

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

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## 1   **Abstract**

2   We evaluated effects of top-soil scarification by heavy machinery on growth of two valuable  
3   and shade-intolerant tree species- *Nothofagus dombeyi* (evergreen and considered very plastic  
4   to different soil fertility levels) and *Nothofagus alpina* (deciduous and considered sensitive to  
5   soil fertility)- seedlings underplanted in *Nothofagus* old-growth forests subjected to  
6   shelterwood cuttings without the final cut in the Chilean Andes. We related tree basal  
7   diameter growth as it responds to light availability and soil compaction (as measured by  
8   resistance to penetration) by fitting a growth model based on the Michaelis-Menten equation.  
9   Predicted growth of *N. dombeyi* was greater than *N. alpina* in high- and low-light levels, but  
10   without differences between species. Both species showed significant differences at high  
11   levels of penetration resistance ( $>2,000\text{kPa}$ ). Differences for *N. dombeyi* occurred above ~40%  
12   in total light, and for *N. alpina* above ~20%. However, they were not different when compared  
13   at low and intermediate levels of penetration resistance. The results suggest that partial  
14   shelterwood cuts may provide adequate light levels to achieve appropriate growth of  
15   underplanted *Nothofagus* seedlings. However, if regeneration of *N. alpina* is desired,  
16   scarification of topsoil needs to be implemented with more caution in canopy openings, as  
17   traffic and soil removal by heavy machinery can have detrimental effects on growth of this  
18   and other species that are more sensitive to soil compaction.

19   **Key words:** Michaelis-Menten, Shade-tolerance, Soil resistance to penetration, stress  
20   conditions, Underplanting.

# 1   **Introduction**

2   Silvicultural practices manage canopy structures with the objective of regenerating and  
3   reallocating growing space for desired crop species (Nyland 2002; Puettmann et al. 2008a).  
4   Questions on which resource levels or environmental factors most significantly influence  
5   seedling performance have been a topic of discussion in the last decades (e.g., Walter and  
6   Reich 1997; Kobe 2006). On moist sites in temperate forests light availability seems to be the  
7   most important factor that determines seedling establishment, survival, and growth (e.g.,  
8   Canham et al. 1990). Understanding the response of seedlings to variations in light levels is  
9   fundamental to predict effects of forest management practices on future ecosystem  
10   development (Carter and Klinka 1992; Coates and Burton 1999); they vary by species due to  
11   species-specific light requirements (Canham et al. 1990; Pacala et al. 1994; Carter and Klinka  
12   1992). A species' shade tolerance determines the performance of seedlings under low-light  
13   conditions and eventually can affect the composition and structure of forest stands (Pacala et  
14   al. 1996). The chance of seedlings and saplings of a given species to reach the canopy is often  
15   determined by their performance in young stages (Canham 1988; Kobe 1999), but recent  
16   studies have shown that even in temperate forests other resources, such as nutrients and water  
17   availability, also can have a significant influence on the performance of these young trees in  
18   the understorey (Walters and Reich 1997; Finzi and Canham 2000; Kobe 2006), even affecting  
19   their shade tolerance (Carter and Klinka 1992; Drever and Lertzman 2001).

20   In the Andes of south-central Chile, environmental conditions apparently have not been  
21   suitable for successful natural regeneration after harvesting highly productive and valuable  
22   *Nothofagus*-dominated forests (*Nothofagus dombeyi* and *Nothofagus alpina*). For decades  
23   these forests have been harvested either through selective cuts (cut the best and leave the

1 worst; *sensu* Nyland 2002), exploitation or incomplete shelterwood cuts, where the final cut  
2 has not been conducted. This incomplete or partial shelterwood could be confused with  
3 irregular shelterwood, but the latter is aimed to regenerate tree species tolerant or midtolerant  
4 to shade (Raymond et al. 2009), whereas in the Chilean Andes the objective is to regenerate  
5 the light-demanding *Nothofagus* species. Regardless of prescriptions, harvesting operations  
6 have resulted in high-graded forests, in the sense that these two *Nothofagus* species, the most  
7 valuable tree species in the Andes, have been unable to regenerate. The lack of tree  
8 regeneration may be partially caused by the cyclic nature of seed production of *Nothofagus*  
9 (Donoso 1993). However, another explanation is that invasive dense patches of bamboo  
10 (*Chusquea* spp) in the understory are very competitive and inhibit tree regeneration of these  
11 species (Veblen et al. 1981; González et al. 2002; Muñoz and González 2009).

12 Some silviculturists in Chile have opted to manipulate light conditions to reduce or delay the  
13 dominance and growth of competing understory species, such as bamboo (*sensu* Smidt and  
14 Puettmann 1998; Coates and Burton 1999; Maas-Hebner et al. 2005) and thus improve the  
15 success when regenerating these forests. This approach by itself, however, has not been  
16 successful in the Chilean Andes (personal communication Luis Molina, former manager in the  
17 Neltume-Carranco forest company between 1999 and 2014). A technique that has been  
18 applied is scarification of top soil with heavy machinery (e.g. bulldozer trails in harvested  
19 areas), which basically eliminates the rhizomes of *Chusquea* spp., the main competing species  
20 for *Nothofagus*. In addition, this technique creates microsites that provide better seed beds for  
21 natural regeneration of *Nothofagus* species (Veblen et al. 1981) and/or better planting spots.  
22 This silvicultural practice has been implemented in selected locations in Chile with good

1 results in terms of establishing regeneration (Reyes et al. 2013), but its specific impacts on  
2 seedling growth have not been studied.

3 Any operation with heavy machinery in forests, including soil scarification, has the potential  
4 to cause soil compaction, as reflected in decreased porosity, and increased bulk density and  
5 resistance to penetration (*sensu* Kozlowski 1999). These impacts may limit access to nutrients  
6 and water by roots and thus compromise seedling establishment, survival, and growth  
7 (Kozlowski 1999; Berger et al. 2004; Resco de Dios et al. 2005; Yoshida et al. 2005).

8 However, specific effects of soil compaction on plant growth are very complex and can vary  
9 from beneficial to detrimental (Kozlowski 1999; Ares et al. 2005). On most soils, studies  
10 suggest harmful effects of soil compaction on plant growth (Greacen and Sands 1980;  
11 Kozlowski 1999; Ares et al. 2005). For instance, 2 MPa of resistance to penetration (a  
12 surrogate of soil compaction) has been considered an upper threshold above which there is a  
13 negative influence on plant growth (Greacen and Sands 1980; Kozlowski 1999). On the other  
14 extreme, soils with very low resistance to penetration (~0.6 MPa ) also have detrimental  
15 effects on plant growth since high porosity increases the aerated conditions, and the soil can  
16 desiccate during dry spells in the summer season (Bassett et al. 2005). In between,  
17 intermediate values of resistance to penetration (e.g. around 1 MPa) provide conditions  
18 suitable to plant growth (Kozlowski 1999; Ares et al. 2005; Bassett et al. 2005). The actual  
19 thresholds are obviously a function of the specific measurement tool and conditions and vary  
20 considerably by species according to their tolerance to soil compaction (Kozlowski 1999;  
21 Bassett et al. 2005) and other traits such as crown architecture, phenotypic plasticity or plant  
22 ontogeny (Arvidsson 1999).

1 In Chile there is little information about effects of soil compaction upon tree growth of native  
2 species, but the silvics of some species illustrate that they differ in terms of their growth in  
3 various soil conditions (Donoso 2006). *N. dombeyi* is known for its plasticity and grows well  
4 in a wide range of soil conditions (Donoso et al. 2005, 2006a; Soto et al. 2014). In contrast, *N.*  
5 *alpina* is usually restricted to well-aerated, coarse-textured and deep soils (Donoso et al. 1993,  
6 1999, 2006b). Both species naturally regenerate after large-scale disturbances in the Andes of  
7 southern South America (Chile and Argentina) create open conditions, sometimes exposing  
8 volcanic slag (Donoso 1993; Veblen et al. 1996), i.e., well aerated and poorly-developed soils  
9 (Inceptisols). Overall, both species are adapted to growing in well aerated soils, but their  
10 specific performance under these conditions has not been evaluated.

11 In this study we evaluated the impacts of a wide range of light and soil compaction conditions  
12 created after harvesting and soil scarification on growth of underplanted seedlings of *N.*  
13 *dombeyi* and *N. alpina*. We expect that the wide range of conditions created on the study site  
14 will highlight species-specific responses to this forest management practice. Therefore, the  
15 objectives of this study were; 1) to evaluate and quantify the short-term performance of  
16 underplanted *N. dombeyi* and *N. alpina* as a function of light availability, and 2) to evaluate  
17 and quantify the influence of soil compaction (low, intermediate and high levels of resistance  
18 to penetration) on seedling performance of these species under a wide range of light levels.  
19 We hypothesized that the performance of both species will decline under low light conditions,  
20 but the magnitude of decline will be greater in *N. dombeyi* due to its higher shade-intolerant  
21 character compared to *N. alpina* during early ontogenetic stages. We also hypothesized that  
22 *N. alpina* (typically found on sites with higher soil fertility) will be more sensitive to soil  
23 compaction than *N. dombeyi* (typically found on sites with lower soil fertility).

# 1   **Methods**

## 2   Study site

3   This study was carried out on a southeast-facing gentle slope (< 15%) of the Mocho-  
4   Choscuenco volcano in south-central Chile (39°35'S, 72°05'W) between 910 and 990 m a.s.l..  
5   The forest belongs to the *N. dombeyi*, *N. alpina* and *Laureliopsis philippiana* forest type  
6   (Donoso 1981; Donoso et al 1986). The original old-growth forest likely had a structure  
7   similar to that reported for these types of Andean forests by Veblen et al. (1980, 1981).  
8   Typically, these forests have basal area close to 100 m<sup>2</sup> ha<sup>-1</sup>, and a multilayered canopy  
9   dominated by emergent *Nothofagus* species (i.e., *N. dombeyi* and *N. alpina*) above a canopy of  
10   shade-tolerant species (i.e., *Saxegothaea conspicua*, *L. philippiana*, and/or *Dassyphylum*  
11   *diacanthoides*). More details about structure, composition, and dynamics of these forests can  
12   be found in Veblen et al. (1981) and Donoso et al. (1986).

13   The climate is Andean polar, with short and dry summers (December-March) and humid  
14   winters (June-September). The annual precipitation is between 3,000 and 3,500 mm (Oyarzún  
15   et al. 2011) mainly as snow during winter months. The mean annual temperature is 9°C, with  
16   4°C and 16°C mean temperature for the coldest (August) and warmest months (February),  
17   respectively. Extreme temperatures can range from less than -10°C to more than 30°C (Soto  
18   et al. 2009). Frost events must be common at the elevation of the study site considering that  
19   from 30 to 50 annual frosts occur from August through September at lower elevations (550 m  
20   a.s.l.) in this same region (Soto et al. 2009).

21   Soils on the study site correspond to a transition between Acrudoxic Hapludand (andisol) and  
22   Andic Dystrudepts (inceptisol); both are coarse mixed and mesic soils (CIREN 2001), which

1 have a stratified structure and medium textures (sand: 60%, silt: 45% and clay: 5%; Reyes et  
2 al. 2014) through the entire profile. These soils are acid to moderately acid (pH 5.3 to 5.7),  
3 have an A horizon about 20 cm deep, high organic matter content (35%), high water retention  
4 capacity (> 250 mm in 1 m depth), a good C/N relation (12), and low values in terms of total  
5 N content (0.6%), available P (Olsen P 20 mg kg<sup>-1</sup>), K (305 mg kg<sup>-1</sup>), and Al saturation (2%);  
6 Reyes et al. 2014). The soil consists of different layers of volcanic materials such as slag and  
7 sand with a medium coarse texture (CIREN 2001).

#### 8 Harvest and site preparation

9 The forest on the study site was cut during summer of 2007 with a shelterwood harvest,  
10 leaving an average residual basal area of 20-30 m<sup>2</sup> ha<sup>-1</sup> and 150-180 trees per hectare (Luis  
11 Molina, personal communication- former manager of the Neltume Carranco forest company  
12 between 1999 and 2014). However, the final cut was never conducted, i.e. this was a partial  
13 shelterwood cut. In spite of leaving this basal area, after the shelterwood cut was applied  
14 dense-thickets of *Chusquea culeou*, considered a shade-tolerant bamboo species (Veblen 1982,  
15 Gonzalez et al. 2002), developed quickly in the understory and four years after the cut there  
16 was a scarce tree regeneration. It was then when soil scarification was carried out, expecting  
17 that this would allow successful regeneration. The scarification removed between 20 and 40  
18 cm of soil, altering chemical and physical properties of the remaining top soil (Reyes et al.  
19 2013, 2014). In the top 20 cm of the scarified areas nutrient supply decreased (organic matter:  
20 4%, total N: 0.07%, P (Olsen) 3.2 mg kg<sup>-1</sup>, K: 19 mg kg<sup>-1</sup>). In contrast, Al saturation (30%),  
21 and bulk density and resistance to penetration increased in unscarified areas (mean 0.8g cm<sup>-3</sup>  
22 and 1.1 MPa, respectively). More details of the effects of top-soil scarification on soil features  
23 are given by Reyes et al. (2013, 2014).



## 1 Source of seedlings

2 *Nothofagus dombeyi* and *N. alpina* seeds were collected from seed-trees in the San Pablo de  
3 Tregua experimental forest of the Universidad Austral of Chile (50 km north of the study site  
4 at 700 m a.s.l.). Seeds were produced in black polyethylene containers (393 seedlings m<sup>-2</sup>;  
5 130 cm<sup>3</sup> and 16 cm tall). The substrate was composted *Pinus radiata* bark mixed with a slow-  
6 release fertilizer (18N-6P-12K; Osmocote ®; 5kg per m<sup>3</sup> of bark). The one-year seedling  
7 production protocols followed the recommendations of Duryea and Landis (1984). Further  
8 details about seedling production of *Nothofagus* are given by Bustos et al. (2008) and Soto et  
9 al. (2014). Seedlings selected for the study were homogeneous in size (ranged from 25-35 cm  
10 in height and 3-4 mm in root-collar diameter), thus any potential biases due to differences in  
11 initial seedlings sizes are likely minor (*sensu* MacFarlane and Kobe 2006).

## 12 Planting design and environmental and resource measurements

13 Sixty canopy openings, in which understory vegetation was removed through scarification,  
14 were selected for planting. The areas of planting were defined as areas with a canopy  
15 openness (uncovered fraction of the hemispherical view estimated through Gap Light  
16 Analyzer; GLA, Fraser et al. 1999) after harvesting of at least 5%. The range of canopy  
17 openness planted with *N. dombeyi* (mean 28.9 ± SD 7.9%; range 9.6-50.2%) and *N. alpina*  
18 (mean 25.6 ± SD 7.5%; range 5.36-43.2%) was similar. In each opening 15 seedlings were  
19 planted in a rectangular layout with distances between seedlings reflecting opening sizes (Fig.  
20 1). For instance, in large openings (e.g. > 40% of canopy openness) the distance between  
21 seedlings was 4x4 m and in some cases 5x4 m. In medium-sized (20-40% of canopy  
22 openness) and small openings (<20% canopy openness) the distance was 3x3m and 2x2m,

1 respectively. No seedlings were placed beneath tree crowns at opening edges (Fig. 1). Thirty  
2 forest openings were planted with each species. Seedlings were planted at the end of May  
3 2010 (late fall, before snow covered the study area).

4 *Light availability.* We took nine photographs per forest openings during the second growing  
5 season, one at the apex of each selected seedling using a Coolpix D4500 digital camera (Nikon  
6 CO., Japan) with a fisheye Nikkor (8mm) lens that has a 182° field of view (Nikon CO.,  
7 Japan; Fig. 1). Photographs were taken under homogeneous diffuse sky light conditions near  
8 the middle of the growing seasons and light index was calculated using the Gap Light  
9 Analyzer 2.0 software (Frazer et al. 1999) as an indicator of light availability during the  
10 growing season (Messier and Puttonen 1995, Parent and Messier 1996, Lieffers et al. 1999).  
11 Light availability was estimated as total radiation (a combination of diffuse and direct beam  
12 radiation) and calculated as percentage of growing season (e.g., October 1<sup>st</sup> until March 30<sup>th</sup>)  
13 incident radiation (% transmitted total radiation; Frazer et al. 1999). Some input parameters  
14 used into GLA were the solar constant ( $1,370 \text{ W m}^{-2}$ ), cloudiness index (0.5), spectral faction  
15 (0.45), bean fraction (0.85), clear sky transmission coefficient (0.65) and standard overcast  
16 sky-regions brightness.

17 *Measurement of soil compaction.* Top-soil scarification by heavy machinery was characterized  
18 as resistance to penetration (kPa) on mineral soil next to each selected seedling (~10 cm from  
19 root collar) with an Eijkelkamp soil cone penetrometer (American Society of Agricultural  
20 Engineers 1990). Since top-soil scarification affects several soil variables, measuring  
21 resistance to penetration has been documented as a generic and inclusive measure of soil  
22 compaction (Kozlowski 1999; Berger et al. 2004; Ares et al. 2005; Zenner et al. 2007;  
23 Puettmann et al. 2008b; Soto et al. 2014). Resistance to penetration was measured by pressing

down the penetrometer with a uniform force close to  $\sim 2 \text{ cm seg}^{-1}$ . A  $2 \text{ cm}^2$  base area cone was used, and readings were taken once the cone reached 15 cm of soil depth (*sensu* Puettmann et al. 2008b). Four measurements (one in each cardinal points - N, E, W, S) 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. 2008b). Readings were ignored when the penetrometer cone hit rocks or roots. The median value was used for each seedling in order to minimize effects of extreme readings and readings that were influenced by hitting e.g, fine roots. Soil measurements were taken in early fall (April) two years after planting in the driest period of the year, and taken during two contiguous days (*sensu* Berger et al. 2004; Puettmann et al. 2008b), 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 2012. We selected nine live seedlings per canopy opening (9 seedlings x 30 canopy openings = 270 seedlings per species), where three seedlings were located each in the north, center and south 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 ( $d$ : 1 cm above ground) using a digital caliper ( $\pm 0.01 \text{ mm}$  of precision; Litz professional; Germany) and total seedling height ( $h$ ) using a

1 manually graduated tube (cm). In addition we took hemispherical photos and measured  
2 resistance to penetration for each seedling as described above. All seedlings with mechanical  
3 damage, herbivory, dieback, defoliation or dead were not considered in the analysis, because  
4 such reductions in leaf area can produce reductions in growth not related to light or soil  
5 compaction (Table 1).

## 6 Statistical analyses

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

$$9 \quad RGR = \frac{\ln d_1 - \ln d_0}{t_1 - t_0}, \quad (1)$$

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

17 We modeled the relationship between seedling *RGR* and light using the Michaelis-Menten  
18 equation (*sensu* Pacala et al. 1994), which has been widely used in similar studies (e.g., Pacala  
19 et al. 1994; Coates and Burton 1999; Drever and Lertzman 2001; Kobe 2006). The model  
20 parameters are easily interpreted, and allow statistical testing of interspecific differences in

1 growth responses as a function of light levels (*sensu* Pacala et al. 1996; Coates and Burton  
2 1999). The Michaelis-Menten model is as follows:

$$3 \quad RGR_i = \frac{\alpha L_i}{\left(\frac{\alpha}{\beta}\right) + L_i} + \varepsilon_i, \quad (2)$$

4 where:  $RGR_i$  and  $L_i$  are the relative growth rate of basal diameter and light level for the  $i$ th  
5 seedling;  $\alpha$  and  $\beta$  are parameters, and  $\varepsilon_i$  is the random error term of the model for the  $i$ th  
6 observation (Pacala et al. 1994; Coates and Burton 1999) assumed to be normally distributed,  
7 with mean equal to zero and variance  $\sigma_\varepsilon^2$ . When fitted to all data, we referred to Eq. (2) as the  
8 “general model”, and its parameters were estimated by non-linear least squares using the  
9 nlstools package in R (R Development Core Team 2010). The biological interpretation of the  
10 parameter are as follows:  $\alpha$  is the asymptote of the model, and  $\beta$  is the slope of the relationship  
11 at zero light, with the model passing through the origin (Coates and Burton 1999; Drever and  
12 Lertzman 2001).

13 To explore effects of soil compaction on seedling growth, the seedlings were segregated into  
14 three categories according to associated values of resistance to penetration: low ( $< 600\text{kPa}$ ),  
15 intermediate ( $600\text{--}2,000\text{ kPa}$ ), and high ( $\geq 2,000\text{ kPa}$ ). These levels have been suggested to be  
16 reflective of soil that is too compacted, adequate, or too porous for optimal plant growth,  
17 respectively (Greacen and Sands 1980; Kozlowski 1999; Ares et al. 2005; Bassett et al. 2005).  
18 Eq. (2) was fitted for penetration resistance category, and the fitted models were named after  
19 their respective resistance levels. We assessed all the fitted models by computing the residual  
20 standard error ( $\sigma_\varepsilon^2$ ), and the following prediction-oriented statistics as defined by Salas et al  
21 (2010): the aggregated difference or mean residuals  $AD = \left(\frac{1}{n} \sum_{i=1}^n \hat{e}_i\right)$ ; and the root mean

- 1 square differences  $RMSD = \sqrt{\frac{1}{n} \sum_{i=1}^n \hat{e}_i^2}$ , where:  $\hat{e}_i = y_i - \hat{y}_i$ ;  $y_i$  and  $\hat{y}_i$  are the observed and
- 2 predicted  $RGR$  for the  $i$ -th seedling, respectively; and  $n$  is the sample size.

## 1   **Results**

### 2   Effects of light availability on seedling growth

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

12   Effects of soil compaction on growth responses of seedlings were related to light availability,  
13   with species-specific variation in parameter estimations, when separating seedlings by soil  
14   condition, i.e., by low, intermediate and high rates of resistance to penetration values, (Table  
15   2, Fig. 3). Changes in seedling performance were observed through the estimated parameters  
16   of the models for *N. alpina* when comparing resistance to penetration classes (Table 2; Fig. 3).  
17   For instance, the asymptotic growth rate (parameter  $\hat{\alpha}$  ) for *N. alpina* at low rates of resistance  
18   to penetration was higher than the general model (1.858 vs. 1.297; Table 2). On the other  
19   hand, asymptotic growth parameters of *N. dombeyi* were insensitive to low and intermediate  
20   levels of resistance to penetration (Table 2, Fig. 3). The estimated asymptotic growth  
21   parameters for *N. dombeyi* and *N. alpina* at intermediate levels of resistance to penetration  
22   were similar to the general model for both species (Table 2; Fig. 3). At high levels of

1 resistance to penetration both species had lower asymptotic growth parameters than the  
2 general model (Table 2), with *N. alpina* showing a stronger response (Fig. 3). Confidence  
3 intervals overlapped for low and intermediate resistance to penetration models, suggesting no  
4 significant differences between them, but at high resistance levels both species exhibited  
5 differences. These differences for *N. dombeyi* were detected above ~40% in total light, and  
6 for *N. alpina* above ~20% (Fig. 3).

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



## 1 Discussion

2 Effects of light availability upon growth of underplanted seedlings of *N. dombeyi* and *N.*  
3 *alpina*.

4 Both *Nothofagus* species showed increasing growth rates with increasing light levels during  
5 the second growing season after planting. However, *N. dombeyi* had a higher asymptotic light  
6 growth parameter at greater light levels than *N. alpina* (Table 2 and Fig. 3). Species with a  
7 higher asymptotic light parameter ( $\hat{\alpha}$ ) are considered more shade intolerant, and those with a  
8 higher low light parameter ( $\hat{\beta}$ ) are considered more shade tolerant species (Pacala et al. 1994;  
9 Kobe 1999). Our study quantitatively reflects no difference in shade tolerance between these  
10 two species, which is not consistent with previous studies that have reported that natural  
11 regeneration of *N. dombeyi* appears to be more successful in larger forest canopy openings  
12 compared to regeneration of *N. alpina* (Donoso 1993; Weinberger and Ramírez 2001). This  
13 results also contradicts the results obtained in plantations where the two species were  
14 underplanted at a slightly lower elevation in the Andes, with *N. alpina* having a growth pattern  
15 that was indifferent to light availability after the first two growing seasons (Donoso et al.  
16 2013), while growth of *N. dombeyi* seedlings was very sensitive to light levels in the  
17 understory (Donoso et al. 2013).

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

20 The strongest detrimental effects of soil resistance to penetration on growth were detected  
21 under high resistance levels for both species (above of >2,000 kPa; Fig. 3). However, growth  
22 of *N. alpina* was reduced more than growth of *N. dombeyi* (Fig. 3). Under these resistance

1 levels, growth of *N. alpina* was impacted above 20% light availability, while growth of *N.*  
2 *dombeyi* was only affected at light levels above 40% of full sunlight (Fig. 3). However, levels  
3 of soil resistance to penetration at low and middle light levels were not significant for *N.*  
4 *alpina* and *N. dombeyi*. Thus, our study confirms the soil resistance to penetration levels that  
5 have been widely documented as thresholds above which there are detrimental effects on  
6 seedling growth, i.e. ~2,000 kPa (e.g., Greasen and Sands 1980; Kozłowski 1999) despite  
7 potential differences in measurement tools, methodology, or soil conditions. These findings  
8 for our study species refute the hypothesis that low levels of soil compaction also lead to  
9 reduced plant growth (see Kozłowski 1999; Bassett et al. 2005).

10 In general, it is well known that high soil compaction can be a stressful factor which  
11 negatively affects plant growth (see Greasen and Sands 1980; Bates et al. 1993; Kozłowski  
12 1999). Several studies have shown that high levels of soil compaction impact plant  
13 metabolism, such as increasing plant demand for photosynthates, decreasing photosynthesis,  
14 reducing foliage area and root growth and eventually stagnating above-ground growth  
15 (Arvidsson and Jokela 1995). In general, effects of soil compaction on seedlings growth are  
16 varied, and depend on the species' traits and soil types (*sensu* Kozłowski 1999). These  
17 multiple and variable impacts confound the effects of forest management operations (e.g.  
18 logging activities) or mechanical site preparation (e.g. scarification) upon growth. For  
19 instance, some studies have shown that heavy soil compaction reduced tree growth in natural  
20 regeneration (Cheatle, 1991; Bates et al. 1993; Gebauer and Martinková 2005; Basset et al.  
21 2005), but others have documented a positive effect of soil compaction on plant growth  
22 (Miller et al. 1996; Örlander et al. 1997; Ares et al. 2005; Fleming et al. 2006; Alameda and  
23 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 response 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, limitation to below ground resources, such as moisture and nutrients, appear to have a stronger impact on growth in high-light 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 upon silvical characteristics (Walter 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*, where 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

1 To put the practical implications of our results in context, it is relevant to compare responses  
2 of *N. dombeyi* and *N. alpina* to light gradients at middle and high elevations in the Andes with  
3 results of plantations in open field conditions or with some lateral protection. In the Andes of  
4 south-central Chile, where climatic conditions become harsh (>700 m; Donoso et al. 2007;  
5 Soto et al. 2009), partial shade (e.g. lateral in open field or from overstory trees in canopy  
6 openings) has been shown to improve growth and survival (Donoso et al. 2013; Soto et al.  
7 2014) of *Nothofagus* species. Previous studies also suggested that some shelter from neighbor  
8 vegetation (Álvarez and Lara 2008; Soto et al. 2009) or from a partially open overstory  
9 (Donoso and Soto 2010; Donoso et al. 2013; Soto et al. 2014) provide a protection that  
10 improve seedling performances. On the other hand, growth rates obtained for both species in  
11 this study were lower than those reported in open field plantations established on abandoned  
12 grasslands (e.g. in full-light conditions in mesic sites) at low elevations in south-central Chile  
13 (Wienstroer et al. 2003; Donoso et al. 2009, 2011), but higher than those reported for open-  
14 field plantations at elevations >700 m in the Andes (Donoso et al. 2005, 2007; Soto et al.  
15 2014).

16 In general, higher light levels after harvesting in the understory of forests in the Chilean Andes  
17 promote the invasion of bamboo from rhizomes, which eventually create dense patches that  
18 inhibit natural and artificial regeneration of *Nothofagus* species (González et al. 2002; Muñoz  
19 and González 2009). Top-soil scarification is a potentially efficient tool to improve seedbed  
20 conditions for natural regeneration and/or provide open areas for underplanting (Donoso and  
21 Soto 2010, Reyes et al. 2013, Soto et al. 2014). In this context, one of the most important  
22 research challenges is to investigate impacts and effectiveness of top-soil scarification upon  
23 regeneration of *Nothofagus* species (Donoso and Soto 2010; Reyes et al. 2013). Our studies

1 and practical experiences suggest that shelterwood harvesting when combined with soil  
2 scarification appears to create adequate regeneration niches for pioneer species (Donoso and  
3 Soto 2010; Reyes et al. 2013). However, site preparation may also lead to soil compaction  
4 levels that are detrimental especially to *N. alpina*. Thus, scarification has to be carefully  
5 implemented, e.g., during the dry season or with machinery that use low-pressure tires to  
6 minimize detrimental soil compaction levels. Also, so far we know that scarification with  
7 heavy machinery works well in coarse-textured soils (Reyes et al. 2013), which is common in  
8 the Andes of southern South America (Andisols and Inceptisols), but studies must be  
9 conducted to know its applicability in more fine-textured soils.

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1 Table 1. Characteristics of seedlings, light availability, and soil conditions. Absolute growth  
2 in the period 2011-2012 in  $d$  (root-collar diameter in cm) and  $h$  (stem height in cm).  $d$ ,  $h$ , and  
3 light availability are presented as mean values  $\pm$  standard deviation and ranges. Median and  
4 ranges are presented for soil compaction (resistance to penetration).

| Species           | $n$ | $d$ (cm)        | $h$ (cm)          | Light<br>availability<br>(%<br>transmitted<br>radiation) | Soil compaction<br>(kPa) |
|-------------------|-----|-----------------|-------------------|----------------------------------------------------------|--------------------------|
| <i>N. dombeyi</i> | 257 | $0.36 \pm 0.19$ | $32.58 \pm 17.38$ | $46.8 \pm 12.7$                                          | 1346.8                   |
|                   |     | 0.05 – 1.00     | 0.00 – 97.00      | 13.3 – 73.7                                              | 467.1 – 3459.6           |
| <i>N. alpina</i>  | 238 | $0.44 \pm 0.28$ | $30.36 \pm 18.82$ | $40.7 \pm 14.7$                                          | 1207.2                   |
|                   |     | 0.00 – 1.50     | 0.00 – 96.40      | 3.7 – 74.8                                               | 467.2 – 3609.2           |

5

Table 2. Estimated parameters ( $\pm$  standard error) of the Michaelis-Menten model for RGR of basal diameter as a function of light availability (95% of confidence intervals in parenthesis), separated by soil compaction levels (low: <600kPa; intermediate: 600-2,000 kPa; high: >2,000 kPa).  $\hat{\alpha}$  is reflecting the asymptotic growth rate in high light and  $\hat{\beta}$  is representing growth at low light.  $\sigma_{\varepsilon}^2$  is the residual standard error, AD is the aggregate difference and RMSD is the root mean square differences of the residuals. .

| Species           | Model        | <i>n</i> | $\hat{\alpha}$                          | $\hat{\beta}$                           | $\sigma_{\varepsilon}^2$ | AD<br>(%) | RMSD<br>(%) |
|-------------------|--------------|----------|-----------------------------------------|-----------------------------------------|--------------------------|-----------|-------------|
| <i>N. dombeyi</i> | Base         | 257      | 1.384*** $\pm$ 0.150<br>(0.986 – 1.578) | 0.029*** $\pm$ 0.004<br>(0.023 – 0.042) | 0.183                    | -0.012    | 26.5        |
|                   | Low          | 24       | 1.748** $\pm$ 0.537<br>( 0.633– 2.864)  | 0.025*** $\pm$ 0.005<br>(0.015 – 0.036) | 0.091                    | -0.034    | 13.4        |
|                   | Intermediate | 196      | 1.320*** $\pm$ 0.174<br>(0.976 – 1.664) | 0.033*** $\pm$ 0.005<br>(0.022 – 0.045) | 0.189                    | -0.023    | 26.4        |
|                   | High         | 37       | 0.884*** $\pm$ 0.241<br>(0.393 – 1.374) | 0.038* $\pm$ 0.037<br>(-0.004 – 0.080)  | 0.155                    | 0.006     | 25.9        |
| <i>N. alpina</i>  | Base         | 238      | 1.297*** $\pm$ 0.213<br>(0.963 – 1.805) | 0.033*** $\pm$ 0.004<br>(0.020 – 0.037) | 0.217                    | 0.085     | 34.8        |
|                   | Low          | 24       | 1.858* $\pm$ 0.764<br>(0.273 – 3.443)   | 0.027*** $\pm$ 0.006<br>(0.014 – 0.041) | 0.127                    | -0.056    | 19.8        |
|                   | Intermediate | 195      | 1.558*** $\pm$ 0.302<br>(0.961 – 2.154) | 0.027*** $\pm$ 0.004<br>(0.019 – 0.036) | 0.220                    | 0.029     | 33.9        |
|                   | High         | 18       | 0.795** $\pm$ 0.207<br>(0.354 – 1.236)  | 0.018** $\pm$ 0.005<br>(0.006 – 0.030)  | 0.092                    | -0.48     | 23.0        |

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

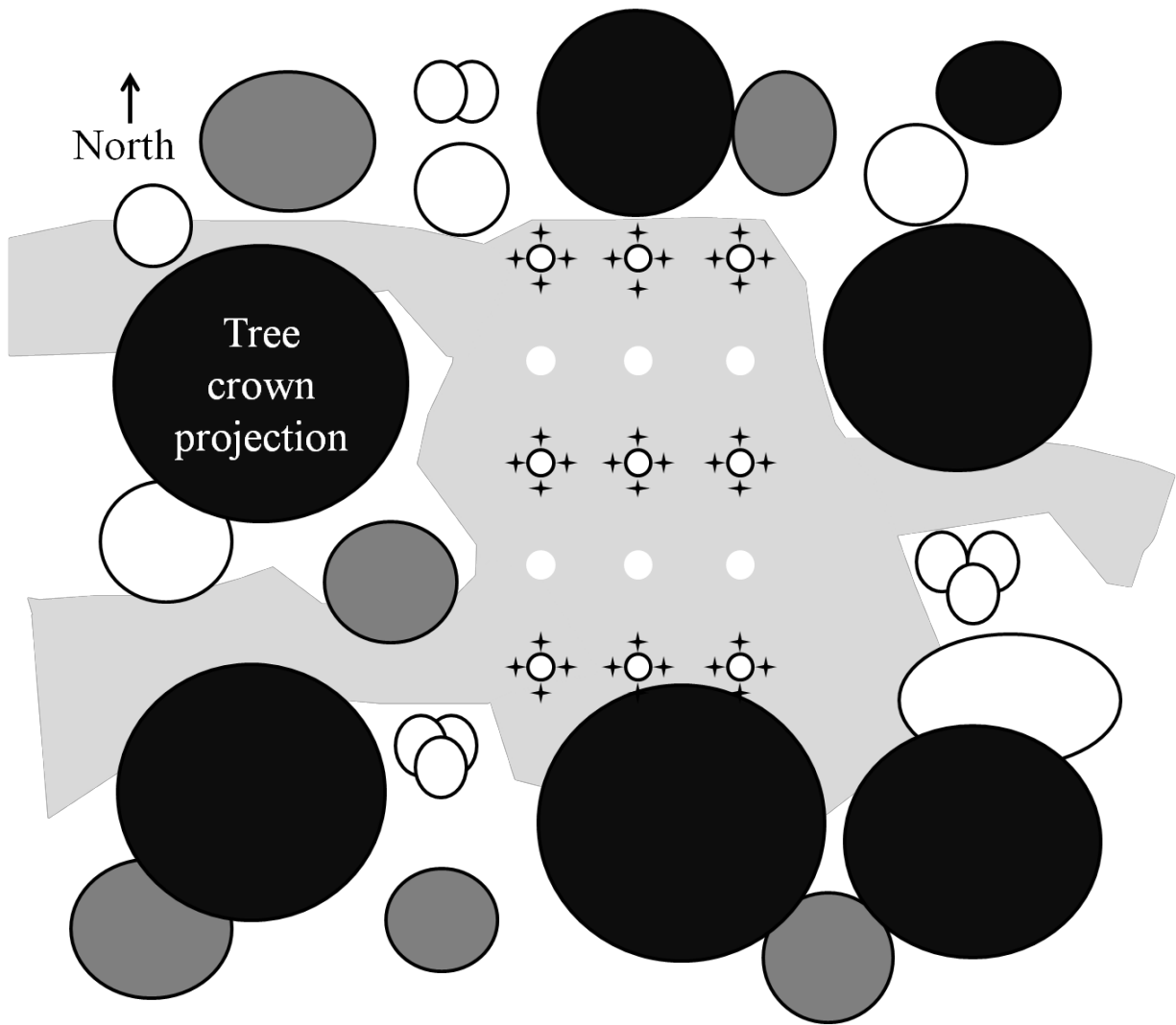
## 1 **Figure captions**

2 Fig. 1. Schematic layout of underplanted seedlings in canopy openings. Seedlings are shown  
3 in white circles and, for illustration, crowns of remnant trees are shown in black (*N. dombeyi*)  
4 dark grey (*N. alpina*) and white (*S. conspicua*). The scarified area is in light grey with the  
5 irregular tracks of the bulldozer. Sampled seedlings are shown in circles with black rings (9  
6 seedlings per opening). Finally, crosses (4 around each seedling) correspond to the point  
7 where resistance to penetration was measured with an Eijkelkamp soil cone penetrometer.

8 Fig. 2. Observed values (circles) and fitted general models (lines) for relative growth response  
9 in basal diameter as a function of light availability. Area in grey scale are the confidence  
10 intervals at 95% per each species.

11 Fig. 3. Observed values (circles) and fitted models of *RGR N. dombeyi* and *N. alpina* in  
12 response to light availability separated by soil compaction levels. Areas with different colors  
13 represent the confidence intervals at 95% per compaction levels.

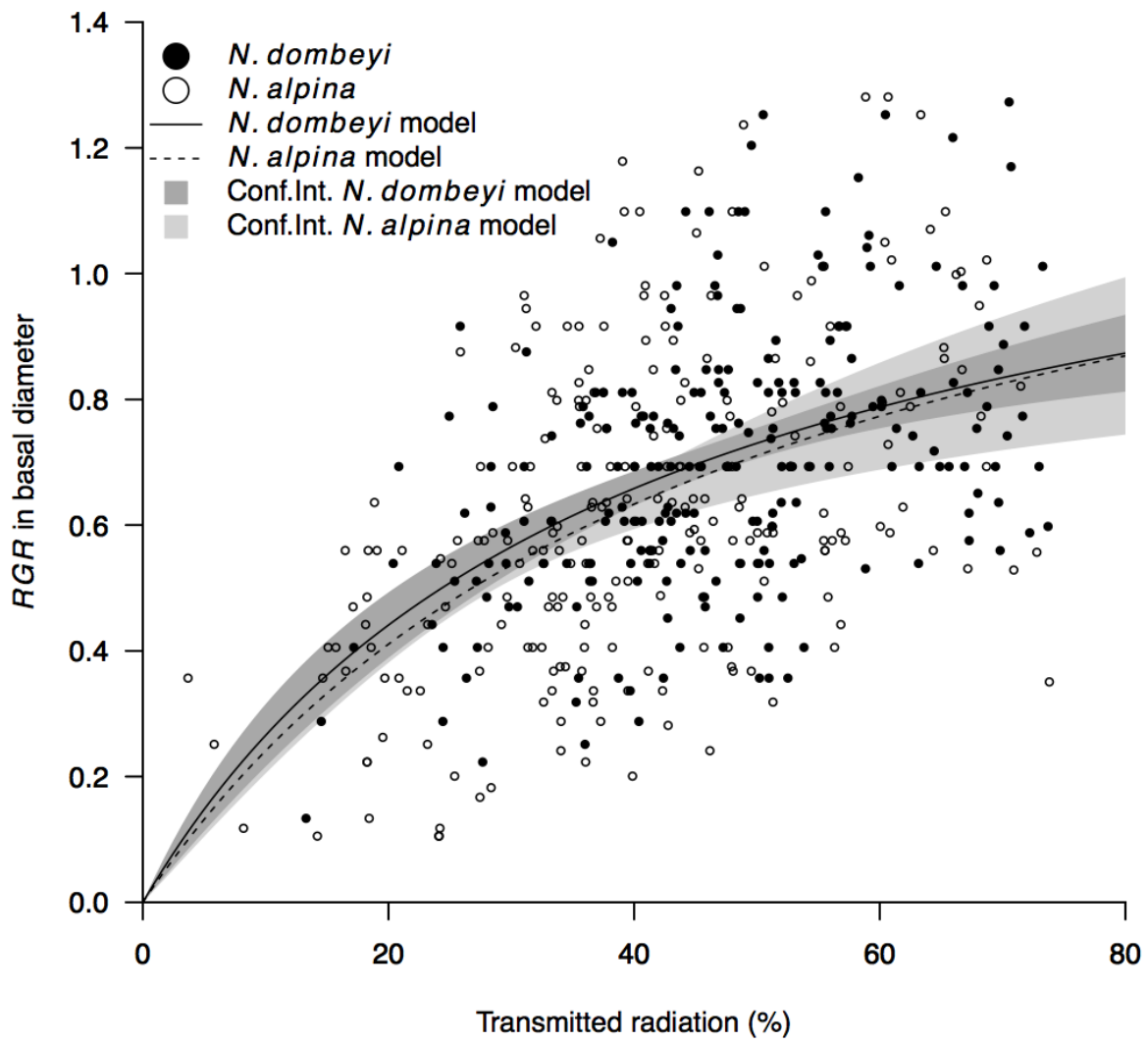
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2 **Fig. 1.**

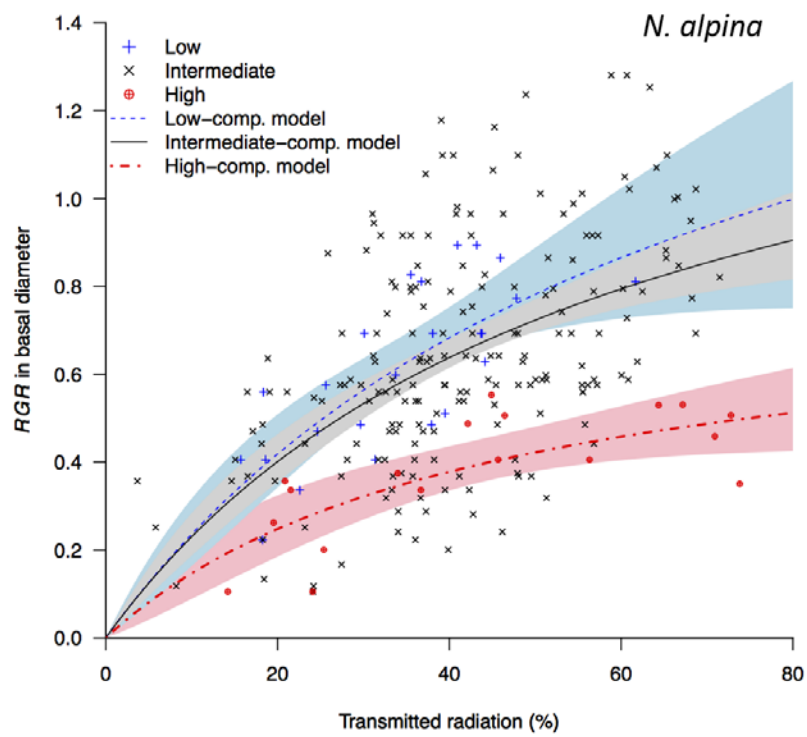
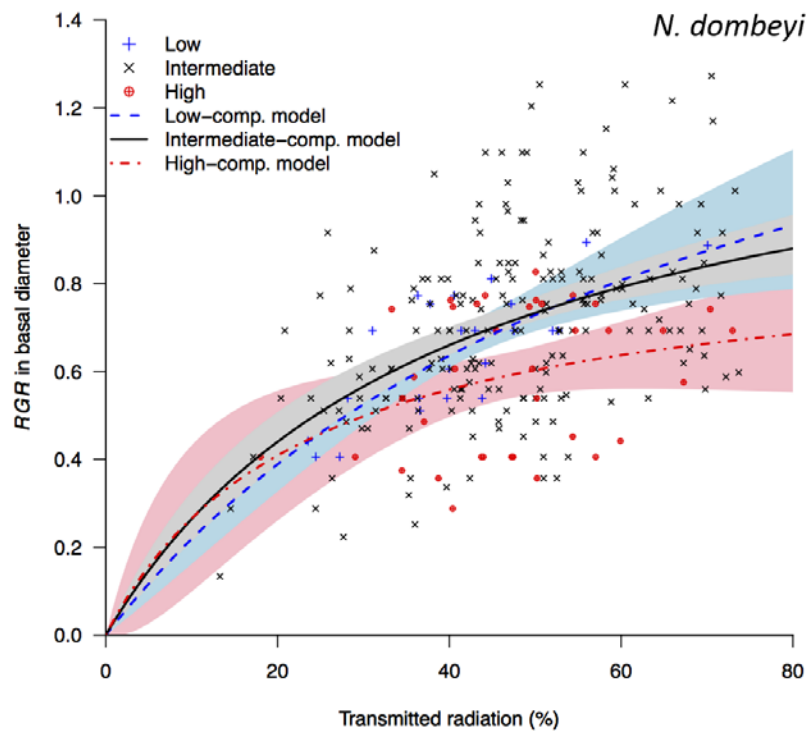
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2 **Fig. 2.**

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2 **Fig. 3.**