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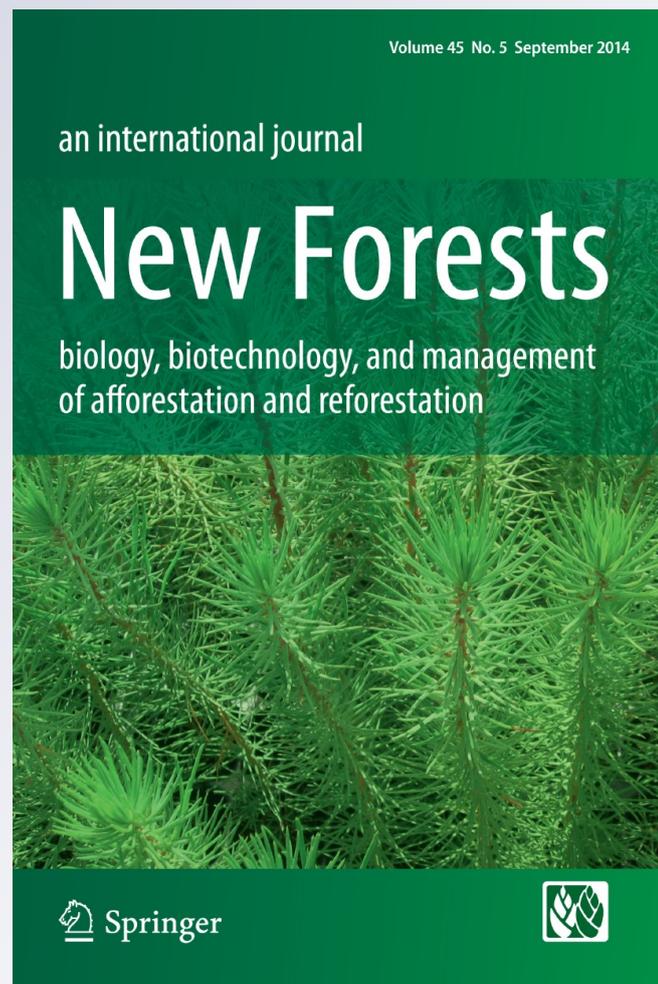
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Mortality in relation to growth rate and soil resistance varies by species for underplanted *Nothofagus* seedlings in scarified shelterwoods

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Abstract This study evaluated early mortality patterns of planted *Nothofagus dombeyi* (Mirb.) Blume (evergreen, shade intolerant) and *Nothofagus alpina* (P. et E.) Oerst. (deciduous, mid-tolerant to shade) seedlings established in scarified gaps in a *Nothofagus* old-growth forest in the Chilean Andes that was subjected to a shelterwood cut. Soils were scarified with heavy machinery that removed up to 40 cm of the upper horizons (e.g. it completely removed the litter layer and organic horizon, and in some cases partially the A horizon) to eliminate bamboo (*Chusquea culeou* E. Desv) shoots and rhizomes from the scarified areas. Two years after planting, seedlings were growing free of understory competition and mortality patterns were assessed using logistic regression models with the following predictor variables: (1) basal diameter growth in the prior year, and (2) soil strength measured as resistance to penetration. The probability of mortality of both species was highly predictable based on recent basal diameter growth. *N. dombeyi* seedlings appeared to be less affected by mortality, as reflected in lower sensitivity of mortality at lower growth rates compared to *N. alpina*. High values of resistance to penetration (>2,000 kPa) induced a higher probability of mortality in *N. alpina* (up to 40 % at 3,500 kPa). In contrast, *N. dombeyi* mortality was not significantly influenced by soil strength, which illustrates the more stress-resistant and pioneer character of this species. This study showed that recent growth rates can be used as a predictor of future mortality, but these relationships need to be calibrated for each species. In addition, our results suggest that species characteristics that relate to resource limitations, such as shade tolerance, are not adequate to understand effects of other stressors, such as soil disturbance, on mortality patterns.

Keywords Logistic regression · Resistance to penetration · Carbon balance · Shade-tolerance · Stress adaptation · Soil scarification

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Introduction

Mortality patterns in juvenile stages play an important and profound role in forest dynamics, succession, and future species composition and diversity (Pacala et al. 1996). Mortality varies by species due to different silvical characteristics, especially the capacity of plants to obtain resources and maintain an adequate carbon balance in a stressful, low-resource environment (Kobe and Coates 1997). Shade tolerance, an important silvical characteristic, is viewed as a key concept to understand the species-specific performances in different stages of tree development, especially under an overstory canopy (Valladares and Niinemets 2008). By definition, shade-intolerant species do not grow well under low-light environments. In contrast, shade-tolerant species modify their growth patterns to be able to survive in the long-term even under heavily shaded conditions (Valladares and Niinemets 2008).

Researchers have used various plant measurements to predict mortality, including recent growth, seedling morphology and photosynthesis levels (e.g., Walters and Reich 1996; Kobe et al. 1995; Morrissey et al. 2010). Absolute differences in morphology and photosynthesis are not necessarily reflected in seedling mortality patterns, due to species-specific responses that depend on light use-efficiency at leaf levels, shade tolerance and morphological adaptation of the species (Walters and Reich 1996; Löf et al. 2007). Various studies have shown that growth is an indicator of resource levels and thus a good predictor of mortality for seedlings and saplings (Kobe et al. 1995; Kobe and Coates 1997). For this reason, models of seedling and sapling mortality incorporate recent growth prior to seedling death as a proxy variable and as a surrogate for carbon balance (Kobe et al. 1995; Pacala et al. 1996; Kobe and Coates 1997).

The functional relationship between species mortality and recent tree growth has been soundly established (e.g., Kneesshaw et al. 2006; Morrissey et al. 2010). However, at the landscape level these patterns can change as a function of water and nutrient availability. Moisture and nutrient availability, or in more general terms site quality, usually varies according to climate, topography, geology, and soil conditions. For example, Carter and Klinka (1992) reported that probability of mortality within a species was influenced by site quality, specifically a lower shade tolerance was found in stands with higher soil moisture levels. In contrast, Caspersen and Kobe (2001) suggested a diffuse pattern of mortality as a function of soil moisture in several hardwoods species, but concluded that soil moisture did not modify the species-specific shade-tolerance ranking. However, forest management activities can also change site quality, especially through their effects on soil properties, e.g., through logging and site preparation with heavy machinery. Some studies have shown that sensitivity to tolerate soil compaction can vary considerably among species (Kozłowski 1999; Smith et al. 2001), presumably due to species-specific tolerance to soil conditions, such as soil compaction, that play an important role for seedling performance (Kozłowski 1999). The impacts of soil compaction on plant mortality during early stages of development in managed forest areas have been poorly documented (Resco de Dios et al. 2005; Yoshida et al. 2005), and not studied in *Nothofagus* forests in Chile.

Natural regeneration of commercially valuable tree species after different forest management operations in *Nothofagus* old-growth forests in Chile is generally poor (González et al. 2002). The main reasons include competition from dense thickets of bamboo, an invasive, fast-growing and light demanding species that typically proliferates in forest understories (Veblen et al. 1980; González et al. 2002). Planting into bamboo thickets is not practical and often not even feasible, thus for decades landowners tried to overcome this problem by planting *Nothofagus* seedlings in strips where weeds, especially bamboo, are manually controlled. Still, most of these efforts failed (personal communication by Luis

Molina, CEO of Neltume-Carranco S.A., a large forest company in the Andes of Chile). Also, the intensive labor for site preparation and the control of bamboo regrowth for at least 2 years is quite expensive (Siebert 1999). As an alternative, silviculturists in Chile started to apply site preparation techniques in the last decade that consists of scarification of top soil to a depth of about 40 cm by heavy machinery (e.g. Bulldozers) to (1) control dense patches of competing vegetation by eliminating bamboo rhizomes (see Veblen 1982; González et al. 2002), (2) create microsites to improve seedbed conditions for regeneration of *Nothofagus* species (pioneer tree species adapted to regenerate after stand-displacing disturbances—Veblen et al. (1980)), and (3) generate open areas to facilitate planting as an alternative to natural regeneration in years without sufficient viable seed production (Donoso and Soto 2010). Although early results seem promising, the impact of soil disturbance on chemical and physical soil characteristics, such as soil strength, water availability, bulk density, porosity and nutrients has not been investigated. Alterations of these variables can potentially modify site quality and compromise seedling survival and growth (Kozłowski 1999). Since many variables are affected by soil disturbance, a generic and inclusive variable commonly used to quantify soil disturbance is the resistance to penetration, as a surrogate of soil compaction or soil disturbance (e.g., Berger et al. 2004; Zenner et al. 2007; Puettmann et al. 2008).

Relationships between radial growth and seedling or sapling mortality have been widely focused on natural regeneration with limited consideration given to growth history, soil conditions (e.g. nutrients and water availability), microclimate conditions, and seedling age and size (Kobe 1999). Consequently, conflicting results have limited the acceptance of general patterns of tree seedling mortality as impacted by microsite conditions and silvical characteristics of the species (see Kobe 1999). Using planted seedlings with homogeneous history in terms of nursery production and size will help minimize the variability inherent in field studies (Kobe 1999), but care must be taken when extrapolating results to natural regeneration, as e.g., rooting patterns and mycorrhizae inoculation likely differ between planted and naturally regenerated seedlings.

In this study our objective was to quantify the early mortality of underplanted *Nothofagus dombeyi* and *N. alpina* as a function of two variables: recent diameter growth prior to death and soil resistance to penetration. This approach will provide information about the sensitivity of these two pioneer tree species (*N. dombeyi* evergreen and shade intolerant; *N. alpina* deciduous and mid-tolerant to shade) to resource and soil conditions found in the understory of managed forests, i.e., in canopy gaps after site preparation treatments have been applied. Specific questions were: (a) Is there a relationship between seedling mortality and recent diameter growth prior to death? (b) Does soil resistance to penetration impact mortality of these species? and (c) Does recent basal diameter growth and soil resistance to penetration improve the ability to predict seedling mortality, and does this differ among species? Early predictions of seedling mortality as impacted by heavy soil disturbance following forest operations will allow to make timely decisions (e.g. land-owners) to secure adequate regeneration, a key to successful forest management.

Materials and methods

Study site

This study was conducted in forests owned by the Neltume Carranco company on a southeast-facing gentle slope of the Mocho-Choscuenco volcano in south-central Chile

(39°35'S, 72°05'W) between 910 to 990 m a.s.l. in the sector called Piedras Negras. The forest is classified as *N. dombeyi*, *N. alpina* and *Laureliopsis philippiana* forest type (tipo forestal Coihue-Rauli-Tepa; Donoso 1981). The original old-growth forest likely had structures similar to that reported for these types of Andean forests by Veblen et al. (1980) and Donoso et al. (1986). Typically, these forests had basal area of about 100 m²/ha and a multilayered canopy dominated by emergent *Nothofagus* species (*N. dombeyi* and *N. alpina*) above a canopy of more shade-tolerant species (*Saxegothaea conspicua* and in some cases *Dassyphyllum diacanthoides* and *Laureliopsis philippiana*). More details about the typical structure, composition, and dynamics of these forests can be found in Veblen et al. (1980) and Donoso et al. (1986).

The climate of the study area is Andean polar with short and dry summers (December–March) and humid winters (June–September). The annual precipitation during the last 10 years averages 4,000 mm, which mainly falls as snow during the winter months (data from the nearby meteorological station in Neltume Carranco company). Mean annual temperature is 9 °C, with a mean of 16 °C for the warmest (February) month and 4 °C for the coldest (August) month. Extreme temperatures can range from –10 to 30 °C, and frosts events are common (50 annual frosts at 600 m a.s.l. were reported by Soto et al. (2009), in the same area.

Soils in the study area correspond to a transition between Acrudoxic Hapludand (andisol) and Andic Dystrudepts (inceptisol); both are coarse mixed and mesic soils (CI-REN 2001). The soil has a stratified structure and medium texture through the entire profile. It is acid to moderately acid (pH from 5.3 to 5.7), has an A horizon of about 20 cm deep, high organic matter content (35 %), high water retention capacity (>250 mm in 1 m depth) and low total N content (0.6 %), available P(Olsen P 20 mg Kg⁻¹), K (305 mg Kg⁻¹) and a good C/N relation (12), in addition to a low Al saturation (>2 %; Reyes 2012). The soil consists of different layers of volcanic materials such as slag and sand with a medium coarse texture (CI-REN 2001).

The study area is a 20 ha tract that was cut during summer of 2007 as a shelterwood harvest, leaving an average residual basal area of 20–30 m²/ha and 150–180 trees per hectare (Luis Molina, personal communication, Neltume Carranco company). Following harvest, increased light conditions allowed the development of dense thickets of *Chusquea culeou* in the understory that inhibited regeneration of commercial tree species, especially *N. dombeyi* and *N. alpina*. Under this scenario, soil scarification was deemed necessary to establish tree seedlings. A top-soil scarification with a bulldozer had the aim to eliminate the dense thickets of bamboo in places where the machine had access (on average one-half of the area) and to stimulate the natural regeneration of tree seedlings. The scarification removed between 20 and 40 cm of soil with typical bulldozer blade, altering chemical and physical properties of the remaining top soil. In the top 20 cm nutrient supply decreased (organic matter: 4 %, total N: 0.07 %, P (Olsen) 3.2 mg kg⁻¹, K: 19 mg kg⁻¹) and Al saturation increased (30 %). Due to top soil removal the soil increased in bulk density (0.8 ± 0.1 g cm⁻³) and resistance to penetration (1.1 ± 0.2 kg cm⁻²). More details of the effects of top-soil scarification on soil conditions are given by Reyes (2012).

Source of seedlings

Nothofagus dombeyi and *N. alpina* seeds were collected from seed-trees in the San Pablo de Tregua experimental forest of the Universidad Austral of Chile (50 km north of the study site). Seeds were soaked in a 50 ppm solution of gibberellins for 24 h and then sown in black polyethylene containers (393 seedlings m⁻²; 130 cm³ and 15 cm tall). These

containers have root trainers that consist of internal vertical ribs, which direct roots straight down to prevent spiral growth. The containers were set on frames to allow air-pruning of roots as they emerge from the containers. The substrate was composted *Pinus radiata* bark mixed with a slow-release fertilizer (18-6-12; Osmocote®; 5 kg per m³ of bark; see details in Bustos et al. 2008). Seedlings were grown in a greenhouse from the first week of September (early spring) until the end of November (mid spring), then were placed outdoors under a 50 % shade cloth, and finally hardened during the last month of the growing season (February–March; midsummer). Base fertilization was initiated once all seeds had emerged. Twice a week containers were irrigated with a growth nutrient solution made with a commercial fertilization NPK mixture following production protocols recommended by Duryea and Landis (1984); (for further details about seedling production see Bustos et al. (2008)). The morphology of seedlings selected for the study were homogeneous in size (ranged from 25 to 35 cm in height and 3–4 mm in basal diameter), thus any potential biases due to differences in initial seedlings sizes are likely minor (sensu MacFarlane and Kobe 2006).

Study design

Sixty gaps were selected (30 for *N. dombeyi* and 30 for *N. alpina*) with a minimum canopy openness of 5 %. In each gap center 15 seedlings were planted in a rectangular design with distances between seedlings reflecting gap sizes (Fig. 1). For example, in large gaps (e.g. >40 % of canopy openness) the distance between seedlings was 4 × 4 m and in some cases 5 × 4 m. In medium-sized (20–40 % of canopy openness) and small gaps (<20 % canopy openness) the distance was 3 × 3 m and 2 × 2 m, respectively. No seedlings were placed below tree crowns at gap edges (Fig. 1). The study gaps were randomly assigned to one of the two underplanted species and the gaps for both species have similar elevations and are on gentle sloped terrain (<15 %) (Table 1). The stand structure after the shelterwood cut resulted in similar canopy openness, light availability and leaf area indices in the study gaps for both species (Table 1). Seedlings were planted in the selected gaps at the end of May 2010 (late fall), before snow covered the study area. The study used a nested design, i.e., the sampling units are seedlings with their basal diameter growth and soil disturbance levels nested in gaps.

Soil measurements

Soil strength after top-soil scarification by heavy machinery on seedling growth was characterized as resistance to penetration (Kilopascals) of the mineral soil next to each selected seedling (~10 cm from root collar) with an Eijkelkamp soil cone penetrometer (American Society of Agricultural Engineers 1990). Since top-soil disturbance affects several soil characteristics, measuring the resistance to penetration has been documented as a generic and inclusive measure of soil disturbance (Berger et al. 2004; Zenner et al. 2007; Puettmann et al. 2008). Two years after seedling establishment the resistance to penetration was measured by pressing down the penetrometer with a uniform force close to ~2 cm seg⁻¹. A 2 cm² base area cone was used, and the readings were taken once the cone reaches 15 cm of soil depth (sensu Berger et al. 2004; Puettmann et al. 2008). Four measurements in all cardinal points (N, E, W, S) were taken to obtain the penetration resistance for each seedling (Fig. 1). These data are based on following assumptions and methods: (1) soil texture and moisture are similar across the study site, (2) readings were ignored when the penetrometer cone touched rocks or roots, (3) readings were taken for the

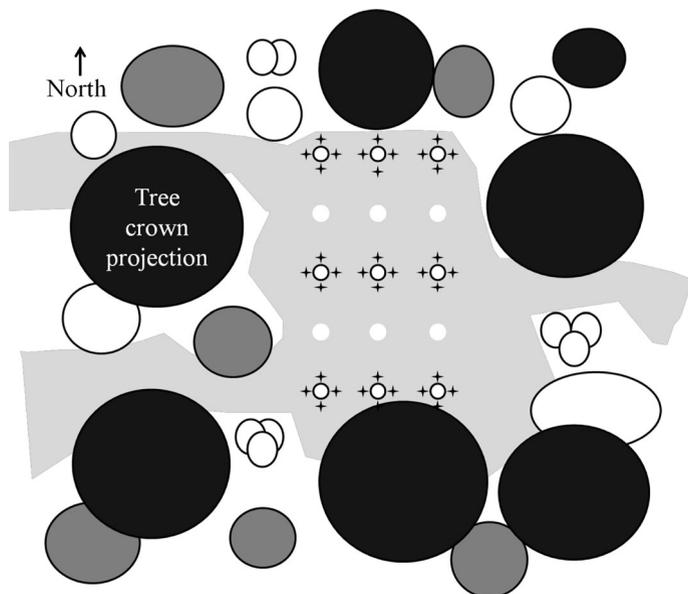


Fig. 1 Example of spatial study layout of underplanted seedlings in gaps. Seedlings are shown in *white circles*, crowns of remnant trees are shown in *black* (*Nothofagus dombeyi*), *dark grey* (*N. alpina*), and *white* (*Saxegothaea conspicua*). Scarified areas are *light grey*, note the irregular tracks of the Bulldozer). Live seedlings selected for sampling are shown in *circles with black rings* (9 seedlings per gap). Finally, crosses (4 per each seedling) correspond to locations where soil disturbances (resistance to penetration) were measured with the Eijkelkamp soil cone penetrometer

first 15 cm of depth because root systems are concentrated within this soil depth, and (4) median values were used in the analysis to minimize effects of outliers (Berger et al. 2004; Puettmann et al. 2008). The measurements were taken during two contiguous days in early fall (April), in the driest period of the year (sensu Berger et al. 2004; Puettmann et al. 2008). Resistance to penetration readings were likely around maximum values for the year at this time, best reflecting potential effects on seedling performance (sensu Ares et al. 2005).

Seedling measurements

Basal diameter at the root-collar of seedlings was measured in each dormant season (mid May) immediately after planting and during the two following years (May of 2010 and 2011). We used a Litz caliper with a precision of 0.05 mm, and the measurements were made 1 cm above ground. We measured basal diameter growth and resistance to penetration for all dead and 9 live seedlings per gap in all gaps (9 seedlings \times 30 gaps = 270 seedlings per species). Of these 9 seedlings, 3 were located in the north, center and south portions of the gaps (Fig. 1) to represent the spatial variability growing conditions (positions) in gaps. For this study, we used the basal diameter growth in the year prior to seedling mortality, which was the growth of year 1 (y_1). We assumed that impacts of nursery practices and initial seedling conditions on field performance were similar for all seedlings and had become negligible after 1 year in the field. To further ensure that mortality was induced only by the conditions after outplanting, we only considered

Table 1 General characteristics of study gaps (mean ± SD (range)) and seedlings in the study sites

Characteristic	<i>N. dombeyi</i>	<i>N. alpina</i>
Elevation (range m a.s.l.)	946–968	964–980
Slope (range %)	0–15	0–10
Canopy openness (%) ^a	28.9 ± 7.9 (9.6–50.2)	25.6 ± 7.5 (3.36–46.2)
Light availability (% full sun) ^a	46.8 ± 12.7 (13.3–73.7)	40.7 ± 14.7 (3.7–74.8)
LAI m ² m ^{-2a}	1.33 ± 0.38 (0.52–2.89)	1.46 ± 0.42 (0.81–3.64)
Sample size (all seedlings) ^b	277	287
Sample size (live seedlings)	257	257
Sample size (dead seedlings) ^c	20	30
Mortality %	7.2	12.6
Basal diameter growth in mm (live) ^d	0.36a ± 0.19 (0.05–1.00)	0.44a ± 0.28 (0.00–1.50)
Basal diameter growth in mm (dead) ^d	0.05b ± 0.04 (0.00–0.15)	0.11b ± 0.05 (0.03–0.20)
<i>P</i> values of <i>t</i> test (dead vs. live)	<0.001	<0.001
Soil strength in kPa (live)	1,346 (467–3,459)	1207b (467–3,609)
Soil strength in kPa (dead)	1,152 (516–2,162)	1821a (591–3,708)
<i>P</i> values of <i>t</i> test (dead vs. live)	>0.05	<0.001

Basal diameter growth mean ± standard deviation and ranges are presented (different letters show statistical differences between live and dead seedlings). Soil strength (measured as resistance to penetration) statistics include the median value and ranges

^a Variables were estimated from a single central hemispherical photography per gap using GLA 2.0 (Frazer et al. 1999)

^b Seedlings without mechanical, browsed or dieback damage

^c Seedlings dead during second growing season after planting

^d Represent the growth for live and dead seedlings used for mortality modeling, i.e., seedling growth during the growing season before death

seedlings without any mechanical damage, herbivory, die back, or defoliation in the analysis.

Statistical analysis

We compared the basal diameter growth (*incd*) and the resistance to penetration (*rp*) between dead and live seedlings by a paired *t* test for each species. We computed the Pearson product-moment correlation analysis (r_p) between *incd* and *rp* in order to test possible interactions. As a way of comparing the distribution of the variables *incd* and *rp* between dead and live seedlings we drew a density plot. We used logistic regression to model the probability of mortality (dichotomous variable; i.e., live or dead) of seedlings as a function of recent radial growth (*incd*); resistance to penetration (*rp*); and both variables together. In order to assess effects of the predictor variables on the probability of mortality, we fit the following logistic models:

$$\text{logit}[\pi_{y=1|x}] = \beta_0 + \beta_1 \text{incd} \tag{1}$$

$$\text{logit}[\pi_{y=1|x}] = \beta_0 + \beta_1 \text{rp} \tag{2}$$

$$\text{logit}[\pi_{y=1|x}] = \beta_0 + \beta_1 \text{incd} + \beta_2 rp \quad (3)$$

where,

$$\text{logit}[\pi_{y=1|x}] = \ln \left[\frac{\hat{\pi}_{y=1|x}}{1 - \hat{\pi}_{y=1|x}} \right] = Z \quad (4)$$

$\pi_{y=1|x}$ is the probability of the occurrence y given x (0 or 1; live or death, respectively); *incd* is the basal diameter growth prior to death; *rp* is the resistance to penetration; and β_0 , β_1 and β_2 are parameters to be estimated. If we are interested in predicting $\hat{\pi}_{y=1|x}$, we use the parameter estimates of the model being assessed using the following formula;

$$\hat{\pi}_{y=1|x} = \frac{1}{1 + e^{-z}} = \frac{e^z}{1 + e^z} \quad (5)$$

Comparisons between models were performed using the Akaike's Information Criterion AIC. The model with smaller value in the AIC statistics provides the better fit, and models within 2 AIC units have similar levels of empirical support (Burnham and Anderson 2002). As a threshold of estimated mortality we use 0.5, i.e., when $\hat{\pi}_{y=1|x} \geq 0.5$ we assume that the seedling is dead, otherwise is alive. We also computed the percentages of total correct prediction, and the sensitivity and specificity indices of the models from a contingency table of dead and live seedlings. Sensitivity corresponds to a fraction of observations that are actually dead (1 values) with a correct predicted classification (e.g., $\hat{\pi}_{y=1|x} \geq 0.5$ for dead seedlings), and on the other hand, specificity is the fraction of observation that are actually live (0 values) with a correct predicted classification (e.g., $\hat{\pi}_{y=1|x} < 0.5$ for live seedlings). All models were fitted by maximum likelihood estimation using a logit link and a binomial probability density function in the software R (R-core Team 2010). Finally, for better graphical representation of logistic models we used the R routine "logi.hist.plot{popbio}" written by de la Cruz Rot (2005).

Results

Summary of seedlings and predictor variables

Overall seedling mortality was low 2 years after outplanting, with 7.3 % for *N. dombeyi* and 12.5 % for *N. alpina*. However, for both species basal diameter growth was significantly higher in live seedlings compared to seedlings that died within the study period (Table 1). The average basal diameter growth of dead seedling was lower for *N. dombeyi* (0.05 mm) than for *N. alpina* (0.11 mm) (interspecific comparison was not tested; Table 1). Density plots illustrate that the basal diameter growth showed obvious differences between live and dead seedlings for *N. dombeyi* and *N. alpina* (Fig. 2a, b). However, live and dead *N. dombeyi* seedlings showed a diffuse pattern in density plots in terms of resistance to penetration (Fig. 2c, d). On the other hand, resistance to penetration was significantly higher for dead than live *N. alpina* seedlings ($P < 0,001$; Table 1), illustrating that dead plants were exposed to higher rates of compaction before dying. The correlation between pre-death basal diameter growth and resistance to penetration (Pearson-moment correlation analyses) was not significant in dead or in live seedlings of *N. dombeyi*. However, dead *N. alpina* seedlings showed a significant correlation ($r_p = -0.536$;

$P = 0.002$) between basal diameter growth and resistance to penetration, suggesting that these variables interacted to influence mortality patterns.

Mortality models as a function of growth and resistance to penetration

The best prediction of the mortality probability for *N. dombeyi* was obtained using only basal diameter growth as a predictor variable ($P < 0.001$, Table 2). In the same way, the probability of mortality in *N. dombeyi* was high for seedlings with slow basal diameter growth (<0.05 mm), and was lower for trees with faster growth (Fig. 3a). For instance, an increase in basal diameter growth from 0 to 1.5 mm reduced the probability of mortality from 99 to 6 % in *N. dombeyi* (Fig. 3a), and from 97 to 30 % in *N. alpina* (Fig. 3b).

Additional models were fitted to evaluate the impact of resistance to penetration (Fig. 3c, d). *N. dombeyi* seedlings were not affected by resistance to penetration ($P > 0.05$). A tendency that lower resistance to penetration indicated higher probability of mortality was present, but not statistically significant (Fig. 3c). The probability of mortality for *N. alpina* was significantly greater with increasing resistance to penetration (Table 2; Fig. 3d) and a maximum probability of mortality close to 50 % occurred at soil strength values of 4,000 kPa.

Models including the basal diameter growth and resistance to penetration for *N. dombeyi* and *N. alpina* had lower Log likelihood compared to models containing only basal diameter growth (Table 2). However, AIC values were very similar for both sets of models and both species (Table 2). Also, models with both variables had non-significant parameters ($\hat{\beta}_2$) associated with resistance to penetration (Table 2). These results may be partially influenced by collinearity, due to the negative significant correlation between both predictive variables (Fig. 2d). For all these reasons, we decided to only test the performance of models with growth as a predictor variable.

The predictive abilities of the best models were excellent for both species (Table 3). The percentages of correct classification were high (94.4 for *N. dombeyi* and 90.1 % for *N. alpina*). Similarly, *N. dombeyi* had high sensitivity (% of correct classification of dead seedlings) and specificity (% of correct classification of live seedlings) respect to *N. alpina*. Therefore, the better prediction was obtained for *N. dombeyi* (Table 3).

Discussion

In this study we reported early mortality patterns of two pioneer tree species planted under a partial canopy of a *Nothofagus* old-growth forests. Seedlings were planted in areas with overstory gaps, no understory competition, and where bulldozer had caused variable levels of soil compaction. These experimental conditions partially replicate those caused by natural large-scale disturbances in the Andes, where landslides following earthquakes or volcanic eruptions uncover mineral soil (Veblen and Ashton 1978). Survival was very high after 2 years for both species. The probability of mortality fitted by logistic regression had a high goodness of fit using only basal diameter growth prior to seedling death for *N. dombeyi* and *N. alpina*, whereas the variable soil compaction did not significantly contribute to explain seedling mortality period. The strength of basal diameter growth as an indicator of future mortality was consistent with several studies that have used this variable as a surrogate of carbon balance in predictions of plant mortality in early stages of seedling

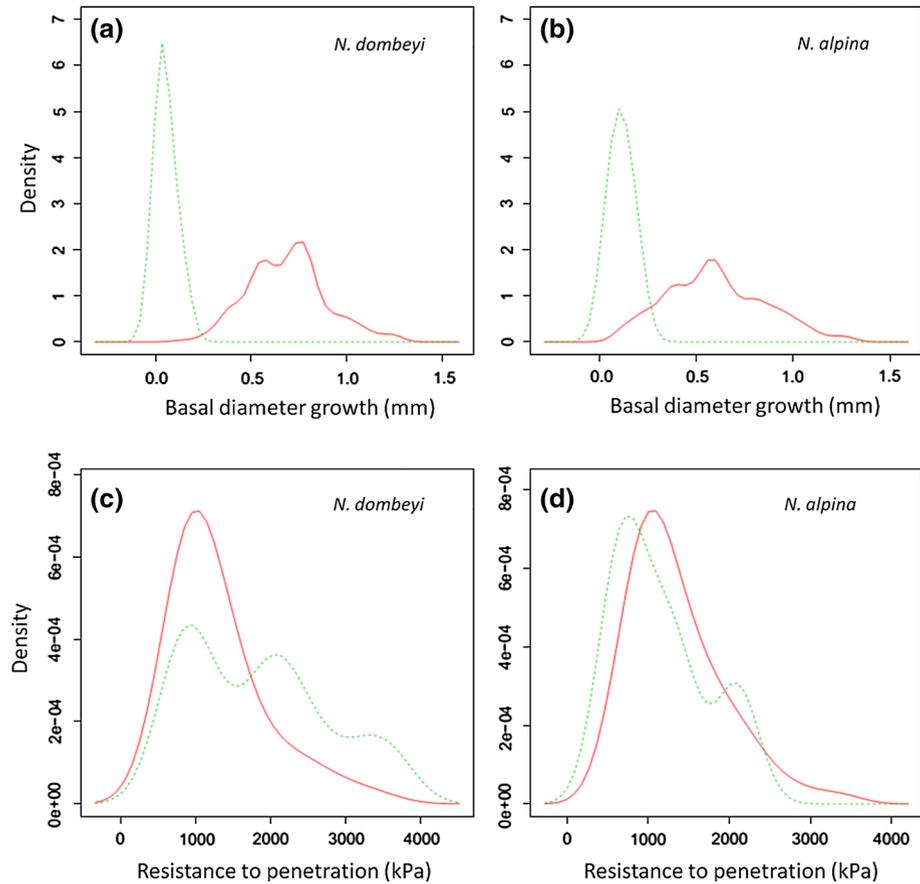


Fig. 2 Density plots for basal diameter growth and resistance to penetration for live (continuous red lines) and dead (dashed green lines) seedlings for *N. dombeyi* (a, c) and *N. alpina* (b, d). (Color figure online)

(Kobe 1999) and sapling development (e.g., Kobe et al. 1995; Kobe and Coates 1997; Löff et al. 2007).

The study shows that species-specific mortality patterns were a function of different relationships between mortality and basal diameter growth, and as such expands on the long-standing discussion about the role of competition in determining tree mortality (Peet and Christensen 1987; Waring 1987). For similar growth rates, mortality differed by more than two orders of magnitude between species. This suggests that shade-tolerant rankings designed to reflect the growth responsiveness to light levels (Holste et al. 2011) do not necessarily imply a higher capacity of species to tolerate stressful condition and resist death at low growth rates. Our findings confirm that the diameter growth–mortality relationship is not simply an extension of the shade–tolerance rankings (Kobe et al. 1995; Kobe 1999; Kneesshaw et al. 2006). This may be partially due to different responses of species to above- and various below-ground resource levels (Davis et al. 1999), for example as reflected in biomass allocation patterns (Canham et al. 1996). Alternatively, or

Table 2 Estimated parameters and standard errors (in parenthesis) of the logistic regression equations, including model Log-likelihood and AIC statistics

Species	Model	$\hat{\beta}_0$	$\hat{\beta}_1$	$\hat{\beta}_2$	Log likelihood	AIC
<i>N. dombeyi</i>	Growth	8.482** (4.858)	-52.179* (33.21)		-2.804***	9.609
	Resistance to penetration	-1.699** (0.610)	-0.0007 ns (0.0005)		-70.668 ns	145.338
	Growth + resistance to penetration	20.738 ns (19.932)	-88.397 ns (73.832)	-0.006 ns (0.008)	-2.166**	10.332
<i>N. alpina</i>	Growth	4.153*** (0.960)	-26.739*** (5.657)		-28.136***	60.273
	Resistance to penetration	-3.505*** (0.450)	0.001*** (0.000)		-89.414***	182.828
	Growth + resistance to penetration	6.446*** (1.748)	-31.140*** (6.997)	-0.0008 ns (0.001)	-26.152***	58.305

ns no significant, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$

in addition, these response patterns may be due to the species' responses to stressors, which may not act in synchronicity with shade tolerance (Packer and Clay 2000). For example, Niinemets and Valladares (2006) showed that shade tolerance is inversely related to the ability of species to tolerate stressors, such as drought or water logging. Their review shows that a great number of species traits apparently interact to determine species response to stress, including crown architecture, leaf phenology, phenotypic plasticity and plant ontogeny (see Valladares and Niinemets 2008 and references therein). Thus, the discussion about shade tolerance may provide insight into growth responses, but our results suggest that information about shade tolerance may not be sufficient to predict mortality patterns of species when other stressors are present (Valladares and Niinemets 2008).

Physiological or morphological adaptation mechanisms to resist stress and mortality have not been studied in these *Nothofagus* species. But, an indirect inference from *Nothofagus nitida* (an evergreen and emergent tree species) could help understand the adaptation of *Nothofagus* to stress. This species has a similar physiognomy, but a smaller maximum size than *N. dombeyi* (e.g. height and diameter). *N. nitida* has a high "light acclimation" at the leaf level and can tolerate more shade in early years (e.g., seedlings) than in later successional stages (Coopman et al. 2008). Therefore, we can assume that in these species the shade tolerance changes with tree ontogeny (sensu Boyden et al. 2009), and seedlings can stay alive with marginal carbon balances in early years (Coopman et al. 2008). In addition, ontogenetic variation, i.e., small plants are more adaptable or plastic to light variation (e.g., low-light) than larger plants, is more pronounced in shade-intolerant than in shade-tolerant species (Lusk et al. 2008). This ontogenetic pattern implies that findings from seedlings, such as the current study provides, should not simply be extrapolated to larger trees (Valladares and Niinemets 2008).

Mortality patterns in *N. alpina* were significantly influenced by soil conditions, with high values of resistance to penetration (e.g., 2,000 kPa) causing higher rates of mortality. This is consistent with several studies that report that *N. alpina* grows better on soils with low bulk density, high aeration, and high nutrient availability (Donoso et al. 1999, 2011, 2013; Donoso 2006; Reyes 2012). *N. dombeyi*, on the other hand, has been labeled as a pioneer species that establishes after large-scale disturbances in Chile and Argentina

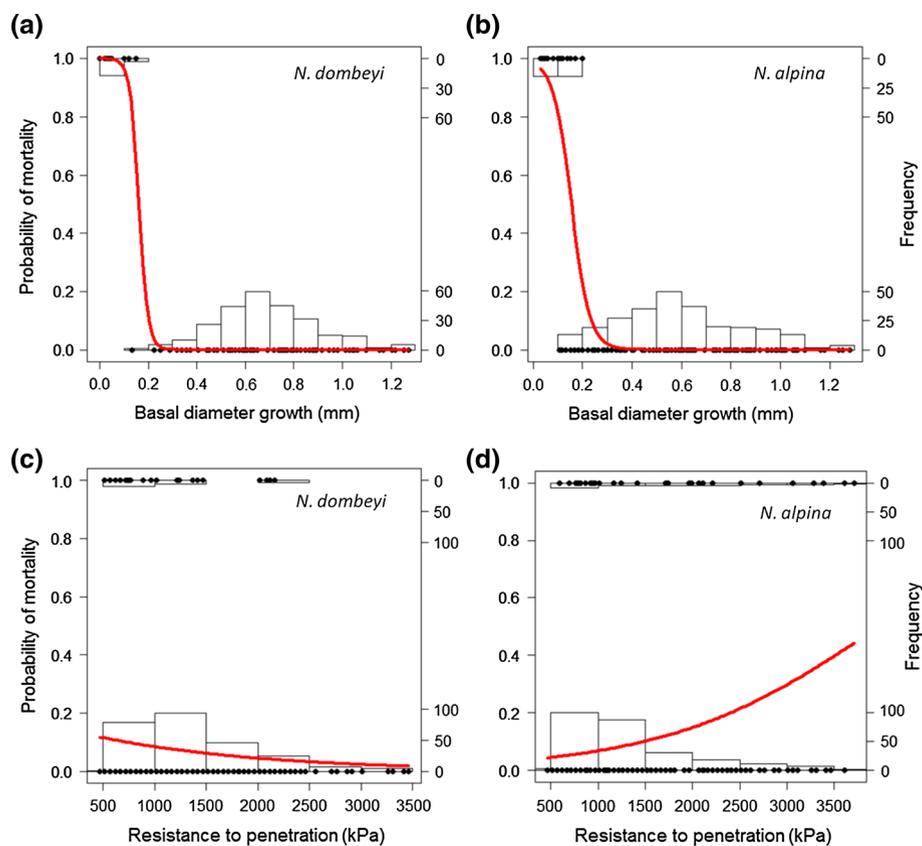


Fig. 3 Logistic models predicting probability of mortality as a function of recent basal diameter growth and resistance to penetration for *N. dombeyi* (a, c) and *N. alpina* (b, d). Black dots show seedling conditions: dead (1) or live (0); their respective frequency is shown in bars for each predictor variable. Red lines show the fitted models. (Color figure online)

Table 3 Performance of best supported logistic models (all statistics in percentage)

Species	Model	Correct model prediction	Sensitivity ^a	Specificity ^b
<i>N. dombeyi</i>	Growth	94.4	91.6	95.6
<i>N. alpina</i>	Growth	90.1	70.7	91.6

^a Corresponds to the power of the model to identify the dead seedlings or 1 values of the model prediction

^b Corresponds to the power of the model to identify the live seedlings or 0 values

(Veblen et al. 1980; Donoso 1993; 2006), and as a species that can tolerate low soil fertility and grows well on a wide variety of sites (Donoso et al. 1999; Donoso 2006). We did not find any indication of frost damage, even though this species is very sensitive to frosts in early spring and summer in young stages of plantations, and seems to need partial protection or shelter in sites above 600 m a.s.l. in the Chilean Andes (Donoso et al. 2007; Soto et al. 2009; Donoso and Soto 2010). Even though we did not assess seedling quality directly (Mattson 1997), the overall success of the planting suggests that the seedling

quality was very high and seedling had high vigor, little damage, (Burdett 1990) and sufficient root growth potential (Grossnickle 2005), at least in adequate soil conditions.

Management implications

Mechanical site preparation is currently utilized as an important tool in underplanting and restoration efforts, and considered a viable option to improve the regeneration of desired tree species in forest ecosystems (Löf et al. 2012; Oliet and Jacobs 2012), such as the Andes. In these settings, the top-soil scarification practices in disturbed old-growth forests of the Chilean Andes, is aimed to control dense carpets of bamboo, but can also stimulate natural regeneration (e.g. for pioneer species on mineral soil) and generate open areas for underplanting. Due to the lack of natural regeneration in many years resulting from natural cyclical seed production in adult trees of *Nothofagus* species, especially in *N. alpina* (Donoso 1993; Donoso and Soto 2010) underplantings may be necessary to ensure consistent regeneration results. Underplanted seedling had high survival and this study documented the effectiveness of underplanting and soil scarification in high-elevation sites in the Andes. *N. dombeyi* seedlings responses were more plastic, and this species can be recommended for plantings in areas with higher equipment traffic without concerns about high mortality rates. On the other hand, *N. alpina* was sensitive to soil conditions and should be preferentially planted on microsites that were not impacted heavily by equipment traffic. In practice, lower compaction, conditions that are relatively better for *N. alpina*, occur on the edges of the gaps, and therefore this species should be located preferentially in this positions, leaving *N. dombeyi* to be planted in gap centers.

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