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EARLY DEVELOPMENT OF *Nothofagus* (NOTHOFAGACEAE) SPECIES FROM THE SUBANTARCTIC FOREST UNDER EXPERIMENTAL CONDITIONS OF LIGHT, SUBSTRATE AND ECOLOGICAL INTERACTION

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HIGHLIGHTS

In *Nothofagus*, positive correlation between seed weight and emergence in laboratory and nursery tests would be linked to the higher nutrient content of heavier seeds.

High emergence and survival of *N. obliqua* and *N. alpina*, and higher growth of three *Nothofagus* species with high irradiation, would be adaptations to colonize open areas.

The experimental results are compatible with patterns and processes found in this *Nothofagus* mixed forests, in which the interaction with *Chusquea culeou* plays a key role.

In *Nothofagus*, deep mineral soil with large moisture increased emergence and survival, whereas litter reduced emergence; germination of *C. culeou* was very abundant and increased tree mortality.

ABSTRACT

The entry of trees into a community is an irregular process often constrained by species interactions and regeneration niche. We experimentally examined the effect of light intensity (high, medium and low), substrate type (mineral and cover with litter) and presence of *Chusquea culeou* (Poaceae), on the performance of regeneration of *Nothofagus dombeyi*, *N. obliqua* and *N. alpina* (Nothofagaceae). These species constitute the natural forest within the lake Lácar watershed (40° 08' W, 71° 30' S). Populations of *C. culeou*, an abundant understorey component that restrict tree regeneration, experimented in 2001 a gregarious flowering and subsequent mortality comprising 200,000 ha and the development of an abundant seedlings cohort. During tests, *Nothofagus* species exhibited a very low germination (< 2.2%) positively correlated with seed weight. Plant emergence and size was larger and mortality smaller under high irradiation, probably as an adaptation to colonize open areas. Reduced germination of seeds on organic substrate was ascribed to the role of litter as a physical barrier. *Nothofagus* exhibited 76% of increased mortality under the presence of *C. culeou*, whose germination was very abundant (93% in laboratory) and occurred preferably with high irradiance and litter. However, *C. culeou* also showed a good response with lower light levels. After senescence, *C. culeou* would form an abundant and fast-growing cohort that probably limits *Nothofagus* ability to establish, given increased mortality and litter accumulation. These results contribute to a better understanding of succession, which is crucial for implementing a sound management of this valuable ecosystem.

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INTRODUCTION

Major determinants controlling the structure and dynamics of forest ecosystems are physical, related to conditions and resources, spatial heterogeneity and disturbance and stress, and biological, related to pool and performance of species (Gurevitch et al., 2006; Keddy, 2017). Colonization is a key performance process that basically comprises seed production and dispersal, determining the spread of propagules, and post-dispersal recruitment, governing the survival and growth of immature plants (Martin and Canham, 2010; Treveset et al., 2013). Recruitment can be also limited by the specificity of the regeneration niche, that explains the coexistence of tree species that otherwise could not co-occur indefinitely due to competition (Grubb, 1977; Martin and Canham, 2010). Understanding the physical and ecological mechanisms of tree regeneration is crucial to designing sustainable strategies at management unit level (Coates and Burton, 1997; Raison et al., 2001).

Patterns and processes of forest stands in which the frequency of large-scale exogenous disturbances is greater than the lifetime of a cohort, are regulated by small-scale endogenous perturbations that create gaps of reduced size (Canham and Marks, 1985; Platt and Strong, 1989). Within these small openings the inhibition of regeneration of light-demanding, pioneer species, prevails due to a high cover of understory plants or a large amounts of litter (Coates and Burton, 1997; Veblen et al., 1996). The amount of resources of the seed also plays a central role in stand dynamics. Seed weight tend to be correlated with the temperament of species; usually, heavier seeds have a greater reserve of nutrients, a lower anemophilic dispersal and are adapted to shady habitats, while lighter ones disperse at a greater distance and develop in canopy clearings (Seiwa and Kikuzawa, 1991; Moles and Westoby, 2006). Seedlings originating from heavy seeds tend to exhibit a rapid and vigorous growth that allows overcoming this stage more successfully (Rees, 1996).

In Argentina, along the eastern foothills of the Cordillera de los Andes (39° 29' - 40° 22' S) up to 1,000 m a.s.l., with annual precipitation from 1,000 to 2,000 mm and on deep well drained volcanic soils, mixed forests occur. Here, stands are dominated by the evergreen *Nothofagus dombeyi* ((Mirb.) Oerst., coihue), and the deciduous *Nothofagus obliqua* ((Mirb.) Oerst., roble pellín) and *Nothofagus alpina* ((Poepp. & Endl.) Oerst., raulí) (Nothofagaceae), and occupy 50.240 ha (CIEFAP-MAyDS, 2016). These trees re-colonize open sites and develop even-aged populations following the

occurrence of large-scale, natural or anthropogenic disturbances. In the absence of such events, small-scale perturbations produce environmental heterogeneity that promotes a shifting forest mosaic (Veblen et al., 1996).

Nothofagus species are dicline monoecious with wind-dispersed seeds, and exhibit masting and a transitory soil-seed bank (Figueroa et al., 2004; Donoso et al., 2014; Dezzotti et al., 2016). During a three-year period (2001-2003), mean seed production was 4,900 seeds·m⁻², from which 86% belonged to *N. dombeyi*, 11% to *N. obliqua* and 3% to *N. alpina* (Dezzotti et al., 2016). All tree species showed an analogous masting pattern, with 3%, 46% and 51% of production corresponding to the first, second and third period, respectively (Dezzotti et al., 2016). Although seedlings are gap-dependant, they are highly sensitive to desiccation and freezing, and therefore silviculture is mainly practiced through shelterwood methods (Chauchard et al., 2008). *Nothofagus dombeyi* is the most light-demanding whereas *N. alpina* is the most shade-tolerant species. Niche differentiation related to light tend to manifests early, and it would explain the variability in stand composition and structure of this vegetation type (Müller-Using and Schlegel, 1981; Weinberger and Ramirez, 2001; Donoso et al., 2013).

In this mixed forest, *Chusquea culeou* (E. Desv., Poaceae, caña colihue) is the most abundant native component in the understory and clearings of different size and origin (Veblen et al., 1996). This bamboo forms a continuous and thick cover of litter and aerial biomass, generating a physical barrier and low levels of light, that inhibits rooting and growth of *Nothofagus* seedlings (Burschel et al., 1976; Giordano et al., 2009; Marchesini et al., 2009). *Chusquea culeou* shows a vegetative phase of between 14 and 50 yr, after which it flowers and dies in a gregarious and synchronous mode (Lusk, 2001; Jaksic and Lima, 2003). In the study area, the most recent massive flowering occurred in 2001 and comprised 200,000 ha, the subsequent 97% of culm mortality, a seed production of 4,400 seeds·m⁻² and the formation of an abundant seedlings cohort (Marchesini et al., 2009; Dezzotti et al., 2016). This process dramatically changed in a short period, light, temperature, soil organic matter, nutrient cycling and granivorous demography (Jaksic and Lima, 2003; Sage et al., 2007; Austin and Marchesini, 2012).

We searched for experimental evidence about the effect of light, substrate, seed weight and ecological interaction with *C. culeou*, on germination and growth of *N. dombeyi*, *N. obliqua* and *N. alpina*. Given the relatively low shade tolerance and high susceptibility to extreme seasonal temperatures of young and succulent plants, the challenge related to forest management based in natural regeneration,

is to determine the role of these factors for optimum species performance. Though there are experiments on early performance of *Nothofagus* under both controlled and natural environments (Müller-Using and Schlegel, 1981; Weinberger and Ramírez, 2001; Dezzotti, 2008; Donoso et al., 2013), those also including *C. culeou* are scarce given the intermittent availability of seeds.

The study comprised five tests that included the analysis of I: germination of *Nothofagus* species and *C. culeou* (laboratory), II: performance of *Nothofagus* seeds and seedlings related to species, light and substrate, III: growth of *Nothofagus* saplings related to species and light, IV: performance of *C. culeou* related to light and substrate, and V: performance of *Nothofagus* seedlings related to species, light and presence of *C. culeou* (nursery). Additionally, we investigated the role of tree seed weight on regeneration dynamics. We hypothesized that in this mixed forests, there are intraspecific similarities and differences in emergence, growth and survival of young phases of *Nothofagus* trees, which are mainly related to intrinsic (seed weight), abiotic (light intensity, substrate type) and biotic factors (presence of *C. culeou*). The interaction of these components would contribute to explain significant patterns and processes occurring in these *Nothofagus* stands.

MATERIAL AND METHODS

Study area

Seeds were collected in the sampling sites Quilanolahue, Yuco Alto Oriental, Yuco Alto Occidental and Pucará (Lanín National Park) (Figure 1). Here, climate is humid temperate with two pronounced precipitation gradients, a W - E caused by the rain-shadow of the Cordillera de los Andes, and a seasonal determined by

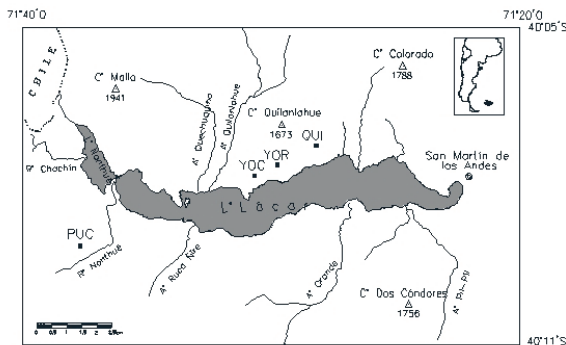


FIGURE 1 Location of the sampling sites Quilanolahue (QUI), Yuco Alto Oriental (YOR), Yuco Alto Occidental (YOC) and Pucará (PUC), the weather station Quechuquina and the city of San Martín de los Andes within the lake Lácar watershed from Argentina.

annual displacements of the Pacific pressure centre (Peel et al., 2007). In western sectors, precipitation is abundant and distributed regularly throughout the year, while in those more eastern it is drastically reduced and concentrated during cold months. In the weather station Quechuquina (730 m a.s.l.), mean temperature and total rainfall were 9.3 °C and 1,889 mm-yr⁻¹, respectively (Figure 1).

Phytogeographically, this temperate mixed forest is part of the Subantarctic Forest ecoregion. Here, forest is well preserved from recent, intense and large-scale anthropogenic disturbances. Stands were even-aged and at different stages of development. Young stands exhibited high density and low tree diameters (stem exclusion stage), whereas mature stands presented lower density and large tree size (understorey reinitiation and old-growth stages) (Dezzotti et al., 2016). These population structures are compatible with the early successional temperament of *Nothofagus* species, and with the regime of natural perturbation of varying intensity and scale, which promotes the existence of mosaic forests (Veblen et al., 1996).

General methodology

Seeds of *N. dombeyi* (Nd), *N. obliqua* (No), *N. alpina* (Na) and *C. culeou* (Cc) were collected during 2001, through 10 circular traps with a catching area of 0.058 m², placed randomly at 1.4 m height in each sampling sites (Figure 1). Seeds were stored in airtight bags refrigerated at 4 °C for 120 d, then layered with moist sand at 4 °C for 21 d and subsequently washed with running water for 12 d. This treatment imitated the promoting effect on plant emergence that cold and high precipitation would have under natural conditions (Muñoz, 1993; Escobar and Donoso, 1996). At sampling sites, substrate for the different tests was collected digging the ground (shovel): on the one hand, litter composed of leaves and small branches, and on the other hand, superficial (2-cm deep) and deep (8-cm) mineral soil; this material was sieved to remove *Nothofagus* and *C. culeou* seeds.

For the different tests, light corresponded to the photosynthetically active radiation (PAR) measured instantaneously with the LI-250 digital radiometer and the quantum sensor LI-190SA (LI-COR, Inc.). Measurements were carried out on a clear summer day during the morning (at 9), noon (at 12) and afternoon (at 18). Relative high light intensity (LH) corresponded to that of open sky (PAR₀), whereas relative intermediate (LI) and low light intensity (LL) corresponded to that below two plastic meshes with different pore size (PARs), initially placed at 0.5 m height and covering completely the experimental unit. Three light measurements per treatment and time

of the day were made (27 measurements in total). PAR in the morning was estimated to be $20.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (SE = 1.1), at noon $1,820.0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (SE = 114.5) and in the afternoon $122.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (SE = 15.9). LI was approximately 60% and LL 10%; these values were estimated according to [1]:

$$L = (PAR_s / PAR_o) \cdot 100 \quad [1]$$

In nursery, four tests were carried out to evaluate performance of *Nothofagus* and Cc in relation to light intensity, substrate type and ecological interaction. The nursery was located in San Martín de los Andes at $40^\circ 10' \text{ S}$ and $71^\circ 20' \text{ W}$, and 640 m a.s.l. (Figure 1). Soil moisture was maintained high and constant with an automated micro-sprinkler irrigation system. We carried out manual control against weeds, and chemical control against fungi with Benomyl ($1.2 \text{ g}\cdot\text{l}^{-1}$) and Captan ($1.8 \text{ g}\cdot\text{l}^{-1}$), and insects with Abamectin (1.8% , $0.6 \text{ g}\cdot\text{l}^{-1}$). For nursery tests, experimental designs were multi-factorial and completely randomized with fixed effects, of the general type [2], where N: amount of experimental units, r: amount de replicates, E: amount of levels for factor “species”, L: amount of levels for factor “relative light intensity”, S: amount of levels for factor “substrate type” and P: amount of levels for factor “presence of Cc”. Variables for all nursery tests were measured every 21 d from January 2 to April 17 (five measurements during 106 d).

$$N = r(ELSP) \quad [2]$$

Seed weight and germination

In laboratory, seed wet weight (Ws) of *Nothofagus* was assessed from 10 experimental units composed of 120 healthy seeds of each species, selected at random from traps samples (scale, precision 0.001 g). In laboratory, seed wet weight (Ws) was assessed from 10 experimental units composed of 120 healthy seeds of each species, selected at random from traps samples (scale, precision 0.001 g). Test I was performed based on a completely randomized design with 10 replicates. The experimental unit was composed of 100 seeds per species, placed in a Petri dish on a moistened paper, to which the chemical control against fungi were regularly applied. These pre-treated seeds were placed in a germination chamber at 25° C with 12 h of artificial light during 56 d and germinated propagules were counted every 7 d (test I).

Nothofagus seeds and seedlings performance

Test II consisted of the analysis of the effect of light intensity and substrate type on germination and seedlings mortality and height of *Nothofagus*. Factors and levels were E (Nd, No, Na), L (LH, LI, LL) and S (SA, “deep mineral”: seeds covered by deep mineral soil, SB, “superficial mineral”: seeds covered by surface mineral soil, SC, “organic 1”: seeds covered by litter, SD, “organic 2”: seeds above litter ($r = 3$, $N = 108$) (Table 1). Number of seeds sown in each experimental unit (Ns) was 325 for Nd, 350 for No and 375 for Na. Emergent plants (Ng) were marked with a plastic tag, counted and measured for plant height (H, calliper). At the end of the test, number of alive plants (Nm) were counted, and germination (G) and mortality (M) were estimated according to [3] and [4]

$$G = (N_g / N_s) \cdot 100 \quad [3]$$

$$M = (N_m / N_g) \cdot 100 \quad [4]$$

Nothofagus saplings growth

Test III was performed to analyse the effect of L on diameter (ld) and height growth (lh) of two-year saplings of *Nothofagus*, produced in nursery from seeds collected in the study area. One hundred individuals of Nd, No and Na were selected, from which a random sample of 10 per species was taken and H and root collar diameter (D) (calliper) were measured. The rest of saplings were intercalating in the nursery with a spacing of 20 cm. In the experimental unit 10 individual of each species were planted and factors and levels were E (Nd, No, Na) and L (LH, LI, LL) ($r = 3$, $N = 27$) (Table 1). ld and lh were estimated dividing D and H by the extent of the sampling period.

Chusquea culeou performance and interaction

Test IV consisted in the analysis of the effect of L and S on G and H of Cc. In each experimental unit $N_s = 450$ and factors and levels were L (LH, LI, LL) and S (SB, SC). At the end of test, Ng and H was measured ($r = 9$, $N = 54$) (Table 1). Test V involved the analysis of the effect of Cc, on G, M and H of *Nothofagus* seedlings. Factors and levels were E (Nd, No, Na), L (LH, LI, LL), and P (1: Cc present, 0: Cc absent) ($r = 3$, $N = 54$) (Table 1). In each experimental unit, 325 seeds of Nd, 350 of No and 375 of Na were sowed together with 450 seeds of Cc in half of the experimental units. Subsequently Ng, M and H for *Nothofagus* were recorded. All data were statistically analysed using parametric techniques because they fulfilled the assumptions of ANOVA. The existence of significant differences of means among species and

treatments was evaluated through multifactorial ANOVA and the LSD multiple comparisons test ($p < 0.05$).

RESULTS

Nothofagus seeds and seedlings performance

Ws of Nd, No and Na seeds were 1.56 mg (SE = 0.03), 6.15 mg (SE = 0.15) and 9.53 mg (SE = 0.29), respectively; these values differed significantly (LSD test, ANOVA $F_{2,29} = 449.7$, $p < 0.001$, $n = 10$). After 56 d during test I, G was 6.1% (SE = 0.97) for No and 7.6% (SE = 0.80) for Na; G for Nd was null ($n = 10$) (Figure 2). During test II, G for Nd = 0%, No = 1.0% (SE = 0.16) and Na = 1.8% (SE = 0.29); these values differed significantly (ANOVA, $p < 0.05$), and emergence difference between Na and No was equal to 71.2%. M for No = 16.1% (SE = 3.30) and Na = 32.8% (SE = 4.69); these values did not differ significantly (ANOVA, $p \geq 0.05$) (Figure 3A). H was 2.4 cm for No and Na; this value represents a $lh = 0.67$ $\text{cm}\cdot\text{month}^{-1}$ (Figure 3B) (Table I).

G for *Nothofagus* with LH = 1.3% (SE = 0.25), LI = 0.9% (SE = 0.24) and LL = 0.7% (SE = 0.19). Emergence was on average 67.8% higher with LH than with LI and LL (ANOVA, $p < 0.05$); there were no significant differences of germination between LI and LL (ANOVA, $p \geq 0.05$) (Figure 3C). H did not differ among the different light levels and was on average 2.4

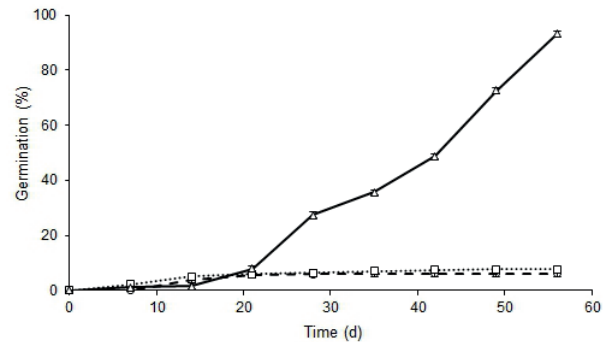


FIGURE 2 Germination along time of *N. obliqua* (circle, dashed line), *N. alpina* (square, dotted line) and *C. culeou* seeds (triangle, continuous line). Vertical bars indicate SE for $n = 100$ (Test I).

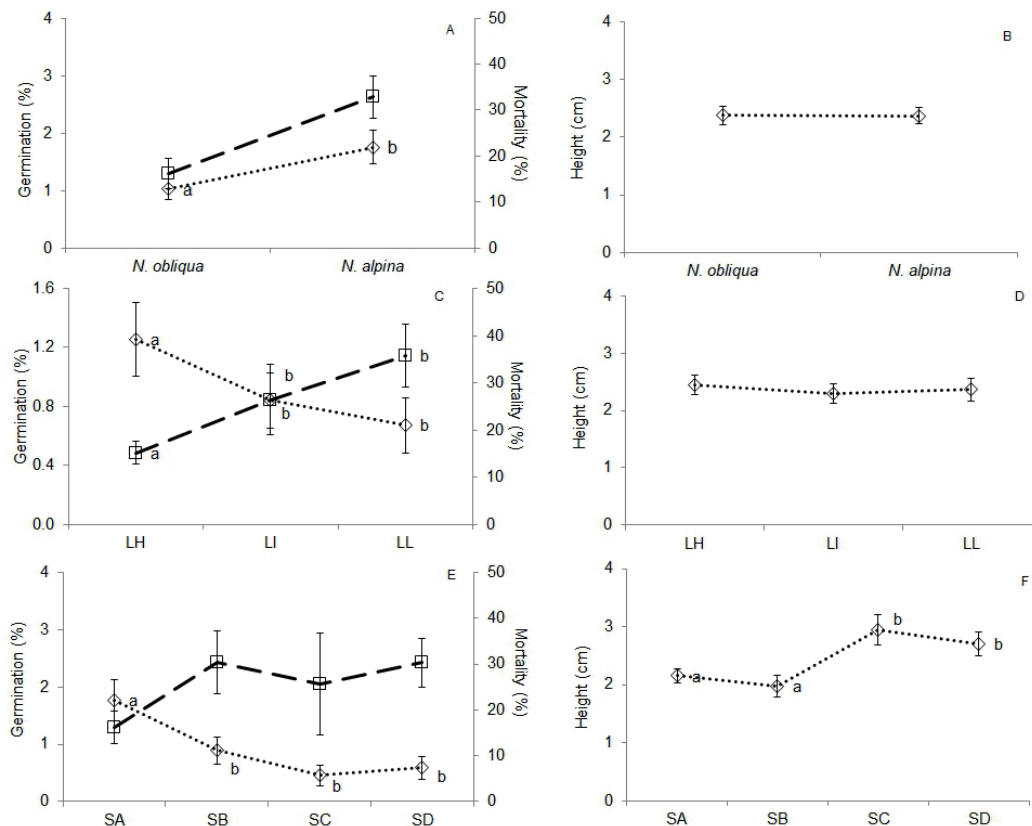


FIGURE 3 Germination (rhombus, dotted line), mortality (squares, dashed line) and height in relation to species (*N. obliqua* and *N. alpina*), relative light (LH: high, LI: intermediate, LL: low) and substrate (SA: deep mineral, SB: superficial mineral, SC: organic 1, SD: organic 2). Vertical bars indicate SE and unequal letters significant differences of means among treatment levels (ANOVA, $p < 0.05$) (Test II).

TABLE I Analysis of variance of tests II to V relating species (E, Nd: *N. dombeyi*. No: *N. obliqua*. Na: *N. alpina*), light (L, LH: high. LI: intermediate. LL: low), substrate (S, SA: deep mineral. SB: superficial mineral. SC: organic 1. SD: organic 2) and presence of *C. culeou* (P, I: present). Number of replicates (r), size (e) and number of experimental units (N), source of variation (SV, main effects and interactions), degrees of freedom (DF), F-quotient (F), and sample size (n) are showed. Unequal letters in homogeneous groups (HG) indicate significant differences of means among levels, *: significant, ns: non-significant ($p < 0.05$). Only significant interactions are showed.

TEST	VARIABLE	SV	DF	F	p	Level	HG	n
<i>Nothofagus</i> seeds and seedlings performance r = 3 e=0.3 x 0.3 m N=108 t = 106 d (II)	Germination	E	2	39.37	<0.001*	Nd No Na	a b c	36
		L	2	4.58	0.013*	LH LI LL	a b b	36
		S	3	13.34	<0.001*	SA SB SC SD	a b b b	27
		E x S	6	10.07	<0.001*	-	-	-
		E	1	3.86	0.056ns	No Na LH	- a b	24
		L	2	4.81	0.013*	LI LL SA SB SC SD	b b - - - -	36
	Mortality	S	3	1.64	0.195ns	-	-	27
		E	1	0.30	0.586ns	No Na LH	- - -	24
		L	2	0.49	0.615ns	LI LL SA SB SC SD	- - a a b b	36
	Height	S	3	3.45	0.026*	-	-	27
		E	1	43.23	<0.001*	Nd No Na	a b c	9
	<i>Nothofagus</i> saplings growth r = 3 e = 0.6 x 0.6 m N = 27 t = 106 d (III)	Diameter growth	L	2	81.42	<0.001*	LH LI LL	
E			2	42.67	<0.001*	Nd No Na LH LI LL	a b c a ab b	
Height growth	L	2	3.09	0.047*	-	-	27	
	E	1	206.4	<0.001*	LH LI LL	a b c	18	
<i>C. culeou</i> performance r = 9 e = 0.3 x 0.3 m N = 54 t = 106 d (IV)	Germination	S	1	272.6	<0.001*	SB SC	a b	27
		L x S	2	190.5	<0.001*	-	-	-
	Height	L	2	53.72	<0.001*	LH LI LL	a b c	18
		S	1	53.06	<0.001*	SB SC	a b	27
<i>Nothofagus</i> - <i>C. culeou</i> interaction r = 3 e = 0.3 x 0.3 m N = 54 t = 106 d (V)	Germination	E	2	6.91	0.010*	Nd No Na	a b c	18
		L	2	0.64	0.528ns	LH LI LL	-	
		P	1	0.65	0.421ns	I 0	-	
	Mortality	E	1	9.48	0.029*	No Na	a b	18
		L	2	3.25	0.044*	LH LI LL	a a b	
		P	1	13.64	0.004*	I 0	a b	
	Height	E	1	0.16	0.692ns	No Na	-	27
		L	2	0.92	0.402ns	LH LI LL	-	
		P	1	0.06	0.808ns	I 0	-	
		P	1	0.06	0.808ns	I 0	-	

cm (ANOVA, $p \geq 0.05$) (Figure 3D) (Table I). G in SA = 1.8% (SE = 0.35); this value was on average 196.7% significantly higher than in SB, SC and SD (ANOVA, $p < 0.05$); G under this last three substrates did not significantly differ (ANOVA, $p \geq 0.05$). M did not differ significantly among substrate types (ANOVA, $p \geq 0.05$) (Figure 3E). H in SA and SB was on average 2.1 cm (SE = 0.06) and in SC and SD was 2.8 cm (SE = 0.09); these values differed significantly (ANOVA, $p < 0.05$) (Figure 3F) (Table I).

The analysis of the simultaneous effect of levels for E, L and S showed only significant interactions between E (No and Na) and S (SA, SB, SC and SD) on G. For both species, G was maximum in SA (No = 1.3%, SE = 0.17; Na = 4.0%, SE = 0.36) and minimum in SC (No = 0.83%, SE = 0.39; Na = 0.53%, SE = 0.31) (Table I, Figure 4). The analysis of the simultaneous effect of the factor levels for E, L and S indicated that treatments with the highest G were Na-LI-SA (4.3%, SE = 0.92), Na-LH-SA (4.1%, SE = 0.71), Na-LL-SA (3.6%, SE = 0.24), Na-LH-SB (2.8%, SE = 1.2) and No-LH-SC. Treatments with the lowest G were Na-LL-SC (0.3%, SE = 0.15), No-LI-SC (0.2%, SE = 0.19), Na-LI-SC (0.2%, SE = 0.18), No-LL-SD (0.1%, SE = 0.09) and No-LL-SC (0).

Mean G differed among treatments (LSD test, ANOVA $F_{35,107} = 6.23$, $p < 0.001$, $n = 3$) (Figure 5A). Treatments that showed the highest M were Na-LL-SC (69.3%, SE = 19.5), Na-LI-SB (55.7%, SE = 18.2), Na-LL-SB (50.0%, SE = 15.0), No-LI-SD (40.0%, SE = 10.0) and No-LL-SD (37.5%, SE = 12.5). Treatments that showed the lowest M were No-LL-SA (7.7%, SE = 4.9), No-LH-SA (4.7%, SE = 4.7), No-LH-SC (4.5%, SE = 4.5) and Na-LI-SC and No-LI-SC (0%). Mean M differed among treatments (LSD test, ANOVA $F_{22,58} = 2.18$, $p = 0.018$, $n = 3$) (Figure 5B). Treatments that exhibited the highest H were Na-LI-SC (3.5 cm, SE = 0.92), Na-LH-SC (3.5 cm, SE = 0.16), No-LL-SB (3.3 cm, SE = 0.61), No-LI-SC (3.3 cm, SE = 1.2) and Na-LL-SD (3.2 cm, SE = 0.23).

Treatments with the lowest H were Na-LL-SB (1.7 cm, SE = 0.37), Na-LL-SC (1.7 cm, SE = 0.04), No-LL-SD (1.6 cm, SE = 0.18), No-LH-SB (1.6 cm, SE = 0.09) and Na-LI-SB (1.5 cm, SE = 0.34). Mean H differed among treatments (LSD test, ANOVA $F_{22,56} = 2.49$, $p = 0.008$, $n = 3$) (Figure 5C).

Nothofagus saplings growth

Initial D for Nd, No and Na saplings was 2.3 (SE = 0.16), 2.3 (SE = 0.09) and 2.2 cm (SE = 0.08), respectively; these values did not differ significantly

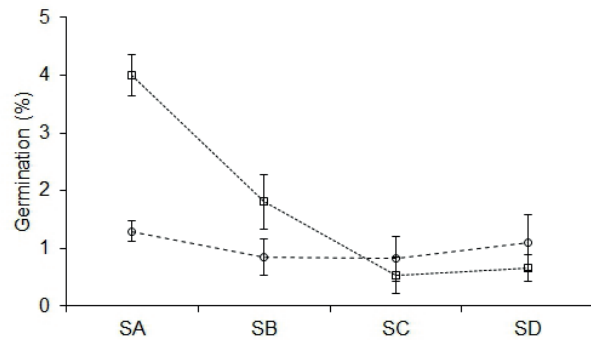


FIGURE 4 Germination of *N. obliqua* (circle, dashed line) and *N. nervosa* seeds (square, dotted line) as a function of substrate (SA: deep mineral, SB: superficial mineral, SC: organic 1, SD: organic 2). Vertical bars indicate SE of the mean for $n = 9$. There is a significant interaction between substrate and species on germination (ANOVA, $p < 0.05$) (Test II).

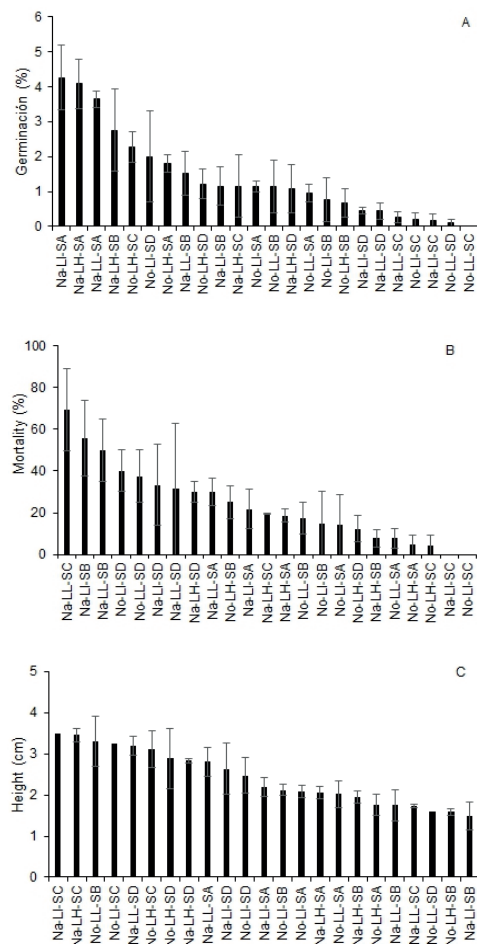


FIGURE 5 Germination (G), mortality (M) and height (H) in relation to species (No: *N. obliqua*, Na: *N. alpina*), light (LH: high, LI: intermediate, LL: low) and substrate (SA: deep mineral, SB: superficial mineral, SC: organic 1, SD: organic 2). Vertical bars indicate SE of the mean. There are differences of means among treatments only in G and M (LSD test, $p < 0.05$) (Test II).

(ANOVA, $F_{2,29} = 0.28$, $p = 0.755$). Initial H for Nd, No and Na was 7.60 (SE = 0.73), 8.45 (SE = 0.47) and 7.43 cm (SE = 0.08); these values did not differ significantly (ANOVA, $F_{2,29} = 0.63$, $p = 0.539$). During test III, Id for Nd = 0.14 mm·month⁻¹ (SE = 0.02), No = 0.33 mm·month⁻¹ (SE = 0.02) and Na = 0.20 mm·month⁻¹ (SE = 0.02); these values differed significantly (LSD test, ANOVA, $p < 0.05$). Mean lh for *Nothofagus* was 0.87 cm·month⁻¹. lh for Nd = 0.65 cm·month⁻¹ (SE = 0.09), No = 1.59 cm·month⁻¹ (SE = 0.14) and Na = 0.29 cm·month⁻¹ (SE = 0.03); these values differed significantly (LSD test, ANOVA, $p < 0.05$) (Table I) (Figure 6A).

Id for *Nothofagus* with LH = 0.38 mm·month⁻¹ (SE = 0.02), LI = 0.16 mm·month⁻¹ (SE = 0.01) and LL = 0.13 mm·month⁻¹ (SE = 0.19); these values differed statistically (LSD test, ANOVA, $p < 0.05$). lh for *Nothofagus* with LH = 1.03 cm·month⁻¹ (SE = 0.11), LI = 0.88 cm·month⁻¹ (SE = 0.12) and LL = 0.69 cm·month⁻¹ (SE = 0.12); these values did not differ statistically (ANOVA, $p \geq 0.05$) (Table I, Figure 6B). Analysis of the simultaneous effect of levels of factors E and L indicated that treatments exhibiting the highest Id were No-LH (0.54 mm·month⁻¹, SE = 0.03), Na-LH (0.35 mm·month⁻¹, SE = 0.04) and Nd-LH (0.26 mm·month⁻¹, SE = 0.03). Treatments that exhibited the lowest Id were Nd-LL (0.05 mm·month⁻¹, SE = 0.03), Nd-LI (0.10 mm·month⁻¹, SE = 0.01) and Na-LL (0.11 mm·month⁻¹, SE = 0.02).

Mean Id differed among treatments (LSD test, ANOVA $F_{8,257} = 31.36$, $p < 0.001$). Treatments that exhibited the highest lh were No-LH (1.74 cm·month⁻¹, SE = 0.19), No-LI (1.69 cm·month⁻¹, SE = 0.25) and No-LL (1.35 mm·month⁻¹, SE = 0.29). Treatments that exhibited the lowest lh were Na-LL (0.18 cm·month⁻¹, SE = 0.06), Na-LI (0.28 cm·month⁻¹, SE = 0.06) and Na-LH (0.40 cm·month⁻¹, SE = 0.05). Mean lh differed among treatments (LSD test, ANOVA $F_{8,257} = 11.56$, $p < 0.001$) (Figure 6C).

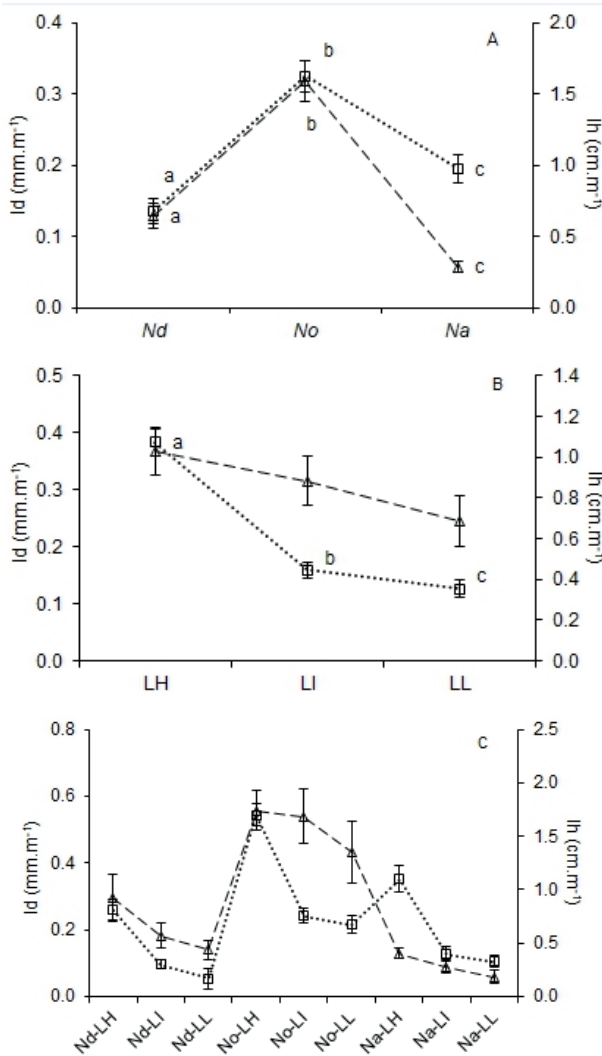


FIGURE 6 Diameter (Id, square, dotted line) and height growth of saplings (lh, triangle, dashed line) as a function of species (Nd: *N. dombeyi*, No: *N. obliqua*, Na: *N. alpina*) and light intensity (LH: high, LI: intermediate, LL: low). Vertical bars indicate SE and unequal letters significant differences of means among treatment levels (LSD test, $p < 0.05$) (Test III).

Chusquea culeou performance

After 56 d of laboratory test I, G for Cc was 93.1% (SE = 1.88) (n = 10) (Figure 2). Mean G for Cc (test IV) with LH, LI and LL was 8.7% (SE = 2.09), 2.7% (SE = 0.73) and 0.8% (SE = 0.32), respectively; these values differed significantly (ANOVA, $p < 0.05$). G with LH was 215.7% higher than that with LI and 937.0% with LL. Mean lh was 1.36 cm·month⁻¹. Mean H with LH, LI and LL was 2.9 cm (SE = 0.14), 5.5 cm (SE = 0.24) and 6.4 cm (SE = 0.38), respectively; these values differed significantly (ANOVA, $p < 0.05$). H with LL was 122.4% higher than that with LH and 15.4% with LI (Table I, Figure 7A).

Mean G for Cc (test IV) with SB and SC was 1.4% (SE = 0.21) and 6.8% (SE = 1.60), respectively; these values differed significantly (ANOVA, $p < 0.05$). G with SC was 394.6% higher than with SB. Mean H with SB and SC was 1.9 cm (SE = 0.15) and 4.5 cm (SE = 0.38), respectively; these values differed significantly (ANOVA, $p < 0.05$). H with SC was 133.3% higher than that with SB. Mean lh = 1.36 cm·month⁻¹, which represented a value 56.5 and 101.6% higher than that for *Nothofagus* seedlings and saplings, respectively (Table I, Figure 7B).

The analysis of the simultaneous effect of factor levels on G showed significant interactions between light and substrate (ANOVA, $p < 0.001$) (Table I, Figure 8).

The treatment that exhibited the highest G was LH-SC (15.6%, SE = 0.0), while that with the lowest was LL- (null value). Mean G differed among treatments (LSD test, ANOVA. $F_{5,35} = 213.25$, $p < 0.001$) (Figure 9). Treatment that exhibited the highest H was LI-SC (4.7 cm, SE = 0.5) and LH-SC (3.9 cm, SE = 0.0), whereas that with the lowest was LI-SB (1.6 cm, SE = 0.4). Mean H differed among treatments (LSD test, ANOVA $F_{4,17} = 16.48$, $p < 0.001$).

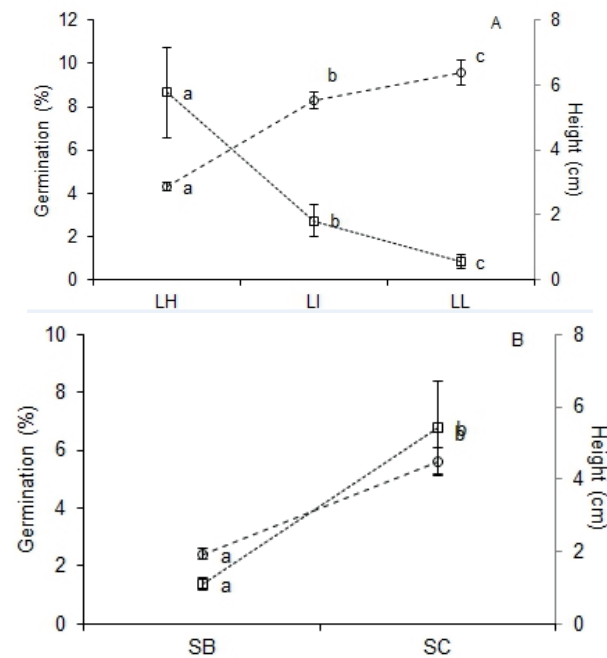


FIGURE 7 Germination (square, dotted line) and height (circle, dashed line) of *C. culeou* related to light intensity (LH: high, LI: intermediate, LL: low) (A) and substrate type (SB: superficial mineral, SC: organic I) (B). Vertical bars indicate SE. Means differ significantly among treatments (ANOVA, $p < 0.05$) (Test IV).

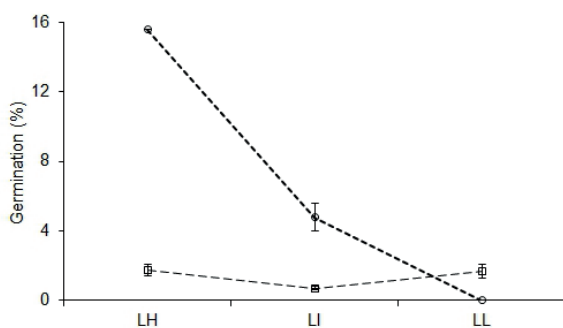


FIGURE 8 Germination of *C. culeou* related to light intensity (LH: high, LI: intermediate, LL: low) and substrate type (SB: superficial mineral, square, dashed line; SC: organic I, circle, dotted line). Vertical bars indicate SE for $n = 27$. There is a significant interaction between substrate and light on density (ANOVA, $p < 0.05$) (Test IV).

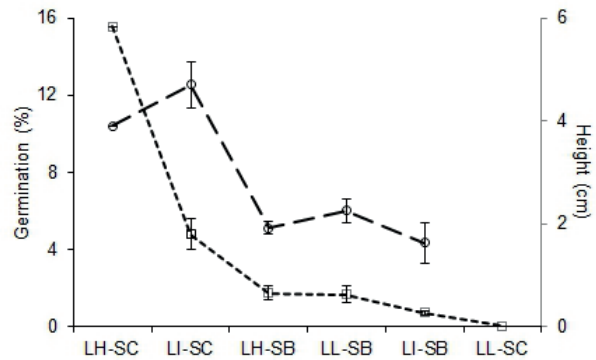


FIGURE 9 Germination (dotted line) and height (dashed line) of *C. culeou* related to light intensity (LH: high, LI: intermediate, LL: low) and substrate type (SB: superficial mineral, SC: organic I). Vertical bars indicate SE. Means differ significantly among treatments (ANOVA, $p < 0.05$) (Test IV).

Nothofagus - *C. culeou* interaction

During test V, G for Nd = 0%, No = 1.2% (SE = 0.28) and Na = 2.2% (SE = 0.28). These values differed significantly (ANOVA, $p < 0.05$) and G difference between No and Na was 83.9%. M for No = 31.5% (SE = 4.97) and Na = 53.4% (SE = 5.27); these values differed significantly (ANOVA, $p < 0.05$) (Figure 10A). Mean H was 2.4 cm for No and Na (Table I, Figure 10B). G for *Nothofagus* with LH = 1.9% (SE = 0.32), LI = 1.4% (SE = 0.32) and LL = 1.9% (SE = 0.19); these values did not differ significantly (ANOVA, $p \geq 0.05$). Mean M for *Nothofagus* with LH, LI and LL was 37.0% (SE = 5.82), 33.7% (SE = 5.66) and 56.7% (SE = 7.46), respectively. G with LH and LI was significantly higher than with LL (ANOVA, $p < 0.05$) (Figure 10C).

H for *Nothofagus* seedlings did not differ among light levels, and was on average 2.4 cm (ANOVA, $p \geq 0.05$) (Table I, Figure 10D). G for *Nothofagus* in presence and absence of Cc was 1.6% (SE = 0.35) and 1.9% (SE = 0.20), respectively; these values did not differ significantly (ANOVA, $p \geq 0.05$). M for *Nothofagus* in presence and absence of Cc was 56.1% (SE = 6.32) and 28.9% (SE = 3.78), respectively; these values differed significantly (ANOVA, $p < 0.05$), and G difference between species was equal to 94.4%. (Figure 10E). H for *Nothofagus* did not differ among those that developed in presence and in absence of Cc and was on average 2.4 cm (ANOVA, $p \geq 0.05$) (Table I, Figure 10F).

DISCUSSION

Although throughout the geographic distribution of *Nothofagus* species, seed weight varies annually and

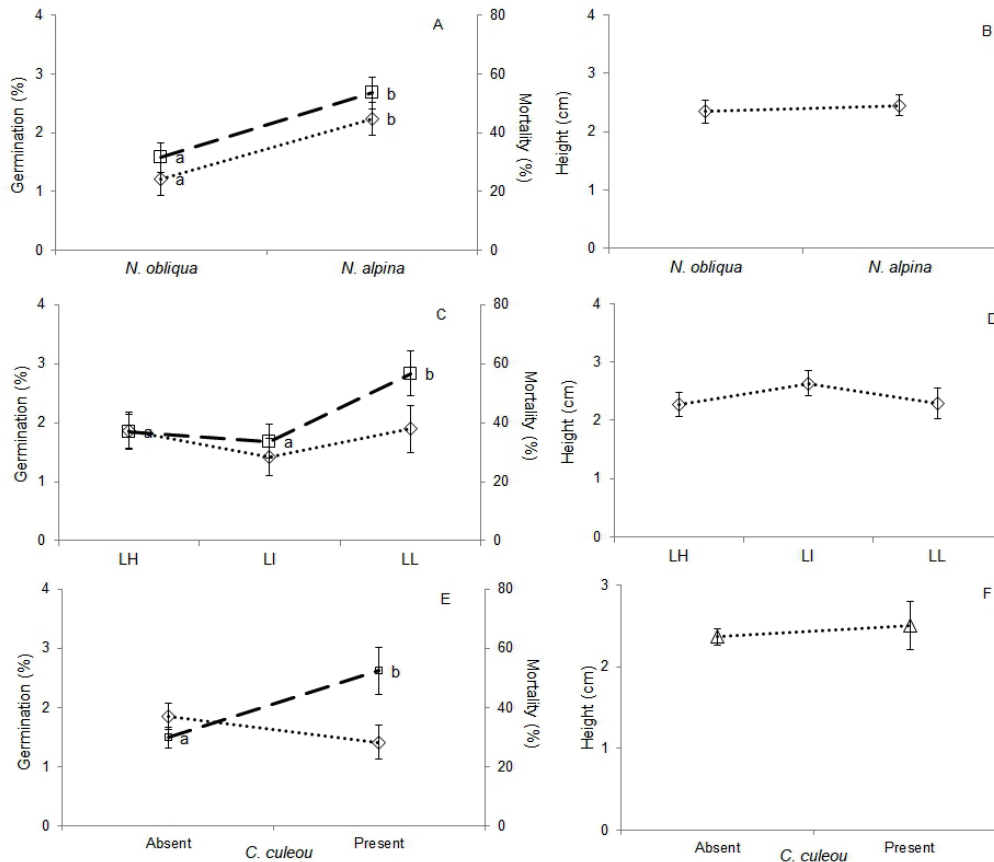


FIGURE 10 Germination (rhombus, dotted line), mortality (squares, dashed line) and height in relation to species (*N. obliqua* and *N. alpina*), relative light (LH: high, LI: intermediate, LL: low) and presence of *C. culeou* (present, absent). Vertical bars indicate SE and unequal letters significant differences of means among treatment levels (ANOVA, $p < 0.05$) (Test V).

between individuals and populations, in a particular site *N. dombeyi* seeds are intrinsically lighter than that of *N. obliqua* (4 times in this study) and *N. alpina* (6 times) (Burschel et al., 1976; Marchelli & Gallo, 1999; Donoso et al., 2014). In laboratory and nursery, seeds exhibited a null or low germination ($\leq 2.2\%$). The low germination capacity, even compared to other autochthonous species but that increases during the most fertile annual periods, was previously cited by Burschel et al. (1976), Donoso et al. (1993) and Muñoz (1993).

Recently fallen *Nothofagus* seeds are frequently vain, probably because of self-fertilization, or subjected to pre- and post-dispersal predation (Burschel et al., 1976; Bustamante, 1996). Calderón-Valtierra et al. (1995), Escobar and Donoso (1996) and León-Lobos and Ellis (2005) proposed combinations of temperature, humidity, substrate and hormones to improve emergency. Germination of *N. alpina* was always greater than that of *N. obliqua*, both in laboratory (25% higher) and nursery (80%), and germination of *N. dombeyi* was null in both settings. Within these species, positive correlation

between seed weight and emergence rate would be linked, at least partially, to the higher nutrient content of heavier seeds (Donoso et al., 2014).

Higher emergence and lower mortality of *N. obliqua* and *N. alpina* seedlings, and higher diameter growth of saplings in the three species with high irradiation, would represent an adaptation to colonize open areas. Dezzotti (2008) found that regeneration of *N. dombeyi*, *N. obliqua* and *N. alpina* exhibited higher growth in sunny centres than in shaded peripheries of artificial canopy gaps. However, mortality in openings can be high due to the extreme temperatures of climates with marked seasonality (Dezzotti, 2008; Donoso et al., 2013). High emergence and survival of *Nothofagus* under a deep mineral substrate would be related to the air and moisture content of this soil horizon (Hilhorst, 2013). The reduced germination of seeds covered by litter can be ascribed to its role as a physical barrier (Burschel et al., 1976). Chauchard et al. (2008) recommended to weaken the thick litter layer to promote regeneration.

The interspecific differences in seed weight could explain, at least partially, the lower diameter growth of *N. dombeyi* saplings observed in nursery; a similar result was also found in natural forests (Dezzotti, 2008). Usually, large seeds have a greater reserve of nutrients, and the resultant seedlings exhibit a rapid and vigorous growth that allows overcoming this stage (Donoso et al., 2014). Müller-Using and Schlegel (1981) proposed that the early higher growth and development (e.g., during the first year) of *N. alpina* and *N. obliqua*, compared to that of *N. dombeyi*, was strongly influenced by the reserves stored in the seed, and that light was important later (e.g., during the second year). In contrast, as adult *N. dombeyi* exhibit one of the greatest growth potential found within the genus (Chauchard et al., 2008).

Growth differences among species related to light were slightly observed only in saplings. However, the more shade-tolerant character of *N. alpina* and the more light-demanding of *N. dombeyi* was previously cited. For example, in virgin natural forests, *N. alpina* mature trees presented an asymmetric left-handed size distribution, due to greater abundance of individuals of smaller sizes under the canopy (Donoso et al., 2014). Within these stands, artificial thinning did not maintain the original balanced composition, due to the lower competitive ability of *N. alpina* regeneration under the increased radiation of the forest floor. Immature trees of this species constituted the advance regeneration and exhibited the highest biomass in the shaded edges of gaps (Dezzotti, 2008; Sola et al., 2016).

In mixed plantations, Grosse (1988) and Donoso et al. (2013) found a better response of *N. dombeyi* to larger gaps whereas *N. alpina* to smaller gaps. In addition, seed size and weight tended to correlate with trees temperament: larger and heavier seeds exhibit less anemocory and plants are adapted to shaded habitats under the canopy (e.g., *N. alpina*), while smaller and lighter ones are dispersed by wind at greater distance and plants develop in sunny areas of canopy gaps (e.g., *N. dombeyi*) (Moles and Westoby, 2006). The persistence of *N. alpina* in intermediate shade was related to low respiration and light compensation point (Read and Hill, 1985).

The performance of *C. culeou* showed a similarity and differences compared to *Nothofagus*. Similarity was related to a higher emergence with intense irradiation. Differences were related to a higher plant performance with intermediate and low light levels, and in the substrate covered by litter. Although open areas would constitute favourable microsite, the dehydration and freezing

prevailing here may be harmful for this species (Veblen et al. 1996; Holz and Veblen, 2006; Marchesini et al., 2009). Presence of *C. culeou* was related to an increase in mortality of *Nothofagus* seedlings, particularly with high luminosity; in this condition, plant death was similar to that observed with intermediate light. These results are compatible with the effect of interspecific competition, although this interaction did not affect germination or height of surviving *Nothofagus* seedlings.

After flowering and massive senescence of *C. culeou*, *Nothofagus* would occupy sites through seed, sprout (*N. obliqua* and *N. alpina*) or advance regeneration (particularly *N. alpina*). However, the ability of *Nothofagus* to compete with *C. culeou* would be reduced because of a lower seed production (Dezzotti et al., 2016) and seedlings emergence, growth and survival. Giordano et al. (2009) found that *C. culeou* flowering created short-term opportunities for *N. obliqua* germination in response to increased radiation, thermal amplitude and red: far-red ratio. Muñoz and González (2009) found that mortality of *Chusquea quila* (Kunth) promoted tree colonization although, after a decade, it recovered dominance and only shade-tolerant trees with vegetative reproduction persisted. Holz and Veblen (2006) found that mortality of *Chusquea montana* (Phil.) encouraged rapid growth but not recruitment of *N. dombeyi* and *Nothofagus pumilio* (Poepp et al.) Krasser.

CONCLUSIONS

After a large-scale disturbance, *Nothofagus* species would colonize the site early from seeds as long as *C. culeou* populations were in the vegetative phase. Although the intrinsic viability of *Nothofagus* seeds tend to be low, it would increase considerably during masting. After a major disturbance, the physical environment characterized by high irradiation and low litter content, would promote establishment, survival and growth of tree species as long as there is water available on the ground. The lower seed viability of *N. dombeyi* would be offset by a greater individual fertility, and its lower initial performance would have reversed over time. After a sexual phase, *C. culeou* would arrive later to sites from seeds, coming from distant sources, and expanding later from rhizomes. The massive biotic disturbance caused by the gregarious, post-flowering mortality of *C. culeou* would provide habitat, highly viable seeds and huge amount of litter, promoting its persistence and also affecting establishment and survival of *Nothofagus*. Small-scale endogenous disturbances would create conditions for the alternative colonization of *Nothofagus*, depending

on the parameters of disturbance (particularly gap size), physical variables (particularly light) and regenerative strategies. It is necessary to continue investigating this successional dynamics, to provide sounder scientific basis for the sustainable management of this complex and valuable forest ecosystem.

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