
K	CP	0.67 ± 0.05^a	0.97 ± 0.09^b	0.93 ± 0.12^b	1.03 ± 0.14^b
	FP	0.57 ± 0.08^a	0.87 ± 0.08^b	0.94 ± 0.18^b	0.89 ± 0.07^b
T_{95}%	CP	4.56 ± 0.34^a	3.23 ± 0.35^b	3.47 ± 0.45^b	3.11 ± 0.40^b
	FP	5.80 ± 0.93^a	3.56 ± 0.36^b	4.00 ± 1.08^b	3.47 ± 0.27^b

Values are mean ± SE. Different letters indicate significant differences between litter types $p < 0.01$. No significant differences ($p < 0.05$) were detected among treatments.

34 °C. The minimum temperatures were similar between control and flowered plots (mean minimum 18 °C). Consequently, the control had the largest thermal amplitude.

No differences were detected between control and flowered plots in terms of soil water potential, litter layer depth and bamboo dry mass (Table 1). Similarly, no differences were observed in PO_4–P, total annual of NO_3–N and NH_4–N and in annual ammonification, nitrification and net mineralization rates between control and flowered plots (Table 1). No seasonal differences were found in the monthly values of NO_3–N and NH_4–N contents between control and flowered plots, but both were variable along the year (d.f. 11, $F = 5.71$, $p < 0.001$, for NO_3–N and d.f. 11, $F = 13.33$, $p < 0.001$ for NH_4–N) (data not shown). Values of total nitrogen content (NO_3–N + NH_4–N) were not correlated with soil water content ($p > 0.05$; data not shown).

Bamboo leaves had lower values of carbon (32%) than culms, branches or leaves of *S. bonplandii* and higher value was found in bamboo culms ($F = 68.85$, $p < 0.001$) (Table 2). Percentage of sugar on bamboo leaves was higher compared with the other bamboo organs ($F = 13.92$, $p < 0.05$). Lignin concentration varied between 13% and 18% for all bamboo organs and the highest value was present in bamboo branches ($F = 20.08$, $p < 0.01$). Decomposition rates of bamboo leaves branches and culms were high at the beginning of the experiment and decreased after 6 months (data not shown). Dry matter loss for each type of litter throughout the year followed a negative exponential decay ($r^2 > 0.9$ and $p < 0.05$ for all cases). Rates of litter decomposition were not different between control and flowered plots ($n = 5$, d.f. 32, $F = 1.22$, $p = 0.27$) and no significant interaction was found among litter type and treatments ($n = 5$, d.f. 32, $F = 0.18$, $p = 0.90$). Among litter types, on the other hand, significant differences in decomposition rate were found ($n = 5$, d.f. 32, $F = 4.23$, $p = 0.012$). Leaves of *C. ramosissima* exhibited a slower decomposition rate in comparison to culms and branches of the same species and leaves of *S. bonplandii* (Table 2). The 50% of the initial dry matter of *C. ramosissima* leaves was lost during the first year of the study and consequently between 4 and 5 years of exposure in the soil surface will be needed to lose 95% of the original dry matter (Table 2). The other types of bamboo litter and *S. bonplandii* leaves will require approximately 3 years to lose 95% of their mass (the 50% of the initial dry matter was decomposed during the first 8–9 months) (Table 2).

3.2. Tree sapling growth and plant understory composition after flowering

We identified 586 and 565 tree saplings in control and flowered plots, respectively, belonging to 72 species and 18 families at the beginning of the study (2003) (Appendix A). Mean sapling density (±SE) was similar in control and flowered plots (1.22 ± 0.13 and 1.12 ± 0.17 individuals per m^2, respectively). Contrary to our expectations, no differences in species richness (16.5 ± 4.25 SD and 19 ± 6.87 SD in control and flowered plots respectively) and Shannon diversity index (3.06 in control and 3.24 in flowered plots) were found between control and flowered plots. Moreover, no statistical differences were detected during the 3 years of the study for these indexes. Control and flowered plots did not disperse significantly along NMDS dimensions based on sapling species composition (*r* values of correlation among site scores and saplings composition per site varied between 0.3 and 0.4 and $p > 0.05$ in all cases). Similarly, we did not detect significant changes in the species composition of saplings during the 3 years of the study in control and flowered plots. The dominant sapling species in all plots were shade-tolerant medium or small-size trees such as *S. bonplandii*, *Inga marginata*, *Allophyllus edulis* and some

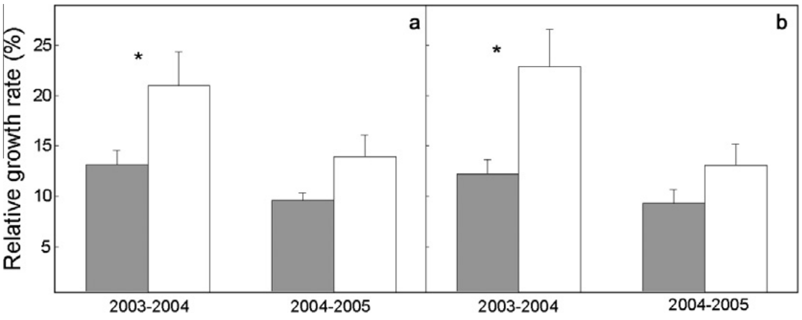

Fig. 2. Annual relative growth rate (%) in height (a) and diameter (b) for tree saplings during the first (June 2003–July 2004) and second (July 2004–June 2005) periods of measurements in control (solid bars) and flowered (open bars) plots. The saplings were naturally established before bamboo die-back. Bars are means + SE ($n = 10$). A total of 432 healthy saplings in control and 471 saplings in flowered plots were analyzed during 2003–2004, and 318 and 410 saplings in control and flowered plots, respectively during 2004–2005. *Indicates significant differences ($p < 0.05$), *t*-test for independent samples.

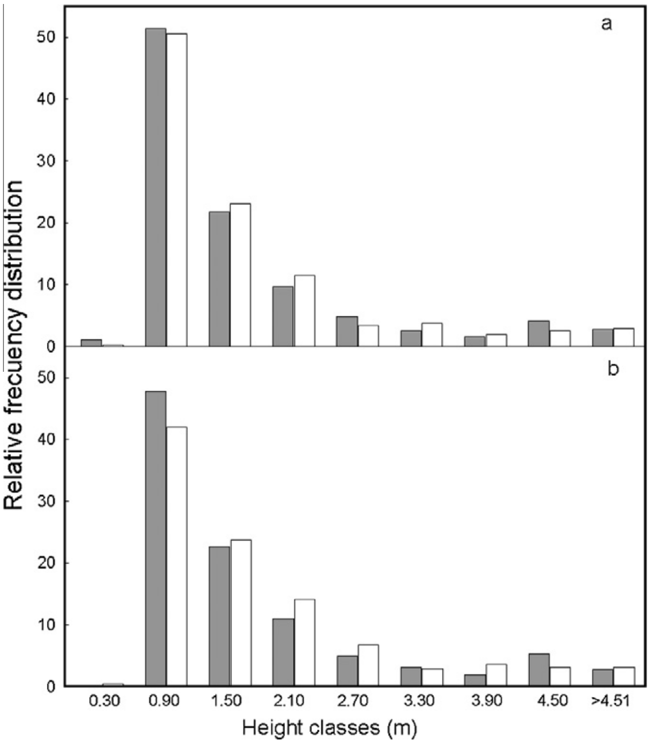

Fig. 3. Relative abundance of tree saplings by height class in control (solid bars) and flowered plots (open bars) during two consecutive years 2004 (a) and 2005 (b).

canopy species such as *N. megapotamica*, *Lonchocarpus* spp., *Balforoudendron riedelianum, Machaerium* spp. (Appendix A).

The flowering and death of *C. ramosissima* had a positive effect on tree sapling growth in the first year after flowering (2003–2004), which increased more than 50% compared to non-flowering plots (Fig. 2). During this period, saplings growing in flowered plots showed higher relative growth rates in height ($n = 10$, d.f. 18, $t = -2.16$, $p < 0.05$) and in stem diameter ($n = 10$, d.f. 18, $t = -2.69$, $p < 0.05$) compared to saplings growing in control plots. Some species such as *N. megapotamica* and *C. fissilis* exhibited high values of height growth (near 20 cm year^{-1}) with some individuals having large height increments (almost 40 cm year^{-1}) in the flowered plots (data not shown). The number of saplings in each height class (Fig. 3a) was similar between control and flowered plots ($\chi2 = 7.50$, $p > 0.05$). This effect was not observed during the second year of sampling (2004–2005), when differences in relative growth rates were marginally non-significant between control and flowered plots ($p = 0.08$ and $p = 0.15$ for height and diameter, respectively) (Fig. 2). However, the number of saplings in each height class (Fig. 3b) was different between control and flowered plots ($\chi2 = 32.62$, $p < 0.05$). During 2005 more than 51% of the total saplings exceeded the height mean in flowered plots compared to 30% in control plots. A total of 432 and 471 healthy saplings were measured in control and flowered plots respectively during 2003–2004 and 318 *y* 410 during 2004–2005. At the end of the 3 year study (2005), tree saplings in the flowered plots exhibited lower damage and mortality than tree saplings growing in the control plots ($U = 12$, $p < 0.01$ and $U = 24$, $p < 0.05$, respectively) (Fig. 4).

After flowering, control and flowered plots were different (d.f. 1, $F = 48.80$, $p = 0.001$) and in sequential surveys (d.f. 1, $F = 5.43$, $p = 0.004$) in terms of environmental characteristics and understory composition, interaction between years and treatments was not significant (d.f. 1, $F = 1.206$, $r^2 = 0.013$, $p = 0.279$). The first three axes of the PCoA of plots by environmental and understory composition variables explained more variation than expected for a random (broken-stick) partitioning of variance. Of the 20 possible eigenvectors, one had zero eigenvalues and eight had negative eigenvalues but nearly 65% of the variance was explained by the first three axes (which explain 46.7%, 9.3% and 7% of the variation, respectively). Four of the 10 variables were significantly related to the first ordination axis; % cover of bamboo was correlated negatively and fraction of radiation transmitted (FRT), % cover of ferns

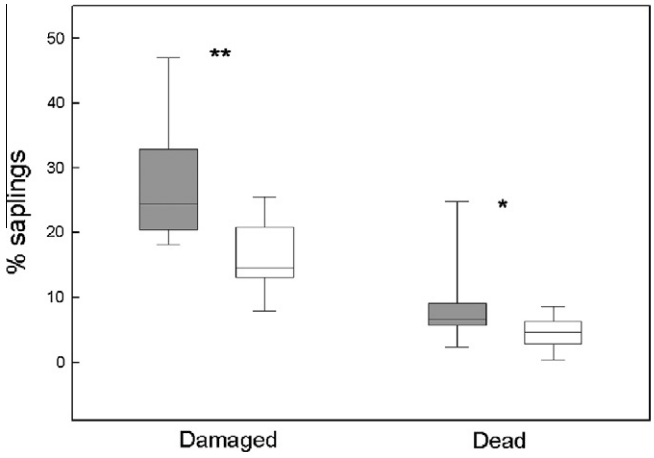

Fig. 4. Percentage (%) of damaged and dead tree saplings during the period 2003–2005 in control (solid bars) and flowered (open bars) plots. Medians, 25–75% quartiles, minimum and maximum values are shown. Statistical significant differences were observed between control and flowered plots (*$p < 0.05$ and **$p < 0.01$) Mann–Withney *U* test. Total of 586 and 565 tree saplings were identified in control and flowered plots respectively on 2003.

Table 3
Cumulative percentage of variance explained by principal component analysis (PCoA) of 20 plots based on 10 environmental and understory composition variables on the first three axes by the PCoA. Bold numbers indicate significant values.

	Axis 1	Axis 2	Axis 3
Percentage variance explained (%)	46.7	9.3	7
FRT	**0.54**[*]	0.13	0.20
Soil humidity	−0.01	0.11	0.04
Soil PO_4–P	0.19	0.20	0.10
Soil NO_3–N	−0.21	0.24	0.03
Soil NH_4–N	−0.18	−0.12	0.28
%C Bamboo	**−0.73**[*]	0.03	−0.22
%C Lianas	0.15	**−0.72**[*]	0.10
%C Ferns	**0.75**[*]	0.02	−0.14
%C Herbs	0.29	**−0.56**[*]	−0.05
%C *Piper* spp.	**0.60**[*]	0.19	**0.33**[**]

FRT = fraction of solar radiation transmitted, %C = percentage cover of each understory vegetation class.

[*] $p < 0.001$.

[**] $p < 0.05$.

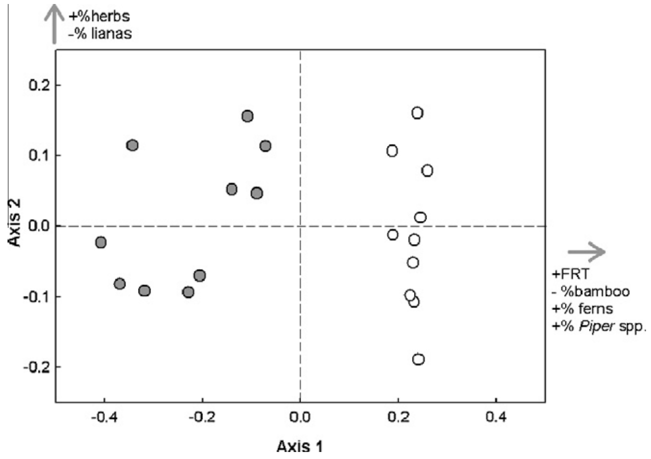

Fig. 5. Principal component analysis (PCoA) of 20 plots based on 10 environmental and understory composition variables along the first two axes. Solid and open circles show control and flowered plots, respectively. The traits listed are those integrated by each of these axes; they are enumerated in sequence from strongest to weakest strength of association with each axis; signs indicate the direction of association. Bamboo refers to *Chusquea ramosissima*.

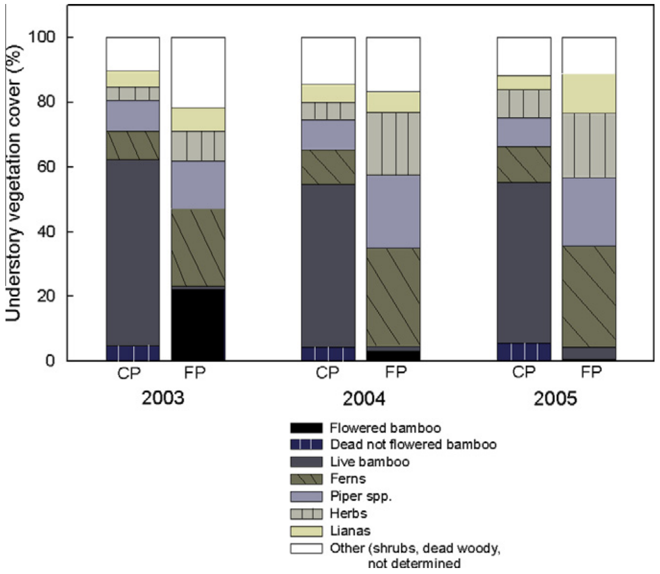

Fig. 6. Stacked bar graph of understory vegetation cover in control (CP) and flowered (FP) plots in three consecutive measurement periods (2003, 2004 and 2005) after *C. ramosissima* bamboo flowering and die-back. Total hits (100%) per years and treatment were: 572 ± 50 in CP and 440 ± 37 in FP on 2003; 526 ± 65 in CP and 380 ± 31 in FP on 2004 and 544 ± 60 in CP and 395 ± 25 in FP.

and % cover of *Piper* spp. were correlated positively (Table 3). The second PCoA axis was correlated negatively with % cover of herbs and positively correlated with % cover of lianas (Fig. 5 and Table 3). The lower percentage of variance explained by other axes demonstrated a reduced power of them in explaining differences between control and flowered plots (data not shown).

Understory vegetation cover in control and flowered plots in 2003, 2004 and 2005 is shown in Fig. 6. Each bar was divided into different classes of understory vegetation such as flowered, dead not flowered and alive bamboo, ferns, lianas and three others classes. The interaction of time and treatment (control vs. flowered plots) had a strong effect on % of non-bamboo cover (the sum of ferns, herbs, lianas and others) (time × treatment $F = 8.08$, $p < 0.001$). The flowered plots had the highest values of non-bamboo cover ($F = 60.81$, $p < 0.001$), and had a significant difference in these categories of understory vegetation through time. In flowered plots *Piper* spp., ferns, herbs and lianas showed a significant increment in % cover from 2003 to 2005 ($U = 2$, $p = 0.0002$; $U = 4$, $p = 0.0005$; $U = 22$. $p = 0.034$ and $U = 15$, $p = 0.008$, respectively) (Fig. 6). Standing flowered bamboo cover significantly decreased between 2003 and 2004 because senescent biomass fell to the ground. At the same time near 1% of vegetation cover that corresponded to live bamboo (non-flowered) was present in the flowered plot during 2003 and 2004 (Fig. 6). During 2005, we counted 1.492 and 0.135 living culms per m^2 in control and flowered plots respectively, that corresponded to more than 50% of the total vegetation cover in the understory of control plots and about 5% in the understory of flowered plots ($U = 4$, $p < 0.05$) (Fig. 6). This increment in live bamboo resulted from the vegetative growth of plants that did not flower and from bamboo established seedlings (plants that had developed more than three culms and had more than 50 cm of height) (data not shown). No flowered bamboo was measured in control plots during the study (Fig. 6).

4. Discussion

4.1. Environmental conditions, nutrient cycling and litter decomposition after flowering

C. ramosissima die-back resulted in a substantial increase of solar radiation at the forest floor in this subtropical forest, similar to the changes observed in forests dominated by other monocarpic bamboo species after flowering (Taylor and Qin, 1992; Taylor et al., 2004; Giordano et al., 2009; Marchesini et al., 2009; Budke et al., 2010). The increment of solar radiation was higher during the first summer and winter after flowering (2002–2003), but was not significant the following summer. The first year after flowering and die-back the solar radiation reaching the understory was similar to the values observed after experimental removal of *C. ramosissima* in a similar forest type (Campanello et al., 2007a). During the summer of 2003–2004, radiation in flowered plots reached the same values than in control plots, due to the fast growth of other understory plant species such as ferns and *Piper* spp. that colonized the space released by bamboo die-back. The recovery of *C. ramosissima* in flowered plots began during the last year of the study (2005) suggesting that a re-colonization of bamboo can be expected after flowering (Montti, 2010; Montti et al., 2011).

According to some studies, water use of trees is negatively affected by the presence of woody bamboos (Takahashi et al., 2003; Griscom and Ashton, 2003; Ishii et al., 2008); consequently, we expected an important effect of *C. ramosissima* die-back on soil water availability. However, no changes were found in soil water potentials after bamboo die-back. Similar results were obtained by others (Gratzer et al., 1999; Takahashi et al., 2007; Marchesini et al., 2009). It is possible that the high rainfall characteristic of this site maintained soil close to saturation and it was not affected by bamboo die-back. In other words, water supply overshadowed any potential differences in water uptake between control and flowered plots.

Several studies suggested that the presence of bamboo vegetation improves soil fertility (Tripathi and Singh, 1992; Christanty et al., 1997; Singh and Singh, 1999), although other studies have observed reduced fertility in areas of dominant bamboo cover (Shanmughavel and Francis, 1997) and argued that soil nutrient availability can increase if bamboo is removed due to a reduction in nutrient uptake (Raghubanshi, 1994; Takahashi et al., 2003; Tripathi, 2006). Litter decomposition following bamboo flowering has not been evaluated yet in tropical forests. In our study site, after 1 year of *C. ramosissima* die-back, nitrogen availability and turnover was similar in control and flowered plots. These results could be explained by the similar slow decomposition rates and litter mass accumulation of *C. ramosissima* in control and flowered plots. Decomposition of bamboo litter was slower on average than rates of mass loss in other subtropical forests (Deka and Mishra, 1982; Singh and Singh, 1999), and substantially reduced compared to the subdominant tree species such as *S. bonplandii*. Our results were similar to the findings of Liu et al. (2000) in a subtropical mountain forest in China for the bamboo *Sinarundinaria nitida*, which requires more than 6 years to lose 95% of their initial mass, and consistent with another study of *Chusquea* bamboo flowering which demonstrated significantly slower decomposition of bamboo litter, particularly stem tissue (Austin and Marchesini, 2011). The slow decomposition rates of *C. ramosissima* leaves could be the result of several factors. Liu et al. (2000) observed that leaves of bamboo are thinner and less rigid than leaves of canopy trees, but have lower N and P concentrations, and higher lignin/N, lignin/P, and N/P ratios, characteristics that can affect litter decomposition rates (Lisanework and Michelsen, 1994). The differences in decomposition rates among leaves and other bamboo organs can be also explained by differences in litter quality, especially carbon content (Table 2, Montti, 2010). Nevertheless, although differences in litter quality and decomposition were observed, they did not appear to affect nutrient availability in the soil during the period of study. In temperate forest ecosystems, the impacts of synchronous bamboo flowering on biogeochemical cycling may be perceived in the medium to long-term, when low quality senescent material is decomposed and incorporated into the soil organic matter pools, and microbial immobilization of nutrients occur (Austin and Marchesini, 2011). In contrast in this subtropical forest, the input of senescent material (dead bamboo) aboveground was immediate and litter quality of bamboo does not differ strongly among leaves, branches and stems due to the relatively rapid decomposition overall and the similar contribution to aerial senescent biomass in control and flowered plots, ecosystem-level decomposition was not impacted by the flowering event. In addition, plant growth rates are more rapid such that vacant spaces are quickly colonized, and nutrient uptake may not be substantially impacted by the bamboo mortality. If this was the case, the potential effect of bamboo flowering on nutrient cycling would be undetectable in subtropical ecosystems where bamboo could not entirely dominate the understory or where flowering events were not synchronous, which is consistent with the results observed in this study. The rapid colonization by other species appears to quickly compensate for the loss of vegetative cover due to the flowering event, and given that there were no significant effects in the first years post-flowering, it is not likely that there will be medium or long-term impacts on carbon and nutrient cycling.

4.2. Effects on tree growth and understory composition

In temperate forests, the sudden decline of bamboo cover after a flowering event is thought to be an important process regulating tree seedling establishment and forest stand development (Nakashizuva and Numata, 1982; Nakashisuka, 1987; Taylor and Qin, 1992; Abe et al., 2002; González et al., 2002; Holz and Veblen, 2006; Giordano et al., 2009). In the subtropical forests of northeastern Argentina, *C. ramosissima* flowering and die-back enhanced growth and reduced mortality rate of tree saplings. However, the positive effect observed in tree saplings in the flowered plots occurred only during the first year after flowering, and tree species richness and sapling density did not change as expected. This short-term effect on tree saplings growth could be explained not only by the significant increment in light availability during the first year after bamboo died-back, but also by the decline of physical damage to established canopy saplings by bamboo. The high density of culms and aerial biomass of bamboo caused physical damage on tree saplings by mass-loading and crushing, which affected the growth of saplings reducing the height stem, and also causes tree mortality. These effects on growth along with a reduced mortality probably resulted in differences in sapling abundance and height-class distribution. Physical damage in tree saplings was also observed in other studies of woody bamboos (Griscom and Ashton, 2003; Silveira, 2001). The absence of differences in tree sapling growth rates between control and flowered plots during the second growing season after bamboo die-back could be explained by a decreased in solar radiation in flowered plots in the summer 2003–2004 that became similar to control plots. This result reinforces the idea that light is the main limiting resource for tree saplings growing under the bamboo canopy in the study area. Favorable light conditions after bamboo die-back enabled also the growth of other plants such as ferns, lianas and *Piper* spp. in the understory and gaps. These understory species may have also limited tree saplings growth by intercepting a percentage of the incoming solar radiation during the second growing season after flowering (summer 2003–2004) and are a critical influence on the growth rate and composition of canopy species regeneration.

Some authors (Nakashizuva and Numata, 1982; Taylor and Qin, 1992; Taylor et al., 1995; Abe et al., 2001; Giordano et al., 2009) suggested that bamboo flowering and die-back enhance synchronized tree canopy regeneration and germination. However, Montti et al. (2011) showed that *C. ramosissima* die-back did not result in the establishment of new tree seedlings. Contrary to our prediction, pioneer or light-demanding tree species such as *Solanum* spp., *Trema* spp., *Cecropia* sp. or *Cestrum* spp. were not observed in flowered plots. Recently, Budke et al. (2010) in a similar ecosystem of the Atlantic Forest showed that gaps were colonized by tree saplings 2 years after synchronous flowering of *Merostachys multiramea*, another Atlantic Forest monocarpic bamboo species. It would be interesting to know if the effect persists in the long-term or instead the bamboo re-colonizes the areas it had previously occupied. Medium to long-term studies were necessary to establish whether tree regeneration was enhanced or not by bamboo die-back in temperate forests where bamboos with synchronic flowering are a dominant component of the understory (Abe et al., 2005; Holz and Veblen, 2006; Muñoz and González, 2009). These studies and our results showed that bamboo recovered after flowering, and that the positive effects of bamboo die-back on tree regeneration were restricted to a short period of time and that other ecological factors (e.g., canopy tree, seed production, seed predation, vegetative reproduction of canopy tree, understory vegetation or micro-environmental condition) should be also considered. Vegetation response to bamboo flowering should be then considered as an ongoing process rather than a discrete event (Holz and Veblen, 2006).

Martins et al. (2004) argued that the success of pioneer and light-demanding tree species depends on the gap size created by bamboo die-back. It is possible that tree species composition in flowered plots did not change because the gaps generated by the death of *C. ramosissima* were relatively small. Furthermore, *C. ramosissima* produces a compact and thick low quality litter layer (aprox. 4 cm thick) that accumulates at the soil surface. This could have affected seed germination or seedling establishment in flowered plots and ultimate tree seedling abundance, species richness and diversity. This hypothesis is consistent with previous observations by Campanello et al. (2007a) that light-requiring species' regeneration was improved in skid-trails after soil disturbance and litter and live biomass removal. Also, Larpkern et al. (2010) performed an experiment of litter removal in a tropical forest in Thailand, and observed that bamboo litter reduces tree regeneration.

Finally, it is important to note that bamboos have different flowering patterns that range from continuous non-semelparous to synchronous, and that periods between flowering events are quite variable among species (Janzen, 1976; Pohl, 1991; Widmer, 1994; Judziewicz et al., 1999). *C. ramosissima* showed a spatially discontinuous flowering pattern (i.e., asynchronous) and, in consequence, flowering and non-flowering culms can be intermingled in patches of different size at any time (Montti, 2010; Montti et al., 2011). This flowering behavior is quite different to the synchronous (or gregarious) flowering of many woody bamboo species described in the literature, which involve flowering of all culms and/or individuals at regular intervals over extensive areas (Janzen, 1976; Veblen, 1982; Campbell, 1985; Franklin, 2004; Marchesini et al., 2009). This aspect of the reproductive biology of *C. ramosissima* and their ability to re-colonize gaps after die-back by new seedling production and vegetative growth of the remaining live culms can also diminish or shorten the effects of bamboo die-back on tree regeneration.

5. Conclusions

Most woody bamboo species are monocarpic and their mortality after flowering can have consequences at the population and ecosystem scale, but contrasting responses to flowering events suggest that ecosystems may behave differently depending on climatic and edaphic constraints and also, on the flowering patterns and their synchronicity. Our study contributes to this query by evaluating the effects of an abundant and widespread neotropical bamboo species in the dynamics of a subtropical forest. In northeastern Argentina, *C. ramosissima* flowering and die-back enhanced growth and reduced mortality rate and damage of tree saplings only during the first year after flowering, but without changes in tree species richness or sapling abundance. The short-term effects on tree sapling growth were due to significant increment in light availability during the first year after bamboo flowering which was quickly reverted due to rapid colonization by other herbaceous understory species. At the same time, many other environmental characteristics such as litter decomposition and soil nutrient concentrations were largely unaffected by the flowering event, which is contrasts with results from temperate Argentine forests (Giordano et al., 2009; Austin and Marchesini, 2011). Successful tree growth in gaps following bamboo flowering appears to be restricted to a very narrow window of increased resource availability, and only some already established individuals were able to take advantage of the increasing resources. Consequently, these flowering events do not appear to play a major role in the regeneration of canopy species in this subtropical forest ecosystem.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.06.029.

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