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Tree regeneration responses to *Chusquea montana* bamboo die-off in a subalpine *Nothofagus* forest in the southern Andes

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Abstract

Question: The aim of the present study is to examine how a rare flowering and massive die-off event of a dominant understorey bamboo affected tree regeneration processes in a subalpine *Nothofagus* forest. In particular, we assess the effects of the die-off event on tree seedling demography (establishment and survival) and on the height growth of previously established juveniles, and we determine how these effects vary in relation to stand age and canopy conditions.

Location: Carirriñe Pass and Choshuenco Volcano at 1200 m a.s.l. in a mixed subalpine temperate forest in northern Patagonia (40°S, 71°W), spanning the Chilean and Argentinian border.

Methods: Regeneration processes in *Nothofagus pumilio* and *N. dombeyi* were examined under different canopy conditions (closed or gap), in both young and old stands, and in patches of flowered and non-flowered *Chusquea* bamboo during the first three growing seasons following the simultaneous flowering and die-off of *Chusquea montana* f. *montana* in November–December 2001. We installed permanent plots under all forest conditions and measured seedling and sapling height growth and new seedling establishment following the bamboo die-off. To assess potential variation in tree seed sources, seed fall was collected and seed viability was measured. To assess for potential variation in the understorey light conditions and infer its influence on tree regeneration, hemispherical photographs of the canopy were taken at each plot.

Results: Bamboo die-off triggered accelerated growth in height of *Nothofagus* seedlings and saplings in gaps in old stands. Bamboo die-off did not result in new tree seedling establishment; however, die-off did increase the survival of newly established seedlings.

Conclusion: The predominant response of *Nothofagus* spp. to the bamboo die-off event was the accelerated height growth of previously established juveniles (i.e. a re-organization response). Successful recruitment into the canopy of these relatively shade-intolerant tree species appears to be dependent on previously existing canopy gaps. It is likely that the release in height of previously established juveniles of *Nothofagus* after the bamboo die-off will eventually result in development of even-sized and relatively even-aged, patches of canopy trees.

Keywords: *Chusquea* bamboos; Regeneration dynamics; *Nothofagus pumilio*; *Nothofagus dombeyi*; Northern Patagonia.

Nomenclature: Muñoz (1966); Matthei (1997).

Introduction

In many forests, abundant and/or large understorey plants may have a controlling influence on tree regeneration processes by either inhibiting successful tree seedling establishment and survival, or by impeding the growth of tree juveniles and their recruitment into the main canopy (Mitchell et al. 1997; Nilsen et al. 2001; Mallik 1995; Denslow et al. 1991). Bamboos, because of their rapid growth rates to large sizes and high culm (stem) densities, often impede tree regeneration as shown by numerous studies in forests in tropical and temperate latitudes (Widmer 1997; Tabarelli et al. 2000; Narukawa & Yamamoto 2002; Abe et al. 2002; Nakashizuka & Numata 1982; Gratzer et al. 1999; Taylor et al. 1995). The peculiar life-cycle of many bamboo species in which populations remain in a vegetative state for decades and then flower and die gregariously, raises the obvious question: In some forests does tree regeneration depend on a window of opportunity created by a synchronous die-off event that reduces understorey competition and releases resources? The massive flowering and die-off of a *Chusquea* bamboo species in subalpine *Nothofagus* forests in the southern Andes (ca. 40 °S) provided a rare opportunity to examine the consequences of bamboo flowering on tree regeneration processes.

The flowering, seeding, and subsequent death of large populations of bamboo can extend over thousands of hectares, and may occur at intervals of up to many decades depending on the species (Gadgil & Prasad 1984; Nelson 1994; Makita 1995; Franklin 2004). Given the rarity of flowering events of bamboo species, there is little understanding of the effect of synchronous bamboo flowering and die-off on tree regeneration dynamics (but see Nakashizuka 1988; Taylor et al. 1988b, 2004; González et al. 2002). In a mesic forest with a potentially closed canopy, changes in understorey conditions and the transient pulse of resources associated with a massive bamboo flowering and die-off are likely to result in tree regeneration responses that can be classified as either *re-organization* or *new establishment* patterns (Marks 1974; Canham & Marks 1985). The *re-organization response*

includes accelerated growth or 'releases' of plants already established at the time of the tree-fall, as well as asexual sprouting from damaged tissues after tree-falls. The *new establishment response* refers to the new recruitment of individuals from propagules either newly dispersed to the site or from dormant seeds buried in the soil. This conceptual framework was used in the current study to pose specific questions about the nature of tree regeneration responses to a massive bamboo die-off.

In south-central Chile (ca. 38 - 43 °S) several species of *Chusquea* bamboos dominate forest understories from sea level to alpine tree line at ca. 1200 m, and have been shown to impede the regeneration of many tree species, in particular that of the relatively shade-intolerant *Nothofagus* spp. Below ca. 700 m, the climbing bamboo *C. quila* reaches culm lengths of up to 20 m, dominates natural tree-fall gaps, and proliferates where forests have been disturbed by logging or burning (Veblen 1982; Donoso 1993). At mid-elevations (ca. 500 to 1000 m), forest understories are typically dominated by *C. culeou*, which proliferates where either natural or anthropogenic disturbance creates canopy openings in the forests that typically are a mixture of a few relatively shade-intolerant *Nothofagus* spp. and abundant shade-tolerant tree species. On the Argentine side of the Andes where forest canopies typically are less dense and are formed primarily by *Nothofagus* spp., this species is particularly dominant. The understories of the subalpine forests (ca. 950 - 1200 m) of the Andes over a broad north-south extent (at least from 37 to 43 °S) are dominated by *Chusquea montana* f. *montana* (syn. *Chusquea tenuiflora*, see Matthei 1997). It attains densities of 100 000 culms/ha, forming a relatively continuous understory cover at a height of ca. 1 - 2 m, which inhibits the regeneration of the dominant *Nothofagus pumilio*, *N. dombeyi*, and *N. betuloides* of these forests (Veblen 1982; Veblen et al. 1981).

In the subalpine forests of south-central Chile and adjacent areas in Argentina, the regeneration of the dominant *Nothofagus* spp. (*N. pumilio*, *N. dombeyi* and *N. betuloides*) depends either on coarse-scale disturbances such as snow avalanches, mass movements or severe fire, or on large or small tree-falls (Veblen et al. 1981, 1996). Severe coarse-scale disturbances that remove the understory create opportunities for new establishment of the relatively shade-intolerant *Nothofagus* spp. Tree-falls, which leave the bamboo understory intact, favour tree regeneration by creating raised sites (logs, tree butts) for seedling establishment and altering microclimatic conditions in ways that favour the growth of *Nothofagus* juveniles relative to bamboo growth (Veblen et al. 1981). Although the inhibitory effects of *C. montana* on tree regeneration have been widely documented (Veblen 1979, 1982; Veblen et al. 1981), this is

the first study to document a widespread, massive flowering and die-off of this species and to examine its consequences for tree regeneration.

The overall aim of this study is to determine the effects of a massive flowering and die-off of *C. montana* on the regeneration processes of *Nothofagus* spp. Our specific objectives are to describe: (1) height growth and survival of tree juveniles that established prior to bamboo die-off (i.e. a re-organization response), and (2) establishment of tree seedlings following the bamboo die-off. For both these objectives we compare the two dominant tree species (*N. pumilio* and *N. dombeyi*) and consider the potential influences associated with stand age and canopy conditions.

Study area

In September-October 2001, a large flowering event of *Chusquea montana* occurred near Carirriñe Pass (40 °S, 71 °W) at 1200 m in a mixed forest of *Nothofagus pumilio* and *N. dombeyi*, spanning the Chilean and Argentinian border. By January 2002, the culms were dead; most seeds were already on the ground, but some were still attached to the bamboo spikes on standing culms. We were not able to establish a control (non-flowered) site in the Carirriñe area because we could not locate non-flowered populations within a radius of several km of the site. The nearest non-flowered population occurring under similar environmental conditions where access was feasible was at 1200 m on the slopes of Choshuenco Volcano, ca. 25 km to the Southwest. Both sample sites are similar in floristic composition, forest structure, and abiotic site factors. The disjunct location of the second site disqualifies it as a true replicate in an experimental sense (Hurlbert 1984), and the limitations associated with this pseudo-replication are considered in our interpretations. Hereafter, Carirriñe and Choshuenco will be referred as the dead- and live-bamboo sites, respectively.

At both the dead- and live-bamboo sites, glaciated surfaces covered by extensive, recent andesitic volcanic deposits have produced undulating but gentle slopes (i.e. 5-25 %). The southern Andes have a coastal maritime climate influenced by mid-latitude westerlies (Miller 1976). Annual precipitation generally exceeds 3000 mm (Anon. 1966), and above 1000 m forest understories are typically under a snow cover from May through November. Mixed stands of evergreen *N. dombeyi* and deciduous *N. pumilio* form a narrow altitudinal belt between ca. 900 and 1200 m, and *N. pumilio* forms pure stands at higher elevations.

The understory of these forests is dominated by abundant densely distributed clumps of *C. montana* that reach heights of ca. 1 to 2 m. The longevity and flowering intervals of *C. montana* are unknown (Veblen 1982;

Matthei 1997). There is only one flowered herbarium specimen that explicitly documents its gregarious flowering habit and that is from ca. 43 °S: Schlegel N° 7651, CONC; cited by Matthei 1997). However, there is no documentation or local or scientific awareness of a previous massive flowering event of this species extending over a large (> a few km²) area anywhere in the southern Andes (Veblen 1982; Donoso 1993). Given that extensive field research has been conducted in these forests for several decades, this implies that massive flowering events in *C. montana* occur at long intervals of probably at least several decades.

Methods

Field methods

In February of 2002, and for the two following growing seasons, we measured height growth of already established juveniles and frequency of new tree seedling establishment. Ten 15 m × 15 m permanent plots were located at both the dead- and live-bamboo sites under primarily mixed stands co-dominated by *Nothofagus pumilio* and *N. dombeyi*. At each site, half of the plots were in young stands and half in old stands. In the old stands, three plots were in gaps and two beneath closed-canopy. In every plot, ten 2-m² seedling quadrats were systematically distributed on a regular grid.

Stand characteristics

To assess potential variation in tree seed sources at each site, wooden seed boxes (0.25 m width × 0.5 m length × 0.2 m height) were placed in half of the plots at both sites. Seed fall was collected at the end of the growing seasons of 2001/2002 and 2002/2003.

Age and size data on trees were obtained to determine whether our initial subjective classification of young and old stands was accurate. At each site, species and DBH were recorded in the plot, and if necessary outside the plot, for a minimum of thirty trees (≥ 5 cm in DBH and ≥ 2 m tall). To age trees, increment core samples were extracted as close to the soil as possible from every third tree systematically encountered while walking straight lines through the plot. Twelve tree seedlings (< 2 m tall) per species (i.e. *N. pumilio* and *N. dombeyi*) were harvested at each site by cutting at the root-shoot boundary to estimate the time for trees to grow to the coring height.

Understorey light conditions (i.e. gap fraction; Anderson 1964) were inferred from hemispherical photographs (Anderson 1964) of the canopy. From the centre of each 15 m × 15 m plot, the photographs were

taken during the growing season of 2002/2003 using a fisheye lens from a height of 1.80 m, eliminating the influence of the bamboo understorey on light conditions.

Monitoring of tree juveniles that had established prior to the bamboo die-off

Tree saplings (< 5 cm in DBH and ≥ 2 m tall) within each 15 m × 15 m plot and tree seedlings (< 5 cm in DBH and < 2 m tall) within each 2-m² quadrat were labeled, identified, and their heights were recorded in three successive years. Tree saplings were classified into three height classes: 1: 2 - 4 m; 2: 4 - 6 m; 3: 6 - 8m; the saplings and seedlings were measured vertically, i.e. perpendicular to the ground.

Monitoring of post-die-off populations

In the 2-m² quadrats, new tree seedlings were identified, labeled and their heights recorded throughout the study period. Newly emerged tree seedlings were sometimes labeled as 'unknown *Nothofagus*' due to their immaturity for identification at the species level. These individuals were properly identified in the following field season, except for the last field season.

Data processing and statistical analysis

Stand characteristics

Number of seeds.m⁻².a⁻¹ and seed viability (%) by species were measured; seed viability (%) was obtained by cutting the seeds (Daniel et al. 1982). Differences in seed fall and seed viability (%) between live- and dead-bamboo sites were tested using Dunn's procedure for non-parametric multiple comparisons (Zar 1999).

In order to estimate tree ages, cores were mounted and sanded following standard procedures (Stokes & Smiley 1968; McBride 1983). For incomplete tree cores (i.e. cores with a missing pith), the number of missing rings was estimated using a geometric model (Duncan 1989). If the estimated number of rings was > 20, the minimum age was used instead. Cores that included less than 75% of the geometric radius of the tree were rejected.

The 12 tree seedlings that were harvested to estimate the number of rings missed due to coring height, were sectioned in discs, sanded, and aged every ten cm from the root collar up to 150 cm above ground. For these sectioned seedlings, age/height regressions were computed and used to estimate the number of years that the coring procedure missed at a given height. In stands where the *R*² was below 0.75, the median age at a given coring height was chosen to adjust tree ages. At both sites, and for each stand structure age (young and old stands), tree species were combined together, and the frequency

distributions of tree ages and sizes were obtained (Fig. 1). In old stands, 42% of the sampled trees were *N. pumilio* and 58% *N. dombeyi* at the dead-bamboo site, while 74% of the trees were *N. pumilio* and 26% *N. dombeyi* at the live-bamboo site. In young stands, 97% of the sampled trees were *N. pumilio* and 3% *N. dombeyi* at the dead-bamboo site, while 96% of the trees were *N. pumilio* and 4% *N. dombeyi* at the live-bamboo site.

The percentage of the understorey light conditions was obtained by subtracting the area blocked by the canopy from the maximum total sunlight (i.e. 100%), which was assumed to be the open clear sky (Anderson 1964). The understorey light condition was assumed to be roughly similar to the percentage of visible sky beneath the canopy, or gap fraction (Anderson 1964). At both sites, the percentage of understorey light conditions was obtained for each plot. Differences in the understorey light conditions (medians) were tested between different stand ages and canopy conditions using Mann-Whitney test.

Juvenile tree population responses to bamboo die-offs

For tree juveniles that had established prior to the bamboo die-off, for each growing season, differences in mean seedling heights and frequencies in height class of saplings were tested between the two sites by species for each stand age and canopy condition using non-parametric Mann-Whitney and *G*-tests (Zar 1999). The Wilcoxon test was also used to test differences in seedling height within each site throughout the study period. New establishment responses of post-die-off populations

For newly established tree seedlings, non-parametric Mann-Whitney and Wilcoxon tests were used to test differences in density between the sites by species for each stand age and canopy condition.

Results

Stand characteristics – Light conditions and seed fall and seed viability

The gap fraction was slightly higher at the live-bamboo site than at the dead-bamboo site, especially beneath closed-canopy (Table 1).

Differences in the seed fall of the two *Nothofagus* spp. were found between the two seasons that seed fall was measured. During the first growing season similar quantities of seeds were found at both sites, but during the second growing season the amount of seeds collected at the dead-bamboo site was fivefold greater than that at the live-bamboo site (Table 2). Whereas in young stands the majority of seeds were produced by *N. pumilio*, in old stands the majority of seeds were produced by *N. dombeyi* (Table 2).

Seed viability was found to be relatively low (< 5%; Table 2). In old stands seed viability was highest at the live-bamboo site, while in young stands seed viability was highest at the dead-bamboo site (Table 2).

Height growth of tree juveniles that established prior to bamboo die-off

In gaps in old mixed stands, seedlings of *N. dombeyi* were slightly shorter at the dead-bamboo site than those at the live-bamboo site in 2001/2002 (Table 3). However, after two growing seasons (2003/2004), the seedlings at the dead-bamboo site were significantly taller compared to those at the live-bamboo site ($p < 0.05$, Mann-Whitney test; Table 3). Beneath closed canopy in young stands, seedlings of *N. pumilio* were found exclusively at the live-bamboo site, where these seedlings did not increase significantly in height (Table 3; Wilcoxon test).

In gaps in old stands, saplings of *N. pumilio* were slightly taller at the live-bamboo site than at the dead-bamboo site in 2001/2002 (Table 4). However, after two growing seasons (2003/2004), saplings of this species were significantly taller at the dead-bamboo site than at the live-bamboo site ($p < 0.001$, *G*-test; Table 4). Beneath closed canopy in young stands, saplings of *N. pumilio* were exclusively found at the dead-bamboo site

Table 1. Light conditions* (%) for all canopy and stand age conditions in mixed *Nothofagus pumilio*-*N. dombeyi* forests at both bamboo sites in 2002/2003. For each characteristic, values are medians (range). Differences are test between stand ages and sites. Medians in the same row followed by the same superscript are not statistically different ($p < 0.05$; Mann Whitney test).

Stand age/Canopy condition	Old/Gap	Live-bamboo		Dead-bamboo		
		Old/Canopy	Young/Canopy	Old/Gap	Old/Canopy	Young/ Canopy
Total site factor	40.42 ^a (29-52)	47.08 ^a (23-50)	29.52 ^b (22-46)	34.01 ^a (25-49)	23.31 ^a (18-28)	23.47 ^b (21-30)

* Light conditions are defined as Gap fraction (Anderson 1964); see Methods section.

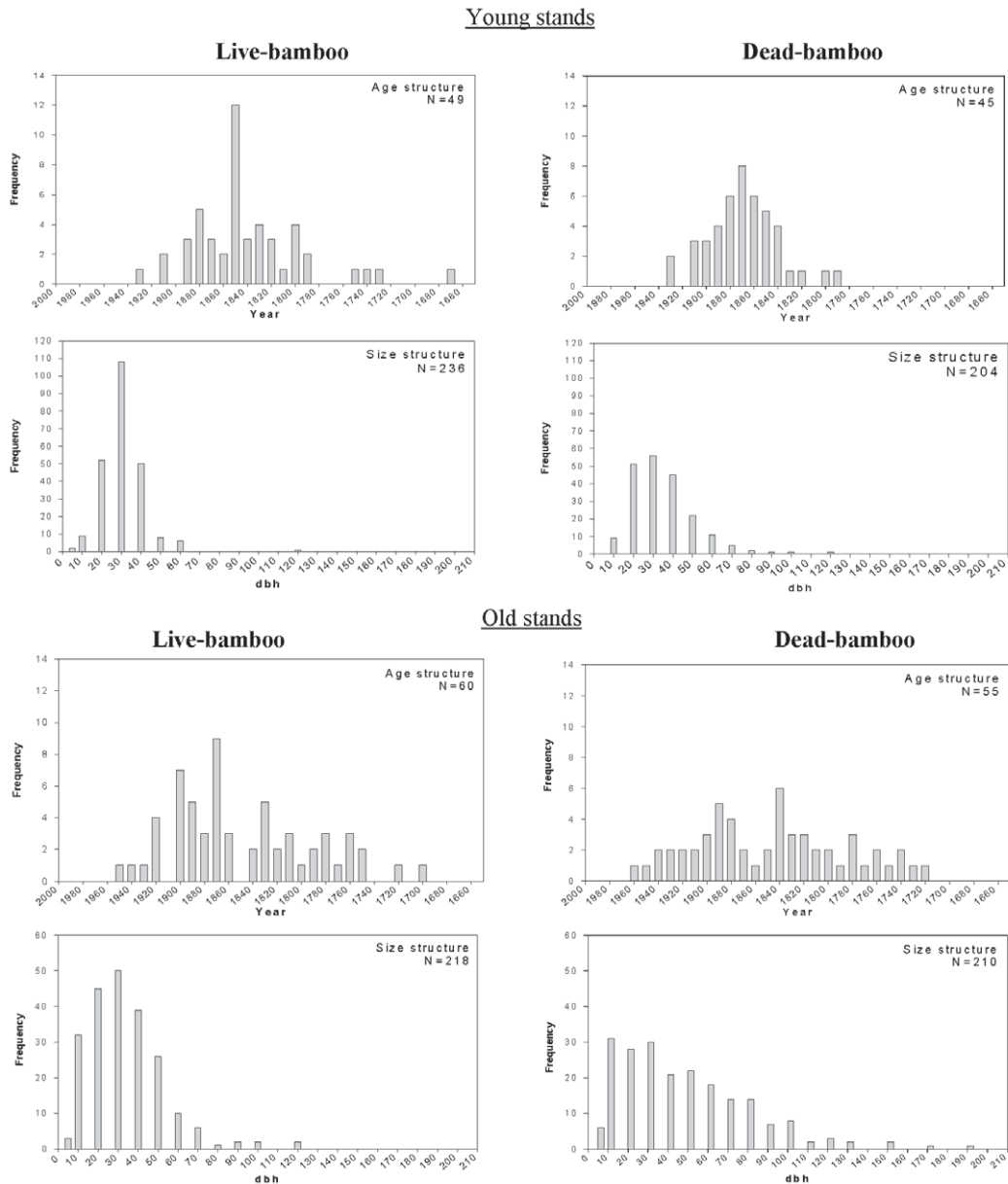


Fig. 1. Frequency distributions of tree ages and sizes of both *Nothofagus* spp. at both bamboo sites in young and old stands. N indicates the sample size, and DBH indicates the diameter at breast height. The years missed by the coring procedure at a given height were estimated and added using the median age of the harvested seedlings at that height. Saplings were included.

in 2001/2002 (Table 4). After two growing seasons (2003/2004), saplings of this species were significantly taller than during the 2001/2002 growing season ($p < 0.001$, G -test; Table 4). A similar trend occurred with saplings of *N. dombeyi*, but this result is not presented here due to the small sample size (see Holz 2004).

Establishment of tree seedlings following bamboo die-off

In general, in old mixed stands, new seedling establishment of both *N. pumilio* and *N. dombeyi* increased in density from the first to the second year of measurements beneath closed canopy and gaps at both bamboo sites (Table 5). No new tree established during the year of the bamboo die-off. An increase in the number of seedlings of both species was observed in 2002/2003, especially at the live-bamboo site. In the second growing season after the bamboo die-off, however, the

Table 2. Tree seed fall (/ha), and seed viability (%) of *Nothofagus pumilio* (Np) and *N. dombeyi* (Nd) for all canopy and stand age conditions in mixed *N. pumilio*-*N. dombeyi* forests at both bamboo sites. Values are medians (range). For each species, differences are test among years and sites. Medians in the same row followed by the same superscript are not statistically different ($p < 0.05$; Dunn test).

Stand age/ Canopy condition	Year	Live-bamboo						Dead-bamboo					
		Old/Gap		Old/Canopy		Young/Canopy		Old/Gap		Old/Canopy		Young/Canopy	
		Np	Nd	Np	Nd	Np	Nd	Np	Nd	Np	Nd	Np	Nd
Seed fall (No/ha), in thousands	2001/ 02	0 (0)	3200 (2480-5360)	0 (0)	6920 (5600-8240)	200 (80-400)	0 (0-80)	80 (0-160)	2200 (560-6720)	0 (0)	4240 (2080-6400)	480 (160-2800)	0 (0)
	2002 /03	0 (0)	6000 (5680-6320)	0 (0)	3840 (3840-400)	680 (400-960)	0 (0)	400 (0-800)	12840 (11920-13760)	0 (0)	18080 (18080)	6320 (4220-8400)	0 (0)
Seed viability (%)	2001/ 02	0 (0)	0 (0-8)	0 (0)	5 (0-10)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	2002/ 03	0 (0)	5 (0-10)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.02 (0-2)	0 (0)	0 (0)	4.35 (0-9)	0 (0)

density of newly established seedlings of *N. pumilio* was significantly higher at the live-bamboo site than at the dead-bamboo site, particularly in old stands ($p < 0.01$, Mann-Whitney test; Table 5). In contrast, the density of newly established seedlings of *N. dombeyi* was significantly higher at the dead-bamboo site than at the live-bamboo site, especially in old stands ($p < 0.001$, Mann-Whitney test; Table 5). In addition, establishments of the ‘unknown *Nothofagus*’ occurred exclusively in old stands in gaps at the dead-bamboo site.

In young stands, newly established seedlings of *N. pumilio* showed similar patterns at both bamboo sites (Table 5). There was almost no new establishment of seedlings during the growing season of the year of the bamboo die-off event. A peak occurred during the subsequent growing season, with fairly low density of

establishments during the second growing season after the die-off (Table 5). There was no new establishment of seedlings of *N. dombeyi* in young stands during the study period at either of the bamboo sites (Table 5). New establishments of the ‘unknown *Nothofagus*’ occurred during the second growing season after the bamboo die-off at both sites.

Seedling survival

Almost no new seedlings established during the year of the bamboo die-off. Therefore, the new seedling survival was only comparable in 2003/2004 for the seedlings established in 2002/2003 (Table 6). Aside from the new seedlings of *N. dombeyi* in gaps in old stands, all newly established seedlings beneath any canopy and forest condition increased their survival at the dead-bamboo site (Table 6), although the *N. dombeyi* result is not presented here, due to its small sample size (see Holz 2004).

Table 3. Height (cm) of seedlings of *Nothofagus pumilio* (Np) and seedlings of *N. dombeyi* (Nd) for all canopy and stand age conditions in mixed *N. pumilio*-*N. dombeyi* forests at both bamboo sites. Beneath closed canopy in young stands, seedlings of *N. pumilio* were found at the live-bamboo site, exclusively. For each characteristic, values are medians, (range) and [sample size]. Differences in seedling height were tested among years and sites. Medians in the same row followed by the same superscript are not statistically different ($p < 0.05$; Mann Whitney test). Results presented here include only forest conditions that have seven or more seedlings at the end of the study period.

Stand age/ canopy condition	Live-bamboo		Dead-bamboo
	Young/Closed (Np)	Old/Gap (Nd)	Old/Gap (Nd)
2001/2002	12.5 ^a (2-80) [42]	31 ^b (3-160) [50]	22 ^b (3-110) [16]
2002/2003	20 ^a (3.5-61) [37]	32 ^b (4-160) [42]	38 ^b (6-132) [13]
2003/2004	21 ^a (3-52) [27]	35.5 ^b (4.5-157) [34]	76 ^c (30-170) [7]

Table 4. Frequency per height size class of saplings of *Nothofagus pumilio* for all canopy and stand age conditions in mixed *N. pumilio*-*N. dombeyi* forests at both bamboo sites. Saplings in closed canopy in young stands were found exclusively at the dead-bamboo site. The size classes are 1 = 2 - 4 m; 2 = 4 - 6 m; 3 = 6 - 8 m. Frequencies between groups of three columns followed by the same superscript are not statistically different ($p < 0.001$, *G*-test). Frequencies in the same row, as well as within the last group of three columns followed by the same superscript are not statistically different ($p < 0.001$, *G*-test).

Stand age/ canopy condition	Live-bamboo						Dead-bamboo		
	Old/Gap			Old/Gap			Young/Closed		
Size class	1	2	3	1	2	3	1	2	3
Year									
2001/2002	13 ^a	8 ^a	0 ^a	13 ^a	2 ^a	0 ^a	14 ^a	5 ^a	0 ^a
2002/2003	14 ^a	7 ^a	0 ^a	10 ^a	4 ^a	0 ^a	8 ^a	9 ^a	0 ^a
2003/2004	13 ^a	3 ^a	2 ^a	0 ^b	2 ^b	6 ^b	1 ^b	4 ^b	6 ^b

Table 5. Density (ha^{-1}) (mean \pm SE) of new establishments of seedlings of *Nothofagus pumilio* (Np), *Nothofagus dombeyi* (Nd), and ‘unknown *Nothofagus*’ (uN) for all canopy and stand age conditions in mixed *N. pumilio*-*N. dombeyi* forests at both bamboo sites. For each species, averages between sites are tested for the same species under similar canopy and stand conditions; columns followed by the same superscript are not statistically different ($p < 0.01$; Mann Whitney test). No new establishments were found during the year 2001/2002.

Year	Live-bamboo							Dead-bamboo						
	Old/Gap		uN	Old/Canopy		Young/Canopy		Old/Gap		Old/Canopy		Young/Canopy		uN
	Np	Nd		Np	Nd	Np	uN	Np	Nd	uN	Np	Nd	Np	
2002/2003	6333 ^a ± 2065	250 ^a ± 142	0 ^a ± 0	9375 ^a ± 3248	875 ^a ± 875	4050 ^a ± 699	0 ^a ± 0	5750 ^a ± 2139	83 ^a ± 83	0 ^a ± 0	125 ^a ± 125	375 ^a ± 211	2250 ^a ± 1041	0 ^a ± 0
2003/2004	22833 ^a ± 4420	0 ^a ± 0	0 ^a ± 0	17250 ^a ± 5664	0 ^a ± 0	400 ^b ± 353	6750 ^b ± 2764	0 ^c ± 0	333 ^b ± 162	3333 ^b ± 918	125 ^{bc} ± 125	375 ^b ± 276	150 ^b ± 86	26450 ^c ± 3476

Discussion

The re-organization response

Seedlings of *N. dombeyi* and saplings of *N. pumilio* released significantly more in height at the dead-bamboo site than at the live-bamboo site, especially after the second growing season after the die-off (2003/2004; Tables 3 and 4). These patterns in height growth can in part be explained by the differences in shade-tolerance between both the tree and the bamboo species, as well as by pre-die-off differences in the light conditions between both bamboo sites (Table 1).

The tendency of *N. dombeyi* seedlings to experience height growth releases was greater in canopy gaps than in closed canopies. This is consistent with the faster growth of this species under slightly less than full sunlight in shading experiments (Müller-Using & Schlegel 1981). In the lowlands of southern Chile, advanced tree regeneration of shade-tolerant species released in height after *Chusquea quila* die-off, especially those originated from root suckers (González et al. 2002).

Regardless of the canopy conditions, a release in height-growth of *N. pumilio* seedlings was also expected; this did not occur. Previous studies have shown

Table 6. Survival (%) of the newly established seedlings of *Nothofagus pumilio* (Np) in 2003/2004 in all canopy and stand age conditions in mixed *N. pumilio*-*N. dombeyi* forests at both bamboo sites. For each characteristic, values are medians (range). Only the medians with \geq seven seedlings per forest and canopy conditions are shown. Medians in the same row followed by the same superscript are not statistically different ($p < 0.05$; Mann Whitney test).

Stand age/ Canopy condition	Live-bamboo		Dead-bamboo	
	Old/ Gap	Young/ Canopy	Old/ Gap	Young/ Canopy
Survival (%)	0 ^a (0)	0 ^b (0-100)	0 ^b (0-100)	50 ^c (0 - 100)

that beneath trees of the deciduous *N. pumilio*, the depth of snow is greater, its persistence is longer, and the sunlight conditions that reach the understory during the summer are lower when compared to conditions beneath evergreen *N. dombeyi* (Veblen et al. 1977, 1979). Consequently, beneath deciduous *N. pumilio* trees, clumps of *C. montana* have shorter growing seasons for development, resulting in slightly shorter and more sparsely distributed clumps than those beneath evergreen *N. dombeyi* (Veblen et al. 1981). Hence, the lack of response in growth of *N. pumilio* seedlings may be an issue of timing; seedlings of this species may simply release more slowly in the years following the die-off than those of *N. dombeyi*, or the small sample size underrepresented the pattern of *N. pumilio*. Additionally, growth differences during the first years of seedling development seem to persist over time for *Nothofagus* spp. (Smulders 1988; Donoso et al. 1991a, b, 1993).

Even though during the year of the die-off the number of saplings of *N. pumilio* in gaps in old stands was higher at the live-bamboo site, saplings of *N. pumilio* rapidly increased their heights at the dead-bamboo site in comparison to the live-bamboo site, particularly during the two growing seasons following the bamboo die-off (Table 4). During the 2002/2003 field season, we noticed that at the live-bamboo site, some saplings of both *Nothofagus* spp. were crushed by tree branches and fallen trees damaged during the 2002 austral winter. Therefore, the percentage of individuals in the shorter height class slightly increased in the year after the die-off (Table 4). The difference in slope aspect and its influence on the microclimatic conditions of each sample site may explain this last finding. In general, both bamboo sites should be equally affected by the regional climate; both are on the same slope of the Andes, they lie at the roughly same elevation, and are close in proximity to each other. However, the forest in the live-bamboo site faces the predominant *westerlies* winds

(i.e. directly exposed to wind and snow storms), whereas the forest at the dead-bamboo site faces south and north and is slightly less exposed to the westerlies.

Beyond the shade-intolerance of both species and the micro-environmental conditions that may explain these height growth differences, an additional factor could be the fact that we defined saplings as those seedlings taller than 2 m, which is roughly similar to the average height of *C. montana* bamboo. Therefore, saplings of the less shade intolerant *N. pumilio* might not have been suddenly over-exposed to high solar radiation or thermal oscillations after the bamboo die-off, as was likely the case for this species' seedlings.

The new establishment response: Tree seedlings that established following bamboo die-off

New establishment of *Nothofagus* seedlings were not related to the bamboo conditions, given that similar general densities and trends throughout the study period were found at both the live- and dead-bamboo sites (Table 5). In the lowlands of southern Chile, new establishment of tree species occurred in the first and second (1995-1996) growing season after the flowering and die-off of *C. quila* (González et al. 2002). Even though the relation between new establishments and seed availability of *N. dombeyi* was only slightly stronger than that of *N. pumilio* (Tables 2 and 5), these results suggest that new seedling establishments depended more on variations in other aspects, such as seed fall and seed viability, rather than bamboo conditions (Tables 2 and 5).

High seed crops of *N. pumilio* normally occur every six to eight years (Mascareño 1987; Schmidt et al. 2003), which is conducive to episodic seedling establishments (Cuevas 2002) with no or few seedling establishments in between the mast seeding years (Martínez-Pastur et al. 1999). In contrast, other studies have shown main seed productions of *N. dombeyi* at intervals of two to three years (Burschel et al. 1976).

In general, seed fall is highly variable in *Nothofagus* spp. (Mascareño 1987; Schmidt et al. 2003; Heinemann et al. 2000) and positively correlated with seed viability (Donoso 1993). This high variability does not allow for the development of a persistent seed bank (Veblen et al. 1996). Our data suggest that the timing and forest conditions of the highest seed viability only partially coincided with those of the highest seed fall production (Table 2).

Even though the bamboo die-off did not result in differences in new establishment of seedlings, the die-off did increment the survival of new seedlings (Table 6). In general, the survival of new establishments of both *Nothofagus* spp. increased under the dead-bamboo (Table 6; see also Holz 2004). It is likely that the change in the micro-environmental conditions due to the with-

ering of the bamboo may have favoured new seedling development. Furthermore, decomposition of bamboo litter could favour seedling establishment in the near future (i.e. before the bamboo closes the understorey again) of both shade-intolerant species by allowing them to more easily reach the mineral soil.

The flowering and die-off of *C. montana* can be interpreted as allowing the coexistence of the relatively shade-intolerant tree species with the bamboo which is a superior competitor. Coarse-scale disturbances such as mass movements and fire in creating regeneration opportunities for *Nothofagus* spp. which otherwise may regenerate poorly in competition with bamboos and/or shade-tolerant tree species has long been recognized (Veblen & Ashton 1978; Veblen 1982). To the extent that bamboo die-off is considered a coarse-scale disturbance, the findings of the present study are consistent with that non-equilibrium interpretation of species coexistence.

Vegetation responses to a bamboo die-off is an ongoing process, rather than a discrete event. This is a significant limitation to the interpretation of the patterns documented in our three-year study. A further limitation is the lack of availability of non-flowered bamboo populations spatially intermingled with the flowered population. Thus, variables in addition to flowering behaviour may have differed between the sites of flowered and non-flowered bamboo populations. For example, some of the results may have been related to differences in the forest physiognomy between sites, rather than to the bamboo die-off itself.

We conclude that the seedlings and saplings of both *Nothofagus* spp. that were growing in canopy gaps and rapidly responded to the release of resources caused by the bamboo die-off may recruit into the main forest canopy as a new relatively even-aged cohort. In contrast, seedlings and saplings of both *Nothofagus* spp. that responded to the die-off in closed forest canopy may be suppressed in the future due to the lack of gaps in the main canopy. The accelerated recruitment of *Nothofagus* regeneration into the main forest canopy in gaps could lead to a patchy distribution of an even-aged cohort that is likely to persist into the future forest structure, affecting the dynamics of these subalpine forests.

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