



Light and nitrogen interact to influence regeneration in old-growth *Nothofagus*-dominated forests in south-central Chile



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ARTICLE INFO

Article history:

Received 16 July 2016

Received in revised form 9 November 2016

Accepted 10 November 2016

Available online 16 November 2016

Keywords:

High-grading

Ground disturbance

Michaelis-Menten equation

Species acclimation

ABSTRACT

Light is one of the most important factors governing development of understory vegetation in forest ecosystems, including tree establishment and growth. Information about interactive effects of light with other resources such as water and nutrients is relatively scarce. How varying resources affect tree growth in forest understories is still unclear and current knowledge is largely confined to the northern hemisphere. A field experiment in which high-grading of an old-growth forest in the Andes of south-central Chile was followed by ground disturbance provided data about tree basal diameter growth responses under a wide range of light conditions, total nitrogen (tN) concentration in leaves, and water potential. We used a model selection approach to determine whether light is co-limiting with tN and water potential (or their interactions) for three species typically found in these forests and are known to vary in resource-use strategies. Species differed in growth response to light and tN, but not to water potential. For instance, radial growth of the tree species (*Nothofagus dombeyi*) with greatest light demand was strongly related to tN at high-light conditions only. The mid-shade tolerant species (*Nothofagus alpina*) had better basal diameter growth with high tN at high- and low-light environments. Contrary to expectations, radial growth of the late-successional shrub species (*Drimys andina*) was positively affected by light and tN in low-light environments only. Our results suggest that the species differences in regards to the impact of tN concentration along a light gradient are important factors that could influence plant community development. Restoration and management treatments can be more efficiently targeted if they are based on information about species sensitivities to interacting resource levels.

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1. Introduction

Resource availability affects plant growth, thereby potentially influencing successional trajectories of forest ecosystems (Canham et al., 1996; Pacala et al., 1996) depending on the set of interacting ecological and environmental variables (Lambers et al., 2008; Harpole et al., 2011). Among these variables, light availability is considered one of the most important limiting factors in determining seedling and sapling growth in understories of forest stands (Canham et al., 1990; Pacala et al., 1996). However, studies have also shown a consistent association between tree species performances and light and soil conditions (Coomes and Grubb, 2000; Finzi and Canham, 2000; Hostle et al., 2011),

specifically nutrient and water availability (Carter and Klinka, 1992; Bigelow and Canham, 2007), but these effects vary according to species-specific resource requirements (Drever and Lertzman, 2001; Kobe, 2006; Hostle et al., 2011). Thus, plant growth may be influenced by an interaction of soil moisture, nutrient and light availability (Carter and Klinka, 1992; Kobe, 2006). Nitrogen (N) has been recognized as the element that globally is most limiting to plant growth in natural (Waring and Schlesinger, 1985; Catovsky and Bazzaz, 2002; Lambers et al., 2008) and managed temperate forest ecosystems (Binkley, 1985; Harpole et al., 2011; Goodman et al., 2013a; Mainwaring et al., 2014). In many settings, water availability limits N uptake and this co-limitation affects plant growth, and thus the development of forest communities (Waring and Schlesinger, 1985; Drever and Lertzman, 2001; Lambers et al., 2008). Although several studies have provided insights into the mechanisms how light limitations affect plant

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growth and its subsequent influence on forest ecosystem dynamics (Pacala et al., 1996; Bloor and Grubb, 2003), understanding the processes of how light is in co-limitation with other resources, such as N and water availability, is still unresolved.

The effects of water and nutrient limitations on tree growth in forest understories are complex and responses vary by species, associated with species' life history traits and the combination of the specific resource levels (Chapin et al., 1987; Reich et al., 1997; Lambers et al., 2008). For example, high foliar N content influenced growth at high light conditions in temperate conifers and hardwoods forests, while soil water availability affected growth in low-light conditions (Carter and Klinka, 1992; Drever and Lertzman, 2001; Finzi and Canham, 2000; Kobe, 2006). In contrast, multiple resource limitations in northern hardwoods in North America produced differing results. For example, calcium and N were equally important for growth of some tree species, while at other times, N alone had the greatest effect (Kobe, 2006; Bigelow and Canham, 2007). Such reports of contrasting growth responses within a species highlight the ambiguity of our understanding of tree responses to multiple resources. On the other hand, a consistent positive relationship between high foliar N levels and high light conditions has been observed in studies that focused on photosynthesis (Walters and Reich, 1997; Lambers et al., 2008; Goodman et al., 2013b). In contrast, soil nutrients and water availability do not appear to have a major influence on plant growth under low light conditions (Walters and Reich, 1997). Thus, plant reaction and its synergistic interactions with varying resource availability in ecosystems are complex and not well understood. Furthermore, most current knowledge is based on results from studies in northern hemisphere forest ecosystems.

In this study, we investigated how co-existing species of differing successional status respond to multiple, interacting resource limitations. These data will enable us to better predict differential responses to disturbance within managed forests. This will provide insights about possible mechanisms and implication for plant community development in disturbed forests. To this end, we used a gradient of light, leaf tN concentration and plant water potential conditions in disturbed, high-graded stands in the south-central Chilean Andes to investigate how multiple conditions and their interactions influence basal diameter growth patterns of *Nothofagus dombeyi*, *N. alpina* and *Drimys andina*, species that are known to differ in terms of their resource use. Specifically, we hypothesized that: (a) the light demanding tree species (*N. dombeyi*) is more sensitive to tN limitations under high-light conditions than the late successional species; (b) the basal diameter growth of species with intermediate shade tolerance (*N. alpina*), but high sensitivity to tN concentration under the full light gradient, i.e., between the light demanding species and the shade tolerant species, respectively; (c) the shade tolerant species (*D. andina*) is less sensitive to tN and water potential levels under any light level.

2. Methods

2.1. Study sites

We selected four disturbed *Nothofagus* old-growth forest stands with a wide range of site productivity within the Coihue-Rauli-Tepa forest type in the Huilo-Huilo biological reserve (between 39 and 40°S and 500 to 1400 masl). Each stand consists of a homogeneous patch dominated in most cases by *Nothofagus dombeyi* (coihue) and *Nothofagus alpina* (rauli). The general stand and soil characteristics for each site are presented in Table 1.

The climate in Huilo-Huilo is considered as Andean polar, with short and dry summers (December–March) and humid winters (June–September). The annual precipitation reaches 3500 mm (Reyes et al., 2014) mainly as snow during winter months. The

mean annual temperature $\sim 9^\circ\text{C}$, with a mean of 4°C and 16°C for the coldest (August) and warmest month (February), respectively. Extreme temperatures can range from below -10°C to above 30°C , and 30–50 annual frost events concentrated from August through September are common above of 550 m a.s.l. (Soto et al., 2009). On the other hand, soils in these sites correspond to a transition between Andisol (Acruoxic Hapludand) and Inceptisol (Andic Dystrudepts); both are coarse mixed and mesic soils that have a stratified structure and medium texture through the entire profile (Reyes et al., 2014).

In high altitudes the studied forests are dominated by *N. dombeyi*, *N. alpina* and *Nothofagus pumilio* (lenga), which is a species adapted to harsh environmental conditions in the treeline (Donoso, 1993; Pollmann and Veblen, 2004). At lower altitudes this forest consists in a more complex and stratified vertical structure, showing the typical uneven-aged stand structure (i.e. reverse j-shape diameter size structure), where *N. dombeyi* and *N. alpina* are the dominant trees, and mid canopies are comprised mainly of shade-tolerant tree species, such as *Saxegothaea conspicua* (manio hembra or manio de hojas cortas), *Laureliopsis philippiana* (tepa) and *Dasyphyllum diacantoides* (trevó) (Donoso and Lusk, 2007). The understory vegetation in these forests is commonly comprised of bamboo (*Chusquea* spp.) and the shrub *Drimys andina* (canelo enano). Dense thickets of bamboo (*Chusquea* spp.) that proliferate quickly in understories affects ecosystem dynamics (Veblen et al., 1980; Veblen, 1982; González et al., 2002) by stalling forest recovery and succession (González et al., 2002; Reyes et al., 2013; Soto et al., 2015). To overcome this condition, forest managers started to implement ground disturbance through topsoil scarification with heavy machinery (i.e., bulldozer) after harvesting. Goals of these operations include to creation of “safe sites” for establishment and growth of early-seral *Nothofagus* tree species during the initial stages of post-disturbance succession by effectively controlling bamboo (Reyes et al., 2014; Soto et al., 2015). Further details about structure, composition and stand dynamics of these forests can be found in Veblen et al. (1980) and Pollmann and Veblen (2004).

2.2. Overstory removal and ground disturbance

The four stands were disturbed through operational high-grading harvests during southern summer of 2000–2001, leaving on average residual basal areas between 50 and 63 $\text{m}^2 \text{ha}^{-1}$ and 137–273 trees ha^{-1} (Table 1). Due to natural variability of spatial arrangement and size and quality of trees, harvesting only the

Table 1
Study site and stand characteristics.

Characteristic	Rincón del diablo	Lago Chan-chan	Piedras negras	Valle Hermoso
Latitude ($^\circ$)	39°49'20	39°49'53	39°54'33	40°01'07
Longitude ($^\circ$)	71°52'27	71°50'34	71°56'50	71°52'32
Altitude (masl)	1050	1200	1030	970
Top-height* (m)	41	34.6	39	44
Density (trees per ha)	145	137	273	285
DBH (cm)	44.0	40.5	34.1	35.4
Basal area ($\text{m}^2 \text{ha}^{-1}$)	50.6	55.8	54.9	63.3
Slope (%)	0–15	0–20	0–15	0–20
Aspect	SE	SW	E	SE
Soil texture	Sandy loam	Sandy loam	Coarse sands	Loam
pH (water)	5.3	5.0	5.7	5.7
tN (%)	0.12	0.28	0.12	0.18
tC (%)	8.4	10.2	5.2	6.5
SB ($\text{cmol} + \text{kg}^{-1}$)	2.9	4.0	1.5	5.6
CEC ($\text{cmol} + \text{kg}^{-1}$)	3.7	5.7	1.9	5.7

* Measured to the 10 highest trees in 1 ha.; variables without ground disturbance mapped in 1 ha permanent plot. CEC: cation-exchange capacity, and SB: sum of basis.

Table 2

Ecological niche requirements for the study species. The number of + signs indicates the strength of the sensitivity for a given resource (maximum degree for each category is 3 + signs).

Species	Shade-tolerance	Light	Water	Nitrogen	Sources
<i>Nothofagus dombeyi</i>	Intolerant	+++	+	++	Donoso (1993), Donoso et al. (2006a, 2011, 2015), Soto et al. (2014, 2015), Piper et al. (2009)
<i>Nothofagus alpina</i>	Mid	++	++	+++	Donoso (1993), Reyes et al. (2007), Donoso et al. (2006b, 2011, 2015), Soto et al. (2014, 2015)
<i>Drimys andina</i>	Tolerant	+	+	+	Veblen et al. (1977) and Donoso (2006)

largest, high quality trees led to spatial heterogeneous conditions, e.g., light conditions ranged from 4.5% to 80.5% of full sunlight (Table 1).

Topsoil removal through mechanical scarification was conducted by heavy machinery (Komatsu D4 bulldozer of 5400 kg, with a horizontal blade) in the summer of 2005–2006. These operations removed the rhizomes and culms of *Chusquea* spp. and 20–40 cm of the upper soil layers (Reyes et al., 2014; Soto et al., 2015). As indicated above, ground disturbance of this type creates a complex spatial pattern, as the machine movement depends on the distribution of residual trees and the presence of snags and logs on the forest floor. This typically leads to larger treatment areas connected by narrower pathways, reflecting a node-network (D. Soto, personal observation). In addition, such operations typically avoid removing already existing *Nothofagus* spp. regeneration. Scarification will not extirpate *Chusquea* spp. from the sites, and impacted around 24–46% of the total area in our study sites (Table 1). Technically, ground disturbance altered the chemical and physical properties of the remaining soil. Reyes et al. (2013, 2014) documented that in the top 20 cm of the soil, nutrient supply decreased (organic matter: $4 \pm 2.8\%$, total N: $0.07 \pm 0.05\%$, P (Olsen) 3.2 ± 2.0 mg kg⁻¹, K: 19 mg kg⁻¹), and Al saturation increased (30%); physically, the soil increased in bulk density (0.8 ± 0.1 g cm⁻³) and penetration to resistance (1.1 ± 0.2 kg cm⁻²). Further details on the effects that this restoration technique has on soil chemistry are given in Reyes et al. (2013, 2014).

2.3. Study design, species and measurements

In each of the four selected stands, we installed a 1-ha permanent rectangular plot with 100 circular regeneration plots of 2 m² (radii 0.8 m) in a 10 m by 10 m grid. The four stands exhibited a range of productivity, as reflected in top heights of the 10 tallest trees of *Nothofagus dombeyi* per stand, Table 1). We selected the tallest sapling of the three species (see below) in each regeneration plot (Table 4). Furthermore, measurement trees had to be free-to-grow, i.e., without apparent lateral understory competition quantified as having at least 75% of the upper crown free of competition, and any biotic and abiotic damage (e.g., chlorosis and clipping by browsing).

2.4. Characteristics of the species under study

We chose three species common in scarified and unscarified soil conditions in the four stands selected; these species are known to differ in resource utilization strategies (Table 2): (1) *Nothofagus*

dombeyi, an evergreen, light demanding, early seral, tree species, considered plastic in terms of below-ground resource use. The plasticity in terms of resource use is evident by the variety of resource conditions in which the species can be found (Donoso et al., 2005, 2006a); (2) *Nothofagus alpina*, a deciduous early seral species that is mid-shade tolerant when young (Donoso et al., 2006b, 2013, 2015). This species is known to be very sensitive to below-ground resource, as it can only be found on soils that are well aerated with medium to high nutrient availabilities and high soil water holding capacity (Donoso et al., 2006b; Reyes et al., 2007; Soto et al., 2015). Finally, *Drimys andina* is a shade tolerant, late successional understory shrub species with low water and nutrient requirements. It is considered a species with a plastic response to environmental stresses such as those characteristics of high mountain conditions near timber line (Veblen et al., 1977; Donoso, 2006). More details about species resource requirements are presented in Table 2.

2.5. Plant sampling

We harvested a total of 250 saplings and seedlings: 90 *N. dombeyi*, 100 *N. alpina*, and 60 *Drimys andina*. The harvesting and soil disturbance treatment and the grid sampling design ensured that the harvested plants had grown in a wide range of light, nutrients, and water availability (Table 3). A basal disc was removed from selected seedlings (1 cm above the seedling root collar) and we measured periodic annual radial growth for the last five years. Basal radial growth has been widely used as an integrated measure of whole-plant carbon balance in seedlings, which has been shown to be sensitive to resources (Coates and Burton, 1999; Drever and Lertzman, 2001; Finzi and Canham, 2000; Soto et al., 2015). The sampled discs were air dried for 2 weeks in a well-aerated environment (to avoid infection by fungi), and then gradually sanded in the laboratory. The tree ring widths were measured in two directions (wider and thinner, used the average of both as radial growth) of the sampled discs using a high precision digital caliper (resolution of 0.01 mm; Mitutoyo Absolute Digimatic caliper Series 500).

2.6. Light conditions

Before the plant harvest, a hemispherical photograph was taken at the apex of each selected seedling to estimate the light availability using WinSCANOPY Pro 2013c software (Regent instruments, 2013). The software works with 24MP DSLR compact self-labeling O-Mount system with a calibrated fisheye lens, and

Table 3

Seedling size, light availability, water potential, and tN concentration (mean (standard deviation) and minimum and maximum) of the study plants. *d* is the root-collar diameter; *h* is total height. Light was estimated with hemispherical photographs. Water potential was measured with pressure bomb. tN was determined as total N concentration in leaves through Kjeldahl digestion.

Species	<i>n</i>	<i>d</i> (mm)	<i>h</i> (mm)	Light (% transmitted radiation)	Water potential (MPa)	tN (%)
<i>Nothofagus dombeyi</i>	90	17.2 (15.4) 3.2–84.2	155.4 (44.8) 20.2–214.0	36.4 (18.6) 4.5–80.5	0.8 (0.3) 0.3–1.8	1.3 (0.2) 0.8–1.9
<i>Nothofagus alpina</i>	100	19.5 (13.3) 3.5–63.1	169.8 (87.8) 30.0–330.2	33.4 (18.1) 5.0–80.2	1.1 (0.4) 0.4–2.6	1.7 (0.3) 0.7–2.7
<i>Drimys andina</i>	60	10.6 (3.5) 3.8–30.1	91.2 (34.5) 15–210	28.87 (17.5) 4.6–78.0	0.9 (0.3) 0.3–2.2	1.3 (0.2) 0.8–1.7

automatic north finder (for further details about software and hardware see http://regent.qc.ca/assets/winscanopy_about.html). Light availability was estimated as the total transmitted radiation (the sum of diffuse and direct beam radiation) computed as the percentage of growing season transmitted radiation (e.g., light index as% of full sun; Canham, 1988). Photographs were taken during the growing season under homogeneous diffuse sky light conditions, i.e., during cloudy days or at dawn or dusk.

2.7. Water potential

Prior to plant harvest, we collected the terminal shoots and measured midday xylem water potential (Ψ_{xylem} , MPa) as an indicator of plant water status. At least three complete leaves were cut from each terminal shoot and immediately measured with a portable pressure chamber (PMS Instrument Co., Corvallis, Oregon) in the field. All measurements were taken between the end of March and early April (the driest period of the year in that location) and between 11 and 15 h. Thus, sampling conditions should reflect highest water limitations during the yearly and daily water use cycle.

2.8. Nitrogen concentration

Total nitrogen (tN) concentration (%) was measured following standard Kjeldahl digestion procedures with colorimetric determination (Binkley, 1985; Sadzawka et al., 2004) for all plants used for measuring water potential and growth. We collected the plant material during the end of the growing season to ensure exposure to stressful conditions and the fluctuations of nutrient concentrations typically present during the growing seasons (sensu Sadzawka et al., 2004; Goodman et al., 2013a). We sampled a minimum of 10 g of green leaves without signs of chlorosis or mechanical damage by defoliation or herbivory from the upper crown (1/3 crown position) from each seedling. Leaves were stored in polyethylene bags and placed in an ice container to avoid sample degradation and desiccation for a period not exceeding 24 h in the field. Subsequently, plant material was air dried in an open and ventilated environment for 2 weeks. Next, the samples were dried for 24 h in a drying oven at $72^\circ \pm 5^\circ \text{C}$ and then pulverized into small particles. The analysis was carried out by the Laboratory of Forest Soils and Plant Nutrition, Universidad Austral de Chile.

2.9. Statistical analysis

For each one of the species, we considered different models using the periodic (last 5 years) annual radial increment (hereafter radial growth) at the root-collar diameter as a measure of the plant response to growing conditions. Specifically, we used variations of the non-linear Michaelis-Menten model to describe radial growth as a function of various variables, including light availability (% transmitted radiation), water potential (MPa) and tN concentration (%), as fixed effects variables, and ground disturbance (disturbed and undisturbed soil conditions; categorical variable) and site quality (4 stands; categorical variable) as random effects. The inclusion of random effects terms helps account for possible correlations in the error structure. The choice of Michaelis-Menten model is partially justified because of its flexibility and parsimony to describe non-linear relationships, and the biological interpretability of its parameters. For these reasons, they have been widely used in forestry and ecological studies and allow for statistical assessment of interspecific differences in growth response as a function of light availability (see Pacala et al., 1994; Coates and Burton, 1999; Drever and Lertzman, 2001; Coomes et al., 2009; Soto et al., 2015).

We consider first the model:

$$y_i = d_i^\theta \frac{\alpha L_i}{\left(\frac{\alpha}{\beta}\right) + L_i} + \varepsilon_i, \quad (1)$$

where y_i is radial growth (mm/yr), L_i is light availability (transmitted radiation, %) and d_i is the plant size (root-collar diameter, mm), for the i th seedling. The coefficients α , β and θ are unknown parameters of interest and ε_i is the error term, which we assume to be normally distributed and with mean zero and constant variance (Pacala et al., 1994; Coates and Burton, 1999). The biological interpretation of the parameter α is the growth rate at a high-light level (model asymptote), and β is the growth rate at a low-light level or statistically the slope of the relationship at zero light (Pacala et al., 1994; Coates and Burton, 1999; Drever and Lertzman, 2001). Finally, the parameter θ corresponds to the initial plant size and is introduced to control the disproportionate size effects of plants (Kobe, 2006). Values of $\theta < 0$ reflect conditions where larger saplings induce less growth per unit of initial size than smaller saplings, while values of $\theta > 0$ indicates that larger saplings produce greater growth per unit of initial size than smaller seedlings (Kobe, 2006; Coomes et al., 2009).

Table 4
Selected models and ecological interpretation of their parameters and of the model as a whole (modified from Kobe, 2006). Model parameters are defined in Section 2.9.

Model	Parameters	Biological interpretation
1.- Base $y_i = d_i^\theta \frac{\alpha L_i}{\left(\frac{\alpha}{\beta}\right) + L_i} + \varepsilon_i$	α : asymptotic growth β : growth at low light d : power constant of tree size θ : plant size effect	Non-linear positive effect of light. Saturation of growth at high light levels
2.- High light growth effect $y_i = d_i^\theta \frac{(\alpha R_i) L_i}{\left(\frac{\alpha R_i}{\beta}\right) + L_i} + \varepsilon_i$	$\hat{\alpha}$: Resource term affects high light asymptotic growth β : see model 1 d : see model 1 θ : see model 1	tN or water potential or both modifies high-light growth
3.- Low light growth effect $y_i = d_i^\theta \frac{\alpha L_i}{\left(\frac{\alpha}{\beta R_i}\right) + L_i} + \varepsilon_i$	α : see model 1 $\hat{\beta}$: Resource term affects low light term d : see model 1 θ : see model 1	tN or water potential or both modifies low-light growth
4.- Proportionate effect at high- and low- light $y_i = d_i^\theta \frac{(\alpha R_i) L_i}{\left(\frac{\alpha R_i}{\beta R_i}\right) + L_i} + \varepsilon_i$	$\hat{\alpha}$: see model 2 $\hat{\beta}$: see model 3 d : see model 1 θ : see model 1	tN or water potential or both proportionally modifies low- and high-light growth
5.- Simultaneous limitations at high- and low- light $y_i = d_i^\theta \frac{\alpha L_i R_i}{\left(\frac{\alpha}{\beta}\right) + L_i + \left(\frac{\alpha R_i}{\beta R_i}\right) + R_i} + \varepsilon_i$	α : asymptotic growth term at high light and high resource terms (N or water or both) β : see model 1 d : see model 1 θ : see model 1 β low: Growth term at zero resource (N or water or both)	Simultaneous limitation of light and a tN or water potential or both

To incorporate effects of additional single (i.e., water potential and tN) or multiple conditions (i.e., water potential \times tN) we considered the following variations of the model, as proposed by Kobe (2006):

- 1- *High-light growth effects*: non-linear positive effect of light on growth with effects of other variables (R_i : 1.- water potential, 2.- tN and 3.- its interaction) more pronounced at high light.
- 2- *Low-light growth effects*: variables (R_i) modify growth at low-light levels only.
- 3- *Proportionate effect at high- and low-light*: proportional effect of variables (R_i) on growth along the light gradient, i.e., higher effect at high light levels than at low light levels.
- 4- *Simultaneous growth limitation at high- and low-light*: simultaneous limitation of light and other variables (R_i) on plant growth (see Kobe, 2006; Finzi and Canham, 2000). For instance, below-ground resources could affect growth negatively at low light and positively at high light levels, or vice versa.

The mathematical expressions of all the models and the corresponding interpretation of the parameters are shown in Table 4. Model parameters were estimated using maximum likelihood and model comparisons were made using the corrected Akaike's information criterion (AICc), in order to avoid possible issues with the approximations due to the sample sizes. In this context, models with smaller AICc values are better supported by the data, and models within 2 units of AICc are considered equivalent (Burnham and Anderson, 2002). To facilitate comparisons, we also computed the Δ AICc, that is, the difference between AICc values of the best-fitting model and the other models, and the AICc-weights (w_a) that can be interpreted as a measure of strength of evidence favoring a specific model (Burnham and Anderson, 2002). Finally, we used the coefficient of determination R^2 as an additional indicator of model performance. All modeling was conducted in nlme package in R (Pinheiro et al., 2016).

3. Results

3.1. General resource and resource-growth patterns

The levels of light, water potential, and tN showed no evidence of multicollinearity (even when data were separated by species). On the other hand, preliminary examinations also showed

evidence of association between radial growth and all predictors (i.e., light, tN, water potential) for *N. dombeyi* and *N. alpina* (Fig. 1). In contrast, radial growth of *D. andina* was only significantly related to light availability ($r = 0.380$, $p = 0.002$). The correlations between radial growth with light availability ($r = 0.578$, $p < 0.001$), tN ($r = 0.497$, $p < 0.001$) and water potential ($r = -0.457$, $p < 0.001$) were stronger for *N. alpina* than *N. dombeyi* (Fig. 1). Also, in isolation tN had a stronger influence on plant growth ($r = 0.615$, $p < 0.001$) in *N. dombeyi*, even more than light ($r = 0.522$, $p < 0.001$) and water potential ($r = -0.219$, $p = 0.038$). The strength of association between these variables becomes more evident when the nonlinear Michaelis-Menten model was used, as shown in Fig. 2.

3.2. Effect of initial plant size on plant growth

All species showed the trend that smaller plants produced less radial growth per unit radius than larger plants ($\theta > 0$ in all cases, $p < 0.001$). In general, (based on the performance of the base model and the best supported model) *N. alpina* was the most sensitive to initial size differences, followed by *N. dombeyi* and by *D. andina* (see Appendix A). Thus, size of plant evaluated for the studied species played an important role in determining growth patterns.

3.3. Effect of light availability on plant growth

All parameters were significant ($p < 0.001$) in the base models for the three species, when only light were used as predictor variable (Appendix A). The models for the different species had similar statistical support, as evident by the overlapping confidence intervals (Appendix A). However, *N. alpina* had the lowest growth under high light conditions, as reflected by $\hat{\alpha} = 0.181$, followed by *D. andina* ($\hat{\alpha} = 0.276$) and *N. dombeyi* ($\hat{\alpha} = 0.333$). Similarly, *N. alpina* had the lowest low light parameter $\hat{\beta}$ (0.03) followed by the *N. dombeyi* ($\hat{\beta} = 0.036$) and *D. andina* ($\hat{\beta} = 0.069$), even though the three confidence intervals overlapped (see Appendix A).

3.4. Species-specific growth responses to light availability, tN and water potential

The best model for *N. dombeyi* (light demanding species) was the model that reflected a tN concentration effect on radial growth

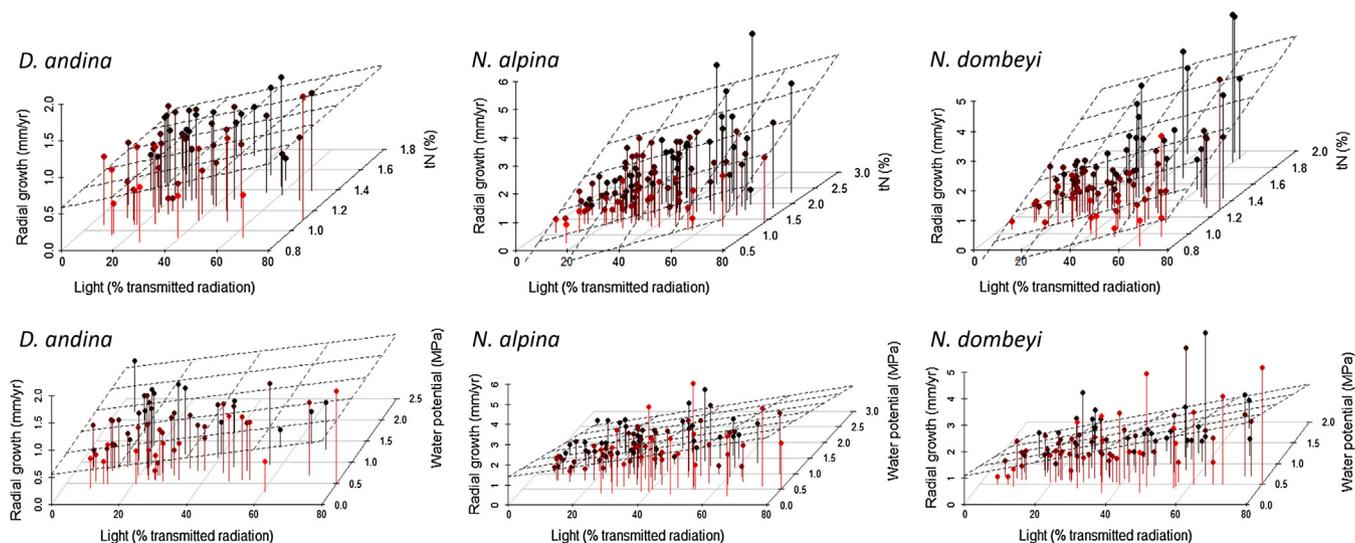


Fig. 1. Tridimensional relationship between radial growth (mm/yr) with light (% transmitted radiation), N concentration (tN%), and water potential (MPa) for the study species. Gradient from red to black dots represent the low to high conditions in tN and water potential, respectively. The surface planes are the linear relationships among variables. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mostly in high light environments (Table 5). There was high evidence that this model was superior $w_i = 0.892$ and had a high predictive ability (i.e., relationship between observed and predicted radial growth; $R^2 = 0.797$, $p < 0.001$). The second best supported model was the simultaneous effect of N at high- and low-light environments ($\Delta_i = 4.400$), supporting the notion that – in addition to light – tN concentration have a strong effect on radial growth (Table 5, Fig. 2).

For *N. alpina* (the intermediate shade-tolerant species with high sensitivity to N and water availability), the best supported model reflected a proportionate effect of N in low- and high-light environments ($w_i = 0.768$) and a high predictive ability ($R^2 = 0.880$, $p < 0.001$). The second best supported model reflecting tN concentration effects only at high light had a Δ_i of only 2.4, but these models differed when compared with likelihood ratio test ($p < 0.05$). This species also showed that high tN concentration increased the radial growth (Table 5, Fig. 2).

The best model for *D. andina* (late successional species) reflected a tN concentration effect only at low light environments ($w_i = 0.758$) and a high predictive ability ($R^2 = 0.569$, $p < 0.001$, Table 5). The base model was the second supported model with a Δ_i of 2.4 (Table 5). Despite the minor differences in terms of AICc values, these models differed according to the likelihood ratio test ($p < 0.05$). The tN concentration effects in the best model are shown in Fig. 2.

4. Discussion

4.1. Species-specific growth responses to resource availability

Our study highlights the sensitivity of light demanding species (*N. dombeyi*, coihue) to N under high conditions. This behavior appears to be generally accepted, as has been documented for different functional groups and individual tree species worldwide (Grubb et al., 1996; Finzi and Canham, 2000; Catovsky and

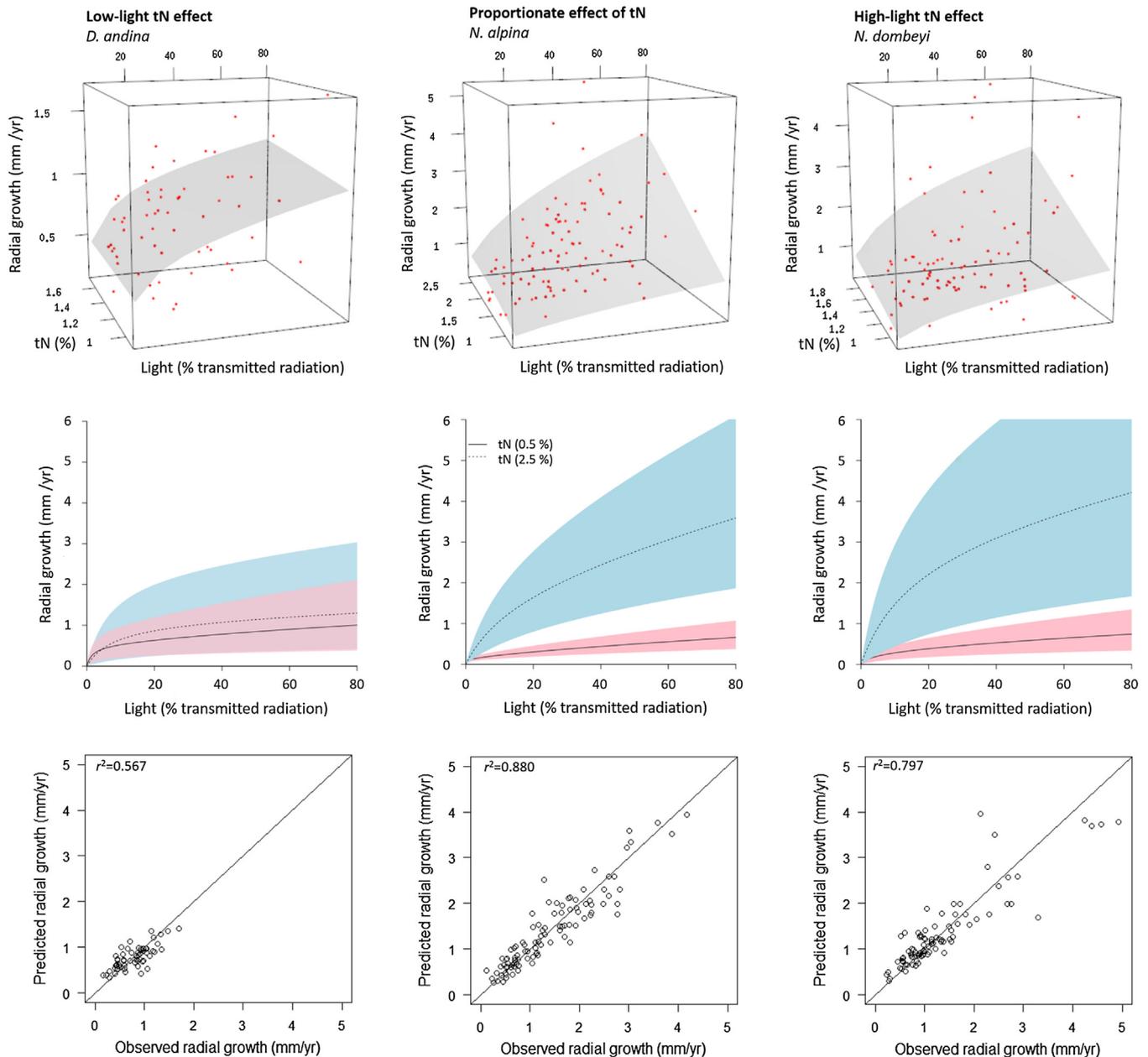


Fig. 2. Best supported models and observed growth values for each studied species (upper row). Middle row shows the effects of high (2.5%)- and low (0.5%)-levels of tN concentrations in leaves, the shaded areas show the Confidence intervals at 95%. Lower row shows the relationship between predicted vs. observed values for the best supported models.

Bazzaz, 2002; Kobe, 2006). Light demanding species have been shown to increase their metabolism as light availability increases (Lambers et al., 2008). This mechanism allows increased nutrient and water uptake and thus enhanced photosynthesis and carbon fixation (Field and Mooney, 1986; Lambers et al., 2008). Thus, light demanding species take advantage of the increased N that is often released after disturbances (Bormann and Likens, 1979; Kimmins, 1997). According to our results, growth of the light demanding species (*N. dombeyi*) benefitted from higher tN concentration when light levels were above 10–15% of light availability. Under lower light levels, increases in tN concentration in leaves did not result in increased growth, likely because these light-demanding species are not able to allocate carbon under low light conditions (Walters and Reich, 1997; Lambers et al., 2008).

The proportionate response of the mid shade-tolerant, N-demanding tree species (*Nothofagus alpina*, rauli) reflected the species' known niche, i.e., its reputation for being sensitive to resource availability and as a poor competitor in natural forests and planted settings when resources are not highly available (Reyes et al., 2007; Donoso et al., 2011, 2015; Soto et al., 2015). Under high light conditions this species acted similar to the light demanding species in terms of the response to tN concentration in leaves (see Fig. 2). However, in contrast to the light-demanding species, this species was extremely sensitive to tN under all light conditions, which is indicative of the resource demanding nature (Donoso et al., 2006b; Soto et al., 2015). Thus, even though not considered a late successional species, this species reacted positively to N inputs in shaded conditions, likely because high levels of N increased leaf chlorophyll concentration and thus photosynthesis, albeit modestly (Field and Mooney, 1986; Walters and Reich, 1997; Holste et al., 2011). This finding may contradict the postulates of previous studies showing that increased N availability reduces the growth and, in extreme cases increase the mortality at low light conditions for light demanding and mid shade-tolerant tree species (Grubb et al., 1996; Catovsky and Bazzaz, 2002), indicating that these mechanisms still need more ecological and functional clarification.

Contrary to our hypothesis, the late successional shrub species (*Drimys andina*, canelo enano) was most influenced by light availability and showed only minor impact of tN concentration on plant growth under low light conditions. These results are consistent with postulates that late-successional species are unresponsive to

light, water and N availability, such as that documented for eastern hemlock (*Tsuga canadensis*) (Walters and Reich, 1997; Catovsky and Bazzaz, 2002; Bigelow and Canham, 2007). However, contrary to our expectations, this late successional species reacted positively to light after disturbance (see Fig. 2), despite being known as a shade tolerant species that typically suffers photo-inhibition in response to canopy openings (*sensu* Strauss-Debenedetti and Bazzaz, 1991; Valladares et al., 2002). The potential explanations include that this species adapts to mid-to-high light conditions presumably through light acclimation mechanisms at the leaf level by increasing tN concentration and light availability (Chazdon, 1992). This finding for this late successional species contradicts previously published claims that species in this functional group are less plastic than co-occurring light demanding species (Strauss-Debenedetti and Bazzaz, 1991; Valladares et al., 2002), although there have been some exceptions reported from tropical rain forests in Panama (Chazdon, 1992) and northern hardwoods in the USA (Abrams and Mostoller, 1995). This shows that more research into these mechanisms is needed to clarify this functional behavior in late successional species.

4.2. Effects of species' differential resource use upon secondary succession

Our study provides insights how autecological species characteristics, specifically light and N requirements in conjunction with an understanding of disturbance effects on light, tN concentration, water potential provide insights about the processes governing plant growth in early stages of succession. The differences in species sensitivities and resource levels found on the study sites were strong enough to have implications for future stand composition and structure (Finzi and Canham, 2000; Kobe, 2006). For example, we found that the fast growth of light demanding species (*N. dombeyi*) during early stages of succession is strongly dependent on N. Similarly, the proportionate growth effects of tN concentration along a light gradient for intermediate shade-tolerant species with a high sensitivity to below-ground resources show that *N. alpina* may have lower competitive ability than light demanding species on dry slopes with heavy and poor nutrients soils that are typical conditions after large-scale disturbances such as landslides, fires, or volcanic eruptions (*sensu* Veblen et al., 1996; Franklin et al.,

Table 5

AICc results for the various models, separated by the hypotheses that the models represent and by species. Δ_i is AICc difference between best supported model (bold numbers) with competitive ones. w_i is the AICc weights. R^2 is the coefficient of determination between observed and predicted values. In bold is shown the best supported model.

Models	<i>Nothofagus dombeyi</i>				<i>Nothofagus alpina</i>				<i>Drimys andina</i>			
	AICc	Δ_i	w_i	R^2	AICc	Δ_i	w_i	R^2	AICc	Δ_i	w_i	R^2
<i>Base</i>												
1. Light	139.5	32.0	0.000	0.710	104.8	36.8	0.000	0.816	−4.7	2.4	0.228	0.552
<i>High-light resources effect</i>												
2. Light, nitrogen	107.5	0	0.892	0.797	70.4	2.4	0.231	0.877	12.8	19.9	0.000	0.435
3. Light, water	–	–	–	–	–	–	–	–	15.3	22.4	0.000	0.490
4. Light, water, nitrogen	177.0	69.5	0.000	0.591	175.4	107.4	0.000	0.702	19.0	26.1	0.000	0.446
<i>Low-light resources effect</i>												
5. Light, nitrogen	145.9	38.4	0.000	0.689	110.7	42.7	0.000	0.816	−7.1	0	0.758	0.569
6. Light, water	136.4	28.9	0.000	0.719	90.9	22.9	0.000	0.849	2.9	26.1	0.000	0.491
7. Light, nitrogen, water	144.2	36.7	0.000	0.695	100.0	32.0	0.000	0.834	1.3	8.4	0.011	0.504
<i>Proportionate effect of resources at low- and high-light environments</i>												
8. Light, nitrogen	116.8	9.3	0.008	0.777	68.0	0	0.768	0.880	6.0	13.1	0.001	0.485
9. Light, water	–	–	–	–	141.0	73.0	0.000	0.778	10.2	17.3	0.000	0.499
10. Light, nitrogen, water	166.8	59.3	0.000	0.613	131.1	63.1	0.000	0.796	14.5	21.6	0.000	0.460
<i>Simultaneous limitation at low- and high-light environments</i>												
11. Light, nitrogen	111.9	4.4	0.098	0.787	87.5	18.5	0.000	0.857	24.4	31.5	0.000	0.364
12. Light, water	249.1	141.6	0.000	0.281	–	–	–	–	32.5	39.6	0.000	0.449
13. Light, nitrogen, water	–	–	–	–	–	–	–	–	–	–	–	–

‘–’: do not converge.

2002). Therefore, *N. alpina* and tree species with similar traits are strongly dependent of tree-fall gaps in mesic sites, which have high N and water availability (Kimmins, 1997; Thiel and Perakis, 2009). Obviously, the whole suite of species needs to be considered in such settings. For example, in the study region, severe competition can occur with released understory vegetation, such as the case of bamboo species in Chile (*Chusquea* spp.), creating a narrow window for regeneration and growth in competitive mesic environments (González et al., 2002; Soto et al., 2015).

In this study, we found that late successional species acclimate well to new conditions after disturbances, and are able to establish and grow in larger openings and disturbed soils, i.e., in areas considered suitable for light-demanding species. Our results also suggest that the late successional species may be well adapted to establishment in areas with little or low disturbance. This is likely due to its adaptation to low N and water along the light gradient and its acclimation mechanism at high light levels. Consequently, we found this species not only in most disturbed soils in areas with low to high light availability, but also in undisturbed and very shaded conditions (D. Soto, personal observation). This observation is consistent with the theory that successional patterns vary as a function of soil conditions, i.e., that the occurrence of light demanding species is greater in high-fertility soils (i.e., N in this study), and late successional species in low-fertility soils (Aerts and Chapin, 2000; Lusk and Matus, 2000; Coomes et al., 2009). The dominance of late successional species in low fertility soils is hypothesized to be a consequence of their nutrient and water conservation strategies (e.g., long-lived sclerophyllous leaves with low carbon assimilation rates) (Valladares et al., 2000; Lusk et al., 2014). This trait makes these species relatively unresponsive in high fertility soils, possibly resulting in low competitive abilities compared to with resource demanding species (Aerts and Chapin, 2000; Valladares et al., 2000; Lusk et al., 2014). Therefore, the existing tradeoff between species' light preference and demand of soil resources may aid in understanding the compositional shifts at different soil fertility gradients (Russo et al., 2005; Coomes et al., 2009). Thus, the stand dynamics of these forests are strongly impacted by the range of resource availability, in addition to light, but also (and may be more importantly) by acclimation mechanisms of the species to resources after disturbances.

4.3. Implication for forest management

Forest management operations have the ability to alter ecological processes and functions and thus successional pathways (Coates and Burton, 1999; Haeussler et al., 2013). This study evaluated the effects of ground disturbance upon regeneration growth in a forest ecosystem where succession had been sequestered after a partial and incomplete shelterwood cut (a partial disturbance) in the Andes of southern South America. These practices generated variable levels of tN, light and soil moisture, but the latter did not have an effect on regeneration growth, while the interaction of tN and light differed for the three relevant species. Silvicultural practices, such as overstory and understory treatments, have different impacts on resource levels and availability that are likely to affect seedling development of these three species, as demonstrated in our study herein. Understanding these differences and interactions, specifically the sensitivity to available resources, can help when designing silvicultural practices to encourage the development of desired stand structures and compositions.

The interacting effects of resources (in our study light and N) is of special importance, suggesting that the emphasis on managing light conditions may be warranted in some regions (e.g., Ligot et al., 2014; Klopčič et al., 2015) but may need to be expanded in

other regions to include other factors, especially nutrients and water (Drever and Lertzman, 2001; Kobe, 2006; Bigelow and Canham, 2007). Thus, simple models, such as prescriptions based only on shade tolerance of a species (e.g., Table 2 in *Silviculture Interpretations Working Group*, 1994) may not warrant the desired regeneration and could lead to alternative successional pathways in some regions if other relevant factors are not considered into these models. Similarly, guidelines that define species tolerance (in general) only by their sensitivity to low light levels (e.g., Hopper and Applegate, 1995) may need to be expanded to also address other resources (and environmental conditions) and their interactions (see also Valladares and Niinemets, 2008). Our study highlights the benefits when assessing silvicultural practices in terms of how they impact several factors that affect growth, both in terms of their individual and interactive effects.

5. Conclusions

In our study, leaf tN concentration played an important role in the radial growth of distinct species in terms of resource use. Leaf tN concentration was strongly related to the growth of shade-intolerant and plastic tree species to N availability at high-light levels. On the other hand, tN concentration was related with the radial growth of mid tolerant and high N demanding tree species to low- and high-light levels. Contrary to our expectation, shade-tolerant growth was related to light and N at low-light levels. On light of our results, we can infer that community organization after disturbances (i.e., overstory harvesting and ground disturbance) in *Nothofagus* old-growth forests is highly impacted by light and N. Higher N availabilities may have an important influence on the presence and dominance of shade-intolerant and (more importantly) in resource demanding species. However, release of understory plants after disturbance could influence the community organization after these disturbances. Therefore, management practices in these forests should consider this ecological information (i.e., species requirements in availability of nutrients (tN), water and light) to design silvicultural practices to promote desirable tree regeneration and early growth.

Acknowledgements

This study was supported by Conaf 15/2013 grant (Fondo de Investigación del Bosque Nativo, Conaf, Chile). DPS thanks the support from Becas Chile doctoral fellowship from CONICYT, Chile, and Robert Tarrant fellowship in ecology and silviculture of hardwoods, Oregon State University. We appreciate the field assistant of Diego Ponce, Carlos Soto P., Rodolfo Santander, Manuel Palacios and Juan Vergara (Huilo-Huilo). We also appreciate the early comments and suggestions made by professor Víctor Gerding from Universidad Austral de Chile, and the help of Mercedes Uscola (plant physiology and N dynamic in plants) and Mike Szuter (R management) from Purdue University, and also to three reviewers during the editorial process.

Appendix A

Estimated parameters (standard error) and confidence intervals at 95% for Michaelis-Menten equation. $\hat{\alpha}$ represents the asymptotic estimated parameter, $\hat{\beta}$ represents the low light parameter and $\hat{\theta}$ represents the parameter of effect of plant size (\emptyset). Bold numbers per species represent the best model estimation (i.e., lowest AICc). Empty spaces are those models without convergence in the estimation.

Model	<i>Drimys andina</i>			<i>Nothofagus dombeyi</i>			<i>Nothofagus alpina</i>		
	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\theta}$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\theta}$	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\theta}$
1. Light, \emptyset	0.276 ^{***} (0.062)	0.069 ^{**} (0.026)	0.482 ^{***} (0.072)	0.333 ^{***} (0.078)	0.036 ^{**} (0.013)	0.604 ^{***} (0.051)	0.1814 ^{***} (0.039)	0.033 ^{**} (0.012)	0.767 ^{***} (0.051)
	0.150–0.402	0.0163–0.122	0.336–0.628	0.176–0.489	0.009–0.063	0.501–0.707	0.103–0.259	0.008–0.059	0.664–0.870
2. Light, N, \emptyset	0.271 ^{***} (0.073)	0.047 ^{**} (0.015)	0.426 ^{***} (0.084)	0.271^{***} (0.051)	0.050^{**} (0.017)	0.549^{***} (0.043)	0.1611 ^{***} (0.025)	0.037 ^{***} (0.009)	0.636 ^{***} (0.038)
	0.125–0.418	0.016–0.078	0.257–0.595	0.169–0.373	0.015–0.085	0.464–0.635	0.109–0.212	0.018–0.057	0.559–0.712
3. Light, W, \emptyset	0.182 ^{**} (0.056)	0.022 ^{**} (0.006)	0.726 ^{***} (0.096)	–	–	–	–	–	–
	0.068–0.296	(0.008–0.036)	0.533–0.919						
4. Light, (NxW), \emptyset	0.194 ^{**} (0.056)	0.026 ^{**} (0.008)	0.621 ^{***} (0.094)	1.415 ⁺ (0.584)	0.012 ^{***} (0.002)	0.482 ^{***} (0.057)	0.672 [*] (0.259)	0.007 ^{***} (0.001)	0.641 ^{***} (0.070)
	0.076–0.313	0.010–0.043	0.432–0.811	0.254–2.577	0.007–0.017	0.367–0.596	0.158–1.186	0.003–0.010	0.502–0.781
5. Light, N, \emptyset	0.275^{***} ± 0.059 (0.156–0.395)	0.086^{**} ± 0.030 (0.024–0.148)	0.486^{***} ± 0.070 (0.345–0.627)	0.261 ^{***} ± 0.054 (0.152–0.370)	0.090ns ± 0.056 (–0.021 to 0.203)	0.644 ^{***} ± 0.050 (0.544–0.743)	0.139 ^{***} ± 0.027 (0.085–0.193)	0.140ns ± 0.123 (–0.105 to 0.386)	0.819 ^{***} ± 0.049 (0.720–0.917)
6. Light, W, \emptyset	0.233 ^{***} ± 0.056 (0.121–0.346)	0.158ns ± 0.122 (–0.087 to 0.404)	0.504 ^{***} ± 0.079 (0.344–0.664)	0.362 ^{***} ± 0.081 (0.201–0.524)	0.024 ^{***} ± 0.007 (0.010–0.039)	0.587 ^{***} ± 0.051 (0.485–0.688)	0.226 ^{***} ± 0.043 (0.139–0.312)	0.031 ^{***} ± 0.006 (0.017–0.044)	0.713 ^{***} ± 0.048 (0.617–0.810)
7. Light, (NxW), \emptyset	0.242 ^{***} ± 0.056 (0.128–0.356)	0.150ns ± 0.150 (–0.029 to 0.330)	0.499 ^{***} ± 0.077 (0.343–0.654)	0.281 ^{***} ± 0.059 (0.163–0.400)	0.053 [*] ± 0.024 (0.004–0.102)	0.630 ^{***} ± 0.050 (0.529–0.731)	0.181 ^{***} ± 0.033 (0.114–0.248)	0.070 ^{**} ± 0.021 (0.027–0.112)	0.762 ^{***} ± 0.048 (0.666–0.858)
8. Light, N, \emptyset	0.283 ^{***} ± 0.069 (0.144–0.421)	0.059 ^{**} ± 0.017 (0.024–0.093)	0.424 ^{***} ± 0.017 (0.268–0.580)	0.234 ^{***} ± 0.040 (0.154–0.314)	0.102 [*] ± 0.046 (0.009–0.196)	0.574 ^{***} ± 0.042 (0.490–0.658)	0.141^{***} ± 0.019 (0.102–0.180)	0.071^{***} ± 0.019 (0.034–0.109)	0.670^{***} ± 0.036 (0.598–0.742)
9. Light, W, \emptyset	0.245 ^{***} ± 0.072 (0.099–0.390)	0.025 ^{***} ± 0.007 (0.011–0.039)	0.633 ^{***} ± 0.092 (0.447–0.819)	–	–	–	0.683 ^{***} ± 0.170 (0.345–1.020)	0.009 ^{***} ± 0.001 (0.005–0.012)	0.661 ^{***} ± 0.060 (0.540–0.781)
10. Light, (NxW), \emptyset	0.224 ^{***} ± 0.064 (0.095–0.354)	0.037 ^{**} ± 0.011 (0.015–0.060)	0.572 ^{***} ± 0.091 (0.390–0.755)	0.742 ^{***} ± 0.174 (0.395–1.089)	0.016 ^{***} ± 0.003 (0.009–0.022)	0.530 ^{***} ± 0.053 (0.424–0.636)	0.331 ^{***} ± 0.071 (0.189–0.473)	0.016 ^{***} ± 0.002 (0.010–0.021)	0.685 ^{***} ± 0.053 (0.578–0.791)
11. Light, N, \emptyset	0.028 ^{**} ± 0.008 (0.010–0.046)	0.003ns ± 0.002 (–0.001 to 0.007)	0.420 ± 0.094 (0.230–0.610)	0.0282 ^{***} ± 0.007 (0.013–0.042)	0.002ns ± 0.001 (–0.001 to 0.006)	0.516 ^{***} ± 0.043 (0.429–0.602)	0.017 ^{***} ± 0.003 (0.001–0.024)	0.001 [±] 0.000 (0.000–0.003)	0.564 ^{***} ± 0.041 (0.004–0.647)
12. Light, W, \emptyset	0.012 ^{**} ± 0.003 (0.004–0.020)	0.001ns ± 0.001 (–0.000 to 0.003)	0.876 ^{***} ± 0.116 (0.644–1.108)	–0.011 ^{**} ± 0.004 (–0.019 to (–0.003))	0.001 [*] ± 0.000 (0.000–0.002)	0.944 ^{***} ± 0.096 (0.752–1.135)	–	–	–
13. Light, (NxW), \emptyset	–	–	–	–	–	–	–	–	–

ns: non-significant.

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

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