Ecological consequences of a massive flowering event of bamboo (*Chusquea culeou*) in a temperate forest of Patagonia, Argentina

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Abstract

Question: What changes occur as a consequence of the massive flowering and senescence of the dominant understory species of bamboo, *Chusquea culeou* (E. Desvaux)? In this study, we documented some of the ecological consequences of this rare event that occurred in 2001, the previous flowering having occurred more than 60 years ago.

Location: *Nothofagus* temperate forest, Patagonia, Argentina.

Methods: We assessed changes in environmental variables and bamboo biomass post-flowering in an old-growth southern beech forest. In addition, we monitored the demography of emergent *Ch. culeou* seedling and *Nothofagus nervosa* saplings, comparing non-flowered (live understory) and flowered (senescent understory) patches within the forest matrix.

Results: Bamboo flowering dramatically increased light availability in the forest understory but, surprisingly, other environmental changes were not observed. Bamboo seedlings emerged in both patch types, and experienced gradual but modest mortality through time. Bamboo dieback promoted higher survivorship and an increment in biomass, height, number of leaves and buds in the saplings of *Nothofagus nervosa*.

Conclusion: The high density of bamboo seedlings 5 years after the flowering event and the independence of emergence from environmental variables suggest that understory regeneration is a gradual process that is not strongly regulated by initial seedling density or resource limitation. In contrast, microenvironmental conditions created after the flowering event significantly increased *Nothofagus* sapling growth and survival. These results suggest that overstory forest regeneration could be enhanced in this temperate forest in the first years after this infrequent bamboo flowering event.

Introduction

Understory vegetation has been recognized to exert a profound influence on the structure and dynamics of diverse forests around the world (Veblen 1982; Young 1991; Taylor et al. 2004), and in South America, bamboo grass species are one of the most conspicuous species dominating the forest understory (Clark 1989; Judziewics et al. 1999). Because of their rapid growth, large biomass, and high litter production (Veblen 1982; Christanty et al. 1996), it has been suggested that bamboos could play an important role in forest ecosystems, affecting competitive interactions, nutrient turnover, and forest regeneration (Taylor & Zisheng 1987).

A particular feature of most bamboo species is an unusual life cycle, which varies from 3 to 120 years (McClure 1993), ending with a single reproductive event that leads to massive flowering and seed production (McClure 1993; Keeley & Bond 1999). In general, these synchronized flowering episodes involve a large fraction of the population, although occasionally, patches of non-flowered clumps remain. Seed production during flowering events is copious; for example, González & Donoso (1999) estimated an input of 50 million seeds ha^{-1} during the flowering of *Chusquea quila* in a southern beech forest in Chile, and frequently there is an associated explosion of granivores (Jansen 1976; Gallardo & Mercado 1999; Jaksic & Lima 2003).

Bamboo flowering events have been recorded for centuries, especially in Asia (Gadgil & Prasad 1984; Taylor & Zisheng 1993), but in the Americas, records are scarce (Seifriz 1950; Filgueiras 1988). Due to long vegetative periods and unpredictable flowering episodes, little is known about the ecological impact of this phenomenon on forest dynamics, particularly in the first years post-flowering. The extensive germination and seedling establishment after flowering events suggests that regulation by density-dependent effects could be important factors controlling the final population size and distribution of bamboo in the understory (Makita 1996).

In North and South America, *Chusquea* is one of the most diverse genera of woody bamboos, extending from Mexico to the Patagonian forests of Argentina and Chile (Clark 1989; Judziewics et al. 1999). In many of these temperate forests, *Chusquea* is the dominant vegetation growing below a *Nothofagus* spp. overstory (Veblen 1982). In particular, *Chusquea culeou* has the most widespread distribution, ranging between 35°S and 47°S (Parodi 1941; Veblen et al. 1996). The dense aggregation of culms in the understory can reach 2 to 6 m in height in a matter of months (Veblen et al. 1980; Pearson et al. 1994). Veblen (1982) observed the influence of *Chusquea tenuiflora* on tree sapling establishment in Chilean forests, with increased tree recruitment in areas without a bamboo understory. Similarly, studies in temperate forests of Asia associated tree sapling density and growth with the presence of understory bamboo (Nakashizuka 1988; Taylor & Zisheng 1992; Narukawa & Yamamoto 2002). Finally, recent studies after flowering events in temperate Chilean forests have shown high sapling density of overstory species in flowered areas (González et al. 2002; Holz & Veblen 2006).

Like many other bamboos, *Ch. culeou* exhibits gregarious and synchronous reproduction, an event that occurred most recently in 2001 in the northwestern Patagonian region of Argentina. Historic records from Pearson et al. (1994) for temperate forests in northwest Patagonia indicate that the last flowering events of *Ch. culeou* occurred in 1900 and 1938. As the last flowering occurred more than 60 years ago, there is little information on the ecological consequences in these temperate forests. In this study, we examined changes in a native old-growth *Nothofagus* forest after the recent *Ch. culeou* massive flowering. Specifically, we tested predictions that, as a result of bamboo flowering, microenvironmental conditions would be substantially altered, with increases in light availability, and air and soil

temperatures in the forest understory. In addition, we hypothesized that soil water availability would increase due to decreased evapotranspiration by the understory bamboo. Finally, we tested predictions that these environmental changes would alter forest conditions, increasing bamboo seedling and overstory sapling survival and growth in areas of bamboo flowering and dieback.

Methods

Study site

In 1998, the Forest Service of the Lanín National Park in the Neuquén Province of Argentina (41°10S, 71°21W) observed some isolated flowered patches of *Ch. culeou* in the south-central portion of the park (Sanguinetti & García 2001). During spring and summer of 2000-2001, the flowering event of *Ch. culeou* extended over more than 200 000 ha of temperate *Nothofagus* forests of Patagonia, principally between 39°-40°S (Kitzberger et al. 2007; Raffaele et al. 2007). The massive flowering and subsequent dieback took place in both humid and dry zones, in high and lowland sites, and involved non-disturbed areas as well as those affected by grazing and recurrent fires (Sanguinetti & García 2001).

Field sampling was conducted from January 2003 to March 2006, at several points during spring, summer, and fall. The study site is an undisturbed forest in the Yuco Station of Lanín National Park, near San Martín de los Andes (800 m a.s.l). This temperate forest site includes two deciduous tree species, *Nothofagus obliqua* and *N. nervosa*, and one evergreen species, *N. dombeyi* (Veblen et al. 1996; Marchelli & Gallo 1999). The site has nearly equivalent proportions of the three *Nothofagus* spp, as represented by basal area (Vivanco & Austin 2008), and *Ch. culeou* almost completely dominates the understory, except for rare shrub (*Aristotelia chilensis* and *Azara microphylla*) and herbaceous species (*Osmorrhiza chilensis* and *Alstroemeria aurea*) (Dezzotti et al. 2003). Annual precipitation is 2300 mm, and mean temperature ranges between 3°C during winter and 15°C in summer (Estación Meteorológica Estancia Quechuquina, Neuquén Province, Argentina). Soils are Andisols, derived from volcanic ash, with a high content of silt, clay, and organic matter (Dezzotti et al. 2003).

Experimental design

In order to evaluate the magnitude of the flowering event at a local scale, we randomly established

21 transects of 50 m within the site. In each transect, we counted the total number of bamboo culms touching the tape, and identified them as non-flowered (live) and flowered (senescent). Considering these categories, we estimated the overall percentage of non-flowered and flowered bamboo within the study site.

More specifically, we also compared bamboo biomass and demography of bamboo seedlings, environmental variables, and survival and growth of saplings of an overstory species, *Nothofagus nervosa* in patches with and without bamboo flowering and dieback. Remnant live bamboo patches (live understory) were used as control microsites, representing forest conditions before the flowering, and were dispersed throughout the study site. Flowered (senescent understory) patches consisted of areas where *Ch. culeou* flowered and died in 2001 and contained all standing dead material. We established eight plots of 25 m^2 in each understory condition (live and senescent understory), with similar overstory conditions (% canopy cover and species composition) and homogeneous bamboo cover. None of the plots were located in gaps or open areas and, as the three *Nothofagus* spp. are interspersed throughout the site, there was no species-specific bias associated with the plots. The plot size (25 m^2) was determined by the minimum size of the remnant live understory patches, to maintain a uniform plot size across replicates and treatments.

Assessment of aboveground biomass after the flowering and dieback of bamboo

We estimated changes in bamboo biomass in live understory and senescent understory patches once a year, in February, from 2003 to 2006. As an alternative to destructive biomass harvests in the principal plots, we used bamboo basal cover as an estimate of aboveground biomass using the line-intercept method (Canfield 1941), and developed a calibration relationship between basal cover and aboveground biomass. In 12 secondary adjacent plots of 1.5 m^2 (*n* = 6 of each patch type), we measured bamboo basal cover using the line-intercept method (Canfield 1941) and harvested all aboveground biomass and weighed it. Oven-dry mass of subsamples (< 20%) was used to determine total dry biomass. A linear regression between basal cover and biomass was used to estimate biomass in the study plots, considering the basal cover measured during the time period 2003 to 2006 (live bamboo $r^2 = 0.89$, $P < 0.001$, senescent bamboo: $r^2 = 0.90$, $P < 0.001$)

Environmental variation as a consequence of bamboo flowering

We measured light, air and soil temperature, relative air humidity, and soil water content in live and senescent bamboo patches. Three dataloggers per patch type were installed to register light intensity, air temperature, and relative air humidity (mod. HOBO® TEMP, RH, LI, EXT. (C) 1996). Each logger was positioned 40 cm above the forest floor and programmed for hourly measurements. In addition, photosynthetically active radiation (PAR) was recorded four times a day (10:00, 12:00, 14:00, and 16:00 h) during three consecutives days in January 2005 using a line quantum sensor (LiCor, LI-191SA Lincoln, NE, USA). In this 3-day period, climatic conditions were very similar; there were clear skies without precipitation. Soil temperature was measured four times a day in January and March of 2005 with soil digital thermometers buried to a depth of 10 cm. Water content was estimated by gravimetric methods. One soil core (0–10 cm) per patch was taken using a PVC tube. After collection, samples were stored in plastic bags to avoid water loss. Once in the laboratory, a subsample of humid soil was weighed and dried in an oven at 105°C for 48 h. We measured soil water content on 15 sampling dates, from January 2003 to March 2005. Considering a soil bulk density of 0.5 g cm^{-3} (L. Vivanco, pers. comm), we estimated volumetric water content.

Monitoring bamboo seedling dynamics

We monitored bamboo seedling dynamics in five subplots of 0.5 m × 0.5 m nested in the principal plots of 25 m^2. Each seedling was counted and marked with a toothpick of different color corresponding to a different sampling date. We recorded seedling emergence and survivorship on five dates from February 2003 (initial seedling density) to March 2005 (final seedling density). Mortality was calculated for each sampling date as $1 - (N_t/N_{(t-1)})$ with N_t = seedling density at the sampling date and N_{t-1} = seedling density at the previous sampling date.

The effect of bamboo dieback on overstory tree saplings

We carried out an extensive search for *Nothofagus* saplings in the forest, but no emergent seedlings or young *Nothofagus* saplings were found at the beginning of the study (February 2003). As a

result of the lack of natural emerged saplings, we planted 20 2-year-old saplings of the overstory *N. nervosa* in each plot of live and senesced bamboo. All saplings had a similar initial height (17 ± 3 cm) at the moment of planting. Saplings were monitored at regular intervals from October 2003 to March 2005. We recorded survivorship and growth variables including height, number of leaves and buds of each sapling located in each patch type. Sapling height and number of leaves and buds were measured only during the spring and summer season, when leaves were present. At the end of the second growing season, we harvested four saplings per plot and estimated biomass, by drying (75°C for 48 h) and weighing aboveground biomass.

Statistical analysis

As most measurements were conducted on the same experimental unit (patch, tree sapling, bamboo seedling) over time, we used a modified repeated measures analysis when appropriate (Littell et al. 1996). We compared bamboo biomass, volumetric water content, density of *Ch. culeou* seedlings, and *Nothofagus* sapling growth between live understory and senescent understory plots across sampling dates in the 2-year period. Bamboo biomass was square-root transformed and bamboo seedling density was log-transformed to reduce heterogeneity of variance. Comparisons of *N. nervosa* sapling growth between patch types (live understory and senescent understory) were performed using only spring-summer measurements, when leaves on the saplings were intact. When the assumption of homogeneity of variance among treatments could not be met, we

used a non-parametrical Mann-Whitney *U*-test. This was the case for light intensity, relative humidity, air temperature, PAR, and bamboo seedling mortality for each sampling date when measurements were taken. *N. nervosa* seedling survivorship among live understory and senescent understory patches was tested using a modified repeated measures analysis for data with a Poisson distribution (Littell et al. 1996). We compared *Nothofagus* sapling biomass between patch types at the end of the experimental period using a one-way ANOVA and the average biomass of the four seedlings in each plot. All analyses were completed using SAS version 6.12 (SAS Institute, Cary, NC, USA).

Results

Changes in aboveground bamboo biomass due to bamboo dieback

Within the study site, the massive bamboo flowering event and subsequent dieback included nearly the entire bamboo population, resulting in 96.5% mortality of *Ch. culeou* culms, with the remnant live culms clustered in isolated clumps of < 200 m^2. In the patches where flowering occurred (senescent understory patches), biomass of standing dead material significantly decreased through time (Fig. 1). Notably, changes in aboveground biomass occurred gradually, with the first 2 years showing small changes, and only in the third year were significant reductions observed in senesced aboveground biomass. In contrast, bamboo biomass in the live understory plots significantly increased through time (Fig. 1). The simultaneous reduction
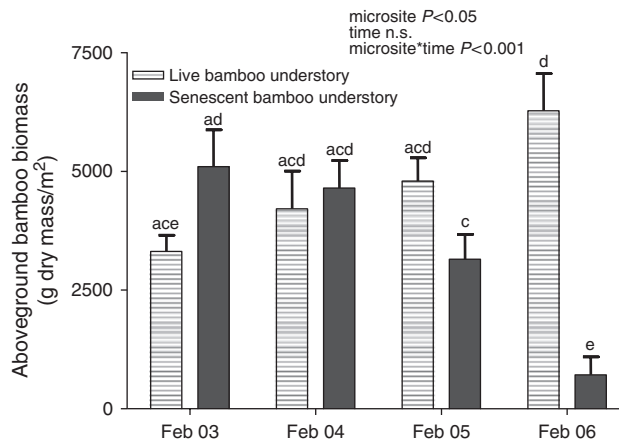

Fig. 1. Aboveground biomass of bamboo in live and senescent bamboo understory. Bars show mean values and standard errors ($n = 8$) for each patch type from February 2003 to February 2006. Different letters indicate significant differences from post-hoc comparisons ($P < 0.05$).

and increase in biomass resulted in a significant interaction between patch type and time ($P<0.001$, *df* 14). As such, aboveground biomass nearly doubled in the live understory plots (from 3.3 to 6.3 kg dry matter m^{-2}, $P<0.01$, *df* 14) and was reduced almost 90% in the senescent understory patches at the end of the study period (from 5.1 kg to 0.71 kg dry matter/m^2, $P<0.001$, *df* 14), such that during the 4-year period, reduction in aboveground biomass resulted in an input of 4.4 kg m^{-2} of bamboo senescent material to the forest floor.

Impact of bamboo dieback on environmental factors: changes in understory conditions

Bamboo dieback significantly increased light levels in the understory and light availability varied with season. The largest differences between patch types and the highest absolute values were found in spring-summer (Fig. 2). PAR was significantly higher in senescent patches, with 15% (SD ± 7%) of full sunlight in senescent understory patches compared with 2% (SD ± 1%) in live understory patches ($P<0.05$, $N=4$). In contrast, there was little difference observed in other environmental variables: air temperature was marginally higher in senescent understory patches (spring–summer average = 12.3 versus 12.8°C in live and senescent understory patches, respectively [$P<0.1$, $N=3$]) but no differences were found for others seasons. Soil temperature, relative air humidity, and volumetric soil water content were not significantly different between live understory and senescent understory plots at any sampling date.

Understory dynamics: demography of bamboo seedlings

A substantial cohort of bamboo seedlings was observed on the first sampling date (Table 1), but simultaneous recruitment of other understory species was not observed. On the subsequent sampling dates (2004-2005), we observed some new seedlings of *Ch. culeou*, but seedling emergence was very low in both patch types (Table 1). Additionally, the recruitment of bamboo seedlings was spatially highly variable, and did not differ between patch types at any sampling date ($P=0.21$, *df* 15).

Over time, bamboo seedling density diminished gradually but significantly ($P<0.001$, *df* 99), and significantly higher seedling mortality was observed in live understory patches in early autumn of both years (Table 1). Seedling mortality did not appear to be associated negatively with bamboo seedling density; the best fitting model for seedling survival and initial seedling densities was a positive linear relationship (proportion survival = 0.00012×initial density, $r^2=0.56$, $P<0.0001$), demonstrating higher survival in plots with higher initial densities.

Tree sapling survival and growth after bamboo dieback

All *N. nervosa* saplings survived at least 3 months after the initial planting in both live and senescent understory plots. Over the study period, patch type significantly affected growth and mortality of *N. nervosa* saplings. Saplings located in senescent understory patches were significantly taller and had more leaves and buds than the saplings growing in the live understory plots (Fig. 3).
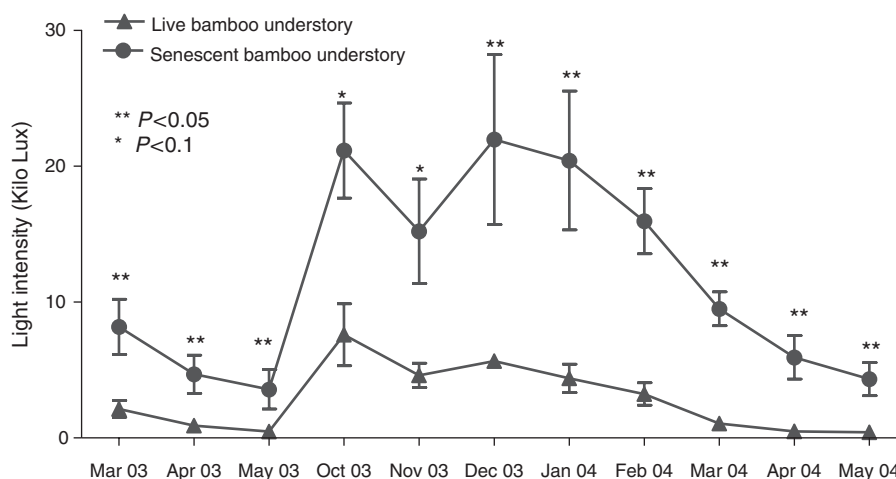

Fig. 2. Light intensity in patches with live and senescent bamboo understory. Mean values ($n=3$) with standard errors for different months in the period March 2003-May 2004. Asterisks indicate level of statistical significance at each time point.

Table 1. Average bamboo seedling density and mortality in live understory and senescent understory patches from February 2003 to March 2005. Mortality was calculated considering the total number of seedlings at any time point (previously emerged + newly emerged seedlings) in each period. Different letters represent significant differences in mortality ($P < 0.05$, Mann-Whitney Test) between patch types for that sampling date.

Cohort/Date	Feb-03	May-03	Oct-03	Jan-04	Jun-04	Oct-04	Nov-04	Jan-05	Mar-05
Live understory (seedlings/m^2)									
Feb-03	76	48	38	34	29	27	26	26	22
May-03		4	2	2	1	1	1	1	1
Oct-03			1	1	0	0	0	0	0
Jan-04				1	0	0	0	0	0
Mortality (%)		0.38[b]	0.25	0.08	0.20	0.06	0.14	0.14	0.31[b]
Senescent understory (seedlings/m^2)									
Feb-03	117	94	83	78	69	59	57	57	54
May-03		4	4	3	2	2	2	2	2
Oct-03			2	1	0	0	0	0	0
Jan-04				1	1	1	1	1	1
Mortality (%)		0.19[a]	0.12	0.10	0.22	0.10	0.03	0.03	0.06[a]

Harvests of selected individuals of *N. nervosa* individuals in the two patch types demonstrated significantly higher total biomass in saplings from senescent patches (1.5 g/sapling $\pm$ 0.5) when compared to live understory patches (1.1 g/sapling $\pm$ 0.4, $P < 0.05$, *df* 14). At the end of the study period in 2005, *N. nervosa* sapling mortality was significantly different among patch types ($P < 0.05$, *df* 14), with 34% mortality on average in live understory plots and < 14% in senescent understory patches.

Discussion

Consequences of bamboo dieback on aboveground biomass

The massive dieback of the understory *Ch. culeou* resulted in an input of organic matter over a 4-year period of 4.4 kg m^{-2}, nearly doubling average litter production of the overstory, estimated at 0.5-0.6 g m^{-2} annually (Vivanco & Austin 2008). The input of senescent material was not immediate, and increased significantly only after the third year post-flowering. These results suggest that there may be some lags in the ecological consequences of this infrequent massive event, depending on the ecosystem process under study. It appears that the impacts on biogeochemical cycling may be seen in the medium to long term as this senescent material is gradually incorporated into the soil organic matter pools.

Aboveground bamboo biomass significantly increased in live understory bamboo patches. Vegetative culms in live understory patches may have benefited from increased light availability and other resources liberated due to the flowering event. Although live understory plots demonstrated considerable growth over the 3-year study period, it is not clear why these patches did not flower with the rest of the bamboo population. More studies are needed to clarify the role of these remnant green patches and how they might interact with the dynamics of bamboo seedling establishment.

Changes in understory conditions after bamboo dieback

Senescent bamboo patches had a light intensity at the soil surface that was intermediate between a full gap and a closed understory in this ecosystem. These values coincide with the radiation data observed in semi-gap areas of a *Nothofagus* mixed forest in southern Patagonia (Peyrou 2002), although closed bamboo (live) sites in this study had 50% less light than in our live sites. Our results contrasted with Abe et al. (2001), who found that after the massive death of the bamboo *Sasa* spp. in Japan, changes in light conditions occurred only when the synchronous bamboo death coincided with a forest gap.

While light availability increased in senescent understory patches, changes were not observed in air or soil temperature, or soil water content, contrary to our predictions. Bamboo senescent patches were large in size compared with remnant live understory patches (average size 30-200 m^2), which were immersed in a senescent bamboo matrix. It is possible that the influence of these large flowered patches on microenvironmental variables reduced differences between senescent and live understory patches. The persistent cover of standing dead material and the possible increased water uptake by overstory trees appear to have minimized differences between senescent and live plots, and in spite of a dramatic change in aboveground live biomass,
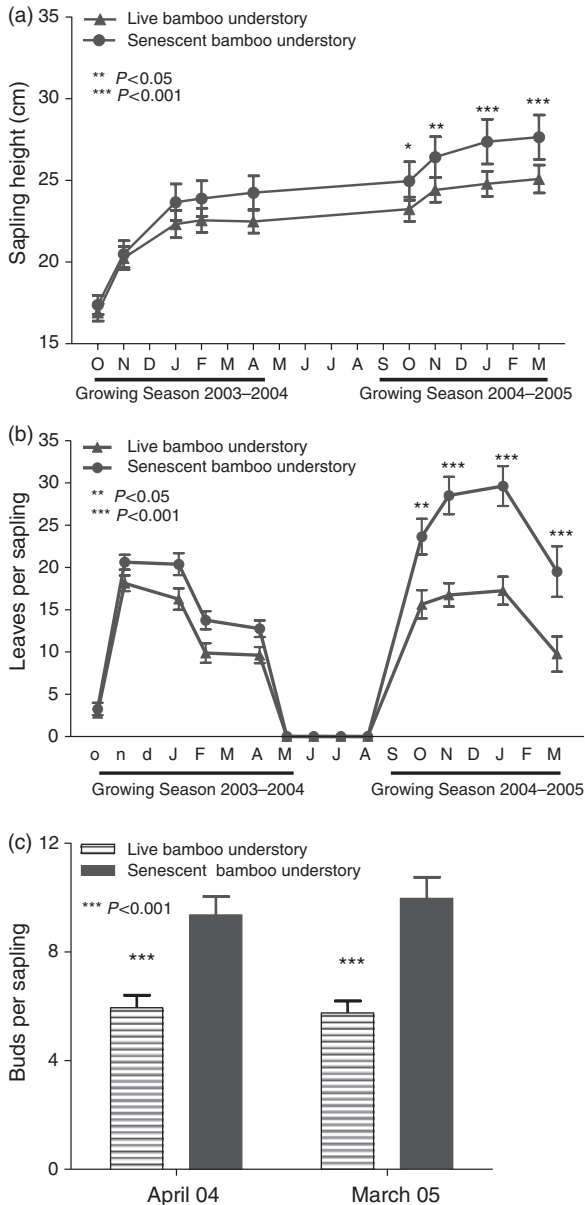
Fig. 3. Sapling height (**a**), number of leaves (**b**) and buds (**c**) of *N. nervosa* saplings in patches with live and senescent bamboo understory. Mean values ($n = 8$) and standard errors for two consecutive growing seasons, measurements taken in spring and summer seasons. Asterisks indicate level of statistical significance at each time point.

the net effect on the water balance of this event seems to have been minimal, at least in the first years after the massive bamboo dieback.

Bamboo seedling dynamics after dieback

Establishment of bamboo seedlings occurred in sites with and without bamboo dieback in equal and highly variable density. In addition, changes in light availability between live and senescent patches did not translate into differences in bamboo seedling mortality except in the early fall, where mortality was significantly higher in remnant live understory patches with lower light availability. Our results contrast with other studies of bamboo regeneration after flowering events, which demonstrated highest recruitment of bamboo seedlings in shaded areas (Taylor & Zisheng 1993; Taylor et al. 2004). In addition, the low emergence rate of bamboo seedlings in the second year of the study (3 years post-flowering) suggests that seed germination only occurred in a limited window of time, and supports the idea that most bamboo species do not form persistent seed banks (Judziewics et al. 1999). Taken together, it appears that mortality of bamboo seedlings in the first years after emergence may be controlled by multiple environmental variables, which can vary with level of disturbance and season.

Results from this study suggest that mortality due to high initial density and resource limitation did not appear to play a dominant role affecting the initial population size of bamboo seedlings. Nevertheless, final densities of adult bamboo individuals of *Chusquea* spp. have been estimated as one clump in an area of 1-2 m^2 (Veblen 1982), which contrasts with observed seedling densities at the end of 3 years of nearly 40 seedlings/m^2 on average. It appears that once germinated, bamboo seedlings demonstrate relatively high resistance to environmental and biological limitation in the first years of growth. At later stages, negative density dependence, resource limitation, or herbivory (Raffaele et al. 2007) could play a more dominant role in affecting the survival and growth and determining final population sizes.

Tree sapling growth and survival after bamboo dieback

In contrast to the effects on bamboo seedling dynamics, *N. nervosa* seedlings demonstrated significantly higher survival and growth in patches where bamboo flowered and died. The three dominant *Nothofagus* species in this forest respond most favorably to intermediate light conditions rather than direct full sunlight (Müller-Using & Schelegel 1981; Read & Hill 1985; Weinberger & Ramírez 2001), suggesting that the light environment at levels similar to those observed in the senescent understory patches may be most advantageous for sapling growth. Enhanced sapling growth has been observed in other southern temperate forests: for *N. obliqua* during the massive flowering of *Chusquea*

quila in Chile in 1991 (González et al. 2002); and after *Ch. montana* die-off in Chile in 2001 (Holz & Veblen 2006). In addition, significantly higher mortality occurred in the live understory patches, suggesting that light or other limitations adversely affected the survival of saplings. These results suggest that environmental changes due to bamboo flowering affect overstory species survival and growth, and have important consequences in the early stages of forest regeneration.

Conclusions

For nearly six decades in this southern temperate forest, *Ch. culeou* dominated the understory and persisted vegetatively. After the massive bamboo flowering and dieback in 2001, the forest understory was significantly modified through (a) the establishment of a large cohort of bamboo seedlings, (b) the input of large quantities of senescent material, and (c) a dramatic increase in understory light availability. Changes in light availability in particular appear to have important significant benefits for the growth and persistence of the overstory species, including *Nothofagus nervosa*. It is important to consider that this study represents observations in a relatively short time frame (3 years post-flowering), and that future changes could have further consequences for both bamboo recruitment and overstory species. Considering that their return to the pre-flowering vegetative state could take more than 15 years (Pearson et al. 1994; Makita 1996), we strongly encourage the establishment of long-term studies that may help to clarify the role of these extraordinary and infrequent events in forest ecosystems around the world.

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