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Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest

Paula I. Campanello [a,*], M. Genoveva Gatti [a], Adrian Ares [b], Lia Montti [a], Guillermo Goldstein [a,c]

[a] *Laboratorio de Ecología Funcional, Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II, 4 piso, Ciudad de Buenos Aires (C1428EHA), Argentina*
[b] *Weyerhaeuser Company, 2730 Pacific Boulevard SE, Albany, OR 97322, USA*
[c] *Department of Biology, University of Miami, P.O. Box 249118, Coral Gables, FL 33124, USA*

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Abstract

We assessed the effect of native bamboo and lianas on microclimate, tree regeneration and forest structure in a semi-deciduous Atlantic Forest subjected to selective timber extraction during the last century. We hypothetized that bamboo and liana cutting would increase incoming solar radiation in the understory promoting establishment and survival of pioneer and light-requiring canopy tree species. A manipulative experiment consisting of bamboo and liana cutting was performed in a native forest stand in northeastern Argentina. In three permanent 1-ha plots bamboo and lianas were cut and allowed to decompose *in situ*, while other three plots were used as a control treatment. We measured solar radiation reaching the understory, soil water availability and air temperature in both bamboo and liana cutting and control plots. Tree sapling abundance and richness, stand basal area, bamboo density, and cover of lianas, herbs, shrubs, fallen trees and branches were also determined. We performed multivariate analyses to relate tree sapling abundance and richness with biotic and abiotic factors. Bamboo and liana cutting increased by 100% the solar radiation reaching the understory. The fraction of solar radiation transmitted at 0.7 m height above ground in control and treated plots was 0.1 and 0.2, respectively. Minimum soil matric potentials after a severe dry spell were less than −2 MPa. Soil water availability was higher under closed-canopy in the treated plots because liana transpiration was prevented by cutting. Although bamboo and liana cutting increased incoming solar radiation, tree seedling and sapling abundance of pioneer and light-demanding species was not improved by the treatment. Instead, an increased abundance of herbaceous plants was observed in gaps and open canopy areas (i.e., sites with amounts of herb cover greater than 75% represented the 11 and 2% of the total number of sites in treated and control plots, respectively). Sapling survival and growth rates, on the other hand, appeared to be promoted by bamboo and liana cutting. Bamboo inhibited tree sapling abundance and richness in gaps, whereas tree basal area had a positive effect. In the semideciduous Atlantic Forest, native bamboos modify gap phase regeneration, and may affect canopy cover and forest composition in the long term. Post-logging management techniques are needed for sustainable timber production in these forest stands.

Keywords: Argentina; *Chusquea ramosissima*; Gap-phase regeneration; Selective timber extraction; Solar radiation

1. Introduction

Solar radiation is a critical factor affecting reproduction, survival and growth of plant species in tropical and subtropical forests (Denslow and Hartshorn, 1994; Fetcher et al., 1994; Chazdon et al., 1996). Forest structure, floristic composition and gap dynamics affect understory solar radiation levels, which display large spatial and temporal variability (Clark et al., 1995). In general, secondary forests have mid-size canopy openings receiving 2–5% of full sun uniformly distributed whereas mature primary forests have many small openings (i.e., less than 2% of full sun) and few large gaps with more than 5% of total solar radiation (Nicotra et al., 1999). Gap size affects not only the fraction of solar radiation reaching the understory but also the frequency and duration of sunflecks (Brown, 1993). Gap formation also increases air and soil temperature and decreases relative humidity (Whitmore et al., 1993). Soil water availability is usually greater in gaps than in undisturbed forest because of decreased evapotranspiration (Cavelier and Vargas, 2002).

* Corresponding author.
E-mail addresses: pcampa@ege.fcen.uba.ar, pcampanello@yahoo.com (P.I. Campanello).

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Gap formation may play a fundamental role in maintaining tree diversity in some tropical forests that have low frequency of large-scale disturbances (Denslow, 1980; Brokaw, 1985; Whitmore, 1990; Phillips and Gentry, 1994). Shade tolerant tropical tree species require a narrow range of gap sizes associated with certain levels of solar radiation (Denslow, 1980; Tuomela et al., 1996; Myers et al., 2000). In large gaps (i.e., larger than 1000 m^2), pioneer or light-demanding plant species with higher growth rates and ecophysiological plasticity have competitive advantages (Denslow, 1980). Although gap-phase regeneration has been considered a major determinant of tree diversity, this paradigm has recently been critically revised (Wright, 2002; Wright et al., 2003). Reasons involve artificial dichotomies used to simplify the complexity of factors shaping tropical forest ecosystems. The first artificial dichotomy is pioneer versus climax species (or light-demanding versus shade-tolerant species). Species usually fall along a continuum, most of them showing intermediate responses (Denslow, 1987; Wright et al., 2003; Santiago et al., 2004; Campanello et al., 2007a). The second artificial dichotomy is gap versus understory. Microsites also fall along a continuum, and continuous variation in microenvironment exists in space and time (Wright et al., 2003).

Large-gaps created after severe natural or anthropogenic disturbances may have a fundamental role in some tropical forest by either increasing tree diversity (Vandermeer et al., 2000; Molino and Sabatier, 2001), or by facilitating encroachment of bamboos and proliferation of lianas (Whitmore, 1990). These two groups of species, which respond fast to sudden increases in solar radiation availability, inhibit tree seedling regeneration and growth (Putz, 1984). Accordingly, in a tropical forest in Panama, development of multistrata forest did not occur in stands with liana-dominated gaps (Schnitzer et al., 2000). In some habitats of the Amazon region and the Atlantic Forest of Brazil, bamboos often ocuppy forest openings and preclude the regeneration of pioneer tree species modifying processes related to forest regeneration and gap succesion (Oliveira-Filho et al., 1994; Tabarelli and Mantovani, 2000; Silveira, 2001; Griscom and Ashton, 2003).

Selective logging is the most common method used for timber extraction in tropical and subtropical areas. A recent study estimated that 12,100–19,800 km^2 of the Brazilian Amazon are affected every year by selective logging (Asner et al., 2005). Gap dynamics is profoundly altered by this method that involves the removal of a few trees per unit area although considerable damage is done to the vegetation adjacent to the felled trees. Selective logging typically creates gaps that are 5–6-fold larger than those in undisturbed forest (Pereira et al., 2002). Main and lower-order logging roads also markedly affect incoming solar radiation, soil temperature, evaporative demand and soil water potential (Van Dam, 2001). Selective logging may also produce soil compaction (Guariguata and Dupuy, 1997; Olander et al., 2004) as well as changes in plant species composition and faunal diversity (Johns, 1992).

The semideciduous Atlantic Forest of South America has a high diversity of liana species (Morellato and Leitão Filho, 1998; Hora and Soares, 2002), and is rich in native bamboo species, some of which may colonize disturbed sites and become the dominant species (Judziewics et al., 1999). Woody bamboos of the genus *Chusquea* and *Merostachys* may form impenetrable thickets in gaps and open canopy areas (Tabarelli and Mantovani, 1999), whereas lianas may affect more than 80% of the canopy trees (Campanello et al., 2007b). Species of *Chusquea* can be aggressive colonizers after human disturbance. They are able to spread rapidly through leptomorph rhizomes while forming clumps through pachymorph tillering (Judziewics et al., 1999). Large-scale forest disturbances such as hurricanes or selective logging also increase liana abundance in tropical and subtropical forests (Schnitzer and Bongers, 2002).

In the Atlantic Forest of northern Argentina, most forests were selectively logged (Montagnini et al., 1997). In these forests, both bamboos and lianas appear to inhibit tree regeneration by changing environmental conditions. If this were the case, bamboo and liana cutting would increase tree recruitment favoring the re-establishing of a multi-stature forest in the long term. The main purpose of this study was to assess the effect of native liana and bamboo species on microclimate, tree regeneration and forest structure in a semi-deciduous Atlantic Forest subjected to selective timber extraction. We hypothetized that bamboo and liana cutting will increase incoming solar radiation in the understory promoting pioneer and light-requiring canopy tree species establishment and survival, which will result on greater sapling and seedling abundance of canopy species after treatment.

2. Materials and methods

2.1. Study area

The research was carried out in a native forest in the Province of Misiones, northeastern Argentina at latitude 25°58′S and longitude 54°13′W. Mean annual precipitation is 2000 mm, 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. During summer, average photosynthetic photon flux density in full sun is about 26 ± 3.5 mol m^{-2} day^{-1}.

The experiment site is placed on gentle to medium slopes (<20%) at approximately 250 m elevation. Soils include stony Alfisols, Molisols and Inceptisols (Soil Survey Staff, 1992) developed from weathered and fractured Jurassic basalt (Ligier et al., 1990). These soils have a relatively large content of exchangeable N (11 and 10 $\mu g\ g^{-1}$ of NH_4^+ and NO_3^-, respectively) and low available P (less than 2 $\mu g\ g^{-1}$ P determined with anion resin beads) in the 0–5-cm soil depth (Campanello, 2004).

The study area comprises 30 ha of forest limiting to the north with a large forest reserve and to the south with commercial plantations of *Pinus taeda* L. The forest was heavily and selectively logged until the end of the 1960s and has been invaded by native lianas and bamboos mainly *Chusquea ramosissima* Lindman, and *Merostachys clausenii* var. *clausenni* Munro.

Lianas are abundant with an average of 50.3 individuals larger than 2.5 cm DBH for 17 different liana species on a 0.1-ha basis. The most abundant liana species belong to the Bignoniaceae and Fabaceae families, and species in the genera *Adenocalymna*, *Arrabidaea* and *Acacia* are common (Campanello et al., 2007b). Some of the dominant canopy trees in the study area are *Balfourodendron riedelianum* (Engl.) Engl., *Nectandra megapotamica* (Spreng.) Mez, *Bastardiopsis densiflora* (Hook. & Arn.) Hassler, *Cedrela fissilis* Vell., *Patagonula americana* L., and *Lonchocarpus leucanthus* Burkart. Common subdominant tree species are *Sorocea bonplandii* (Bailon) Burg., *Actinostemon concolor* (Spreng.) Muell. Arg., *Trichilia catigua* Adr. Juss. and *Trichilia elegans* A. Juss.

2.2. Experimental design

Six permanent 100 m × 100 m (1 ha) plots with similar canopy dominance and understory vegetation were established in May 2000. A 20-m buffer zone was established around each plot to minimize edge effects. All trees greater than 10 cm in diameter at 1.30-m above ground (DBH) were identified, marked, mapped, and their DBH measured with a diameter tape. The experiment contained two treatments: (1) bamboo, mainly *Chusquea ramosissima*, and liana cutting (BLC), and (2) control (CT). Stand basal area in BLC and CT plots was 20.4 ± 0.9 and 19.5 ± 2.5 m^2 ha^{-1} with 329 ± 22 and 280 ± 28 individuals per hectare, respectively. Treatments were replicated three times in a randomized complete block design. Blocking was based on soil type, topographic position, understory vegetation (i.e., *C. ramosissima* abundance) and stand basal area. Selective logging of 2–6 large individuals took place in September 2000 as part of the study. Extraction intensity was adjusted to equalize basal area among plots. Most of the logged trees belonged to the species *Bastardiopsis densiflora* and *Lonchocarpus leucanthus*. Some individuals of *Nectandra megapotamica*, *Balfourodendron riedelianum*, *Lonchocarpus muehlbergianu*s and *Patagonula americana* were also logged. When treatments were imposed, in November 2000, there were 256 ± 19 tree individuals with a mean basal area of 17.1 ± 1.8 m^2 ha^{-1} in CT, and 304 ± 14 individuals with a mean basal area of 18.5 ± 0.2 m^2 ha^{-1} in BLC. These or lower values of basal area are common in the forests of Misiones that are subjected periodically to selective logging. In a less disturbed forest, basal area was larger than 23 m^2 ha^{-1} (Placci et al., 1992; López Cristóbal et al., 1996).

Bamboo and liana cutting was also performed in the 20-m wide buffer strips surrounding the measurement plots. Harvested biomass was left to decompose in situ. Bamboo and liana cutting was repeated in October 2001 when *C. ramosissima* and liana resprouts were cut along with invasive herbs and shrubs. Each 1-ha plot was divided resulting in twenty-five 400-m^2 (20 m × 20 m) subplots per hectare. In July 2002, we installed twenty-five 4-m^2 (2 m × 2 m) regeneration plots centered on the 20 m × 20 m subplots to measure microclimate and vegetation. We counted rooted bamboo culms and liana seedlings and saplings in 4-m^2 plots inside BLC and CT in order to assess treatment effectiveness.

2.3. Microclimate and soil water availability

In August (winter) and December (summer) 2001, we took hemispherical photographs in BLC and CT to determine fraction of solar radiation transmitted with low and high stand leaf area, respectively, as many species are deciduous in winter. Photographs were taken with a digital camera Nikon Coolpix 950 with a Nikkor 8-mm lens on a self-level platform (Delta-T Devices, Cambridge, UK) at 0.7- and 2-m height in the center of ten 20 m × 20 m subplots along two 100-m transects randomly chosen in each 1-ha plots. Measurement heights were selected based on the stature (i.e., 0.5–2 m) of the dominant bamboo (*C. ramossisima*). Measurement locations were marked with stakes for repeated measures. Distance between locations (20 m) was selected to assure independence between contiguous photographs (Clark et al., 1995).

In January 2002, we measured air temperature with HOBO T sensors (Onset Computer Corporation, Bourne, USA) in six 20 × 20 subplots representing two contrasting conditions (gap and closed canopy) inside CT and BLC plots of the same block (totalling 12 subplots). In the same places we measured soil matric potential three times at 5-cm soil depth during dry spells (i.e., 15–30 days without rainfall) in winter and summer, and after rainfall events >100 mm. The filter-paper method was used for soil matric potential estimations (Deka et al., 1995). Precipitation values were obtained from the nearest weather station at 35 km distance in the town of Wanda.

2.4. Tree species diversity and regeneration

In July 2003, we identified and measured all tree saplings (i.e., individuals >30 cm in height and <10 cm in DBH) inside the one hundred fifty 4-m^2 regeneration plots in BLC and CT. In July and August 2004, we remeasured all plots and also counted and identified all tree seedlings (i.e., individuals less than 10 cm height). A total of 150 subplots were surveyed (75 per treatment) of which 60 subplots were located in sites where hemispherical photographs had been taken.

2.5. Determinants of tree regeneration

In July 2003 and August 2004, we counted the number of *Chusquea ramosissima* culms rooted inside the 150 regeneration plots to study the effect of bamboo on tree regeneration. Also, in each regeneration plot cover of *Piper* spp., herbs, other bamboo species (e.g., *M. clausenii*), ferns, fallen logs and branches, and lianas were visually estimated as a percentage of the total 4-m^2 area in each regeneration plot. All trees larger than 10 cm DBH present in the 20 m × 20 m subplots were counted and their stem diameter measured to compute tree basal area in the subplots.

2.6. Data analysis

Hemispherical photographs were analyzed with the Hemiview program (Delta-T Devices Ltd., Cambridge, UK). Fraction solar radiation transmitted (FRT) was calculated as

the proportion of the solar radiation reaching the measurement location relative to the solar radiation on top of the canopy. Non-parametric tests were used for FRT and temperature comparisons as these variables did not have a normal distribution. The Mann–Whitney test (Mann and Whitney, 1947) was used to compare FRT among treatments. Paired measurements of solar radiation, and minimum and maximum temperatures taken in winter and summer were compared with the Wilcoxon test (Wilcoxon, 1945). An ANOVA with log transformed FRT values rendered similar results to those from non-parametric analysis. This latter option was preferred as using the median and quartiles to express central tendency and variability of solar radiation is a more accurate way to describe light enviroments in the forest understory (Smith et al., 1992). Seedling and sapling abundances in CT and BLC plots were compared with a nested ANOVA, being treatment the fixed-effects factor and block the nested factor. A heterogeneity chi-square analysis was carried out to compare height frequency distribution of saplings and seedlings between treatments.

Apart from comparing CT and BLC in terms of microclimate and tree regeneration, tree sapling richness and abundance were related to variables measured in each 4-m^2 plot (*Chusquea* bamboo density, cover of lianas, herbs and shrubs, other bamboo species, ferns and fallen logs and branches) and in each 20 m × 20 m subplots (tree basal area) by using multivariate regression. The Box–Cox transformation (Box and Cox, 1964) was applied to variables to improve normality when needed. The arc-sine square-root transformation was used for data in percent. For each regression model we examined Moran's correlograms (Liechstein et al., 2002) of the residuals to test for independence. Treatment effects on sapling abundance and diversity were analyzed as a mixed model with cutting regime as a fixed effect and block as a random effect (Littell et al., 1996). Comparison of treatment means was made using one degree of freedom orthogonal contrasts. Procedure MIXED in SAS 8.2 (SAS Institute, 1999) that estimates variance components using restricted maximum likelihood methods was used for the statistical analyses.

3. Results

3.1. Microclimate and soil water availability

Fifty-seven percent of the sites in CT had FRT values less than 0.1 (i.e., 10% of the radiation at the crown top) at 0.7 m above ground in winter (Fig. 1a), and 63% of the sites had FRT less than 0.1 in summer (Fig. 1b). In BLC, only 18 and 13% of the sites had FRT below 0.1 in winter and summer, respectively. More than 60% of the sites in BLC showed FRT values between 0.2 and 0.4 in both winter and summer. Bamboo and liana cutting increased FRT at 0.7 m height from a median value of 0.1–0.2 (Mann–Whitney Test; $U = 195.1$, $P < 0.001$). At 2 m above ground, 40% of the sites in both treatments had FRT below 0.2 in winter (Fig. 1c), but in summer 60% of the sites in CT had FRT values lower than 0.2 (Fig. 1d). Thirty to thirty-five percent of the sites in BLC had FRT values between 0.5 and 0.7, while in CT less than 20% of the sites had those values. At 2-m height there were significant differences in FRT between summer and winter in BLC (Wilcoxon Matched Pairs Test; $Z = 2.83$, $P < 0.01$).

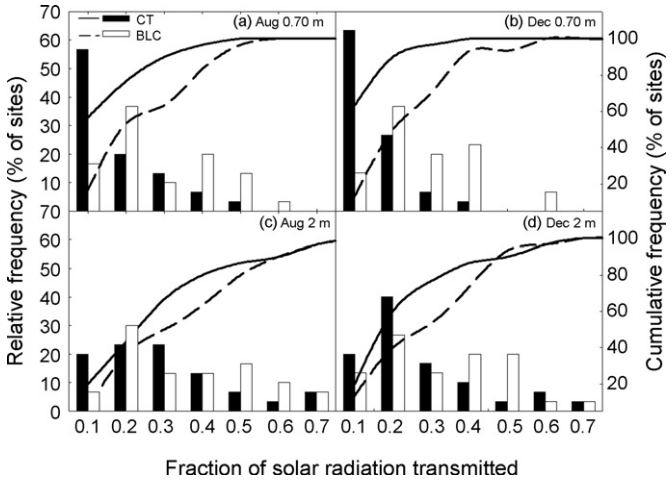

Fig. 1. Frequency of sites in classes of fraction of solar radiation trasmitted (FRT) at 0.7-m (a and b) and 2-m height (c and d) in winter (a and c) and summer (b and d) indicated by dark and white bars in control (CT) and bamboo and liana cutting (BLC) plots, respectively ($n = 60$ sites). Values of FRT correspond to the upper-point of each class. Accumulated frequency is indicated with solid (CT) and dashed lines (BLC).

Precipitation measured from August 2001 to May 2002 amounted to 990 mm with several dry spells (15–30 consecutive days without rain) during this period. In March 2002, after 29 days without precipitation soil matric potential at 0–5-cm depth was less than −2 MPa (Table 1). Soil water availability was greater in gaps than under closed canopy both in CT and BLC. Gaps had similar soil matric potentials in both treatments whereas under closed-canopy, there was higher soil water availability (more positive soil matric potentials) in BLC.

There were significant differences in maximum air temperature between gaps and under closed-canopy within CT (Wilcoxon Matched Pairs Test, $Z = 6.33$, $P < 0.001$) and within BLC (Wilcoxon Matched Pairs Test, $Z = 2.21$, $P < 0.05$). Maximum temperature in gaps was greater in BLC than in CT (Wilcoxon Matched Pairs Test, $Z = 6.33$, $P < 0.01$). The same pattern was observed for closed-canopy

Table 1
Soil matric potential at 0–5-cm depth, and air temperature at 15 cm height under closed-canopy and in gaps for control (CT) and bamboo and liana cutting (BLC) treatments in Misiones, Argentina

	Soil matric potential (MPa)		Summer air temperature (°C)	
	Winter	Summer	Maximum	Minimum
CT				
Closed-canopy	−1.8	−3.8	27.4	21.1
Gap	−0.3	−2.3	29.6	20.1
BLC				
Closed-canopy	−0.8	−3.0	32.1	20.4
Gap	−0.7	−2.7	33.5	20.2

Mean values are shown for soil matric potential and medians for air temperatures.

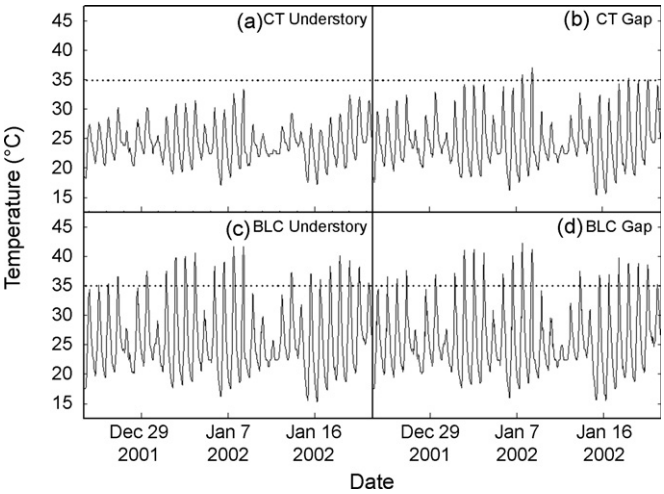

Fig. 2. Daily variation in summer air temperature at 15-cm height under closed-canopy (a and c) and in gaps (b and d) in control plots (a and b) and in plot with bamboo and liana cutting (c and d). Hourly measurements were averaged for each day. A dotted line was depicted at 35 °C for comparative analysis.

sites as well (Wilcoxon Matched Pairs Test, $Z = 6.33$, $P < 0.001$). Gaps and closed-canopy in BLC had the highest maximum and the lowest minimum temperatures (Table 1). In BLC, maximum summer air temperatures in gaps exceeded 35 °C during most of the measurement period (Fig. 2) while minimum temperature was similar in gaps and under closed-canopy (Wilcoxon Matched Pairs Test, $Z = 0.99$, $P = 0.32$).

3.2. Tree species diversity and abundance

We measured 413 and 486 tree saplings belonging to 47 and 51 species in CT and BLC, respectively (Table 2). Mean sapling density per m^2 and species richness per 4-m^2 plot were 1.4 and 3.4 in CT and 1.6 and 3.9 in BLC. In July 2004, there were no significant differences in either tree sapling ($F_{1,144} = 0.27$, $P = 0.60$) and seedling abundance between treatments ($F_{1,144} = 0.08$, $P = 0.77$). The number of saplings in each height class (Fig. 3), however, was different in BLC than in CT ($\chi^2 = 17{,}484$, $P < 0.05$). There was a marked difference in the frequency of saplings in the 1.50–2.7-m classes with 25% of the individuals inside these classes in BLC and 18% in CT plots.

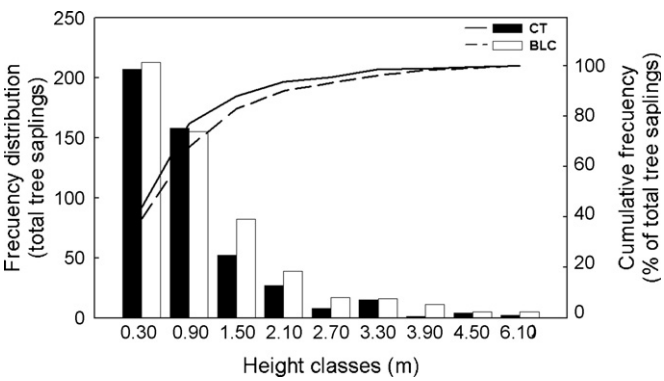

Fig. 3. Sapling abundance by height class in control (CT) and bamboo and liana cutting (BLC) plots are indicated with black and white bars, respectively. Accumulated frequency is indicated with solid (CT) and dashed lines (BLC).

Relative abundances of sapling and adult trees for dominant canopy species, representing approximately 40% of the total individuals are depicted in Fig. 4. Some tree species present as adults in the forest were infrequent among seedlings (e.g., *Cedrela fissilis*, *Bastardiopsis densiflora*, *Cordia trichotoma*, *Patagonula americana*, *Ocotea diospyrifolia*, *Balfourodendron riedelianum*). Dominant tree species in the stand equally or over-represented among the seedlings were *Nectandra megapotamica*, *Lonchocarpus leucanthus*, *Dyatenopterix sorbifolia*, *Myrocarpus frondosus* and *Holocalix balansae*. The most dominant species among saplings (Table 2) were shade-tolerant, small-size trees (*Acinostemon concolor*, *Trichilia elegans*, *Trichilia catigua*, *Sorocea bonplandii*, and *Pilocarpus pennatifolius*), which were scarcely represented among trees larger than 0.1 m in DBH. Saplings of the most abundant species were found in sites with FRT <than 24% at 2-m height, while the least abundant species were found in sites with high FRT. These were pioneer species such as *Solanum* spp., *Dunalia breviflora*, *Trema micrantha*, *Manihot flavelifolia* or light-demanding species that regenerate in gaps such as *Bastardiopsis densiflora*, *Patagonula americana*, *Parapiptadenia rigida*.

3.3. Determinants of tree regeneration

Abundance of *C. ramosissima* and liana saplings and seedlings was significantly lower in BLC than in CT 2 years after the treatment was applied. Median values of liana seedlings per m^2 were 1.25 and 0.75 for CT and BLC, respectively (Mann–Whitney Test, $U = 780$, $n = 50$ 4-m^2 plots, $P < 0.005$). Median number of *C. ramosissima* rooted culms

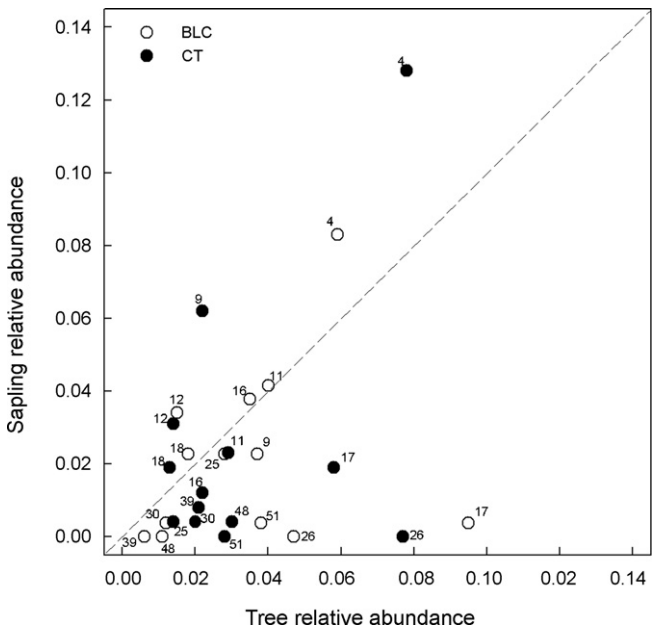

Fig. 4. Sapling relative abundance in relation to tree relative abundance for dominant canopy tree species. The dashed line indicates the expected sapling density if the relative abundance of canopy trees were maintained. Tree abundances were 861 and 950 individuals for CT and BLC plots, respectively. Species number and sapling abundance are in Table 2.

Table 2
Taxonomic identification and abundance of tree saplings (number of individuals in seventy-five 4-m^2 regeneration plots) in control (CT) and bamboo and liana cutting (BLC) plots

	Species	Family	CT	BLC	Total
1	*Actinostemon concolor* (Spreng.) Muell. Arg.	Euphorbiaceae	64	53	117
2	*Trichilia elegans* A. Juss.	Meliaceae	49	45	94
3	*Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. & Boer	Moraceae	30	62	92
4	*Nectandra megapotamica* (Spreng.) Mez	Lauraceae	41	33	74
5	*Pilocarpus pennatifolius* Lem. & Hassler	Rutaceae	27	36	63
6	*Trichilia catigua* A. Juss.	Meliaceae	14	37	51
7	*Chrysophyllum gonocarpum* (Mart. & Eichl.) Engl.	Sapotaceae	18	20	38
8	*Cupania vernalis* Cambess.	Sapindaceae	15	17	32
9	*Lonchocarpus leucanthus* Burkart	Fabaceae	23	9	32
10	*Matayba eleagnoides* Radkl.	Sapindaceae	8	21	29
11	*Holocalyx balansae* Mich.	Fabaceae	9	16	25
12	*Diatenopteryx sorbifolia* Radkl.	Sapindaceae	8	11	19
13	*Machaerium minutiflorium* Tul.	Fabaceae	8	10	18
14	*Campomanesia xanthocarpa* Berg.	Myrtaceae	7	10	17
15	*Allophylus edulis* (A. St. Hil.) Radlk.	Sapindaceae	4	12	16
16	*Lonchocarpus muehlbergianus* Hassler	Fabaceae	5	10	15
17	*Balfourodendron riedelianum* (Engl.) Engl.	Rutaceae	8	6	14
18	*Myrocarpus frondosus* Fr. All.	Fabaceae	5	8	13
19	*Strychnos brasiliensis* (Spreng.) Mart.	Loganiaceae	6	7	13
20	*Parapiptadenia rigida* (Benth) Brenan	Fabaceae	8	2	10
21	*Cestrum laevigatum* Schlecht.	Solanaceae	8	1	9
22	*Sebastiania brasiliensis* A. DC.	Euphorbiaceae	3	6	9
23	*Calliandra twedieii* Benth.	Fabaceae	1	6	7
24	*Cordia ecalyculata* Vell.	Boraginaceae	2	5	7
25	*Cordia trichotoma* (Vell.) Arrab. Ex. Stend.	Boraginaceae	1	6	7
26	*Bastardiopsis densiflora* (Hook. & Arn.) Hassler	Malvaceae	1	5	6
27	*Allophylus guaraniticus* Radlk.	Sapindaceae	4	1	5
28	*Eugenia burkartiana* (D.Legrand) D. Legrand	Myrtaceae		5	5
29	*Manihot flavelifolia* Pohl.	Euphorbiaceae	4	1	5
30	*Ocotea diospyrifolia* (Meissner) Mez	Lauraceae	2	2	4
31	*Solanum granulosum*-leprosum Dun.	Solanaceae	3	1	4
32	*Trema micrantha* (L.) Blume.	Ulmaceae	3	1	4
33	*Albizia hassleri* (Chod.) Burkart	Fabaceae	1	2	3
34	*Chrysophyllum marginatum* (Hook. & Arnott) Radkl.	Sapotaceae	2	1	3
35	*Dunalia breviflora* (Sendtn.) Sleumer	Solanaceae	2	1	3
36	*Inga marginata* Willd.	Fabaceae	3		3
37	*Styrax leprosus* Hook. Et. Arn.	Styracaceae	3		3
38	*Arecastrum romanzoffianum* (Cham.) Becc.	Palmae	1	1	2
39	*Cabralea canjerana* (Vell.) Mart.	Meliaceae	2		2
40	*Campomanesia guazumifolia* (Cambess.) O. Berg.	Myrtaceae	1	1	2
41	*Eugenia involucrata* DC.	Myrtaceae	2		2
42	*Hennecartia omphalandra* Poisson.	Monimiaceae	1	1	2
43	*Maytenus ilicifolia* Reiss.	Celastraceae		2	2
44	*Nectandra lanceolata* Nees & Mart. ex Nees	Lauraceae		2	2
45	*Prunus subcoriacea* Koehne	Rosaceae		2	2
46	*Xylosma* sp.	Salicaceae	1	1	2
47	*Casearia sylvestris* Sw.	Flacourtiaceae		1	1
48	*Cedrela fissilis* Vell.	Meliaceae	1		1
49	*Gleditsia amorphoides* Tabú.	Fabaceae		1	1
50	*Inga uruguensis* Hook & Arn.	Fabaceae		1	1
51	*Patagonula americana* L.	Boraginaceae		1	1
52	*Phytolacca dioica* L.	Phytolaccaceae		1	1
53	*Solanum inaequale Vell.*	Solanaceae	1		1
54	Unknown		3	2	5
	Total		413	486	899

Species were ranked from most to least abundant.

per m^2 was 2 in CT and 0 in BLC (Mann–Whitney Test, $U = 141$, $n = 50$ 4-m^2 plots, $P < 0.001$). The most abundant liana saplings and seedlings belonged to the species *Pristimera andina* Miers, *Seguieira aculeata* L., *Adenocalymna marginatum* (Cham.) DC., *Acacia* sp., *Adenocalymna paulistarum* Bur. Ex. K., and *Macfadyena unguis-cati* (Jacq.) A.H. Gentry. In July 2004, a larger percentage of 4-m^2 regeneration plots with herb cover between 50 and 100% were observed in the BLC treatment

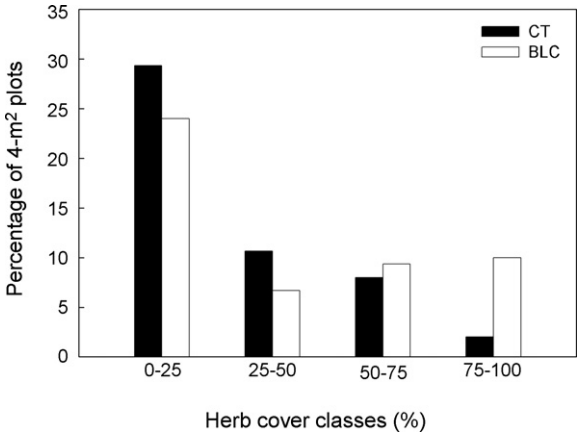

Fig. 5. Frequency distribution of four different herb cover classes (0–25, 25–50, 50–75 and 75–100% of ground cover) in the 4-m^2 plots. Percentages were calculated from all 150 regeneration plots in BLC and CT treatments.

compared to regeneration plots in the control (Fig. 5), suggesting that the cutting of bamboo and lianas promoted the growth of shrubs and herbaceous plants such as *Celtis iguanea* (Jacq.) Sargent, *Piper* spp., *Urera baccifera* (L.) Gaud, *Conyza bonariensis* (L.) Cronq., and *Hybanthus bigibbosus* (H. H.) Hassl.

Sapling density 3 years after imposing the treatments (i.e., year 3, 2003) was positively related to tree basal area, and negatively related to *Chusquea* density, herb cover and FRT at 0.70 m height (Table 3). At year 4, ground cover of fallen trees (not measured in 2003) was negatively related to sapling density. Sapling richness at year 4 was positively related to tree density and inversely related to *Chusquea* density, herb cover and ground cover of fallen trees and branches.

4. Discussion

4.1. Microclimate and soil water availability

Fraction of solar radiation in the understory of the Atlantic Forest studied in northern Argentina was higher than in mature tropical forests, where median FRT reported was less than 0.03 (i.e., 3% of the radiation reaching the top canopy) at any height between 0.6 and 5 m above ground (Smith et al., 1992, Clark et al., 1995). In La Selva, Costa Rica, only 1% of sampled microsites along fifteen 100 m transects had FRT values larger than 0.1 at 1 m height above ground (Clark et al., 1995). In contrast, in the forest of Misiones a large proportion of microsites (more than 36% in both CT and BLC) had FRT values larger than 0.1 at 0.7 m above ground in December, when stand leaf area is high.

A frequency distribution of sites similar to tropical forests (i.e., a log-normal distribution) was observed at 0.7 m in CT, whereas at 2 m a more normal-like distribution was found. Differences in frequency distribution of solar radiation reaching the forest understory between 0.7 and 2 m only observed in CT were caused by bamboo presence. *Chusquea ramosissima* was very abundant in CT (i.e., 23,400 culms per hectare) and formed dense strata 2–3-m in height. Transmitted solar radiation decreased during the summer in CT compared to BLC, because of bamboo and liana leaf expansion and growth.

Apart from increasing FRT reaching the understory, liana and bamboo cutting increased maximum temperatures both in gaps and under closed canopy. A diurnal range of temperature of 25 °C occurring in gaps in BLC, may favor the germination of pioneer species such as *Trema micrantha* and *Solanum granuloso-leprosum*, which are known for colonizing rapidly large gaps and harvested areas (Valio and Scarpa, 2001; Rodrigues et al., 2004).

Soil water availability was greater in gaps than under closed canopy likely because of evapotranspiration differences (Cavelier and Vargas, 2002). Liana and bamboo cutting did not change soil water availability in gaps but increased soil matric potentials (i.e., less negative values) under closed canopies. Differences could be attributed to decreased evapotranspiration as a result of liana cutting and not to site or specific differences because soil water availability was identical among sites after rainfall events. Thus, effects of liana cutting on water availability were likely greater than those

Table 3
Multivariate regression coefficients of models relating sapling density and richness in 4-m^2 plots with explanatory variables

Dependent variable	R^2 adj	p for whole regression model	Explanatory variable	Coefficient	p
Sapling density in 2003	0.22	0.0006	Tree basal area	0.391	0.038
			Chusquea density	−0.041	0.001
			Herb and shrub cover	−0.007	0.004
			FRT 0.70 m	−0.322	0.060
Sapling density in 2004	0.27	0.0008	Tree basal area	0.520	0.002
			Chusquea density	−0.042	0.010
			Herb and shrub cover	−0.009	0.004
			Fallen tree cover	−0.022	0.002
Sapling richness in 2003	0.27	0.0003	Tree basal area	1.845	0.001
			Chusquea density	−0.059	0.030
Sapling richness in 2004	0.29	0.0001	Tree density	0.050	0.066
			Chusquea density	−0.032	0.015
			Herb and shrub cover	−0.006	0.011
			Fallen tree cover	−0.019	0.001

Tree basal area (m^2), *Chusquea* density (number of rooted culms), herb and shrub cover (%), fraction of solar radiation transmitted (FRT), and fallen tree cover (%).

from bamboo cutting. Although performed as a whole treatment, the effects of cutting plants from both functional groups apparently had different impact on soil water dynamics in gaps and under closed canopies. In this forest, lianas are more abundant and occupy primary sites with higher tree density (Campanello et al., 2007b) while bamboo mostly colonizes gaps. Despite lianas comprise a small percentage of the total basal area of the forest, they have generally higher transpiration rates than trees (Restom, 1996), and their cutting may have had a localized effect on soil water availability under closed canopy where they are relatively abundant.

4.2. Tree regeneration

It has been proposed that bamboos and lianas are good competitors in gaps, preclude tree regeneration and slow down gap-phase regeneration processes (Oliveira-Filho et al., 1994; Schnitzer et al., 2000; Tabanez and Viana, 2000; Tabarelli and Mantovani, 2000; Silveira, 2001; Griscom and Ashton, 2003; Schnitzer et al., 2005). A possible explanation is that these functional groups reduce resource availability such as light and nutrients for trees (Tabarelli and Mantovani, 2000). Bamboo-dominated gaps may experience solar radiation conditions similar to forest understory. In the case of lianas, below-ground competition could be more important than above-ground competition, particularly in open forests with high light availability (Schnitzer et al., 2005). In the forest studied, bamboo and liana cutting increased solar radiation, soil water and also nutrient availability. Six months after the treatment was applied, the amount of available N increased from 11.8 ± 2 to 17.8 ± 2.7 μg of NO_3^- per g of soil in the upper 5 cm and from 9.14 ± 1.4 to 14.1 ± 3.3 μg of NO_3^- per g of soil between 5 and 15 cm depth (Arias and Austin, unpubl. data). An increment in the number of tree saplings between 1.5 and 3-m in height was observed in BLC, probably because of lower mortality or greater growth compared to CT. Indeed, enhanced growth was observed for saplings belonging to either light-demanding and shade-tolerant canopy species in BLC plots (Campanello, 2004).

Bamboo and liana cutting, however, seemed to improve slightly the germination and recruitment of canopy tree species. Four years after treatment we did not observe an increase in the abundance of saplings of canopy or fast-growing species which would contribute to reduce the size of gaps produced by selective logging. Regeneration of light-demanding tree species such as *Bastardiopsis densiflora*, *Cedrela fissilis*, *Cordia trichotoma*, *Patagonula americana*, and *Parapiptadenia rigida* were neither boosted by bamboo and liana cutting in gaps despite large increments in solar radiation and nutrients availability. Some of these light-demanding species, which may regenerate in gaps (López et al., 1987; Duz et al., 2004; dos Santos et al., 2006), constitute the group most affected by bamboos, explaining partially the low richness of pioneer trees reported for the Atlantic Forest in southeastern Brazil (Tabarelli and Mantovani, 1999), and also in the present study for the semideciduous Atlantic Forest in Argentina.

4.3. Determinants of tree regeneration

The greatest tree sapling and seedling abundance and richness were found at low FRT values, where tree basal area was high. Liana abundance was also high in these sites and appeared to be correlated with tree basal area (Campanello et al., 2007b). Bamboo negatively affected tree sapling and seedling richness and abundance in the semideciduous Atlantic Forest studied. Similarly, a study of tree pattern regeneration in an *Abies-Betula* forest in China founded that tree seedlings and saplings were scarce in bamboo-dominated stands (Taylor and Qin, 1988). Understory *Chusquea* bamboos have been observed to supress the establishment of trees also in *Nothofagus* temperate forests (Veblen, 1982, 1989) and in Costa Rican *Quercus* forests (Widmer, 1998). In some cases, tree regeneration can be improved by the death of bamboos after mass flowering in gaps (Taylor and Qin, 1992; Taylor et al., 1995; Abe et al., 2001; Martins et al., 2004; Holz and Veblen, 2006). The treatment applied in this study intended to simulate bamboo death after mass flowering, but *Chusquea ramosissima* flowering and death occurring in 2002–2004 in the Iguazú National Park (north of Misiones Province) did not improve tree regeneration (Campanello et al., 2005). *Chusquea ramosissima* leaves and stems have low decomposition rates (i.e., between 3.5 and 4.5 years for 95% of biomass decomposed). It is possible that dead biomass accumulated in a layer of more than 2 cm on the forest floor impeded seed germination or seedling establishment in flowered sites (L. Montti, personal observation) and also in BLC plots. Regeneration of pioneer and light demanding tree species such as *Solanum* spp., *Trema micrantha, Cecropia pachystachya*, *Bastardiopsis densiflora*, *Parapiptadenia rigida*, *Patagonula americana* and *Cordia trichotoma*, was observed in logging traffic lanes, where soil disturbance occurred and litter and live biomass was removed leaving the soil exposed. Some of these species form seed banks in the forest soil (Baider et al., 2001; Valio and Scarpa, 2001; Grombone-Guaratini and Rodrigues, 2002).

Gaps in BLC were invaded by shrubs and herbs including forest and non-forest species (e.g., *Urera baccifera*, *Acacia* sp., *Piper* spp., *Conyza bonariensis*, *Hybanthus bigibbosus*), ferns, graminoids and species in the Commelinaceae family. Shrubs and herbaceous plants cover was negatively correlated to sapling density in the present study indicating that tree regeneration may have been prevented after bamboo and liana cutting. Plants from these functional groups may also stalled succession in gaps, which is similar to effects on succesion observed in forests of Kibale National Park, Uganda, where logging gaps become dominated by herbs and shrubs which inhibit tree regeneration and delay canopy recovery (Chapman and Chapman, 1997; Paul et al., 2004). In the semideciduous Atlantic Forest mainly bamboos, but also herbs, shrubs and lianas, appear to slow-down tree regeneration, growth and survival.

5. Conclusions

Our initial hypothesis that bamboo and liana cutting will promote recruitment of pioneer and light-requiring canopy tree

species cannot be accepted, despite substantial increases in incoming solar radiation due to treatment. In the semideciduous Atlantic Forest studied, tree regeneration occurs mainly under tree canopy and appears to be prevented in gaps by bamboo and by shrubs and herbs after the cutting treatment was applied. In these forests, lianas are also supressed from large canopy gaps by bamboos and by the absence of suitable supports for climbing. Although tree regeneration was not enhanced after bamboo and liana cutting treatment after 4 years, field observations indicated that biomass left to decompose *in situ* after cutting impeded seed germination or seedling establishment and increased sapling mortality. These results have broad implications for timber production as long as sustained harvests over time depends on growth and reproduction by surviving adults, juveniles and seedling regeneration. Furthermore, some of the most valued timber species (i.e., *C. fissilis*, *P. rigida*, *C. trichotoma*) are light demanding and appear to be outcompeted by bamboos in gaps. Although these species were present in the forest canopy, they were not detected among saplings and seedlings in gaps, which support the need of post-logging management techniques for achieving sustainable timber production. Tropical and subtropical forests where bamboo are important components of the ecosystems, particularly in gaps, and where lianas are also conspicuous in the forest canopy, require novel approaches for management and increased timber harvesting.

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