The Influence of Microsite Conditions on Early Performance of Planted Nothofagus Nitida Seedlings when Restoring Degraded Coastal Temperate Rain Forests

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Early performance of *Nothofagus nitida* plantings

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The influence of microsite conditions on early performance of planted *Nothofagus nitida* seedlings when restoring degraded coastal temperate rain forests

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**ABSTRACT**

Widespread impacts of changes in land use, climate, and disturbance regimes continue to affect mature forests and their subsequent post-disturbance recovery. In South American temperate rainforests, the recovery of the original composition, structure, and ecological services of now-degraded old-growth forests is additionally hampered by the aggressive competition that the native *Chusquea* bamboo understory exerts on juvenile trees, thus arresting ecological succession. In this study, we aim to evaluate the early performance of *Nothofagus nitida* seedlings (pioneer tree species that tolerate shade) planted beneath nurse canopy following removal of the understory, and to define which microsite conditions can facilitate *N. nitida* growth. For this, we monitored 45 *N. nitida* plantings established in 2014 in Chiloé Island (North Patagonia, Chile) for five years. After this period, planted seedlings presented relatively good indicators of performance with low mortality (~30% of dead seedlings), good vitality (~60% of
Early performance of *Nothofagus nitida* plantings

healthy seedlings), and relatively high mean periodic annual increments in root collar diameter and height (~1.7 mm/year and ~17.4 cm/year, respectively). Furthermore, our results show that the planted *N. nitida* seedlings can tolerate and grow under low-light conditions, though their diameter and height increase significantly with higher light availability. However, physiological stress of planted seedlings increased in open areas with more available light and planted seedlings were most stressed during the summer season. Increased summer-season stress was attributed to the months with highest depth of the water table, highest maximum and mean photosynthetic active radiation (PAR) values, highest temperature, and lowest precipitation. Our results show for first time with field-based data that different microsite and canopy conditions facilitate the initial performance of *N. nitida* plantings after removal of the *Chusquea* bamboo understory. In this context, we conclude that the removal of the *Chusquea* bamboo understory is the key to overcome arrested succession of coastal temperate rain forests. Furthermore, supplementary planting of pioneer tree species that tolerate shade, like *N. nitida*, assists natural forest recovery, especially in humid and open sites with some protection of a nurse canopy.

**Keywords:** Active restoration, bamboo understory, Chiloé Island, drought stress, fluorescence, seedling growth.

1. Introduction

With more than 75% of the world’s land showing human alteration (IPBES, 2018), restoring ecosystems has become a priority. In fact, last year the United Nations General Assembly declared 2021 – 2030 the UN Decade on Ecosystem Restoration (United Nations, 2019). Thus, the world must work to increase the extent and functionality of native ecosystems by investing in restoration activities, like ecological restoration, that is, the process of assisting the recovery of ecosystems that have been degraded, damaged,
Early performance of *Nothofagus nitida* plantings

or destroyed (SER, 2004; Gann et al., 2019). Today, forest degradation is one of the major drivers of loss in ecosystems goods and services, with ca. 500 million ha of degraded forests in tropical areas alone (Thompson et al., 2013; Ghazoul and Chazdon, 2017). Unlike deforestation (conversion from forested to non-forested land cover), forest degradation refers to human-induced reductions or changes in structural, compositional, and/or functional attributes. From a management and planning perspective, such changes typically occur without modifying the forest land-use condition or classification (Stanturf et al., 2014; Ghazoul and Chazdon, 2017). Degradation of forests is especially sensitive in the case of old-growth forests (defined here as at least 200-year-old stands with high tree basal areas, complex vertical canopy structure, and high tree species richness; Gutierrez et al., 2009), whose annual losses in composition, structure, habitat, timber productivity, and provision of other ecosystem services are proportionally higher than that affecting younger stands (i.e. in relation to the area of undisturbed stands left globally, Bauhus et al., 2009; Donoso et al., 2013; McDowell et al., 2020). In old-growth forests, degradation is mainly caused by high-grading practices which consists in the removal of the most commercially valuable trees, leaving a residual stand composed of poor-timber-quality individuals (Donoso et al., 2013). In this context, restoring high-graded old-growth forests with tree species that tolerate shade is a promising option to recover at least structure and composition in degraded stands (Soto et al., 2014; Soto et al., 2015).

In temperate rainforests of southern South America, there is little information about the extent and effects that forest degradation has on ecosystem services. However, it is known that, as a consequence of severe high-grading, highly commercially valuable forests in southern Chile have been degraded, losing biomass, density and productivity, especially by cutting the dominant tree species (Donoso et al., 2013). Forest degradation, which historically (1800-1900s) was concentrated in the Andes at ca. 37-41°S (Otero, 2006; Bannister, 2018), has gradually advanced in extent south over the last few decades (ca. 1980s-present). Most of this advance in degradation has been through large-scale clear cuts.
Early performance of *Nothofagus nitida* plantings or selective harvesting for firewood and other timber products that create large canopy gaps, where the target trees species have been shade- and mid-shade tolerant species (Echeverria et al., 2008; Heilmayr et al., 2016; Bannister et al., 2017). The recent degradation advance also differs geographically from the historic one, in that it is taking place along the coastal range and in the archipelagos of North Patagonia, where soils are considerably thinner, infertile, frequently waterlogged, and more sensitive to alterations by disturbance events (Bannister and Donoso 2013). In some of these areas, coastal temperate rainforests have remained largely free of stand-replacing disturbances for at least 450 years and instead vegetation dynamics are driven primarily by fine-scale gap-phase dynamics (Gutiérrez et al., 2004). Thus, these forests may be especially sensitive to novel disturbances that create large open-canopy conditions, such as high-grading (Burns, 1993; Parish and Antos, 2006; Bannister, 2012).

Following canopy disturbance, including high-grading, continuous thickets of *Chusquea sp.* bamboos invade and occupied the forest understory. This rapid understory reinitiation (Oliver and Larson 1980) prevents and/or hinders tree regeneration (Veblen, 1982; González et al., 2002; Holz and Veblen, 2006; Muñoz and González, 2009; Donoso et al., 2013; Bannister et al., 2017), which can arrest or stagnate successional development (Soto et al., 2019). Promising management options have been studied to overcome arrested succession in degraded Andean *Nothofagus*-dominated forests following bamboo removal, either through planting of pioneer (shade-intolerant) *Nothofagus dombeyi* and *Nothofagus alpina* in gaps (e.g. Donoso et al., 2013, Donoso et al., 2015; Soto et al., 2014, Soto et al., 2015), or through allowing natural *Nothofagus* spp. regeneration in newly created gaps (Soto et al., 2017, Soto et al., 2019). Those studies have also highlighted the importance of monitoring early performance of planted native tree species, since the likelihood that juvenile planted seedlings will successfully reach the canopy and persist over time is often determined by their performance at younger stages (Soto et al., 2015; Bannister et al., 2020). While the performance of planted juveniles in degraded *Nothofagus*-Andean forests is known to vary by species and to depend on soil conditions, light availability, gap size, and
Early performance of *Nothofagus nitida* plantings

aspect (Donoso et al., 2013; Soto et al. 2014, Soto et al., 2015), it is not known which environmental
variables might control performance of juveniles planted in degraded coastal temperate rainforests of
North Patagonia, or even whether costly, active (versus affordable, passive) restoration is needed.

In this context, a possible option to restore degraded old-growth forest stands in coastal areas is
to remove the dense bamboo understory that develops after a canopy opens and plant species such as
*Nothofagus nitida*, the dominant tree species in coastal Patagonian rainforests, and probably the
*Nothofagus* species that better tolerate shade (Reyes-Díaz et al., 2005; Coopman et al., 2008). *Nothofagus
titida* is a broad-leaved, evergreen species endemic to Chile (between 39°53’S and 48°30’S), that reaches
heights of 35 to 40 m and co-occurs with other broad-leaved species of the coastal temperate rain forests
of North Patagonia (Amigo et al., 2004). The shade tolerance of this species, its relatively fast growth,
and the commercial value of its timber, make this tree species a promising option for restoring degraded
old-growth forests, especially because it can establish after small-scale disturbances, such as in individual
tree-fall gaps (Gutiérrez et al., 2004). This is a competitive advantage in relation to other pioneer species
like *N. dombeyi* that cannot tolerate these low-light conditions. This does not mean that increased light
availability will lead to reduced growth in *N. nitida* seedlings; it means that the species is able to survive
and grow better under low-light conditions than shade-intolerant species. There are many examples
showing that shade-tolerant species (e.g *Fagus sylvatica* in Europe) increase diameter and height growth
with increasing light (van Hees1997, Ammer 2003). Furthermore, during the development from seedling
to sapling, *N. nitida* has the capacity to adjust their photosynthetic apparatus to irradiance and change the
balance of light energy utilization, supporting a phenotypic transition from shade to sun during its early
ontogeny (Coopman et al., 2008). Also, in relation to other *Nothofagus* species, *N. nitida* is restricted to
oceanic climates of the coastal regions and is the only *Nothofagus* species absent from the eastern slopes
of the Andes (Veblen et al., 1996; Amigo et al., 2004; Reyes-Díaz et al., 2005). Some studies have shown
that *N. nitida* has a lower frost tolerance than *N. dombeyi*, with lower capacity to maintain a functional
Early performance of *Nothofagus nitida* plantings

photosynthetic apparatus, tolerating freezing in autumn and winter only at the adult stage (Reyes-Díaz et al., 2005). Also, *N. nitida* has a lower drought tolerance compared to *N. dombeyi*, which has been associated with lower water use efficiency (WUE) and photosynthesis under severe drought stress (Piper et al., 2007).

The overall goal of this study is to evaluate the early performance of planted *Nothofagus nitida* seedlings in degraded coastal rainforests of North Patagonia, following the removal of the *Chusquea quila* bamboo understory, and to define which microsite conditions can facilitate establishment of *N. nitida*. We hypothesize that although *N. nitida* has a relatively high shade-tolerance, early performance of planted *N. nitida* seedlings is facilitated in more open-canopy conditions without a nurse canopy. However, we also hypothesize that due to its low drought tolerance, the physiological stress of *N. nitida* planted seedlings will be higher in open conditions and in the dry season (summer). To address these two hypotheses, we evaluated the early performance of 45 *N. nitida* restoration plantings following removal of the *Chusquea* bamboo understory for five years. Based on our results, we present recommendations for restoration plantings in degraded, coastal temperate rainforests. To our knowledge this is the first study that documents the performance of planted *N. nitida* seedlings.

2. Material and methods

2.1 Study area

The study area was located near Lake Huillinco (~42°43′S and 73°54′W) on the central Chiloé Island, in the northwesternmost region of Patagonia, in southern Chile (Figure 1). Chiloé Island has a cool-temperate climate with strong oceanic influence (Di Castri and Hajek, 1976), and during this work (between 2013 and 2019), the study area had a mean annual temperature of 10.0°C, mean annual relative
humidity of 81.5%, and mean annual precipitation of 1557 mm, ranging from 1004.5 mm in year 2016 to 1917.8 in year 2017 (Tara, Agrometeorological Network, INIA, Chile, approximately 15 km from the study site). This area belongs to the transitional zone between the northern and southern temperate biogeographic region of Chile (Bannister et al., 2012). The landscape has been shaped by the last glaciation (about 13,000 yr. BP), which created a mix of glacial-till hills and shallow valleys that overlay Pre-Cambrian and Tertiary Metamorphic rocks with extremely acidic and frequently poorly drained soils with gley horizons (Villagran, 1988). Elevations range between 50 and 100 m a.s.l and slopes between 0 and 32%.

This area contains extensive old-growth North-Patagonian forests dominated by long-lived, pioneer broadleaf species *Nothofagus nitida* (Nothofagaceae) and emergent *Weinmannia trichosperma* (Cunoniaceae), which are accompanied by codominant shade-tolerant species, including conifer *Saxegothaea conspicua* (Podocarpaceae) and the broadleaf species *Laureliopsis philippiana* (Atherospermataceae) and *Drimys winteri* (Winteraceae). Based on the comprehensive characterization of North-Patagonian old-growth forests made by Gutierrez et al. (2009), we refer to old-growth stands as those with tree basal areas >80 m²/ha, densities of >36% of shade-tolerant tree species in the emergent and dominant canopy layer, species richness >7 tree species, presence of large canopy emergent trees, high vertical heterogeneity, and minimum stand ages older than 200 years. Tree species in these forests have adapted to regenerate beneath small- and medium-size canopy gaps (Gutierrez et al., 2004; Gutiérrez et al., 2008). The understory and lower overstory are dominated by several myrtaceous tree species and a high diversity of non-tree species (Bannister and Donoso, 2013; Bannister et al., 2017). In the last 40 years (1980-2020), these old-growth forests have been exposed to illegal logging (clear cutting or selective logging operations), which have created a wide range of forest structures, including undisturbed, moderately degraded (high-graded), and severely degraded old-growth forests (Figure 2).
Figure 1. Study area on Chiloé Island, North Patagonia, in southern Chile (left), and location of the 45 experimental units in the Huillinco experiment (right aerial photo).

2.2 Experiment design and implementation

In winter 2014, as part of a broader research project, a restoration experiment (Huillinco experiment, 4 ha) was established in the study area near the town of Huillinco (42°43’S, 73°54’W). The general idea behind that broader research project and the establishment of this experiment was to determine whether *Nothofagus nitida* plantings or natural regeneration was a more successful restoration option after the removal of the *Chusquea* bamboo understory, especially whether a less costly natural regeneration approach could be adopted (a common question for foresters, managers, and restorationists). The experiment consisted of 45 experimental units of (20 m x 20 m) 400 m², established in an old-growth North-Patagonian forest that included a gradient with different levels of degradation (in terms of density, dbh, height, and basal area), from totally open areas to close to reference conditions (Bannister et al., 2018). In each experimental unit, the *Chusquea quila* bamboo was fully removed from the understory and a 10 m wide buffer zone between units was retained in order to avoid interference between them. After bamboo removal, plots of 50 *Nothofagus nitida* seedlings (2 m x 2 m) were systematically planted in half (200 m²) of each unit (total of 2,250 seedlings in the complete experiment), while the other half (200 m²) was left for natural regeneration. In this study, only data from the restoration plantings are used. The high range of densities, diameters, and basal areas of the remaining forest in the experiment created a rich gradient of microsites in which to examine the early performance of planted seedlings (Table 1, Figure 2).

Seedlings were transplanted during their first year of life (cotyledons present) from open sites nearby the experiment (near unpaved roads) to a planting bed in a local nursery (42°40’S; 73°53’W) and transplanted as two-year-old, bare-root seedlings in the experimental field plots during the winter (June-
Early performance of *Nothofagus nitida* plantings

July) of 2014. At the time of collection, seedlings height ranged 3-5 cm and at the time of their planting, their mean height was 100.1 cm (±5.1), with a mean root collar diameter of 0.88 cm (±0.07). Cattle were excluded with barbed-wire fences around the perimeter of the experiment in order to avoid browsing from non-native species. Due to the large scale of the experiment (4 ha), and the ineffectiveness of the fences to prohibit browsing by small animals, it was impossible to avoid browsing from *Pudu puda*, a native and near-threatened deer species of the temperate forests of Chile and Argentina (Burger et al., 2019). This deer species is known as one of the smallest deer species in the world, reaching just 40 cm in height (Silva-Rodriguez et al 2010), and it prefers open conditions for browsing (Burger et al. 2019).

Figure 2. Degraded coastal temperate rain forests in Chiloé Island, North Patagonia (a). *Chusquea bamboo* dense understory before removal (b). Experimental units of 400m² where the *Chusquea bamboo* understory was removed (c). Group plantings of *Nothofagus nitida* seedlings (d).

2.3 Measurements

All variables were measured annually (every austral winter) on all *N. nitida* seedlings (2014-2019), including: root collar diameter (*rcd*), total height (*h*), and vitality (1: <10%, 2: 10-25%, 3: 26-50%, 4: >50% of dead foliage). Mortality, survival, and incidence of browsing were recorded and averaged per experimental unit. Competition by native vegetation around each seedling was characterized by measuring cover (%) and maximum height (cm) of naturally regenerated tree seedlings and non-tree species in 1 m² subplots centered on each live seedling in winter 2019. Light availability for each seedling was estimated based on the one-point overcast sky condition method (*sensu* Parent and Messier, 1996). This method considers the percentage of photosynthetic photon flux density (PPFD: µmol m² s⁻¹) reaching each seedling in relation to a simultaneous PPFD measured in an open area (%PPFD). This was
Early performance of *Nothofagus nitida* plantings

carried out for all planted seedlings with a LICOR 1400 Data logger and LI250 point quantum sensors in winter 2015. The physiological stress, or potential photochemical quantum yield of photosystem II (Fv/Fm), was measured from a randomly selected subsample of five living seedlings per experimental unit (1 leaf per seedling) every two months at the end of the experiment between June 2018 and July 2019 (using an OS30p+ chlorophyll fluorometer). Additionally, at least ten leaf samples from the top of living seedlings in each experimental unit were collected for nutrient analysis in the winters of 2015 and 2018.

In order to characterize stand structure degradation, we measured the residual density and basal area at each experimental unit. For this, we counted all living trees > 5cm dbh, registered their species and measured their height and diameter at 1.3 m height (dbh). We measured the depth of the water table every two months during the last experimental year (2018-2019) with a piezometer placed at the center of each experimental unit. To provide more detailed information about light conditions, from June 2018 to July 2019, photosynthetically active radiation (PAR) was measured every hour at 1-m height in the most degraded experimental unit using a PAR sensor and a Em50 Decagon data logger. Precipitation and temperature data for the study area were taken from the nearest official weather station (Tara, Agrometeorological Network, INIA, Chile). Finally, using a soil auger, the soil depth (up to 1m) and pH were measured at the center of each unit. From each experimental unit, soil samples were extracted from the top 10 cm for nutrient analysis using small test pits. The nutrient concentrations of all soil samples were assessed in the Laboratory of Forest Nutrition and Soils at the Universidad Austral de Chile in Valdivia, using the standardized and recommended methods of Sadzawka et al. (2006).

2.4 Statistical analyses
Early performance of *Nothofagus nitida* plantings

For each planted seedling, the current annual increment for rcd \((cai_{rcd})\) and height \((cai_h)\) was computed for each year since plant establishment for growth analysis. The periodic annual increment for rcd \((pai_{rcd})\) and height \((pai_h)\) was also calculated for the five-year period of measurement. Neither browsed seedlings (by the native *Pudu puda* deer) nor dead seedlings were considered for growth analysis.

All variables were analysed with the Shapiro-Wilk, Kolmogorov-Smirnov, and Levene’s tests to assess the distribution and homogeneity of the variance of the data, and since almost all variables had heteroscedastic and non-normal distributions even after various transformations of the data, non-parametric analyses were used. To compare root collar diameter, height, mortality, vitality and browsing from each year between 2014 and 2019, variables were analysed as repeated measurements (Kuehl, 2001), modelling the variance and covariance structure with a 95% level of confidence. Statistical differences between means were performed with a Tukey (HSD) test for multiple comparison. The same two-step statistical procedure was conducted for comparing the depth of the water table and the physiological stress (Fv/Fm values) of seedlings throughout the year (June 2018 to July 2019). In the case of comparing the current annual increment in rcd \((cai_{rcd})\) and height \((cai_h)\) of seedlings between years, the non-parametric Kruskal-Wallis test was used. In this case, when significant differences were found, *post hoc* analyses were performed using the Mann-Whitney U test and the Bonferroni method (Sokal and Rohlf, 1995). To look for differences in foliar nutrient content between years 2015 and 2018, the Wilcoxon signed rank test for paired data was used.

Spearman’s rank correlations were applied to relate stand structure variables, soil properties, and foliar nutrient concentrations with seedling performance attributes \((cai_{rcd}, cai_h, Fv/Fm, Fv/Fm \text{ in December}, \text{vitality, mortality and browsing})\). In order to evaluate the effect of available light on seedlings performance, we fitted quadratic regression models having all models, the corresponding response variable \((Fv/Fm, pai_{rcd} \text{ and } pai_h)\) and relative PPFD as predictor variable. Concordantly, the statistical significance of the treatment was based on the variance estimator of its regression coefficient. The
Early performance of *Nothofagus nitida* plantings

Normality and homoscedasticity of the model residuals were assessed by the Kolmogorov-Smirnov and Levene’s tests, respectively, as suggested by Salas (2002). All of the statistical analyses were performed using the software SigmaPlot (Systat Software, San Jose, CA), the *stats* and *car* packages of software R (R Development Core Team, 2020), and the PROC MIXED procedure (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1 Microsite conditions for seedling growth after removal of the *Chusquea* bamboo understory

The stand structure of the forest inside the experiment was characterized by residual tree densities that ranged between 100 and 977 trees/ha, tree basal areas between 3.86 and 108.99 m²/ha, mean tree diameter at breast height (dbh) between 11.2 and 62.9 cm, and mean tree heights between 8.7 and 22.7 m (Table 1). Seedlings grew over moderately thin (58 – >100 cm thick) and acidic (pH mean: 4.7, range: 4.0-5.1) soils of fluvio-glacial origin, characterized by a clay-loam texture with high values of organic matter (mean: 42.3%, range: 23.0 to 69.0%), total nitrogen (mean: 0.87%, range: 0.47 – 1.88%) and total carbon (mean: 24.6%, range: 13.4 – 39.9%), moderate C/N (mean: 29.6, range: 19.0 – 37.0) and low phosphorus values (mean: 4.3 mg/kg, 1.4 –16 mg/kg). Relative PPFD at seedlings height ranged from 7.3 to 59.8% in the experiment (mean: 30.6%).

During the last 12 months of the study (June 2018 to July 2019) the annual mean depth of the water table in the experiment ranged from 12.28 to 85.5 cm (Table 1). During the same period of time, PAR values (mean and maximum) responded positively to incoming solar radiation in summer, whereas air temperature responded negatively to precipitation. Thus, mean daily PAR values increased from 91.79 µmol/m²s in June 2018 to a peak of 564.74 µmol/m²s in December 2018. Maximum PAR values started
Early performance of *Nothofagus nitida* plantings

at 324.1 µmol/m²s in June 2018 and peaked at 2010.5 µmol/m²s in December 2018 (Figure 3). During the same period, precipitation was concentrated in the Austral winter, with July 2019 (219 mm) reporting the highest values. During the Austral summer, the lowest values were reported for February 2019 (28 mm) (Figure 3). Mean annual temperature at the study area was 9.8°C with max and min values reported for February (33.4°C) and June (-1.8°C), both in 2019 (Figure 3).

Five years after removing the *Chusquea* bamboo understory, planted seedlings faced strong competition from naturally regenerating tree species. Natural regeneration near planted seedlings had a mean cover of 35.04 % (±15.7) and mean maximum height of 100.8 cm (±15.7), and non-tree species presented a mean cover of 3.9 % (±7.4) and a mean maximum height of 9.4 cm (±15.7). In the case of tree species regeneration, mean cover and mean maximum height increased in units with higher relative PPFD (rho: 0.52 and 0.61, respectively, p<0.001). This relationship was not significant for non-tree species.

| Table 1. Stand, soil and microenvironmental variables in each experimental unit across the Huillinco experimental (N=45). Values in brackets represent minimum and maximal mean values. |

Figure 3. (A) Mean minimum and maximum temperatures, and annual precipitation throughout the study period (years 2014-2019) in the study area. (B) PAR values (Photosynthetic active radiation) and precipitation values throughout the year 2018-2019. PAR: values recorded from June 2018 to May 2019 with a datalogger established in extremely degraded conditions inside the experiment. Precipitation and temperature data extracted from the nearest official weather station (Tara, Agrometeorological Network, INIA, Chile, approximately 15 km from the study site).
3.2 Performance of *N. nitida* seedlings during the first 5 years of growth

In general, planted seedlings performed well in the five years following establishment, with 29.4% (±15.9) mortality, 58.7% (±17.59) in healthy condition (i.e. <10% of dead foliage), and mean periodic annual increments in root collar diameter (*pmdi*) of 1.7mm/year (±0.8) and height (*pdimh*) of 17.4 cm/year (±7.3). Final values in 2019 for rcd and height were 16.8 mm (±4.1) mm and 180.6 cm (±35.1), respectively. Although root collar diameter, height, mortality, vitality, and browsing of planted seedlings varied significantly through the different years since establishment (p<0.001), they varied in different ways. While the root collar diameter and height of planted seedlings constantly increased every year, mortality was concentrated in the first year of growth (19.8%) and then increased significantly every year except between 2017 and 2018. Browsing rate increased until 2017 (peak of 23.3% ±19.6), then decreased to a minimum of 3.8% (±5.3) in 2019. The percentage of healthy seedlings decreased significantly to 53.8% (±18.1%) in year 2017 and then began to rise again, but not significantly (p>0.05) (Figure 4). Current annual increment in seedling root collar diameter (*pdmind* and height (*pdmhid*), varied significantly from 2014 (first year of plantation) to 2019 (p<0.001 and p<0.05, respectively). *pdmind* initially increased from 2015 to 2016, then declined and progressively increased significantly with seedling age starting in 2017, from 1.46 mm/year (±1.12) in year 2017 to 2.95 mm/year (±1.46) in year 2019. *pdmhid* steadily increased from 9.1 cm/year (±2.7) in 2015 through 33.6 cm/year (±16.6) in year 2019 (Figure 5). Nitrogen, P and Mg foliar concentrations (all decreased) and the foliar N/P ratio (increased) changed significantly between year 2015 and 2018 (p<0.001). Only foliar K and Ca did not change significantly (p>0.05).
Figure 4. Early performance of all planted N. nitida seedlings. Root collar diameter (A); height (B); mortality rate, % (C); browsing percentage (D) and healthy individuals, % (E), during the 2014 (first year of plantation) – 2019 period. Metrics were measured every Austral winter. Variables were analyzed as repeated measures and statistical differences were performed with a Tukey (HSD) test for multiple comparison. All variables varied significantly through the different years since establishment (p<0.001).

Different symbols indicate statistically significant differences among subsequent years: ns = non-significant; * significant at p < 0.05; ** significant at p < 0.01; *** significant at p < 0.001).

Figure 5. Differences in current annual increment in A) root collar diameter (cai_{rcd}) and B) height (cai_{h}) during the 2014 (first year of plantation) – 2019 period. Cai_{rcd} and cai_{h} varied significantly during this period (p<0.001 and p<0.05, respectively). Differences between years were evaluated with the Kruskal-Wallis test. Values sharing different capital letters in superscript were significantly different at p≤0.001 and with lower case letters at p≤0.05.

Table 2. Median values of foliar nutrient concentrations and N/P ratios for N. nitida in planted seedlings after the first and fourth years of growth (2015 and 2018). Differences between years 2015 and 2018 were evaluated with the Wilcoxon signed rank test for paired data. Values sharing different capital letters in superscript were significantly different at p≤0.001.

3.3 Influence of selected microsite conditions on seedling performance

The periodic annual increment in rcd (pai_{rcd}) and height (pai_{h}) was significantly correlated with most stand and soil attributes and foliar concentrations (Table 3). These seedling performance variables presented significant positive correlation coefficient values with relative PPFD, depth of the water table
Early performance of *Nothofagus nitida* plantings

(annual and during December), pH of the soil, and foliar N (2015 and 2018) and P content (only 2015).

On the contrary they presented significant negative correlations with stand density and basal area, soil organic matter, C and N content, and K (2015 and 2018) and Mg foliar content (only 2015) (Table 3).

Mean Fv/Fm values during the year and during December were negatively associated to relative PPFD and 2015 K foliar content (Table 3). Significant correlation coefficient values were found between annual mean Fv/Fm values and residual stand basal area (positive) and 2018 K foliar content (positive), and between mean Fv/Fm values during December and depth of the water table (negative) and soil C/N (negative) (Table 3). Vitality (<10% seedling dead foliage) was positively and significantly correlated with residual stand basal area and depth of the water table (annual and during December). On the contrary, mortality was negatively associated with the depth of the water table (annual and during December) and positively to soil organic matter, and C and N soil content. Browsing was negatively correlated with stand basal area, soil C/N ratio and B soil content, and positively correlated with relative PPFD and N and P foliar content in year 2015.

Table 3. Spearman rank correlation matrix between seedling performance attributes and stand variables, soil attributes and nutrient foliar concentrations (all at experimental unit level). Variables with no significant correlation with performance were excluded from the table. Pai\(\text{red}\): periodic annual increment in root collar diameter, Pai\(h\): periodic annual increment in height, Fv/Fm: mean annual Fv/Fm of planted seedlings, Fv/Fm\(\text{dec}\): Fv/Fm of planted seedlings during December, Vitality: % of healthy seedlings (<10% of dead foliage), Mortality (%), Browsing (% of browsed seedlings in 2017). Density: total density of the residual forest, RBA: total tree basal area of the residual forest. %PPFD: relative mean photosynthetic photon flux density reaching planted seedlings (%), WT: mean annual depth of the water table, WT\(\text{dec}\): depth of the water table during December, C: carbon (%), OM: organic matter.
Early performance of *Nothofagus nitida* plantings

(%), N: nitrogen (%), C/N: carbon-nitrogen ratio, B: (mg/kg), P: phosphorus (%), K: potassium (%), Mg: magnesium (%). * significant at p < 0.05; ** significant at p < 0.01; *** significant at p < 0.001.

Quadratic models provided highly significant predictive fits (p<0.001) (Figure 6). After five growing seasons, the periodic annual increment in root collar diameter (*pai*<sub>rcd</sub>) and height (*pai*h) of seedlings were positively affected by relative PPFD at seedlings height (*pai*<sub>rcd</sub> = r<sup>2</sup>: 0.598, p<0.001; *pai*h= r<sup>2</sup>: 0.542, p<0.001). An increased dispersion in the *pai*<sub>rcd</sub> response to increased PPFD was observed, whereas the relative PPFD-*pai*h relationship remained stable. On the contrary, Fv/Fm values were generally negatively affected by relative PPFD at seedlings height (r<sup>2</sup>: 0.469, p<0.001), with a tendency to a flat and even positive relationship with high relative PPFD values (Fig. 6c). However, except for the 2015-2016 transition, correlation values between the current annual increment of both variables and relative PPFD did not improve with seedling age (Table 4).

Table 4. Spearman rank correlation values between current annual increment in root collar diameter (*cai*<sub>rcd</sub>) and height (*cai*h), and relative photosynthetic photon flux density (%PPFD) reaching planted seedlings.

Figure 6. Fitted quadratic models representing the relationship between relative photosynthetic photon flux density, PPFD (explanatory variable) and the periodic annual increment in root collar diameter (*pai*<sub>rcd</sub>) (A) and height (*pai*h) (B), and Fv/Fm values (C) (response variables), respectively.

The Fv/Fm values and depth of the water table on the study site varied strongly throughout the year (p < 0.001). Physiological stress was concentrated in the summer months. In the case of Fv/Fm values, they began to decrease (indicating increased physiological stress) significantly in June 2018, with lowest values in the middle of the summer (0.75 in December 2018 and 0.76 in February 2019). Values then
began to increase significantly (indicating decreased physiological stress)– until April 2019 (Figure 7). In the same period, the depth of the water table did not change significantly until October 2018, and then began to increase until December 2018. After that, the depth of the water table began to decrease significantly until July 2019 (Figure 7).

Figure 7. Depth of the water table and Fv/Fm values of N. nitida planted seedlings throughout the year 2018-2019 (left). Variables were analyzed as repeated measures and statistical differences were performed with a Tukey (HSD) test for multiple comparison. Fv/Fm and depth of the water table varied varied significantly during this period (p<0.001). Different symbols indicate statistically significant differences among subsequent years: ns = non-significant; * significant at p < 0.05; ** significant at p < 0.01; *** significant at p < 0.001).

4. Discussion

4.1 Performance of Nothofagus nitida seedlings during the first 5 years of growth

Nothofagus nitida plantings presented relatively good indicators of performance during the first five years of growth with low mortality (~30% of dead seedlings), good vitality (~60% of healthy seedlings) and relatively high mean periodic annual increments in root collar diameter and height (~1.7mm/year and ~17.4 cm/year, respectively). As expected, these growth rates are lower than shade-intolerant species such as Nothofagus dombeyi, but comparable to other mid-tolerant hardwood tree species, including Nothofagus alpina and Eucryphia cordifolia (Donoso et al., 2015; Soto et al., 2020). The growth rates of these other species, however, have been reported after planting them in the Andes, in soils with better quality (e.g. deeper and better nutrition) than the soils of this experiment (in Chiloé Island), and thus
support previous studies that suggest a competitive advantage of *N. nitida* in soils with permanent high-
moisture content (Donoso et al., 2007; Donoso et al., 2019).

According to our results, the first three years after establishment are the most challenging for *N.
nitida* seedlings, since during this period highest mortality (~20% only in the first year), lowest vitality
(~54% of healthy seedlings in third year) and highest browsing damage (peak of ~23% browsed
seedlings in third year) took place. Since bare root plants of ±1 m in height were used, it makes sense
that seedlings were stressed during the initial years after establishment. If newly planted seedlings lack
well-developed root systems; they face multiple hurdles including poor access to available soil-water,
compromising their nutrient status (Grossnickle, 2005). Soil-water access and nutrient status are
especially important for shade-tolerant tree species like *N. nitida* that have low drought tolerance (Piper
et al., 2007) and grow in nutrient poor sites (Bannister and Donoso, 2013). Accordingly, as seedlings
grew, their foliar nutrient concentrations (e.g. N and P) decreased over time (Table 2). This suggests that
seedlings came with high foliar nutrient concentrations from the nursery and had to acclimate to the
nutrient-poor conditions of the experimental site in the first years of growth. In turn, these high nutrient
levels are important for seedlings to develop new roots and foster initial growth (Grossnickle, 2005). Our
results also suggest that N and P foliar content after the first year of growth stimulate root collar diameter
and height growth during the first five years of growth (Table 3).

In summary, and despite the difficult first three years after planting, seedlings grew well,
highlighting this species’ great potential for continuing restoration efforts in the Chilean Coastal Range,
perhaps with higher growth rates than other pioneer hardwood tree species used for planting under nurse
canopy in degraded Andean *Nothofagus*-dominated forests (Donoso et al., 2015; Soto et al., 2020).

**4.2 The influence of microsite conditions on early performance of *Nothofagus nitida* seedlings**
Early performance of *Nothofagus nitida* plantings

460 After the removal of the dense understory of *Chusquea* bamboo, planted seedlings grew in a wide
461 gradient of degradation and stand structures (Table 1), including from undisturbed conditions (>80 m²/ha
462 in basal area, mean dbh >40 cm, mean height >15 m, and relative PPFD <15%), to severely disturbed
463 conditions (<10 m²/ha in basal area, mean dbh <20 cm, mean height <15 m, and relative PPFD >35%).
464 This “degradation” gradient allowed us to evaluate seedling performance in diverse microsite conditions.

465 In this context, our results show that *N. nitida* can grow under low-light conditions, however,
466 planted seedlings grow more robustly in diameter and height under high-light availability. Furthermore,
467 high-light availability was not linked to either seedling mortality or vitality. These findings support our
468 first hypothesis, that despite the relative shade-tolerance of *N. nitida*, the early performance of planted
469 seedlings of the species would be facilitated in open canopy conditions without a nurse canopy. High-
470 growth, high-light relationships also have been reported for other *Nothofagus* species (*N dombeyi, N
471 alpine*) and *E. cordifolia* planted beneath nurse canopy in degraded Andean *Nothofagus*-dominated
472 forests (Donoso et al., 2013; Donoso et al., 2015; Soto et al., 2015, Soto et al., 2020). Furthermore, these
473 relationships have also been reported for shade-tolerant species like *Fagus sylvatica* in Europe (van
474 Hees1997, Ammer 2003). However, our results show that the relation between rcd and height growth
475 and available light did not improve with seedling age after the second year of growth. This partially
476 contradicts previous studies on natural regeneration of this species that stated that as age increases, *N.
477 nitida* seedlings acquire the capacity to grow in higher-light environments (Coopman et al., 2008). It is
478 likely that the pattern shown by Coopman et al. (2008) is only applicable for young and small seedlings
479 (they studied natural regeneration < 73.7 cm in height and <9 years of estimated age). Therefore, our
480 results indicate that an ontogenetic change occurred in the first year of growth, when planted seedlings
481 were relatively small (100-110 cm in height). However, Donoso et al. (2015) showed that *N. dombeyi*
482 and *N. alpina* planted seedlings increase their intolerance to shade (ontogenetic change) during the
483 seedling and sapling stages (years 1, 2, 3 and 6). A possible explanation for this contradictory result is
Early performance of *Nothofagus nitida* plantings

that during the first years of growth, belowground resource availability seems more important than light availability for shade-tolerant tree growth (Ammer et al., 2008), especially in nutrient-poor sites (like those of the study area), where growth may be limited by factors like nutrient availability (Grossnickle, 2005; Bannister et al., 2013). In this context, the high variability in root collar diameter and height growth of *N nitida* seedlings suggest that this tree species is sensitive to local variation in microsites, so that if conditions improve, the correlation between growth and available light should also improve, as was previously seen for *N. alpina* (Soto et al., 2020). But, if nutrient availability does not improve, then higher light availability will not result in the expected increased growth. Surprisingly, our results show that seedling growth was stimulated in more alkaline soils, and that higher soil N and C content and more organic matter were associated with higher seedling mortality and less growth. Further studies should address these contradicting results.

Planted seedlings grew better with more light; however, in these more open settings seedlings faced higher browsing by the *Pudu puda* deer, who prefer such sites for feeding (Burger et al., 2019). Also, according to our results, seedlings with higher growth presented higher N foliar content and they also were more prone to browsing (Table 3). Thus, there was a trade-off between microsite quality for growth and browsing. In addition, physiological stress of planted seedlings was higher in open areas with more available light (lower Fv/Fm values). According to the fitted quadratic model, approximately at >39.7% of relative PPFD planted seedlings of *N. nitida* began to face physiological stress (*sensu* Misra and Singh, 2012). Furthermore, seedlings were most stressed during the peak in incoming solar radiation (December PAR) that co-occurred with highest depth of the water table, prior to late summer (February) with lowest soil moisture content, highest temperature, and lowest precipitation recorded. This in agreement with our second hypothesis that due to its low drought tolerance, physiological stress of *N. nitida* seedlings would be higher in open conditions and during the dry season (summer). Accordingly, seedling physiological stress and depth of the water table both responded rapidly to high incoming solar
radiation, suggesting that there is a threshold in increasing stress levels in late-Spring-early-Summer
(December), but to our surprise, seedlings acclimated under mid and even high relative PPFD values (Fig
6c), higher temperature, and lower (accumulated days without) precipitation in the mid-to-late summer
(Fig. 3). Mortality and vitality of seedlings were not affected by available light, but they were positively
(vitality) and negatively (mortality) affected when the depth of the water table increased. Unfortunately,
we did not have totally open conditions in the experiment (ca. 60% was the maximum relative PPFD
value recorded in the experiment) in order to observe the full range of physiological stress at higher light
availability. However, our results support the idea that *N. nitida* presents low drought tolerance compared
to other *Nothofagus* species. This has been associated with the species’ lower water use efficiency (WUE)
and photosynthesis under severe drought stress compared to other *Nothofagus* species (Piper et al., 2007).
Low drought tolerance could explain the preference of *N. nitida* for permanently saturated soils, as it is
present further south along the rainy Chilean coast (i.e. Archipelagos of North Patagonia) and is mostly
absent along the drier rainshadows of the Chilean Coastal Range and the Andes (Donoso and Escobar,
2006; Donoso et al., 2007; Piper et al., 2007; Vidal et al., 2011). On the other hand, planted seedlings of
the species did not face physiological stress during winter, which differs from previous studies that
suggest a low capacity of *N. nitida* seedlings to maintain a functional photosynthetic apparatus, tolerating
freezing in autumn and winter only at the adult stage (Reyes-Díaz et al., 2005).

**4.3 Nothofagus nitida plantings as a tool for restoring degraded coastal temperate rain forests**

Planting beneath nurse canopy has been proven to be a useful restoration practice to direct successional
trajectories in a more predictable way in many forested habitats around the globe (Paquette et al., 2006;
Donoso et al., 2013; Soto et al., 2015, Soto et al., 2020). To our knowledge, this study reports for the first
time field-based results about *N. nitida* seedlings planted beneath the nurse canopy of degraded forests
Early performance of *Nothofagus nitida* plantings following *Chusquea* bamboo removal. Our results highlight a tradeoff between available light, growth and stress of *N. nitida* seedlings. Seedlings grow more rapidly in root collar diameter and height with higher light availability, but also encounter physiological stress. This suggests that although planting *N. nitida* seedlings in canopy gaps is a reasonable option for achieving growth comparable to other mid-tolerant hardwood tree species proposed for restoring degraded old-growth forests in Chile (Donoso et al., 2015; Soto et al., 2020), because of its low drought tolerance the seedlings are prone to suffer from drought in dry summers. During our experiment, seedling drought stress was not reflected in decreased growth. However, during the 1960-2016 period, precipitation on Chiloé Island was reduced by ca. 5% (ca. 200mm) per decade (Garreaud et al., 2013) and simulation models forecast that drying trends will continue (Boisier et al., 2018). In this context, *N. nitida* plantings will face drought stress problems in the future if planted in dry sites. We also observed that in more open conditions, seedlings faced higher browsing. In order to counteract this problem, physical barriers could be installed around groups or individual plants (Graham et al., 2010; Burger et al., 2019), but due to *Pudu puda* short height, it is very probable that planting seedlings >1 m of height is the best option (Burger et al., 2019).

In summary, the removal of the *Chusquea* bamboo understory is the key to overcome arrested forest succession, and planting beneath nurse canopy is a good way to enable a faster forest recovery of high-graded forests (Donoso et al., 2013; Soto et al., 2015; Soto et al., 2019; Soto et al., 2020). Our results support this management opportunity and we recommend planting *N. nitida* seedlings in degraded coastal temperate rain forests of North Patagonia. These degraded forests present intermediate overstory openings (±7%– to 60% relative PPFD) that are ideal for mid-tolerant species (Paquette et al., 2006). In order to facilitate early growth and avoid physiological stress (because of drought in the summer season or extreme insolation), seedlings should be established in large gaps created after *Chusquea* bamboo removal (>40% relative PPFD) in areas with some nurse canopy protection and humid soil conditions. Further long-term research is needed in order to experiment with other pioneer tree species that tolerate...
Early performance of *Nothofagus nitida* plantings

shade across the complete diversity of degraded temperate rainforests in South America and develop ecologically-based restoration strategies for these forests.

**Author contributions**

JRB: Designed study, performed research, analysed data, and wrote manuscript; GT and NG: Analysed data, performed research and contributed with the creation of figures; MA analysed data contributed to data interpretation; AH: contributed to result interpretation and reviewed the manuscript.

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Early performance of *Nothofagus nitida* plantings


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Early performance of *Nothofagus nitida* plantings


W.H. Freeman and Company.

Early performance of *Nothofagus nitida* plantings


Early performance of *Nothofagus nitida* plantings


Table 1. Stand, soil and microenvironmental variables in each experimental unit across the Huillinco experiment (N=45). Values in brackets represent minimum and maximal mean values.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Mean (range) values</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stand structure</strong></td>
<td></td>
</tr>
<tr>
<td>Density (trees/ha)</td>
<td>392 (100 - 977)</td>
</tr>
<tr>
<td>Dbh (cm)</td>
<td>27.8 (11.2 – 63.0)</td>
</tr>
<tr>
<td>Residual basal area (m²/ha)</td>
<td>45.9 (3.9 – 109.0)</td>
</tr>
<tr>
<td>H (m)</td>
<td>14.0 (8.7 – 22.7)</td>
</tr>
<tr>
<td><strong>Soil properties</strong></td>
<td></td>
</tr>
<tr>
<td>Min Depth (cm)</td>
<td>58 - &gt;100</td>
</tr>
<tr>
<td>pH</td>
<td>4.7 (4.0 – 5.1)</td>
</tr>
<tr>
<td>OM (%</td>
<td>42.3 (23.0 – 69.0)</td>
</tr>
<tr>
<td>Ct (%)</td>
<td>24.6 (13.4 – 39.9)</td>
</tr>
<tr>
<td>Nt (%)</td>
<td>0.87 (0.47 – 1.88)</td>
</tr>
<tr>
<td>P (mg/kg)</td>
<td>4.3 (1.4 – 16.0)</td>
</tr>
<tr>
<td>C/N</td>
<td>29.6 (19.0 – 37.0)</td>
</tr>
<tr>
<td><strong>Micro environment</strong></td>
<td></td>
</tr>
<tr>
<td>% Photos. photon flux density (PPFD) (%)</td>
<td>30.6 (7.3 – 59.8)</td>
</tr>
<tr>
<td><strong>Depth of the water table</strong></td>
<td></td>
</tr>
<tr>
<td>Annual Mean (cm)</td>
<td>53.5 (12.3 – 85.5)</td>
</tr>
<tr>
<td>Minimum (cm)</td>
<td>29.5 (9.0 - 63.0)</td>
</tr>
<tr>
<td>Maximum (cm)</td>
<td>78.5 (44.0 – 106.0)</td>
</tr>
</tbody>
</table>
Early performance of *Nothofagus nitida* plantings

Table 2. Median values of foliar nutrient concentrations and N/P ratios for *N. nitida* in planted seedlings after the first and fourth years of growth (2015 and 2018). Differences between years 2015 and 2018 were evaluated with the Wilcoxon signed rank test for paired data. Values sharing different capital letters in superscript were significantly different at p≤0.001.

<table>
<thead>
<tr>
<th></th>
<th>Year 2015</th>
<th>Year 2018</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (%)</td>
<td>1.00&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.90&lt;sup&gt;B&lt;/sup&gt;</td>
<td><strong>&lt;0.001</strong></td>
</tr>
<tr>
<td>P (%)</td>
<td>0.07&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.06&lt;sup&gt;B&lt;/sup&gt;</td>
<td><strong>&lt;0.001</strong></td>
</tr>
<tr>
<td>N/P</td>
<td>13.70&lt;sup&gt;A&lt;/sup&gt;</td>
<td>16.20&lt;sup&gt;B&lt;/sup&gt;</td>
<td><strong>&lt;0.001</strong></td>
</tr>
<tr>
<td>K (%)</td>
<td>0.35</td>
<td>0.35</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td>Ca (%)</td>
<td>0.56</td>
<td>0.5</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td>Mg (%)</td>
<td>0.17&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.13&lt;sup&gt;B&lt;/sup&gt;</td>
<td><strong>&lt;0.001</strong></td>
</tr>
</tbody>
</table>
Table 3. Spearman rank correlation matrix between seedling performance attributes and stand variables, soil attributes and nutrient foliar concentrations (all at experimental unit level). Variables with no significant correlation with performance were excluded from the table. Pai<sub>pcd</sub>: periodic annual increment in root collar diameter, Pai<sub>h</sub>: periodic annual increment in height, Fv/Fm: mean annual Fv/Fm of planted seedlings, Fv/Fm<sub>dec</sub>: Fv/Fm of planted seedlings during December, Vitality: % of healthy seedlings (<10% of dead foliage), Mortality (%), Browsing (% of browsed seedlings in 2017). Density: total density of the residual forest, RBA: total tree basal area of the residual forest. %PPFD: relative mean photosynthetic photon flux density reaching planted seedlings (%), WT: mean annual depth of the water table, WT<sub>dec</sub>: depth of the water table in December, C: carbon (%), OM: organic matter (%), N: nitrogen (%), C/N: carbon-nitrogen ratio, B: (mg/kg), P: phosphorus (%), K: potassium (%), Mg: magnesium (%). * significant at p < 0.05; ** significant at p < 0.01; *** significant at p < 0.001

<table>
<thead>
<tr>
<th>Variables</th>
<th>Seedling performance attributes</th>
</tr>
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<tr>
<td></td>
<td>Pai&lt;sub&gt;pcd&lt;/sub&gt;</td>
</tr>
<tr>
<td>Stand structure</td>
<td>Density</td>
</tr>
<tr>
<td>RBA</td>
<td>-0.501***</td>
</tr>
<tr>
<td>%PPFD</td>
<td>0.789***</td>
</tr>
<tr>
<td>Soil properties</td>
<td>WT</td>
</tr>
<tr>
<td></td>
<td>WT&lt;sub&gt;dec&lt;/sub&gt;</td>
</tr>
<tr>
<td>pH</td>
<td>0.381**</td>
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Early performance of *Nothofagus nitida* plantings

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Foliar nutrient concentrations</th>
<th>2015</th>
<th>2018</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>-0.377*</td>
<td>0.164</td>
<td>0.112</td>
</tr>
<tr>
<td>N</td>
<td>-0.385**</td>
<td>0.241</td>
<td>0.214</td>
</tr>
<tr>
<td>C/N</td>
<td>0.148</td>
<td>-0.250</td>
<td>0.259</td>
</tr>
<tr>
<td>B</td>
<td>-0.214</td>
<td>-0.024</td>
<td>0.154</td>
</tr>
<tr>
<td>OM</td>
<td>-0.371*</td>
<td>0.151</td>
<td>0.105</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Foliar nutrient concentrations</th>
<th>2015</th>
<th>2018</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>0.404**</td>
<td>-0.173</td>
<td>0.019</td>
</tr>
<tr>
<td>P</td>
<td>0.352*</td>
<td>-0.085</td>
<td>-0.088</td>
</tr>
<tr>
<td>K</td>
<td>-0.458**</td>
<td>0.429**</td>
<td>0.345**</td>
</tr>
<tr>
<td>Mg</td>
<td>-0.524***</td>
<td>0.214</td>
<td>0.031</td>
</tr>
</tbody>
</table>

---

784 785 786 787
Table 4. Spearman rank correlation values between current annual increment in root collar diameter \((cai_{rcd})\) and height \((cai_{h})\), and relative photosynthetic photon flux density (%PPFD) reaching planted seedlings.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Year</th>
<th>rho</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cai_{rcd}</td>
<td>2015</td>
<td>0.533</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2016</td>
<td>0.738</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2017</td>
<td>0.768</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>0.732</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2019</td>
<td>0.589</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cai_{h}</td>
<td>2015</td>
<td>-0.049</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td></td>
<td>2016</td>
<td>0.828</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2017</td>
<td>0.846</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>0.734</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2019</td>
<td>0.739</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Figure 1. Study area on Chiloé Island, North Patagonia, in southern Chile (left), and location of the 45 experimental units in the Huillinco experiment (right aerial photo).
Figure 2. Degraded coastal temperate rain forests in Chiloé Island, North Patagonia (a). Chusquea bamboo dense understory before removal (b). Experimental units of 400 m² where the Chusquea bamboo understory was removed (c). Group plantings of Nothofagus nitida seedlings (d).
Figure 3. (A) Mean minimum and maximum temperatures, and annual precipitation throughout the study period (years 2014-2019) in the study area. (B) PAR values (Photosynthetic active radiation) and precipitation values throughout the year 2018-2019. PAR: values recorded from June 2018 to May 2019 with a datalogger established in extremely degraded conditions inside the experiment. Precipitation and temperature data extracted from the nearest official weather station (Tara, Agrometeorological Network, INIA, Chile, approximately 15 km from the study site).
Figure 4. Early performance of all planted N. nitida seedlings. Root collar diameter (A); height (B); mortality rate, % (C); browsing percentage (D) and healthy individuals, % (E), during the 2014 (first year of plantation) – 2019 period. Metrics were measured every Austral winter. Variables were analyzed as repeated measures and statistical differences were performed with a Tukey (HSD) test for multiple comparison. All variables varied significantly through the different years since establishment (p<0.001).

Different symbols indicate statistically significant differences among subsequent years: ns = non-significant; * significant at p < 0.05; ** significant at p < 0.01; *** significant at p < 0.001).
Figure 5. Differences in current annual increment in A) root collar diameter ($cai_{rcd}$) and B) height ($cai_h$) during the 2014 (first year of plantation) – 2019 period. $cai_{rcd}$ and $cai_h$ varied significantly during this period ($p<0.001$ and $p<0.05$, respectively). Differences between years were evaluated with the Kruskal-Wallis test. Values sharing different capital letters in superscript were significantly different at $p \leq 0.001$ and with lower case letters at $p \leq 0.05$. 

Early performance of *Nothofagus nitida* plantings
Figure 6. Fitted quadratic models representing the relationship between relative photosynthetic photon flux density, PPFD (explanatory variable) and the periodic annual increment in root collar diameter (pไตrcd) (A) and height (pไตh) (B), and Fv/Fm values (C) (response variables), respectively.
Figure 7. Depth of the water table and Fv/Fm values of *N. nitida* planted seedlings throughout the year 2018-2019 (left). Variables were analyzed as repeated measures and statistical differences were performed with a Tukey (HSD) test for multiple comparison. Fv/Fm and depth of the water table varied significantly during this period (p<0.001). Different symbols indicate statistically significant differences among subsequent years: ns = non-significant; * significant at p < 0.05; ** significant at p < 0.01; *** significant at p < 0.001).