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ARTICLE

Light availability and soil compaction influence the growth of underplanted *Nothofagus* following partial shelterwood harvest and soil scarification

Daniel P. Soto, Pablo J. Donoso, Christian Salas, and Klaus J. Puettmann

Abstract: We evaluated effects of topsoil scarification by heavy machinery on growth of two valuable, shade-intolerant tree species — *Nothofagus dombeyi* (Mirb.) Oerst. (evergreen and considered to be very plastic to different soil fertility levels) and *Nothofagus alpina* (Poepp. & Endl.) Oerst. (deciduous and considered to be sensitive to soil fertility) — seedlings that were underplanted in *Nothofagus* old-growth forests, which were subjected to shelterwood cuttings without the final cut in the Chilean Andes. We compared tree basal diameter growth as it responds to light availability and soil compaction (as measured by resistance to penetration) by fitting a growth model based on the Michaelis–Menten equation. Predicted growth of *N. dombeyi* was greater than *N. alpina* in high and low light levels; however, there were no significant differences between the species. Both species showed significant differences at high levels of penetration resistance (>2000 kPa). Differences for *N. dombeyi* occurred above ~40% in total light, and differences occurred for *N. alpina* above ~20% in total light. However, they were not different when compared at low and intermediate levels of penetration resistance. The results suggest that partial shelterwood cuts may provide adequate light levels to achieve appropriate growth of underplanted *Nothofagus* seedlings. However, if regeneration of *N. alpina* is desired, scarification of topsoil needs to be implemented with more caution in canopy openings, as traffic and soil removal by heavy machinery can have detrimental effects on growth of this species and other species that are more sensitive to soil compaction.

Key words: Michaelis–Menten, shade tolerance, soil resistance to penetration, stress conditions, underplanting.

Résumé : Nous avons évalué les effets du scarifiage de la couche supérieure du sol avec de la machinerie lourde sur la croissance de semis de deux espèces d'arbre précieuses et intolérantes à l'ombre, *Nothofagus dombeyi* (Mirb.) Oerst. (espèce à feuilles persistantes qui est considérée comme étant très plastique à différents niveaux de fertilité du sol) et *Nothofagus alpina* (Poepp. & Endl.) Oerst. (espèce décidue qui est considérée comme étant sensible à la fertilité du sol). Ces semis ont été plantés sous le couvert de vieilles forêts de *Nothofagus* soumises à des coupes progressives sans la coupe finale dans les Andes chiliennes. Nous avons relié la croissance en diamètre au collet des semis à la disponibilité de la lumière et à la compaction du sol (mesurée par la résistance à la pénétration) en ajustant un modèle de croissance fondé sur l'équation de Michaelis–Menten. La croissance prédite de *N. dombeyi* était plus grande que celle de *N. alpina* sous des intensités lumineuses forte et faible, mais sans qu'il y ait de différences significatives entre les espèces. Des différences significatives ont été observées chez les deux espèces lorsque la résistance à la pénétration était élevée (>2000 kPa). Les différences ont été observées chez *N. dombeyi* au-dessus de ~40 % de la lumière totale alors qu'elles l'ont été au-dessus de ~20 % dans le cas de *N. alpina*. Toutefois, aucune différence n'a été observée lorsque la résistance à la pénétration était faible ou intermédiaire. Ces résultats indiquent que les coupes progressives peuvent procurer des niveaux de lumière adéquats pour obtenir une croissance appropriée des semis de *Nothofagus* plantés sous couvert. Cependant, si on désire que la régénération de *N. alpina* s'établisse, le scarifiage de la couche supérieure du sol doit être réalisé plus prudemment dans les ouvertures du couvert parce que la circulation et l'enlèvement du sol par la machinerie peuvent avoir des effets néfastes sur la croissance de cette espèce et d'autres qui sont plus sensibles à la compaction du sol. [Traduit par la Rédaction]

Mots-clés : Michaelis–Menten, tolérance à l'ombre, résistance du sol à la pénétration, conditions de stress, plantation sous couvert.

Introduction

Silvicultural practices manage canopy structures with the objective of regenerating and reallocating growing space for desired crop species (Nyland 2002; Puettmann et al. 2008*a*). Questions on which resource levels or environmental factors most significantly influence seedling performance have been a topic of discussion in the last decades (e.g., Walters and Reich 1997; Kobe 2006). At moist sites in temperate forests, light availability seems to be the most important factor that determines seedling establishment, survival, and growth (e.g., Canham et al. 1990). Understanding the response of seedlings to variations in light levels is fundamental to predict effects of forest management practices on future ecosystem development (Carter and Klinka 1992; Coates and Burton 1999); they vary by species due to species-specific light requirements (Canham et al. 1990; Pacala et al. 1994; Carter and Klinka 1992). A species' shade tolerance determines the performance of seedlings under low-light conditions and eventually can affect the composition and structure of forest stands (Pacala et al. 1996). The chance of seedlings and saplings of a given species to

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reach the canopy is often determined by their performance in young stages (Canham 1988; Kobe 1999); however, recent studies have shown that even in temperate forests, other resources such as nutrients and water availability can also have a significant influence on the performance of these young trees in the understory (Walters and Reich 1997; Finzi and Canham 2000; Kobe 2006), even affecting their shade tolerance (Carter and Klinka 1992; Drever and Lertzman 2001).

In the Andes of south–central Chile, environmental conditions apparently have not been suitable for successful natural regeneration after harvesting highly productive and valuable *Nothofagus*-dominated forests (*Nothofagus dombeyi* (Mirb.) Oerst. and *Nothofagus alpina* (Poepp. & Endl.) Oerst.). For decades, these forests have been harvested either through selective cuts (cut the best and leave the worst; sensu Nyland (2002)), exploitation, or incomplete shelterwood cuts, where the final cut has not been conducted. This incomplete or partial shelterwood could be confused with irregular shelterwood, but the latter is aimed to regenerate tree species that are tolerant or mid-tolerant to shade (Raymond et al. 2009), whereas in the Chilean Andes, the objective is to regenerate the light-demanding *Nothofagus* species. Regardless of prescriptions, harvesting operations have resulted in high-graded forests, in the sense that these two *Nothofagus* species, the most valuable tree species in the Andes, have been unable to regenerate. The lack of tree regeneration may be partially caused by the cyclic nature of seed production of *Nothofagus* (Donoso 1993). However, another explanation is that invasive dense patches of bamboo (*Chusquea* spp.) in the understory are very competitive and inhibit tree regeneration of these *Nothofagus* species (Veblen et al. 1981; González et al. 2002; Muñoz and González 2009).

Some silviculturists in Chile have opted to manipulate light conditions to reduce or delay the dominance and growth of competing understory species such as bamboo (sensu Smidt and Puettmann 1998; Coates and Burton 1999; Maas-Hebner et al. 2005) and thus improve the success when regenerating these forests. This approach by itself, however, has not been successful in the Chilean Andes (Luis Molina (former manager in the Neltume-Carranco forest company between 1999 and 2014), personal communication, March 2011). A technique that has been applied is scarification of topsoil with heavy machinery (e.g., bulldozer trails in harvested areas), which basically eliminates the rhyzomes of *Chusquea* spp., the main competing species for *Nothofagus*. In addition, this technique creates microsites that provide better seed beds for natural regeneration of *Nothofagus* species (Veblen et al. 1981) and (or) better planting spots. This silvicultural practice has been implemented in selected locations in Chile with good results in terms of establishing regeneration (Reyes et al. 2013), but its specific impacts on seedling growth have not been studied.

Any operation with heavy machinery in forests, including soil scarification, has the potential to cause soil compaction, as reflected in decreased porosity and increased bulk density and resistance to penetration (sensu Kozlowski 1999). These impacts may limit access to nutrients and water by roots and thus compromise seedling establishment, survival, and growth (Kozlowski 1999; Berger et al. 2004; Resco de Dios et al. 2005; Yoshida et al. 2005). However, specific effects of soil compaction on plant growth are very complex and can vary from beneficial to detrimental (Kozlowski 1999; Ares et al. 2005). On most soils, studies suggest harmful effects of soil compaction on plant growth (Greacen and Sands 1980; Kozlowski 1999; Ares et al. 2005). For instance, 2 MPa of resistance to penetration (a surrogate of soil compaction) has been considered to be an upper threshold above which there is a negative influence on plant growth (Greacen and Sands 1980; Kozlowski 1999). On the other extreme, soils with very low resistance to penetration (~0.6 MPa) also have detrimental effects on plant growth because high porosity increases the aerated conditions, and the soil can desiccate during dry spells in the summer season (Bassett et al. 2005). In between, intermediate values of resistance to penetration (e.g., around 1 MPa) provide conditions suitable to plant growth (Kozlowski 1999; Ares et al. 2005; Bassett et al. 2005). The actual thresholds are obviously a function of the specific measurement tool and conditions and vary considerably by species according to their tolerance to soil compaction (Kozlowski 1999; Bassett et al. 2005) and other traits such as crown architecture, phenotypic plasticity, or plant ontogeny (Arvidsson 1999).

In Chile, there is little information about effects of soil compaction on tree growth of native species; however, the silvics of some species illustrate that they differ in terms of their growth in various soil conditions (Donoso 2006). *Nothofagus dombeyi* is known for its plasticity and grows well in a wide range of soil conditions (Donoso et al. 2005, 2006*a*; Soto et al. 2014). In contrast, *N. alpina* is usually restricted to well-aerated, coarse-textured, and deep soils (Donoso et al. 1993, 1999, 2006*b*). Both species naturally regenerate after large-scale disturbances in the Andes of southern South America (Chile and Argentina) and create open canopy conditions, sometimes exposing volcanic slag (Donoso 1993; Veblen et al. 1996), i.e., well-aerated and poorly developed soils (Inceptisols). Overall, both species are adapted to growing in well-aerated soils, but their specific performance under these conditions has not been evaluated.

In this study, we evaluated the impacts of a wide range of light and soil compaction conditions created after harvesting and soil scarification on the growth of underplanted seedlings of *N. dombeyi* and *N. alpina*. We expect that the wide range of conditions created on the study site will highlight species-specific responses to this forest management practice. Therefore, the objectives of this study were to (*i*) evaluate and quantify the short-term performance of underplanted *N. dombeyi* and *N. alpina* as a function of light availability and (*ii*) evaluate and quantify the influence of soil compaction (low, intermediate, and high levels of resistance to penetration) on seedling performance of these species under a wide range of light levels. We hypothesized that the performance of both species will decline under low-light conditions but that the magnitude of decline will be greater for *N. dombeyi* due to its higher shade-intolerant character compared with *N. alpina* during early ontogenetic stages. We also hypothesized that *N. alpina* (typically found on sites with higher soil fertility) will be more sensitive to soil compaction than *N. dombeyi* (typically found on sites with lower soil fertility).

Methods

Study site

This study was carried out on a southeast-facing gentle slope (<15%) of the Mocho-Choscuenco volcano in south–central Chile (39°35′S, 72°05′W) between 910 and 990 m above sea level (a.s.l.). The forest structure is composed of *N. dombeyi*, *N. alpina*, and *Laureliopsis philippiana* (Looser) R. Schodde (Donoso 1981; Donoso et al. 1986). The original old-growth forest likely had a structure similar to that reported for these types of Andean forests by Veblen et al. (1980, 1981). Typically, these forests have basal area close to 100 $m^2 \cdot ha^{-1}$ and a multilayered canopy dominated by emergent *Nothofagus* species (i.e., *N. dombeyi* and *N. alpina*) above a canopy of shade-tolerant species (i.e., *Saxegothaea conspicua* Lindl., *L. philippiana*, and (or) *Dassyphylum diacanthoides* (Less.) Cabrera). More details about structure, composition, and dynamics of these forests can be found in Veblen et al. (1981) and Donoso et al. (1986).

The climate is Andean polar, with short, dry summers (December–March) and humid winters (June–September). The annual precipitation is between 3000 mm and 3500 mm (Oyarzún et al. 2011), with most of it falling as snow during winter months. The mean annual temperature is 9 °C, with 4 °C and 16 °C mean temperatures for the coldest (August) and warmest (February) months, respectively. Extreme temperatures can range from less than –10 °C to more than 30 °C (Soto et al. 2009). Frost events must be common at the elevation of the study site considering that 30–50 annual frosts occur from August through September at lower elevations (550 m a.s.l.) in this same region (Soto et al. 2009).

Soils on the study site correspond to a transition between Acrudoxic Hapludand (Andisol) and Andic Dystrudepts (Inceptisol); both are coarse-mixed, mesic soils (Centro de Investigación de Recursos Naturales (CIREN) 2001), which have a stratified structure and medium textures (sand: 60%, silt: 45% and clay: 5%; Reyes et al. 2014) through the entire profile. These soils range from acidic to moderately acidic (pH 5.3 to 5.7, respectively) and have an A horizon that is about 20 cm deep, a high organic matter content (35%), a high water retention capacity (>250 mm in 1 m depth), a good carbon (C) to nitrogen (N) relation (12), and low values in terms of total N content (0.6%), available phosphorus (P) (Olsen P, 20 $mg·kg^{-1}$), potassium (K) (305 $mg·kg^{-1}$), and aluminum (Al) saturation (2%) (Reyes et al. 2014). The soil consists of different layers of volcanic materials such as slag and sand with a medium coarse texture (Centro de Investigación de Recursos Naturales (CIREN) 2001).

Harvest and site preparation

The forest on the study site was cut during summer of 2007 with a shelterwood harvest, leaving an mean residual basal area of 20–30 $m^2·ha^{-1}$ and 150–180 $trees·ha^{-1}$ (Luis Molina, personal communication). However, the final cut was never conducted, i.e., this was a partial shelterwood cut. In spite of leaving this basal area, after the shelterwood cut was applied, dense thickets of *Chusquea culeou* É.Desv., considered a shade-tolerant bamboo species (Veblen 1982; González et al. 2002), developed quickly in the understory, and 4 years after the cut there was very little tree regeneration. It was then when soil scarification was carried out, expecting that this would allow for successful tree regeneration. The scarification removed between 20 cm and 40 cm of soil, altering chemical and physical properties of the remaining topsoil (Reyes et al. 2013, 2014). In the top 20 cm of the scarified areas, nutrient supply decreased (organic matter, 4%; total N, 0.07%; P (Olsen), 3.2 $mg·kg^{-1}$; K, 19 $mg·kg^{-1}$). In contrast, Al saturation (30%) and bulk density and resistance to penetration increased in unscarified areas (means, 0.8 $g·cm^{-3}$ and 1.1 MPa, respectively). More details of the effects of topsoil scarification on soil features are given by Reyes et al. (2013, 2014).

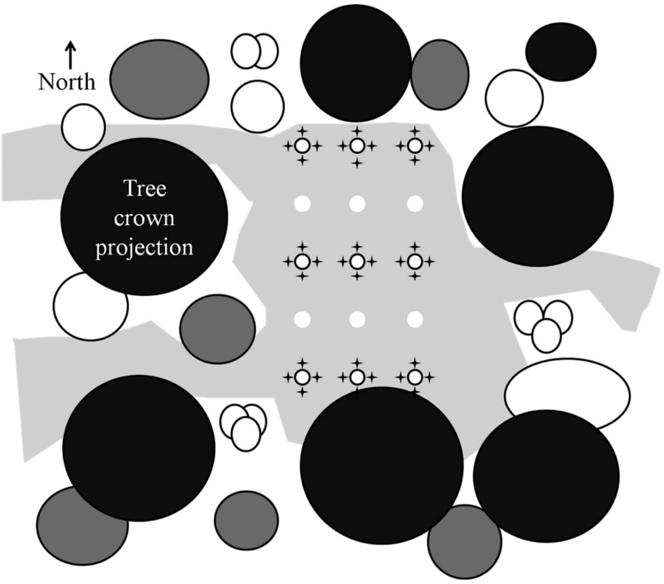
Source of seedlings

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 at 700 m a.s.l.). Seeds were produced in black polyethylene containers (393 $seedlings·m^{-2}$; container, 130 cm^3 and 16 cm tall). The substrate was composted *Pinus radiata* D. Don bark mixed with a slow-release fertilizer (18N–6P–12K; Osmocote; 5 kg per m^3 of bark). The 1-year seedling production protocols followed the recommendations of Duryea and Landis (1984). Further details about seedling production of *Nothofagus* are given by Bustos et al. (2008) and Soto et al. (2014). Seedlings selected for the study were homogeneous in size (height ranged from 25 cm to 35 cm and root-collar diameter ranged from 3 mm to 4 mm), thus any potential biases due to differences in initial seedlings sizes are likely minor (sensu MacFarlane and Kobe 2006).

Planting design and environmental and resource measurements

Sixty canopy openings, in which understory vegetation was removed through scarification, were selected for planting. The areas of planting were defined as areas with a canopy openness (uncovered fraction of the hemispherical view estimated through Gap Light Analyzer (GLA); Frazer et al. 1999) after harvesting at least 5%. The range of canopy openness planted with *N. dombeyi* (mean ± standard deviation (SD), 28.9%±7.9%; range, 9.6%–50.2%) and *N. alpina* (mean ± SD, 25.6%±7.5%; range, 5.36%–43.2%) was similar.

Fig. 1. Schematic layout of underplanted seedlings in canopy openings. Seedlings are shown as white circles, and sampled seedlings are shown as white circles with black rings (nine seedlings per canopy opening). Crosses (four around each seedling) correspond to the point at which resistance to penetration was measured with an Eijkelkamp cone penetrometer. For illustration, crowns of remnant trees are shown in black (*N. dombeyi*), dark grey (*N. alpina*), and white (*S. conspicua*). The scarified area is in light grey with the irregular tracks of the bulldozer.



In each canopy opening, 15 seedlings were planted in a rectangular layout, with distances between seedlings reflecting canopy opening sizes (Fig. 1). For instance, in large canopy openings (e.g., >40% of canopy openness), the distance between seedlings was 4 m × 4 m and in some cases 5 m × 4 m. In medium (canopy openness, 20%–40%) and small (canopy openness, <20%) canopy openings, the distance was 3 m × 3 m and 2 m × 2 m, respectively. No seedlings were placed beneath tree crowns at canopy opening edges (Fig. 1). Thirty forest canopy openings were planted with each species. Seedlings were planted at the end of May 2010 (i.e., late fall, before snow covered the study area).

Light availability

We took nine photographs per forest opening during the second growing season, one at the apex of each selected seedling using a Coolpix 4500 digital camera (Nikon Corporation, Japan) with a fisheye Nikkor (8 mm) lens that has a 182° field of view (Fig. 1). Photographs were taken under homogeneous diffuse sky light conditions near the middle of the growing seasons, and light index was calculated using the GLA 2.0 software (Frazer et al. 1999) as an indicator of light availability during the growing season (Messier and Puttonen 1995; Parent and Messier 1996; Lieffers et al. 1999). Light availability was estimated as total radiation (a combination of diffuse and direct beam radiation) and calculated as percentage of growing season (e.g., 1 October – 30 March) incident radiation (% transmitted total radiation) (Frazer et al. 1999). Some input parameters used in the GLA were the solar constant (1370 $W·m^{-2}$), cloudiness index (0.5), spectral faction (0.45), beam fraction (0.85), clear sky transmission coefficient (0.65), and standard overcast sky-regions brightness.

Measurement of soil compaction

Topsoil scarification by heavy machinery was characterized as resistance to penetration (kPa) on mineral soil next to each selected seedling (~10 cm from root collar) with a hand-held electronic cone penetrometer (Eijkelkamp Agrisearch Equipment,

Table 1. Characteristics of seedlings, light availability, and soil compaction and absolute growth in the period 2011–2012 in *d* (root-collar diameter) and *h* (stem height).

Species	*n*	*d* (cm)	*h* (cm)	Light availability (% transmitted radiation)	Soil compaction (kPa)
Nothofagus dombeyi	257	0.36±0.19 (0.05–1.00)	32.58±17.38 (0.00–97.00)	46.8±12.7 (13.3–73.7)	1346.8 (467.1–3459.6)
Nothofagus alpina	238	0.44±0.28 (0.00–1.50)	30.36±18.82 (0.00–96.40)	40.7±14.7 (3.7–74.8)	1207.2 (467.2–3609.2)

Note: Light availability, *d*, and *h* are presented as mean values ± standard deviation, with the range in parentheses. Median values are presented for soil compaction (i.e., resistance to penetration), with the range in parentheses. *n*, sample size.

Giesbeek, the Netherlands) (American Society of Agricultural Engineers 1990). As topsoil scarification affects several soil variables, measuring resistance to penetration has been documented as a generic and inclusive measure of soil compaction (Kozlowski 1999; Berger et al. 2004; Ares et al. 2005; Zenner et al. 2007; Puettmann et al. 2008*b*; Soto et al. 2014). Resistance to penetration was measured by pressing down the penetrometer with a uniform force close to ~2 cm·second^{-1}. A 2 cm^2 base area cone was used, and readings were taken once the cone reached 15 cm of soil depth (sensu Puettmann et al. 2008*b*). Four measurements (one at each cardinal point, i.e., north, east, west, and south) were obtained for each seedlings (Fig. 1). This methodology is based on the assumption that soil texture and moisture are similar across the study site. Readings were taken for the first 15 cm of the soil, because we assumed that root systems are concentrated within this depth and resistance to penetration measurements would be highest in this layer (Berger et al. 2004; Puettmann et al. 2008*b*). Readings were ignored when the penetrometer cone hit rocks or roots. The median value was used for each seedling to minimize effects of extreme readings and readings that were influenced by hitting, e.g., fine roots. Soil measurements were taken during two contiguous days in early fall (April), which was 2 years after planting in the driest period of the year (sensu Berger et al. 2004; Puettmann et al. 2008*b*), when differences in soil moisture were considered smallest, e.g., between gaps and understory settings. Resistance to penetration readings were likely around maximum values for the year at this time, best reflecting potential effects of stressful conditions for seedling growth (sensu Ares et al. 2005).

Seedling measurements

The following measurement protocols were implemented at the end of the first two growing seasons, i.e., in May 2011 and May 2012. We selected nine live seedlings per canopy opening (9 seedlings × 30 canopy openings = 270 seedlings per species), where three seedlings were located in each of the northern, central, and southern portions of the canopy openings to represent the spatial variability of growing conditions in openings in terms of light availability (Fig. 1). For each seedling, we measured root-collar diameter (*d*; cm, measured at 1 cm above the ground) using a digital caliper (±0.01 mm of precision; Litz Professional, Germany) and total seedling height (*h*; cm) using a manually graduated tube. In addition, we took hemispherical photos and measured resistance to penetration for each seedling as described above. All seedlings with mechanical damage, herbivory, dieback, or defoliation or that were dead were not considered in the analysis, because such reductions in leaf area can produce reductions in growth not related to light availability or soil compaction (Table 1).

Statistical analyses

All analyses were conducted separately for each species. We used relative basal diameter growth rate (RGR) as the response variable in our models, which was computed as follows:

$$\text{(1)} \qquad \text{RGR} = \frac{\ln d_1 - \ln d_0}{t_1 - t_0}$$

where d_0 and d_1 are the root-collar diameters at the beginning (t_0) and at the end (t_1) of a growing season, respectively. Only the second-year (i.e., 2012) growth was used in the analyses to minimize possible effects from nursery operations, planting stress, and acclimation to field conditions (sensu Kobe 1999). We view RGR of root-collar diameter as an integrated measure of whole-plant carbon balance that has been shown to be sensitive to light availability (Pacala et al. 1994; Finzi and Canham 2000). On the other hand, this equation reduced the internal variation of the data and increased that normality of the data (MacFarlane and Kobe 2006).

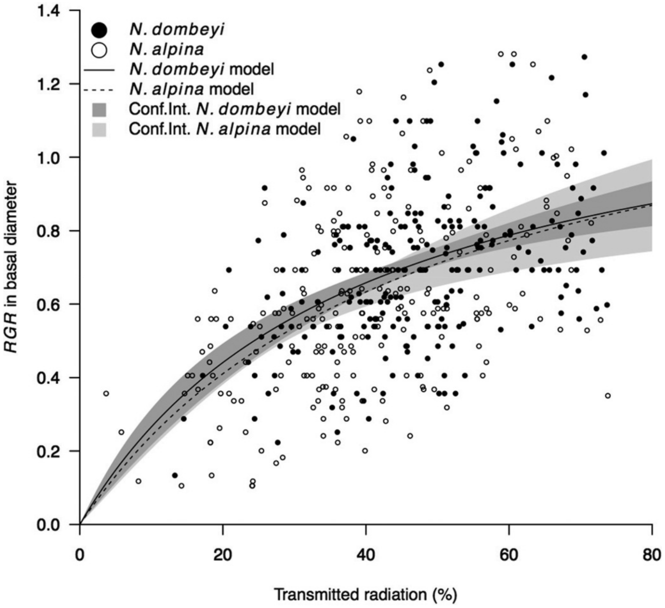


Fig. 2. Observed values (circles) and fitted general models (lines) for the relative growth response in basal diameter as a function of light availability. Areas in the grey shading are the 95% confidence intervals (Conf.Int.) for each species.

We modeled the relationship between seedling RGR and light using the Michaelis–Menten equation (sensu Pacala et al. 1994), which has been widely used in similar studies (e.g., Pacala et al. 1994; Coates and Burton 1999; Drever and Lertzman 2001; Kobe 2006). The model parameters are easily interpreted and allow statistical testing of interspecific differences in growth responses as a function of light levels (sensu Pacala et al. 1996; Coates and Burton 1999). The Michaelis–Menten model is as follows:

$$\text{(2)} \qquad \text{RGR}_i = \frac{\alpha L_i}{(\alpha/\beta) + L_i} + \varepsilon_i$$

where RGR_i and L_i are the relative growth rate of basal diameter and light level for the *i*th seedling, respectively, α and β are parameters, and ε_i is the random error term of the model for the *i*th observation (Pacala et al. 1994; Coates and Burton 1999), which was assumed to be normally distributed, with a mean equal to zero and variance σ_ε^2. When fitted to all data, we referred to eq. 2 as the "general model", and its parameters were estimated by nonlinear least squares using the nlstools package in R (R Development Core

Table 2. Estimated parameters (± standard error) of the base Michaelis–Menten model for RGR of basal diameter as a function of light availability (95% confidence intervals in parenthesis), separated by soil compaction levels (low, <600 kPa; intermediate, 600–2000 kPa; and high, 2000 kPa).

Model	n	$\hat{\alpha}$	$\hat{\beta}$	σ_{ε}^{2}	AD (%)	RMSD (%)
Nothofagus dombeyi						
Base	257	$1.384^{***}\pm0.150$ (0.986–1.578)	$0.029^{***}\pm0.004$ (0.023–0.042)	0.183	−0.012	26.5
Low	24	$1.748^{**}\pm0.537$ (0.633–2.864)	$0.025^{***}\pm0.005$ (0.015–0.036)	0.091	−0.034	13.4
Intermediate	196	$1.320^{***}\pm0.174$ (0.976–1.664)	$0.033^{***}\pm0.005$ (0.022–0.045)	0.189	−0.023	26.4
High	37	$0.884^{***}\pm0.241$ (0.393–1.374)	$0.038^{*}\pm0.037$ (−0.004–0.080)	0.155	0.006	25.9
Nothofagus alpina						
Base	238	$1.297^{***}\pm0.213$ (0.963–1.805)	$0.033^{***}\pm0.004$ (0.020–0.037)	0.217	0.085	34.8
Low	24	$1.858^{*}\pm0.764$ (0.273–3.443)	$0.027^{***}\pm0.006$ (0.014–0.041)	0.127	−0.056	19.8
Intermediate	195	$1.558^{***}\pm0.302$ (0.961–2.154)	$0.027^{***}\pm0.004$ (0.019–0.036)	0.220	0.029	33.9
High	18	$0.795^{**}\pm0.207$ (0.354–1.236)	$0.018^{**}\pm0.005$ (0.006–0.030)	0.092	−0.48	23.0

Note: $\hat{\alpha}$, asymptotic growth rate at high light levels; $\hat{\beta}$, growth at low light levels; σ_{ε}^{2}, residual standard error; AD, aggregate difference; RMSD, root mean square differences of the residuals; n, sample size. *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

Team 2010). The biological interpretation of the parameters is as follows: α is the asymptote of the model, and β is the slope of the relationship at zero light, with the model passing through the origin (Coates and Burton 1999; Drever and Lertzman 2001).

To explore effects of soil compaction on seedling growth, the seedlings were segregated into three categories according to associated values of resistance to penetration: low (<600 kPa), intermediate (600–2000 kPa), and high (≥2000 kPa). These levels have been suggested to be reflective of soil that is too compacted, adequate, or too porous for optimal plant growth, respectively (Greacen and Sands 1980; Kozlowski 1999; Ares et al. 2005; Bassett et al. 2005). Equation 2 was fitted for penetration resistance category, and the fitted models were named after their respective resistance levels. We assessed all the fitted models by computing the residual standard error (σ_{ε}^{2}) and the following prediction-oriented statistics, as defined by Salas et al. (2010): the aggregated difference or mean residuals AD $= \left(\frac{1}{n}\sum_{i=1}^{n}\hat{e}_{\mathrm{i}}\right)$ and the root mean square differences RMSD $= \sqrt{\frac{1}{n}\sum_{i=1}^{n}\hat{e}_{\mathrm{i}}}$, with $\hat{e}_{\mathrm{i}} = y_i - \hat{y}_{\mathrm{i}}$, where y_i and $\hat{y}_{\mathrm{i}}$ are the observed and predicted RGR for the ith seedling, respectively, and n is the sample size.

Results

Effects of light availability on seedling growth

An ample growth dispersion as a function of light occurred for both species (Fig. 2). Model fit and estimated parameters for both species were significant ($P < 0.05$; Table 2). Predictions of the models for *N. dombeyi* had a smaller error (RMSD) and AD than the predictions of the models for *N. alpina* (Table 2). Asymptotic growth at high light levels was higher for *N. dombeyi* ($\hat{\alpha} = 1.384$) than for *N. alpina* ($\hat{\alpha} = 1.297$). Growth under low light levels was also higher for *N. dombeyi* ($\hat{\beta} = 0.029$) than for *N. alpina* ($\hat{\beta} = 0.033$). Thus, on average, the growth performance of *N. dombeyi* was better than for *N. alpina* in both high and low light levels. However, the confidence intervals for both species suggest no statistical differences throughout the light gradient analyzed (Fig. 2).

Effects of soil compaction on growth responses of seedlings were related to light availability, with species-specific variation in parameter estimations, when separating seedlings by soil condition, i.e., by low, intermediate, and high rates of resistance to penetration values (Table 2; Fig. 3). Changes in seedling performance were observed through the estimated parameters of the models for *N. alpina* when comparing resistance with penetration classes (Table 2; Fig. 3). For instance, the asymptotic growth rate ($\hat{\alpha}$) for *N. alpina* at low rates of resistance to penetration was higher than the general model (1.858 vs. 1.297, respectively; Table 2). On the other hand, asymptotic growth parameters of *N. dombeyi* were insensitive to low and intermediate levels of resistance to penetration (Table 2; Fig. 3). The estimated asymptotic growth parameters for *N. dombeyi* and *N. alpina* at intermediate levels of resistance to penetration were similar to the general model for both species (Table 2; Fig. 3). At high levels of resistance to penetration, both species had lower asymptotic growth parameters than the general model (Table 2), with *N. alpina* showing a stronger response (Fig. 3). Confidence intervals overlapped for low and intermediate resistance to penetration models, suggesting no significant differences between them, but at high resistance levels, both species exhibited differences. These differences for *N. dombeyi* were detected above ~40% in total light and for *N. alpina* were detected above ~20% in total light (Fig. 3).

As expected, separating seedlings into resistance to penetration classes generally increased the goodness-of-fit errors (σ_{ε}^{2}) and reduced prediction errors (as estimated by the RMSD (%)) and aggregated differences (AD (%)) for both species (Table 2). For instance, the RMSD of the *N. dombeyi* model was reduced from 26.5% in the base model to 13.4% in the model with low resistance levels (600 kPa). Similarly, RMSDs of *N. alpina* models were reduced from 34.8% in the base model to 19.8% in the model with low resistance levels. Visual analysis of model residuals confirmed that our analysis did not violate statistical assumptions (data not shown).

Discussion

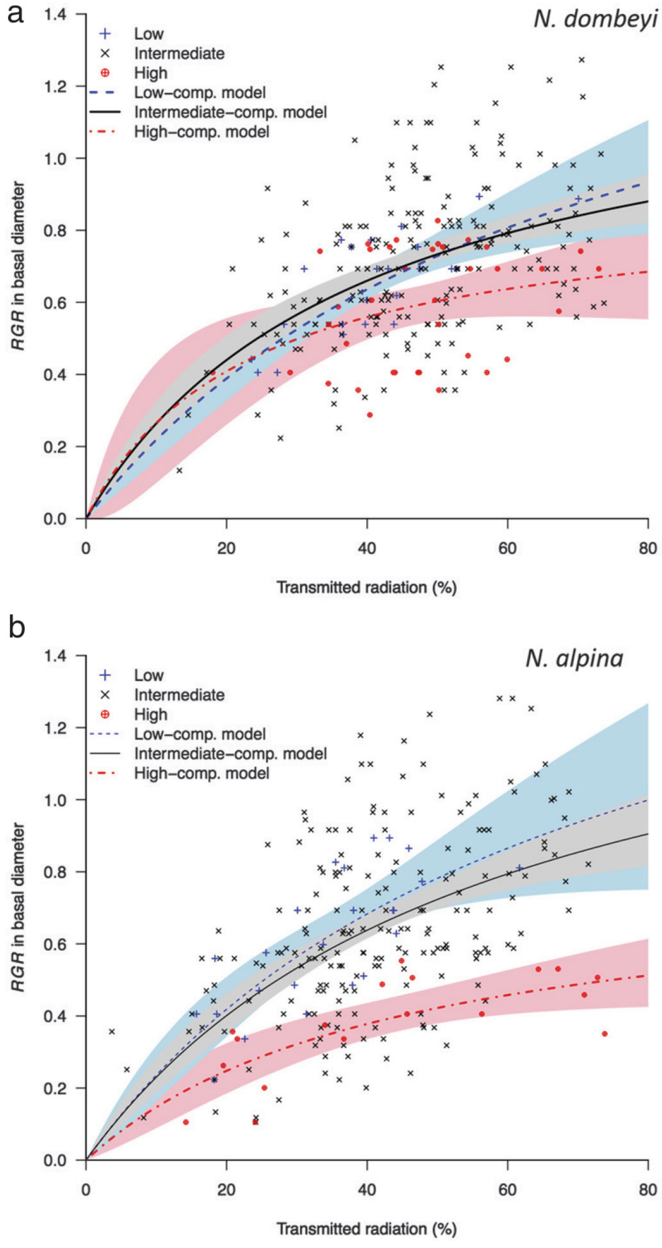
Effects of light availability on growth of underplanted seedlings of *N. dombeyi* and *N. alpina*

Both *Nothofagus* species showed increasing growth rates with increasing light levels during the second growing season after planting. However, *N. dombeyi* had a higher asymptotic light growth parameter at greater light levels than *N. alpina* (Table 2; Fig. 3). Species with a higher asymptotic light parameter ($\hat{\alpha}$) are considered to be more shade intolerant and those with a higher low-light parameter ($\hat{\beta}$) are considered to be more shade-tolerant species (Pacala et al. 1994; Kobe 1999). Our study quantitatively reflects no difference in shade tolerance between these two species, which is not consistent with previous studies that have reported that natural regeneration of *N. dombeyi* appears to be more successful in larger forest canopy openings compared with regeneration of *N. alpina* (Donoso 1993; Weinberger and Ramirez 2001). This result also contradicts the results obtained in plantations where the two species were underplanted at a slightly lower elevation in the Andes, with *N. alpina* having a growth pattern that was indifferent to light availability after the first two growing seasons (Donoso et al. 2013), whereas growth of *N. dombeyi* seedlings was very sensitive to light levels in the understory (Donoso et al. 2013).

Differential effects of light availability and soil compaction on growth of *N. dombeyi* and *N. alpina*

The strongest detrimental effects of soil resistance to penetration on growth were detected under high resistance levels for

Fig. 3. Observed values (circles) and fitted models (lines) for the relative growth response of (*a*) *N. dombeyi* and (*b*) *N. alpina* in response to light availability, separated by soil compaction (comp.) levels. Shaded areas with different colors represent the 95% confidence intervals for each compaction level. This figure is provided in colour online.



both species (>2000 kPa; Fig. 3). However, growth of *N. alpina* was reduced more than growth of *N. dombeyi* (Fig. 3). Under these resistance levels, growth of *N. alpina* was impacted above 20% light availability, whereas growth of *N. dombeyi* was only affected at light levels above 40% of full sunlight (Fig. 3). However, levels of soil resistance to penetration at low and intermediate light levels were not significant for *N. alpina* and *N. dombeyi*. Thus, our study confirms the soil resistance to penetration levels that have been widely documented as thresholds above which there are detrimental effects on seedling growth, i.e., ~2,000 kPa (e.g., Greacen and Sands 1980; Kozlowski 1999), despite potential differences in measurement tools, methodologies, or soil conditions. These findings for our study species refute the hypothesis that low levels of soil compaction also lead to reduced plant growth (see Kozlowski (1999) and Bassett et al. (2005)).

In general, it is well known that high soil compaction can be a stressful factor which negatively affects plant growth (see Greacen and Sands 1980; Bates et al. 1993; Kozlowski 1999). Several studies have shown that high levels of soil compaction impact plant metabolism such as increasing plant demand for photosynthates, decreasing photosynthesis, reducing foliage area and root growth, and eventually stagnating aboveground growth (Arvidsson and Jokela 1995). In general, effects of soil compaction on seedlings growth are varied and depend on the species' traits and soil types (sensu Kozlowski 1999). These multiple and variable impacts confound the effects of forest management operations (e.g., logging activities) or mechanical site preparation (e.g., scarification) on growth. For instance, some studies have shown that heavy soil compaction reduced tree growth in natural regeneration (Cheatle 1991; Bates et al. 1993; Gebauer and Martinková 2005; Bassett et al. 2005), but others have documented a positive effect of soil compaction on plant growth (Miller et al. 1996; Örlander et al. 1996; Ares et al. 2005; Fleming et al. 2006; Alameda and Villar 2009). A recent meta-analysis study showed that effects of soil compaction on growth are often insignificant and vary strongly across soil types and tree species (Ampoorter et al. 2010). Our study highlights the sensitivity of plant response to soil compaction, as we found contrasting responses between two very closely related species (Fig. 3).

The interactions between limiting resources for plant growth have been widely discussed (Finzi and Canham 2000; Drever and Lertzman 2001; Kobe 2006). For example, limitations to belowground resources such as moisture and nutrients appear to have a stronger impact on growth in high-light environments than in low-light environments (Carter and Klinka 1992; Drever and Lertzman 2001; Kobe 2006), but the magnitude of such responses differs among species and depends on silvical characteristics (Walters and Reich 1997; Drever and Lertzman 2001; Kobe 2006). Our study confirms this pattern when comparing growth responses of *N. dombeyi* and *N. alpina* in highly compacted soils (Fig. 3). For example, *N. dombeyi* had a higher growth plasticity to resource limitation than *N. alpina*, as the latter is commonly found on sites of relatively higher quality (sensu Donoso et al. 1999, 2011; Donoso and Soto 2010), suggesting that species adapted to better sites are more sensitive to detrimental soil conditions (Donoso et al. 2011; Soto et al. 2014). The difference in plasticity is reflected in both parameters of the Michaelis–Menten model (Table 2). Although there were no significant differences between species (Fig. 2), *N. dombeyi* had higher $\hat{\alpha}$ (high light) and $\hat{\beta}$ (low light) parameters than *N. alpina*, suggesting that *N. dombeyi* can grow well under wider conditions of light and soil compaction levels (Fig. 3). These findings also suggest that multiple physiological and morphological adaptation mechanisms may explain the strong growth plasticity of *N. dombeyi*.

Management implications

To put the practical implications of our results in context, it is relevant to compare responses of *N. dombeyi* and *N. alpina* to light gradients at middle and high elevations in the Andes with results of plantations in open-field conditions or with some lateral protection. In the Andes of south–central Chile where climatic conditions become harsh (>700 m; Donoso et al. 2007; Soto et al. 2009), partial shade (e.g., lateral protection in open-field conditions or protection from overstory trees in canopy openings) has been shown to improve growth and survival (Donoso et al. 2013; Soto et al. 2014) of *Nothofagus* species. Previous studies have also suggested that some shelter from neighbor vegetation (Álvarez and Lara 2008; Soto et al. 2009) or from a partially open overstory (Donoso and Soto 2010; Donoso et al. 2013; Soto et al. 2014) provide a protection that improves seedling performances. On the other hand, growth rates obtained for both species in this study were lower than those reported in open-field plantations established on abandoned grasslands (e.g., in full-light conditions in mesic sites) at low elevations in south–central Chile (Wienstroer et al. 2003; Donoso et al. 2009, 2011) but higher than those reported for open-field plantations at elevations >700 m in the Andes (Donoso et al. 2005, 2007; Soto et al. 2014).

In general, higher light levels after harvesting in the understory of forests in the Chilean Andes promote the invasion of bamboo from rhizomes, which eventually create dense patches that inhibit natural and artificial regeneration of *Nothofagus* species (González et al. 2002; Muñoz and González 2009). Topsoil scarification is a potentially efficient tool to improve seedbed conditions for natural regeneration and (or) to provide open areas for underplanting (Donoso and Soto 2010; Reyes et al. 2013; Soto et al. 2014). In this context, one of the most important research challenges is to investigate the impacts and effectiveness of topsoil scarification on regeneration of *Nothofagus* species (Donoso and Soto 2010; Reyes et al. 2013). Our studies and practical experiences suggest that shelterwood harvesting when combined with soil scarification appears to create adequate regeneration niches for pioneer species (Donoso and Soto 2010; Reyes et al. 2013). However, site preparation may also lead to soil compaction levels that are detrimental especially to *N. alpina*. Thus, scarification has to be carefully implemented, e.g., during the dry season or with machinery that use low-pressure tires to minimize detrimental soil compaction levels. Also, so far, we know that scarification with heavy machinery works well in coarse-textured soils (Reyes et al. 2013), which is common in the Andes of southern South America (Andisols and Inceptisols), but studies must be conducted to know its applicability in more fine-textured soils.

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