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Short-term effects of variable-density thinning on regeneration in hardwood-dominated temperate rainforests

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ABSTRACT

Second-growth temperate forests usually have simpler composition and structure than comparable old-growth stands. We evaluated the application of variable density thinning (VDT) as a way to increase old-growth attributes, specifically tree species composition and density in two types of second-growth forests: a mixed evergreen-dominated forest (SE, stem exclusion phase) and a *Nothofagus dombeyi*-dominated forest (UR, understory reinitiation stage) in southern Chile (40°S Lat.). Six one-ha plots were established in each forest. We applied VDT in three plots in each forest, which included the following sub-treatments: a thinned matrix (M), large and small patches (LP and SP), and large and small reserves (LR and SR). We also established three one-ha plots in an old-growth forest (OG), which served as a reference for overall stand structural variables and the tree regeneration layer. OG had significantly more total regeneration and shade-tolerant regeneration, than the untreated SE and UR. After VDT, canopy openness was significantly greater in SE than in UR within the treated portions of the plots (M, LP and SP). The similarities in stand characteristics between untreated and pre-harvest treated plots in each second-growth forest suggest that harvesting was responsible for the lower densities observed in thinned plots. Regeneration patterns two growing seasons after harvests were reflective of the interaction between forest type and sub-treatments. While both second-growth forests showed increases in regeneration densities, none of these increases was significant, although proportionally and numerically they were greater in the SE forest. The sub-treatments showed differences only for shade-intolerant and shade-tolerant species in both forests. These differences in general illustrated a preference of shade-intolerant species for patches (only in the smaller height class in both forests), and of shade-tolerant species for the matrix or the reserves in all height classes from > 50 cm through saplings (only in the SE forest). Overall, tree regeneration has been more responsive to VDT in the forest currently in an earlier successional stage, suggesting that second-growth forests in more advanced stages may need to be treated more intensively (larger patches, lower residual densities). Correspondingly, VDT protocols must be developed to account for the interaction between harvest disturbances, developmental stage, and silvics of the component species.

1. Introduction

Old-growth forests represent a small proportion of contemporary landscapes in temperate regions due to historic natural disturbances, agricultural clearing, and past forest harvesting practices. Instead, these areas are generally dominated by second-growth forests that have either returned following agricultural abandonment (Foster, 1992) or regenerated after past natural disturbances or harvesting. Old- and second-growth forests (i.e., developing following application of intensive land use) have substantial differences in key forest attributes, i.e. composition, structure and function (Carey, 2003). Old-growth forests are often dominated by late-successional species and variable and rich understories; their vertical profile is highly variable and characterized by tree species occupying multiple canopy layers; they have a high spatial variability with gaps spanning a range of sizes (e.g., Veblen, 1985; Dahir and Lorimer, 1996; Franklin et al., 2002); and

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detrital pools in these forests are characterized by abundant downed logs representing various stages of decay (Spies et al., 1988; McGee et al., 1999; Schlegel and Donoso, 2008; D'Amato et al., 2008). In contrast, second-growth forests are typically even-aged, dense in terms of numbers of trees, and dominated by few pioneer or early-successional tree species. Structurally, second-growth forests are typically simple, with a vertical profile characterized by a single upper canopy layer with no or limited understory vegetation, including tree regeneration, with structures reflective of the stem exclusion or the understory re-initiation developmental stages (*sensu* Oliver and Larson, 1996).

Given the abundance of second growth, the global rarity of old-growth forests, and the high public and conservation interests (Lindenmayer et al. 2012) in old-growth forests due to their compositional and structural complexity (e.g., Carey, 2003; Wilson and Puettmann, 2007), a range of silvicultural strategies have been proposed to restore old-growth conditions to second-growth forests (Bauhus et al., 2009). These approaches include retention harvests (Gustafsson et al., 2012) and regeneration methods patterned after natural disturbances (Long, 2009; Reuling et al., 2019) in forests subjected to regeneration cuttings. In young second-growth forests, restoration thinning (Keeton, 2006; Dwyer et al. 2010) and variable-density thinning (e.g. Aukema and Carey, 2008; Harrington et al., 2010; O'Hara et al. 2010; Willis et al. 2018) have been proposed and applied. In general, short-term responses have been encouraging, but different stand structural and compositional components have not responded in concert (Puettmann et al. 2016), suggesting the need for more detailed investigation in different ecosystems.

Variable-density thinning (VDT) aims at promoting the biological diversity and structural heterogeneity characteristics typically found in old-growth forests by inducing small-scale variation in homogeneous second-growth forests (Carey, 2003; Aukema and Carey, 2008; Willis et al., 2018). VDT combines thinning and regeneration harvests to enhance stand structural heterogeneity by deliberately thinning at different intensities and in some cases including gaps and reserves (leave areas) of various sizes (Harrington et al., 2010). Subsequent stand development is hypothesized to lead to more varied horizontal and vertical stand structure than generally observed in even-aged forest stands, and thus accelerates development towards old-growth conditions. VDT has been used to increase structural heterogeneity, the proportion of desired late-successional tree species, and accelerate development toward old forest structures in second-growth coast redwood forests, (O'Hara et al., 2010), and in Douglas-fir plantations (Puettmann et al. 2016), and in mixed conifer forests in the Pacific Northwest of the United States (Willis et al., 2018). In addition, VDT has been shown to increase the amount of regeneration (Harrington et al., 2010), understory vegetation (Ares et al., 2010), and tree growth (Roberts and Harrington, 2008; Comfort et al., 2010), and the variety of wildlife habitat and biodiversity (Carey, 2003; Yegorova et al., 2014).

The Valdivian temperate rainforests cover near 6 million hectares in south-central Chile (Lara et al., 2016). Forest stand dynamics, successional pathways, and characteristics of old-growth forests have been well studied in this region over the past several decades (Veblen et al., 1981; Donoso, 1989; Ponce et al., 2017; Loguercio et al., 2018). This work has demonstrated that major disturbances characterizing old-growth forests in the lowlands and Coastal range correspond to tree-fall gaps (Veblen, 1985) with forest regeneration dynamics dominated by mid-tolerant and shade-tolerant species adapted to gap and continuous-recruitment modes (Veblen, 1992). Nevertheless, these forests have been dramatically altered since the end of the XIX century, with many contemporary forests corresponding to second-growth forests establishing after fires, logging, or abandonment of agricultural lands (González et al., 2015a; Ponce et al., 2017). Depending on the type of human disturbance, these second-growth forests may vary in composition (e.g., dominated by *Nothofagus* or by a mix of tree species; Donoso, 1989; González et al. 2015a), and therefore in growth rates, since the shade-intolerant *Nothofagus* species are fast growing (Salas-Eljatib et al. 2016). As with other temperate regions sharing similar land-use histories and conservation priorities associated with restoration of old-growth forest conditions, these different second-growth forests provide opportunities to test the effects of VDT forest structural and compositional development, and prospects for further implementation.

To this end, we conducted a VDT experiment in two second-growth temperate rainforest stands at different successional stages (stem exclusion and understory re-initiation, respectively; *sensu* Oliver and Larson, 1996). This experiment is aimed at conducting long-term ecological and silvicultural research in these temperate rainforests. In the present evaluation, which occurs two years after treatment, our objectives were to a) compare tree regeneration in an untreated old-growth forest and two untreated second-growth forest stands by functional groups according to shade tolerances, b) evaluate regeneration response to VDT treatments and sub-treatments (e.g., gaps, reserves) in the two second-growth forests and c) discuss prospects for VDT in young forests, with a focus on tree species composition.

2. Material and methods

2.1. Study area

The study was conducted in the Llancahue watershed (39° 50′ 20″ S and 73° 07′ 18″ W) in the Coastal Range and its extension to the Central Depression of south-central Chile. Average annual rainfall is 2,300 mm and average annual temperature is 12.2 °C (Núñez et al., 2006). Llancahue lies between 50 and 410 m a.s.l. Soils are dominated by clay derived from ancient volcanic ash deposited on a substrate of metamorphic origin (CIREN, 1999).

Llancahue is dominated by old-growth forests, but second-growth forests cover close to one-third of the area (Fig. 1). This study focused on two second-growth forest types that differ from nearby old-growth forests in several key attributes, including lower total area and volume, very low density and volume of large trees (> 80 cm), especially shade-tolerant species and dominant trees, and higher overall tree densities (Ponce et al., 2017). The old-growth forest (OG) was dominated by one midtolerant species that reaches emergent positions (*Eucryphia cordifolia*; up to 40 m in height) and two shade-tolerant species (*Laureliopsis philippiana* and *Aextoxicon punctatum*). One second-growth forest was in the "stem exclusion" (SE) phase and the other in the "understory re-initiation" (UR) phase (*sensu* Oliver and Larson, 1996) with corresponding old-growth indices of 5 and 28%, respectively (Ponce et al., 2019). The SE forest was dominated by a mixture of tree species with different shade tolerances; trees had a dominant height of 17 m and were close to 70 years old (González et al., 2015a; Donoso et al., 2018a). In this forest, hardwood evergreen species included short-lived pioneer species of the *Proteaceae* family, but the main canopy species were *E. cordifolia*, *L. philippiana,* and *Drimys winteri*. In contrast, the main canopy species in the UR forest was the shade-intolerant *N. dombeyi* (> 50% basal area), with a dominant height of 32 m, and an estimated age of 100 years (González et al., 2015a; Donoso et al., 2018a). *Nothofagus dombeyi* was mixed with common late-successional tree canopy species such as *E. cordifolia*, *L. philippiana*, *A. punctatum* and *D. winteri*. A more detailed description of these forests is provided in Table 1 and in Ponce et al. (2017).

2.2. Experimental design

A total of 15 one-hectare permanent sample plots were established during 2015 (Fig. 1), including six in both the SE and the UR forests, and three plots in the OG forests. Of the six plots in each secondary forest (SE and UR), we randomly selected three to remain untreated and other three to be treated with VDT. These untreated plots were used for comparisons between the two untreated secondary forests and with the

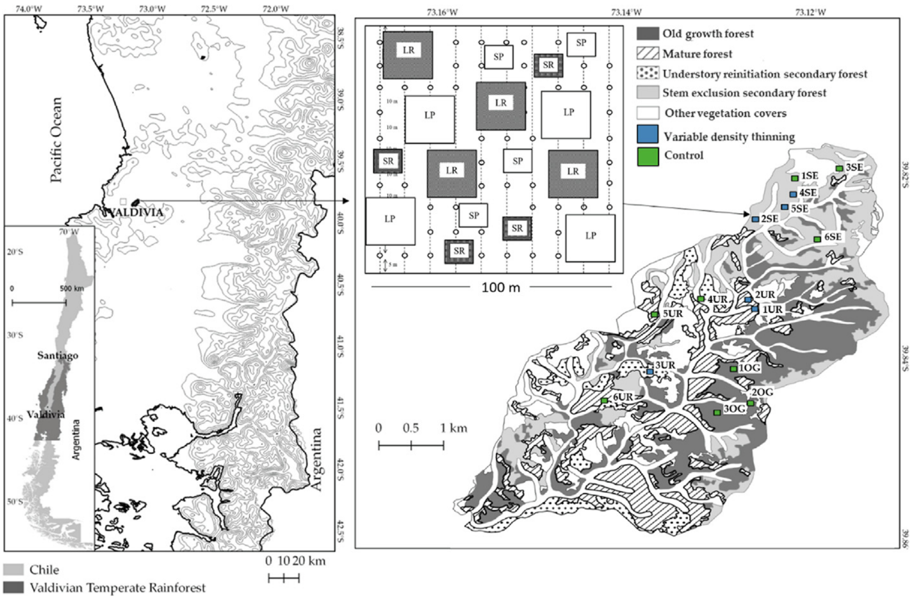

Fig. 1. The Llancahue experimental forest with the 15 study plots. OG: Old-growth forests; SE: Second-growth forest in the stem exclusion phase; UR: second-growth forests in the understory reinitiation phase. Plots treated with VDT are in blue, and those untreated in green. Symbols in the inserted conceptual plot of a VDT include large and small cut patches (LP and SP), and large and small reserves (LR and SR). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

untreated old-growth forest, as well as to serve as a control to evaluate differences with the treated plots within the same secondary forest. These untreated plots were very similar to the ones that were thinned (Table 1) allowing for their use as controls for evaluating regeneration in the thinned plots. We acknowledge that measuring the treated plots before thinning could have been an alternative approach for evaluating regeneration outcomes; however, these untreated plots were necessary to compare untreated forests in different successional stages, and to interpret (cautiously) the impacts of thinning upon regeneration.

The VDTs (see insert in Fig. 1) included cut patches in 16% of the area, and reserves (unthinned patches) in another 16% of the area. The remaining area (the matrix) was treated through restoration thinning, i.e. a thinning aimed to favor late-successional species, reduce relative densities to 50% to favor regeneration and understory development, leave coarse woody material, and girdle trees to create snags. We created two sizes of cut patches and reserves: 300 (17.32 m × 17.32 m) and 100 (10 m × 10 m) m^2, with four replications of each per plot. Thus, we had five types of sub-treatments in each VDT plot: large and small cut patches (LP and SP), large and small reserves (LR and SR), and the matrix treated with restoration thinning (M). Harvesting and skidding were conducted with chain saws and oxen, respectively.

In each untreated plot, we established 100 2 m^2 circular subplots in a 10 × 10 m grid. In the treated plots, we established a variable number of 2 m^2 subplots after the application of VDT. The matrix was systematically sampled along its main axes, excluding patches or reserves. Patches and reserves were sampled using North-South transects placed through their centers. Each patch and reserve was sampled with five plots equidistantly spaced along the North-South axis, with plot centers located 3 m from each other in small patches and reserves, and 5 m from each other in large patches and reserves. Collectively, these subplots represented the range of conditions (center and edges) within the patches or reserves. Overall, each 1-ha plot was sampled using 20 subplots for LP, SP, LR and SR, and the number of plots for the matrix varied, with an average of 46 subplots in the SE forest and 49 subplots in the UR forest.

We recorded, by species, the density of tree regeneration in each subplot for seedlings in different height classes (5- < 50; 50- < 100; 100–200 cm), and for saplings (> 200 cm in height and < 5 cm in diameter at breast height (*dbh*)), and assigned this regeneration to three functional groups according to shade tolerance: shade-intolerant, mid-tolerant, and shade-tolerant species. In addition, hemispherical photographs were taken in the central subplot in each patch or reserve, and in four randomly selected points within the matrix to estimate canopy openness as a surrogate for available light levels in the VDT plots. These photographs were taken at 1.5 m above the forest floor and were processed using the Gap Light Analyzer software (Frazer et al., 1999).

The overall regeneration density in the 1-ha treated forests was estimated by assigning weights to the regeneration density in each sub-treatment by the area of that sub-treatment within the plot. Therefore, regeneration in SP and SR as well as in LP and LS, was multiplied by 0.04 (4 sub-plots of 100 m^2 each) and 0.12 (4 sub-plots of 300 m^2 each), respectively. Similarly, regeneration density in the matrix was multiplied by 0.68 with all units collectively adding up to 1 ha.

The importance value (IV) was calculated for each species based on relative density (seedlings per ha of one species divided by total seedlings per ha) and relative frequency (sum of number of subplots in which a species occurs divided by total number of subplots).

Table 1
Stand variables (mean and standard deviation) for untreated forests (the two second-growth (SE and UR), and the old-growth (OG)), and for the treated SE and UR forests immediately after the VDT implementation conducted in spring-summer of 2015–2016.

		Forest type				
Stand variable		SE	SE VDT	UR	UR VDT	OG
Density (trees/ha)	Pre	4154 ± 300	4094 ± 296	1511 ± 365	2182 ± 454	1145 ± 197
	Post	–	2905 ± 226	–	1339 ± 239	–
Basal area (m^2/ha)	Pre	60.4 ± 5.4	58.7 ± 2.6	61.9 ± 4.8	70.4 ± 3.1	91.8 ± 7.9
	Post	–	44.1 ± 0.2	–	54.0 ± 0.9	–
Quadratic stand diameter (cm)	Pre	13.6 ± 0.9	13.5 ± 0.3	23.3 ± 2.0	20.6 ± 1.9	32.2 ± 2.7
	Post	–	13.9 ± 0.5	–	23.0 ± 2.4	–

2.3. Statistical analyses

Regeneration densities were first compared between forest types in unmanaged stands using a regression model predicting regeneration density based on forest type. Separate models were fit for each functional group. For all models, we verified the assumptions of normality and homoscedasticity of residuals with the Shapiro-Wilks and the Levene tests, respectively (Salas 2002). If forest type was statistically significant, we carried out Tukey's HSD test to compare means among the levels of the factor.

Second, we analyzed the effects of the sub-treatments (LP, SP, M, SR and LR) on regeneration density. Concordantly, we fit generalized linear mixed models where the response variable was tree regeneration, the probability density function followed a Poisson distribution (Korhonen et al., 2016), and forest type (i.e., SE and UR) and sub-treatment were the predictors. We added random effects to fixed-effects parameters of the models to take into account the nesting structure of the data (Salas et al., 2008), i.e., regeneration subplots within sub-treatments at different plots. All mixed-effects models were fit by maximum likelihood using the nlme package (Pinheiro et al., 2017) implemented in R (R Core Team 2017). We also fit these mixed-effects models for each functional group (see SI in Supplementary Material). We computed confidence intervals (using the estimated variance components from the mixed-effects models) of each sub-treatment, using a significance level of 0.05 and identified significant differences by non-overlapping confidence intervals among sub-treatments.

3. Results

3.1. Tree regeneration in the three different untreated forests

Total tree regeneration densities were significantly different among forest types (OG > UR, with SE intermediate). However, when sorted by functional group, the only significant difference occurred for shade-tolerant species with much greater density in OG compared to both second-growth forests (nearly twice as much as in SE, and five-fold difference with UR; Fig. 2).

Tree species richness was 25 in the SE forest, 22 in the UR forest, and 17 in the OG forest (Table 2). Roughly three fourths of the species in the SE and the OG forests were shade tolerant, whereas close to half the species in the UR forest were in this functional group. The five species with highest importance values (IV) accounted for 53–77% of the total IV and varied in terms of shade tolerances (Table 2). In the SE all five species were shade tolerant, including three species of the *Mirtaceae* family, and accounted for roughly 60% of the IV. In UR, the five species with highest importance values included three shade-tolerant species and two midtolerant species, which accounted for 53% of the IV combined. In the OG, a single shade-tolerant species (*A. punctatum*) constituted 49% of the IV, whereas the other four species with largest IVs (one shade-intolerant, two midtolerants and one shade-tolerant) collectively accounted for 29% of the total IV.

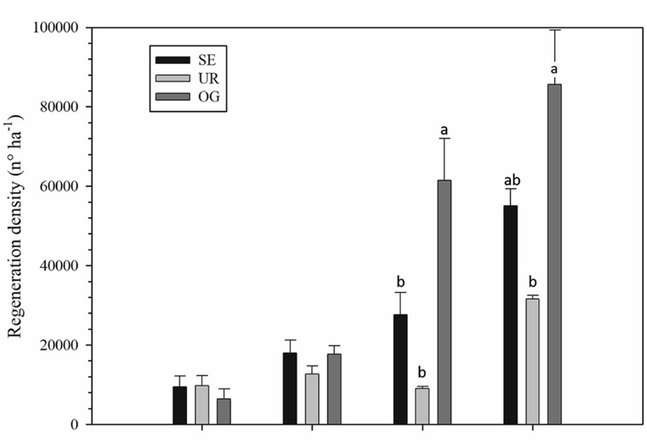

Fig. 2. Density (and standard errors) of regeneration in untreated plots by forest type. Different letters between bars for the same functional group represent significant differences between forest types (p-value < 0.05).

3.2. Effects of VDT upon canopy openness and tree regeneration

Even though the VDT treatments used equal sizes of patches and reserves in both secondary forests, canopy openness in the sub-treatments corresponding to the managed portions of the plots (M, LP, SP) in the SE was significantly higher compared with the same sub-treatments in the UR forest (Fig. 3).

Total tree regeneration density in the SE second-growth forests was significantly lower in the VDT plots compared to the control plots in 2016, as was density of midtolerant and shade-tolerant species (Fig. 4). Two years following the VDT (2018) only regeneration densities of shade-tolerant species remained significantly lower than in control plots in SE. In UR, only regeneration of shade-intolerant species was significantly lower than in control plots, both immediately after the harvest and two years later.

Tree species richness did not change after harvesting in either second-growth forest. The major tree species regenerating two years after the implementation of VDT were partially different from those observed in the untreated plots. The five species with highest importance values (IV) accounted for 56–60% of the total and varied in terms of shade tolerances (Table 2). In the treated SE forest these species included three shade-tolerant species of the *Mirtaceae* family, one midtolerant species, and one short-lived shade-intolerant species. In the treated UR forest these species included two shade-tolerant species, two midtolerant species, and one short-lived shade-intolerant species.

3.3. Regeneration by functional group and sub-treatments

All fixed (forests and subtreatment) and random (nested subplots within sub-treatments in different plots) effects were significant in the fitted models to test tree regeneration for the shade-tolerant and shade-intolerant species, whereas random effects were only significant in the model for midtolerant species. The former models had lower standard deviations than the latter (Table S1 in Supplementary Material).

In the SE forest the density of shade-intolerant species was significantly lower in small patches than in the other sub-treatments (Fig. 5); shade-tolerant species densities were significantly greater in the matrix and in large reserves. In the UR forest, regeneration of shade-intolerant species was significantly lower in the matrix and small reserves, and densities of shade-tolerant species were significantly greater in small patches. Density of midtolerant species did not differ among sub-treatments in either forest.

Regeneration abundance decreased with increasing height classes for both the SE and the UR forests (Fig. 6). In the SE forest the smallest height class showed significant differences only for the shade-intolerant species, which were more abundant in large and small patches compared with the matrix and both sizes of reserves (Fig. 6). For taller height classes, densities of shade-tolerant species were significantly higher in the matrix and in reserves. In the UR forest, densities of shade-intolerant species in the lower height class were significantly greater in large and small patches compared with the matrix and small reserves (Fig. 6), i.e., very similar to the SE forest.

4. Discussion

4.1. Pre-treatment differences in regeneration between second-growth and old-growth forests: Context for the implementation of VDT

The aim of VDT is to restore old-growth attributes such as increased

Table 2
Importance values (%) for species regenerating in each type of untreated forest, and for each treated second-growth forest two growing seasons after VDT. Trees are classified according to functional groups based on shade tolerance, and also according to the potential canopy position they can achieve in mature or old-growth forests. The five species that reached higher importance values in each forest are highlighted in bold letters.

Species by functional group	Canopy position	SE	SE VDT	UR	UR VDT	OG
Shade-intolerant*						
Aristotelia chilensis (Molina) Stuntz	Lower*	0.13	2.3	1.36	3.69	0.19
Embothrium coccineum J.R.Forst. & G.Forst	Lower	3.81	4.29	0.74	0.39	–
Lomatia ferruginea (Cav.) R.Br.	Lower	**8.02**	**11.45**	3.22	4.96	3.19
Lomatia hirsuta Diels ex J.F.Macbr	Lower	0.39	0.16	0.79	0.14	–
Nothofagus dombeyi (Mirb.) Oerst.	Emergent	–	0.03	0.72	0.77	–
Ovidia pillopillo (Gay) Meisn.	Lower	0.26	2.43	0.5	**5.79**	0.04
Raukaua laetevirens (Gay) Frodin	Lower	1.73	1.16	9.08	2.66	0.19
Rhaphithamnus spinosus (Juss.) Moldenke	Lower	3.48	3.22	**12.32**	2.8	**6.85**
Weinmannia trichosperma Cav.	Emergent	0.19	–	0.14	0.14	0.05
Shade-midtolerant						
Dasyphyllum diacanthoides (Less.) Cabrera	Upper	1.12	0.77	0.21	0.18	1.14
Drimys winteri J.R.Forst. & G.Forst.	Upper	0.15	5.71	**10.83**	**16.61**	2.74
Eucryphia cordifolia Cav.	Emergent	6.96	**8.84**	**11.33**	**15.7**	4.19
Gevuina avellana Molina	Middle	2.49	3.32	1.12	1.75	1.64
Laurelia sempervirens (Ruiz & Pav.) Tul	Emergent	–	0.12	1.79	3.28	–
Myrceugenia parvifolia (DC.) Kausel	Lower	0.26	0.09	2.94	1.42	0.17
Podocarpus salignus D.Don	Upper	0.89	2.35	1.37	2.64	**5.34**
Shade-tolerant						
Caldcluvia paniculata Cav. (D.Don)	Lower	0.15	–	0.67	0.32	–
Aextoxicon punctatum Ruiz et Pav.	Upper	5.01	2.52	**10.09**	5.61	**48.67**
Amomyrtus luma (Molina) D. Legrand & Kausel	Lower	8.35	**8.99**	**9.14**	**9.79**	3.66
Amomyrtus meli (Phil.) D. Legrand & Kausel	Lower	**11.84**	**15.21**	7.94	**7.28**	**11.62**
Laureliopsis philippiana (Looser) R.Schodde	Upper	1.57	1.85	6.29	3.56	3.2
Lomatia dentata (Ruiz & Pav.) R.Br	Lower	**9.26**	2.6	2.2	1.47	0.72
Luma apiculata (DC.) Burret	Lower	3.01	0.07	0.07	0.22	0.43
Myrceugenia ovata (Phil.) L.E.Navas	Lower	**19.5**	**15.8**	0.45	1.51	0.41
Myrceugenia planipes (Hook. & Arn.) O.Berg	Lower	1.63	2.38	0.43	1.08	**5.43**
Persea lingue Miers ex Bertero Nees	Upper	**9.55**	2.98	3.46	4.14	0.07
Podocarpus nubigenus Lindl.	Middle	–	–	0.07	0.2	–
Saxegothaea conspicua Lindl.	Upper	0.26	1.37	0.71	1.89	0.07

* Shade-intolerant species classified as only reaching lower canopy positions are short-lived early successional tree species.

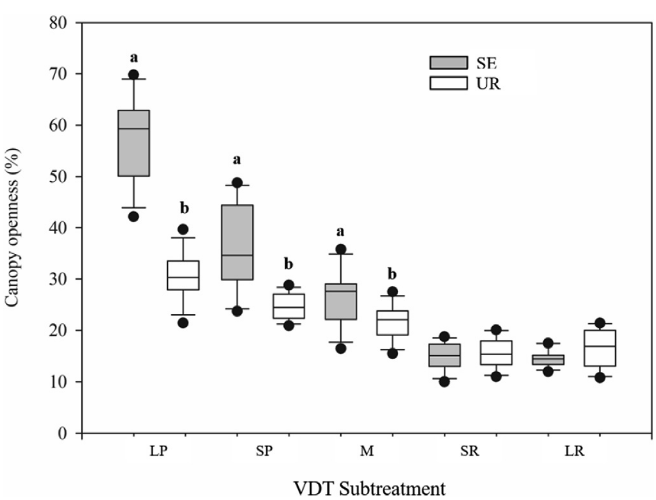

Fig. 3. Canopy openness by forest type and sub-treatment following VDT in each forest. Different letters represent significant differences for a given sub-treatment between the two forests (P-value < 0.05). LP/SP: Large/Small patch; M: Matrix; LR/SR: Large/Small reserve.

regeneration and tree composition of shade-tolerant species (Bauhus et al. 2009). In the present study, the old-growth forest had between 50 and 100% more total tree regeneration, and two to four times more regeneration of shade-tolerant species than the second-growth forests. Despite the differences in stand developmental stage between the two untreated second-growth forests, there were no significant differences between them in terms of total tree regeneration or regeneration by functional groups (Oliver and Larson, 1996). This lack of difference may be due to the similar canopy openness observed in the untreated portions in these forests (Fig. 3). Previous work by Donoso et al. (2018b) indicated that the UR forest had significantly lower regeneration densities in the 100- < 200 cm seedling class and in the sapling class (usually considered as established regeneration), which is contrary to expectations as forests in the understory reinitiation stage are often associated with an established tall regeneration layer (Oliver and Larson, 1996). These findings suggest that second-growth forests dominated by shade-intolerant species (*N. dombeyi* is an evergreen without sprouting capacity in this case), once established, may have a slower understory development, including regeneration of new cohorts, than relatively younger mixed-species forests with many sprouting species. Developmental differences, such as these, need to be accounted for when tailoring VDT to specific forest types and conditions in the landscape.

4.2. Differential effects of VDT sub-treatments on regeneration in each forest

Considering the intensity and variability of this VDT experiment, we expected regeneration dynamics reflective of the sub-treatments to develop rapidly. Although two growing seasons after treatment implementation is a short period for evaluation, there were still several outcomes demonstrating the influence of VDT on regeneration development. Given we did not collect pretreatment regeneration data in the treated plots, we cannot directly relate regeneration densities in these areas to those in untreated plots; however, the extraordinary similarity in stand variables between these areas (Table 1) suggests that cautious comparisons can be made. To this end, thinnings may explain the lower regeneration densities in treated plots than in untreated (control) plots (Fig. 4), presumably due to damage during harvest (Davis and Puettmann, 2009). Differences in tree regeneration between untreated and treated plots suggest greater harvest-related damage in the SE

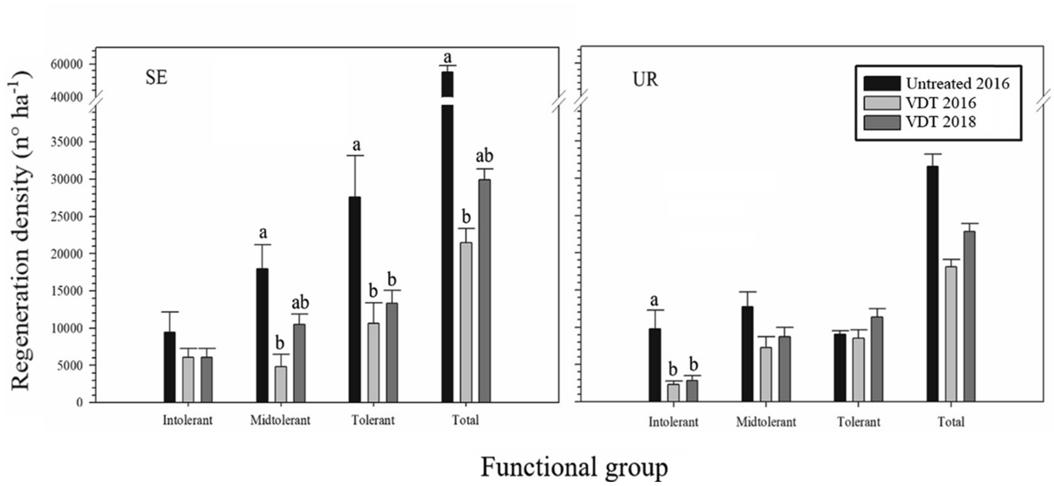

Fig. 4. Density (and standard errors) of regeneration in untreated plots and in VDT plots immediately after harvesting and two years later in each second-growth forest. Different letters above bars for the same functional group represent significant differences among treatments/year (P-value < 0.05).

forest than the UR forest, which might be explained by two factors. First, more trees were felled in the SE (although smaller in size), and second, the crowns of many trees landed inside the patches, due to the smaller tree heights. As a result, both second-growth forests had similar regeneration densities after the cuts (20 to 30 thousand seedlings per hectare), although regeneration abundance in the control plots suggests that the SE likely had more advance regeneration before the cuts (nearly 50 vs. 30 thousand; Fig. 3).

Two-year responses in regeneration differed in the two treated forests. First, while both showed increases in total regeneration densities, none of these increases was significant, although proportionally and numerically they were greater in the SE forest (Fig. 4), which had recruitment levels high enough to result in regeneration densities not significantly different from control plots for all species and for midtolerant species. Second, the sub-treatments showed differences only for shade-intolerant and shade-tolerant species in both forests. These differences generally reflected a preference of shade-intolerant species for patches, and of shade-tolerant species for the matrix or the reserves, while midtolerant species seemed indifferent to sub-treatments (Fig. 5). Third, the evaluation of tree regeneration by sub-treatment and height classes reflected that the pattern observed for shade-intolerant species occurred only in the smaller height class in both forests, while that observed for shade-tolerant species occurred in all height classes from > 50 cm through saplings only in the SE forest (Fig. 6).

These two-year responses in the thinned forests were not compared with any re-measurement of the untreated forests, since we considered this re-measurement was unnecessary for such a short time period. Work in similar secondary forests located to the south of the study area found that early- to mid-successional forests had very similar densities of tree seedlings and saplings, which suggests that these closed-canopy secondary forests have a very stable tree regeneration density (Aravena at al., 2002). These densities increase dramatically as these systems progress to late-successional and old-growth developmental stages (Aravena et al., 2002).

The higher recruitment levels and regeneration dynamics in the SE forest may be explained by a greater level of light penetrating to the understory in this forest. A similar finding was reported by Thyssel and Carey (2001) for the first three growing seasons following VDT in conifer forests. Overall, these results suggest that the size/intensity of treatments used in this study may be more effective when applied in younger versus older stands, especially for midtolerant species. This aspect has received little attention in other regions (Poage and Anderson 2007), as most studies have been designed to address issues reflective of the larger landscape (e.g., Seymour, 2006).

Matrix areas supported the greatest balance of tree species across the different functional groups. In general, the varying abundance and

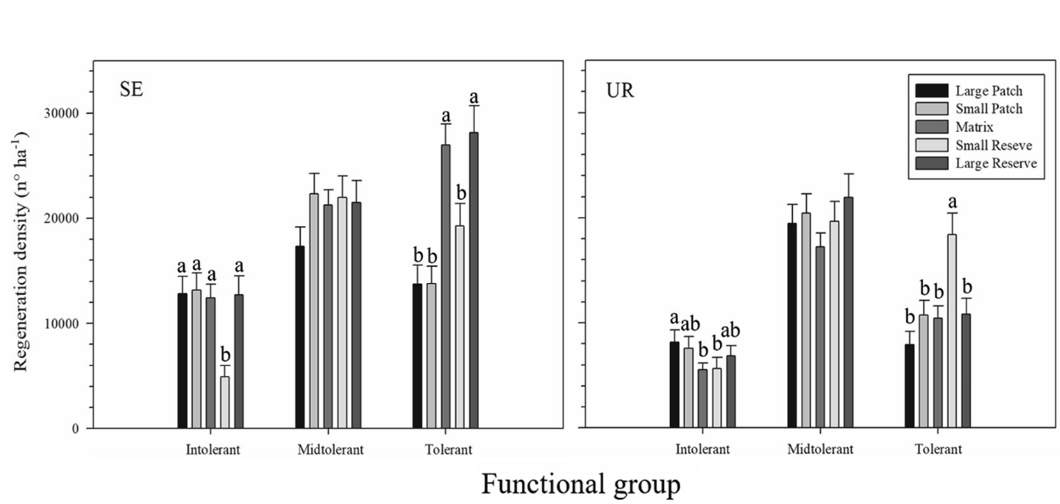

Fig. 5. Density (and standard errors) of seedlings and saplings in each type of forest by sub-treatment (LP: Large patch; SP: Small patch; M: Matrix; SR: Small reserve; LR: Large reserve) and functional group two growing seasons after the implementation of the VDT. Different letters between bars for the same functional group show significant differences among sub-treatments (p-value < 0.05).

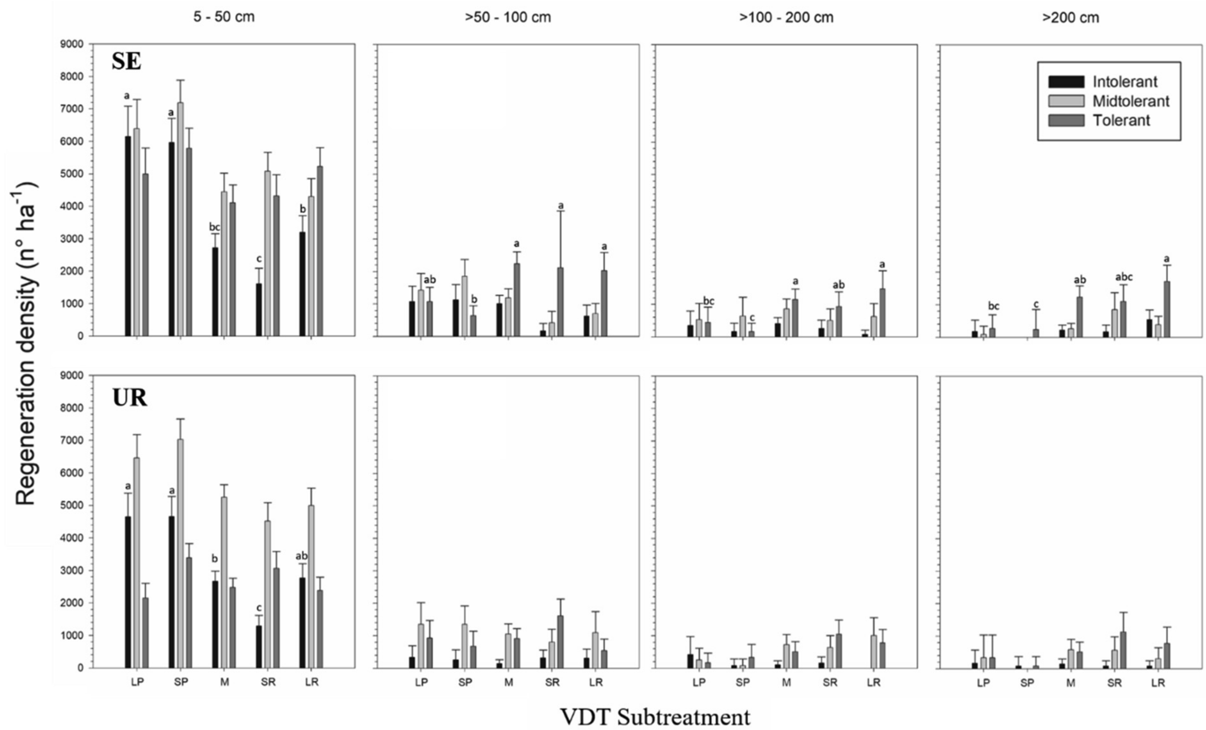

Fig. 6. Density (and standard errors) of seedlings and saplings in both second-growth forests by height class, sub-treatment (LP: Large patch; SP: Small patch; M: Matrix; SR: Small reserve; LR: Large reserve) and functional group two growing seasons after the implementation of the VDT. Different letters represent significant differences among sub-treatments within each regeneration class (*P*-value < 0.05).

shade tolerances of tree species suggest that the various elements of VDT result in a diversity of safe sites for tree regeneration, i.e., tree regeneration was also influenced by small scale conditions (Dodson et al., 2014). In contrast to many conifer forests, the diversity of propagules among tree species in the study included strong vegetative regeneration, except for *N. dombeyi* and *D. winteri* (Donoso, 2006; Donoso et al., 2018a), which results in abundant and diverse regeneration that may not necessarily reflect current light conditions (Burton et al., 2014). Nevertheless, increased light levels following VDT also contributed to the recruitment of two midtolerant species, *D. winteri and E. cordifolia*. As mentioned above, *D. winteri* primarily reproduces from sexual regeneration, whereas regeneration of *E. cordifolia* was primarily from sprouts (especially root suckers), which have been shown to have greater survival than sexual regeneration in more open conditions (Escandón et al., 2013). Overall, increases in light, the variability of microsites and the different types of propagules enabled a suite of tree species to regenerate immediately after the implementation of the cuts.

The VDT treatments have resulted in an initial regeneration response representing species of different shade tolerances. Similar patterns have been found in other regions, even in terms of understory vegetation (Ares et al., 2009), leading to a paradox that early successional species benefit from treatments designed to accelerate development of late successional conditions (Kuehne and Puettmann, 2008; Dodson et al., 2014). In some regions, patches of early successional vegetation are part of old-growth landscapes and as such viewed as valuable in themselves (Swanson et al., 2011; Donato et al., 2012). Even in these regions, our results highlight the importance of applying treatment elements that encourage the establishment and development of late-successional species, e.g., by choosing an appropriate residual density in the thinned matrix or the size of reserves (Shatford and Bailey, 2009). In this context, the challenge with VDT can be viewed as implementing disturbance aimed at accelerating succession, rather than resetting vegetation to an earlier successional stage (Abrams and Scott, 1989).

4.3. Management implications

Our results show that with equal treatments, more light reaches the forest floor in younger/shorter stands resulting in different regeneration patterns following application of VDT. These findings suggest that selecting specific design elements in VDT prescriptions that take into account the initial stand conditions are critical for efficiently promoting heterogeneity in treated stands. In practical terms, care should be taken when implementing VDT designs (e.g., composed of patches, matrix, reserves) to encourage not just a high density of tree regeneration, but to ensure a desirable mix of regenerating species, including regeneration and growth of shade-tolerant and late-successional species. In this regard, natural disturbance patterns may provide direct insight. For example, taller second-growth forests in a more advanced successional stage (e.g., UR in this study) could be treated with patches that reflect gap sizes common in Chilean old-growth forests (Veblen, 1985; González et al., 2015b), or more intense thinnings than used in this study. In contrast, forests of lower stature in a younger successional stage (e.g., SE in this study) could be treated with gaps of smaller sizes than used in our study to promote regeneration of more shade-tolerant species.

Our early results support the notion that VDT can be used to increase complexity and shift species composition in even-aged second-growth stands (Willis et al., 2018). The patterns of regeneration responses in our study appear to support this claim, even after only two years post treatment. In treated stands, regeneration densities have increased in two growing seasons without declines in tree species richness.

Sub-treatments have had differential effects upon regeneration, suggesting the potential for development of patches favorable to shade intolerant species with the matrix and reserves favorable for shade-tolerant species, a late-successional structural attribute typically lacking in second-growth stands, especially stands treated for timber production (Davis and Puettmann, 2009; Bauhus et al., 2009). The early trends observed suggest the potential for future presence of late-successional species in the midcanopy, and later recruitment into the upper canopy layers.

Thyssel and Carey (2001) proposed that VDT showed promise as part of holistic silvicultural systems applied across landscapes, and as a technique to restore vegetative complexity to closed-canopy second-growth forests. This is especially important in regions with concerns over declining late-successional wildlife habitat and biodiversity (Spies et al. 2010), and in regions with continuous demands for timber or firewood, like in south-central Chile (Donoso et al., 2014). Therefore, it is important to acknowledge this first thinning entry can only be the initial part of a long-term silvicultural strategy. The process of converting young and homogeneous forests to more complex forests requires several thinnings that encourage gradual modifications to better attain the objectives of creating old-growth attributes (Nyland, 2003; Shatford and Bailey, 2009; Berger and Puettmann, 2012). In southern Chile, this may be economically and ecologically feasible, since many second-growth forests are mixed-species forests (Loguercio et al., 2018) of high productivity (Salas-Eljatib et al., 2018).

The second-growth forest conditions in the study areas are representative of much of south-central Chile, and to an extent probably many other regions, i.e. fairly homogenous forests that developed following disturbances not historically typical in the respective regions. When aiming to restore old-growth attributes in young forests, VDT approaches should differ as a function of successional stage, type of disturbance initiating the second-growth forest, and the silvics of the tree species. While VDT is a promising approach within the realm of ecological forestry, it needs to be specifically designed, in terms of effective intensities and spatial design (e.g., patches and reserves) to ensure that the treatments accelerate succession towards old-growth structures and compositions.

5. Conclusion

The implementation of the same protocol for the VDT in the two second-growth forests of this study generated a greater canopy openness (a surrogate of light) in the younger forest in the stem exclusion stage forest (SE) compared to the forest in the understory reinitiation stage (UR). Nevertheless, in both forests shade-intolerant species generally preferred sub-treatments with more intense harvesting (the patches), and shade-tolerant species had great abundance in sub-treatments with lower harvesting intensity (the matrix) or no harvesting (the reserves). Tree regeneration of midtolerant species was indifferent to sub-treatments. Responses to these VDT experiments were manifested more clearly in the SE forest. There were two indications of this. In this forest, the increase in tree regeneration densities during two growing seasons reached values not statistically different than the analog untreated forest (which were different after harvesting) for the midtolerant species and for all species. In addition, the preference of shade-tolerant species for the matrix and the reserves in this forest occurred throughout most regeneration height classes, including saplings. Therefore, regeneration dynamics has been more diverse and more rapid in the SE forest. Results in this study allow us to conclude that VDT is a good approach to activate or accelerate forest dynamics towards a more abundant and diverse regeneration, including vigorous regeneration of shade-tolerant species not only in the reserves, but also in the matrix, which comprised about two thirds of the treated areas/plots in the experiment. This outcome is one of the results expected when implementing VDT to attain old-growth attributes, i.e., a dense and hopefully rapidly growing regeneration of shade-tolerant species common in older forests. While this expectation was met more closely in the younger forest, we also conclude that VDT needs to follow differential protocols according to the interaction of initial disturbances, developmental stage, and silvics of the component species, in addition to being part of a long-term silvicultural system that may require several VDT entries.

CRediT authorship contribution statement

Pablo J. Donoso: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing - original draft, Writing - review & editing. **Klaus J. Puettmann:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **Anthony W. D'Amato:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **Diego B. Ponce:** Data curation, Investigation, Methodology. **Christian Salas-Eljatib:** Conceptualization, Formal analysis, Investigation, Methodology, Writing - original draft. **Patricio F. Ojeda:** Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118058.

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