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Mid-term results and prospects for irregular shelterwood systems in hardwood-dominated temperate rainforests in Chile †

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Abstract

Background: When possible, silviculture should aim to develop mixed-species multi-aged forests that can be more productive and resilient to disturbances, provide high-quality timber and sustain greater amounts of biomass. Southern Chile is covered by temperate rainforests dominated by a mixture of tree species, such as the Evergreen forest type (EFT). The irregular shelterwood regeneration method is a novel approach aimed at developing irregular multi-aged forests following the retention of the residual forest (no final cut). Here, we report mid-term results after implementing these cuttings in two EFT forests in the Coastal Range and discuss its prospects for other temperate rainforests.

Methods: Two forests were sampled and evaluated in terms of composition, structure and growth, focusing on the new cohorts developed or released after the irregular shelterwood cuts. One forest was cut in a low-productivity site at 600 m (Hueicolla) in 1983, and the other in a medium-productivity site at 350 m (Llancahue) in 2009. In Hueicolla, 63% of the basal area was harvested from an old-growth forest where the main residual tree species were *Eucryphia cordifolia*, *Laureliopsis philippiana* and *Saxegothaea conspicua*. In Llancahue, 40% of the total basal area was harvested in a mature secondary forest dominated by *Nothofagus dombeyi*.

Results: The understorey developed in Hueicolla had 3,600 trees per ha and a quadratic stand diameter of 15 cm. It was dominated by the mid-tolerant species *Eucryphia cordifolia*, *Gevuina avellana* and *Lomatia ferruginea*, plus the shade-tolerant *Amomyrtus luma*. In Llancahue, a dense lower canopy was dominated by *Podocarpus salignus* and *Drimys winteri*, both mid-tolerant species, which included 81,000 seedlings and saplings < 5 cm per hectare and 560 ingrowth 5-10 cm trees per hectare.

Conclusions: The irregular shelterwood cuts allowed the development of dense understorey tree layers below the residual trees. However, the tree composition of the new cohorts largely differed from that of the residual trees and was dominated by mid-tolerant species, including some short-lived species. The irregular shelterwood method proves appropriate for the EFT and may likely be successful in other forest types with valuable mid-tolerant species.

Keywords: Ecological silviculture; mixed-species silviculture; tree regeneration; diameter growth.

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Introduction

Silvicultural methods aim to regenerate new even-aged or uneven-aged cohorts in stands after mature trees are harvested. The shelterwood method is an approach to develop a new even-aged cohort influenced by the shelter provided by the cover of the residual trees left after the seed cut, which are subsequently cut once the new cohort is established (Matthews 1989; Nyland 2016). The final cut leaves an even-aged new regenerating forest with a tree composition largely dependent on the composition and vigour of the residual trees left after the seed cut. However, during the last decades, alternatives to the classic shelterwodd system have become relevant, which avoid simplifying stand attributes such as regeneration, structure and species composition, and which are framed in new silvicultural strategies such as continuous cover forest management, ecological silviculture or near-natural forestry (D'Amato et al. 2011; D'Amato 2021; Palik et al. 2020; O'Hara 2016; Pukkala & von Gadow 2012; Bannister & Pyttel 2010). Under this scenario the irregular shelterwood cutting method is proposed. This method is defined as a system of successive fellings with a long and indefinite period of regeneration (Raymond et al. 2009), where the tree cover is retained for a longer period and may not even be subjected to a final cut that removes the entire upper canopy, allowing the forest to accommodate different management objectives (Raymond et al. 2009; Raymond & Bédard 2017). Thus, the main objective of the irregular shelterwood cuttings is to establish, in each of the interventions, a new cohort of tree species through longer regeneration periods than in the classical method (Raymond et al. 2009). This extension of the regeneration period means that the new forest is not even-aged but rather has an irregular multi-age structure, maintaining and increasing the heterogeneity of the forests in the long term (Ashton & Kelty 2018; Raymond & Bédard 2017).

Thus, the irregular shelterwood method seems appropriate to apply in forests with tree species with a great range of shade tolerances, and such is the case of the Evergreen forest type (EFT). This forest type is the largest in southern Chile (37 to 45°S Lat, from low to intermediate elevations). It has a relatively high tree species diversity (Donoso 1989ab; Gutiérrez et al. 2009; Gutiérrez & Huth 2012; Donoso 2015; Donoso et al. 2018), although species diversity declines from north to south (Gutiérrez et al. 2012; Bannister et al. 2012) and with elevation (Donoso 1989a). Trees in this forest type include species not only with an ample range of tolerances to shade (Donoso 1989a) but also to soil moisture (Bannister & Donoso 2013; Donoso & Soto 2016; Donoso et al. 2007) and nutrients (Lusk et al. 1996).

Given these considerations, this work aimed to evaluate the implementation of the irregular shelterwood method to EFT forests in two markedly different sites at contrasting elevations within the Coastal range in south-central Chile. We discuss results regarding regeneration and growth in these forests and prospects for applying irregular shelterwood cuttings elsewhere in other temperate rainforests.

Methods

Study site

This work includes two forests managed by irregular shelterwood cuttings in the Coastal range of south-central Chile. One study was established near Hueicolla in 1983 on the western slope of the Coastal Range, between 500 and 610 m a.s.l. (Figure 1). The climate is wet-temperate with average annual temperatures of 9.5°C (Reyes et al. 2009). Precipitation mostly occurs as rain and can reach 4,000 mm per year, with a clear decrease in summer (Donoso 1989b). The soils correspond to the Hueicolla series, which have developed *in situ* on residual metamorphic material of the mica-schist type, are acidic, poorly drained, and of moderate depth (Schlatter & Gerding 1995; CIREN 2003).

The second study was established in 2009 in the Llancahue experimental forest in the Coastal Range, between 340-350 m a.s.l. near the city of Valdivia (Donoso et al. 2014; Figure 1). The average annual rainfall is 2,357 mm, with July being the rainiest month and February the driest. Average annual temperatures are 12.2 °C (Núñez et al. 2006). The dominant soil is clay red, originated by Plio-Pleistocene sediments deposited on metamorphic schists of the Los Ulmos series (Schlatter & Gerding 1995). According to Donoso (2005), the forests at Hueicolla are relatively low-to-medium productivity and at Llancahue, medium-to-high productivity.

Vegetation characteristics

The forest composition at both sites corresponds to the EFT (Donoso 1981), with variations between sites due to latitudinal and longitudinal differences. In Hueicolla, the forest did not have any evidence of recent past human disturbances, being mainly dominated by *Eucryphia cordifolia* Cav., *Aextoxicon punctatum* Ruiz & Pav., *Laureliopsis philippiana* (Looser) Schodde, *Drimys winteri* J.R.Forst. & G.Forst., *Podocarpus nubigena* Lindl., *Saxegothaea conspicua* Lindl., *Dasyphyllum diacanthoides* (D.Don.) Cabrera, *Amomyrtus meli* (Phil.) D.Legrand & Kausel, *Amomyrtus luma* (Molina) D.Legrand & Kausel *Myrceugenia ovata* (Phil.) L.E.Navas, *Gevuina avellana* Molina and, occasionally, individuals of *Weinmannia trichosperma* Cav. (Donoso 1989a). In Llancahue, the history of the vegetation is marked by abrupt changes derived from human-caused fires and land opening for agricultural land use in the past (Donoso et al. 2014, González et al. 2015). Thus, the floristic composition of the site corresponds 20% to old-growth forests, 26% to mature *Nothofagus dombeyi* forests, 19% to mixed evergreen secondary forests, 5% to *N. dombeyi* secondary forests, and 38% to other uses, mainly high-graded forests, hosting a total of 30 arboreal or arborescent species and 41 species of shrubs, herbs, climbing plants and ferns (Donoso et al. 2018). Of these species *N. dombeyi* and *W. trichosperma* are long-lived pioneer species; *G. avellana* is a relatively short-lived pioneer species; *E. cordifolia, P. salignus, D. diacanthoides* and *D. winteri* are mid-tolerant species; *L. philippiana* and *S. conspicua* are upper canopy shade-tolerant species, and the Myrtaceae species are usually

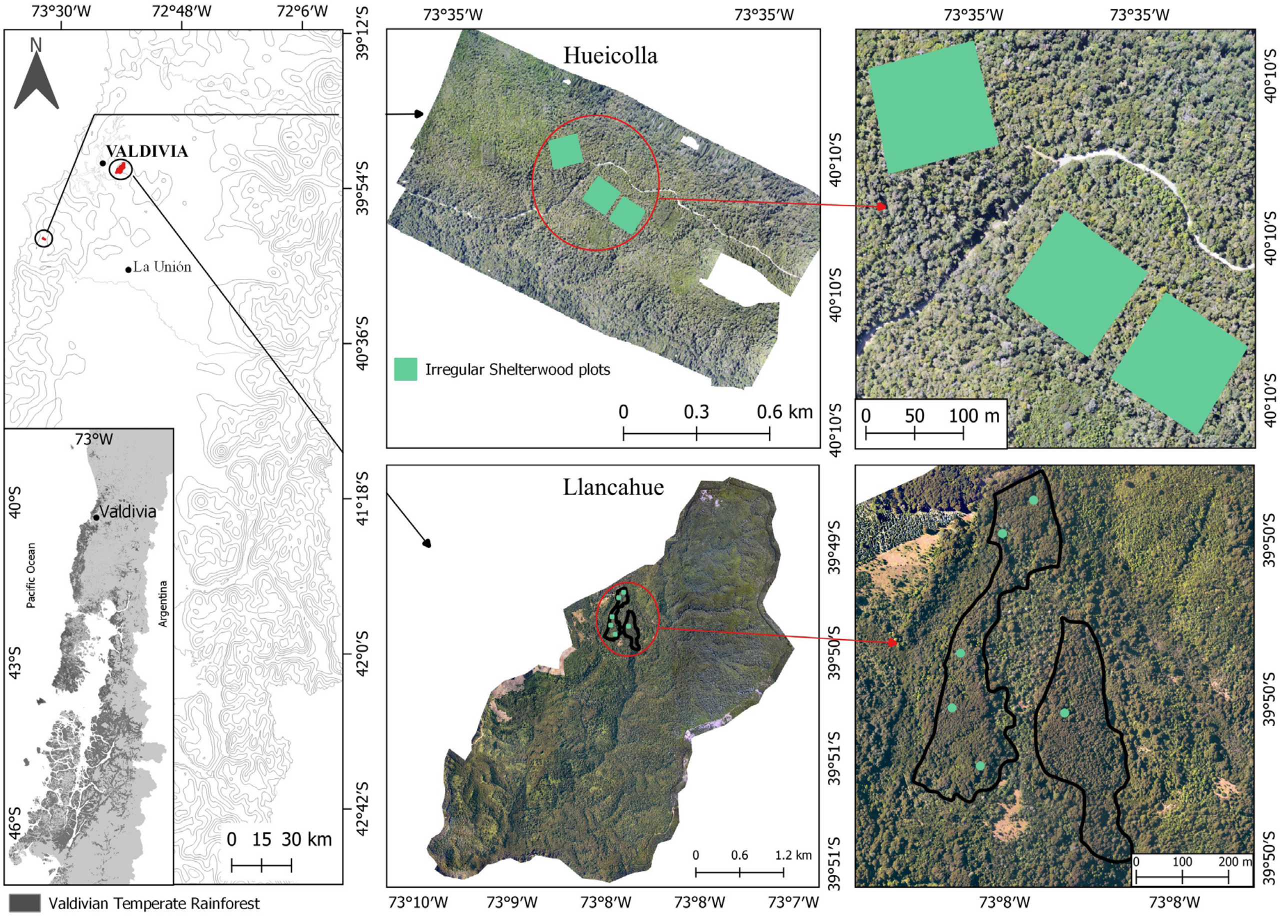

FIGURE 1: Map of the study sites, with the experiment in Hueicolla (upper panel) on the western slopes of the Coastal Range in southern Chile, and the experiment in Llancahue (lower panel) on the eastern slopes of the Coastal Range near the Intermediate Depression.

small trees dominant in the lower canopy of the forest (Donoso 2015; Gutiérrez & Huth 2012; Lusk 1999).

Experimental design

Hueicolla

In 1983, a large experiment was established to evaluate silvicultural methods for the EFT in the Coastal range (Donoso 1989b). The experimental design included three randomly distributed 1-ha plots for each of different silvicultural methods tested. One of these was the irregular shelterwood method, in which on average 63% of the basal area was removed in a regeneration cut (Table 1), and there was no later final cut to remove the residual trees. Stand parameters were evaluated in 1982, before the establishment of the experiment, after the regeneration cut in 1983 (Donoso & Donoso (1987); Donoso (1989b)), and 39 years after the regeneration cut (2022, this study). This last measurement was made by sampling one 1,800 m^2 subplot within each of the original 1 ha plots, which is considered appropriate according to the variability in sizes and densities in these forests (Curtis & Marshall 2005).

Llancahue

In 2009, mature secondary forests dominated by *N. dombeyi* were managed with a shelterwood regeneration cut in which 41% of the basal area was harvested (Table 1) and, like in Hueicolla, there was no later final cut to remove the residual trees. In 2021, we randomly established six 2,000 m^2 (50 x 40 m) plots. In year 2021 the original and residual forest structure following the cut (2009) was reconstructed by using the stand table projection methodology (Avery and Burkhart 1994) but backwards, based upon the diameter growth rates measured from collected increment cores in this study (see Data collection section) and measuring the stumps and species to which they belonged to estimate diameter at breast heigh (dbh) from available linear models.

Data collection

Sampling was conducted in year 2022 at Hueicolla and 2021 at Llancahue. In each sample plot, all tree and arborescent species with a dbh ≥ 5 cm were marked and measured. We recorded species, dbh, tree form and health (each in three categories), and the crown position

TABLE 1: Mean and standard deviation (SD) for number of trees, basal area and volume before and after the irregular shelterwood cuttings at Hueicolla (cut in 1982) and Llancahue (cut in 2009).

		N (Trees/ha)			Basal Area (m²/ha)			Volume (m³/ha)		
Site	**Plot**	**Before**	**After**	**% cut**	**Before**	**After**	**% cut**	**Before**	**After**	**% cut**
Hueicolla	1	775	261	66,3	100,7	45,6	55,7	454	297	35
	2	970	189	80,5	94,9	35,8	62,3	428	219	49
	3	850	200	76,5	108,5	31,8	70,7	456	202	56
Mean±1SD		865±98	217±39	74.4±7.3	101.4±6.8	37.8±7.1	62.5±7.9	447±17	240±51	46±11
Llancahue	1	1262	468	62.9	83.9	41.1	51.0	1035	523	50
	2	1332	851	36.1	75.7	48.0	36.7	882	554	37
	3	1483	799	47.0	71.1	41.9	41.1	838	495	41
	4	1257	704	44.0	68.0	42.8	37.0	790	506	36
	5	1434	775	46.0	69.5	43.7	37.1	784	495	37
	6	1122	716	36.2	73.7	42.7	42.1	868	503	42
Mean±1SD		1315±131	719±134	45.4±9.8	73.7±5.7	43.4±2.4	40.8±5.5	866±92	513±23	40±5

(dominant, codominant, intermediate, suppressed/ submerged) following the forest inventory protocols of Prodan et al. (1997). In addition, we measured the top height of a stratified subsample by tree diameter classes (Table 2) per plot with a VERTEX IV ultrasonic hypsometer (Haglof Inc., Madison, Mississippi, USA) to fit height-diameter functions, and estimate heights and volumes of all trees (according to the functions given in Drake et al. (2003) for Hueicolla and in Donoso et al. (2020a) for Llancahue). We measured 88 trees in Hueicolla and 134 trees in Llancahue from the new cohort (residual trees from the shelterwood cuttings were not included).

In 2 m² subplots established in each plot, distributed every 5 m in two transects (a total of 72 in Hueicolla and 120 in Llancahue), we recorded, by species, the density of tree regeneration for seedlings in different height classes (5-<50; 50-<100; 100–200 cm), and for saplings (> 200 cm in height and <5 cm in dbh). Regeneration was assigned to three functional groups according to shade tolerance: shade-intolerant, mid-tolerant, and shade-tolerant species.

The same individuals measured for height at both study sites were used to analyse their growth in diameter with increment cores extracted at 1.3 m from the ground using Pressler augers, ensuring that they reached the centre of the stem. To visually distinguish the limits of the rings, the extracted and assembled cores were polished in the transverse plane of the core with an orbital sander, starting with coarse-grained sandpaper (100 g cm^{-2}) and ending with fine-grained sandpaper (500 g cm^{-2}). Cores were scanned with a high-resolution digital scanner (EPSON, Perfection V800/V850) at 1200 dpi and measured using CooRecorder computer software version 7.6 (Larsson 2014). Growth ring dating followed the convention of Schulman (1956) for the Southern Hemisphere, and growth series dating was corroborated using the COFECHA program (Holmes 1983). The analysis of the effects of the shelterwood cut upon trees included all trees in Table 2 for Hueicolla (since all of them correspond to the new cohort following the cut), but for Llancahue, it only included trees 17 cm in dbh and smaller, considering that these were the juvenile saplings or small trees that by the time of the cut were the most likely to respond to it.

Estimation of stand variables

With the dbh of each tree per plot, we calculated the basal area (G) and estimated the height (h) and volume (V) of each tree according to species (Drake et al. 2003; Donoso et al. 2020a). With this information, we determined stand level (per ha) values for tree density (N, number of trees), basal area, and volume after treatment (Hueicolla: 1982, Llancahue: 2009) and for the last measurement (2021 to 2022). Total values for each of these variables are composed of trees that correspond to residuals from the cut and to ingrowth, i.e. trees that entered the minimum 5 cm diameter class during the measured period and had a dbh ≤ 25 cm in Hueicolla and ≤ 10 cm in Llancahue in the final measurement (an estimation based on the growth rates evaluated in this study). By these means, we calculated the periodic annual increment (PAI; value at t_1– value at t_0 divided by the number of years) in tree diameter, stand basal area and volume, where the last two variables included ingrowth and mortality. In addition, the PAI in diameter (mm) of the last 10 years in each site was determined through the analysis of ring width by species.

Statistical analyses

The PAI in dbh per species, and in basal area and volume at the stand level, plus regeneration densities (seedlings, saplings), were compared for each site according to functional groups (based upon shade tolerances, i.e.

TABLE 2: Number of trees measured for height and diameter to estimate height and volume per tree according to species and study site. From these trees we also extracted increment cores for the growth analyses.

Site	**Hueicolla**			**Llancahue**		
DBH Class (cm)	**5-<10**	**10-<15**	**15-30**	**5-<10**	**10-<17**	**≥17**
Drimys winteri J.R.Forst. & G.Forst.	0	9	16	5	3	16
Eucryphia cordifolia Cav.	1	22	2	1	11	11
Gevuina avellana Molina	0	9	16	1	10	1
Lomatia ferruginea (Cav.) R. Br*	0	11	0	0	0	0
Laureliopsis philippiana (Looser) Schodde	1	1	0	3	13	4
Podocarpus salignus D.Don	0	0	0	3	15	3
Nothofagus dombeyi (Mirb.) Oerst.	0	0	0	0	0	34
Total	2	52	34	13	52	69

L. ferruginea is considered a short-lived pioneer species, similar to *G. avellana* and other species of the *Proteaceae* family.

shade-intolerant, mid-tolerant, and shade-tolerant species) through analysis of variance (ANOVA). We checked that the residuals of the linear statistical models in each case followed a Gauss distribution using the Shapiro–Wilk test and checked for homoscedasticity of variance through the Levene test. To identify significant statistical differences among PAI and regeneration by functional groups for each site, we used the Least significant difference (LSD) and the Scheffé test in the "agricolae" statistical package (De Mendiburu 2010), in both cases using $\alpha = 0.05$ as a significance level. All the analyses were conducted with the R statistical software (R Core Team, 2020).

Results

Trees, basal area and volume 39 years (Hueicolla) and 12 years (Llancahue) after the seed cuts

In Hueicolla, after 39 years following the seed cut, there has been some loss of the residual trees, but these have increased in basal area and volume (Table 3). Ingrowth (trees ≥ 5 cm of the new cohort established following the cut) reaches almost four thousand trees/ha with a mean annual increment of 0.76 m^2 ha^{-1} in basal area and 3.07 m^3 ha^{-1} in volume. In Llancahue, 12 years after the cut, the ingrowth has been lower, likely because the shorter time after cutting (residual basal area in both sites was

TABLE 3: Number of trees, basal area, and volume at each study site 39 (Hueicolla) and 12 (Llancahue) years after applying the irregular shelterwood cuttings. Total values for each variable include residual trees corresponding to cohorts present before the cuts and ingrowth corresponding to new cohorts that developed after the cuts.

		N (Trees/ha)			**Basal Area (m^2/ha)**			**Volume (m^3/ha)**		
Site	**Plot**	**Res.**	**Ingrowth**	**Total**	**Res.**	**Ingrowth**	**Total**	**Res.**	**Ingrowth**	**Total**
Hueicolla	1	172	3878	4050	41.4	27.6	69	374	112	486
	2	172	3517	3689	45.7	25.9	72	383	103	486
	3	167	4594	4761	37.6	35.2	73	327	144	470
Mean±1SD		170±3	3996±54	4167±545	41.6±4.1	29.6±4.9	72±1.9	361±30	120±21	481±9
Llancahue	1	385	800	1185	52.0	3.5	56	690	17	708
	2	735	470	1205	62.6	2.1	657	759	6	765
	3	790	635	1425	53.1	2.8	569	649	12	662
	4	605	400	1005	54.2	1.8	56	670	6	675
	5	675	485	1160	57.5	2.1	607	686	9	695
	6	495	570	1065	54.4	2.5	57	679	8	686
Mean±1SD		614±152	560±143	1174±145	55.6±3	2.5±0.6	58±4	689±37	10±4	698±36

similar). Mean annual increment in basal area has only been 0.21 m^2 ha^{-1} and 0.83 m^3 ha^{-1} in volume. Residual trees in Hueicolla had a mean annual increment of 0.09 m^2 ha^{-1} in basal area and 3.10 m^3 ha^{-1} in volume, and in Llancahue, 1.02 m^2 ha^{-1} in basal area and 14.67 m^3 ha^{-1} in volume.

Diameter distributions

In Hueicolla, the shelterwood seed cut carried out in 1983 left a residual stand dominated by canopy shade-tolerant species (mainly *L. philippiana* and *S. conspicua* with a modal diameter of 40 cm) followed by the mid-tolerant *E. cordifolia* and understorey shade-tolerant species that corresponded mostly to the Myrtaceae family (Figure 2). After 39 years (Figure 2b), the diameter distribution of the residual trees maintains a similar shape with a modal diameter of 45 cm for canopy shade-tolerant species. There is also a rich understorey of pole-sized trees, saplings and seedlings of mid-tolerant and short-lived shade-intolerant species (Figures 2b and 3a).

In Llancahue, the residual forest was dominated by the long-lived shade-intolerant *N. dombeyi* trees concentrated between 15 and 40 cm in dbh, but with several trees above this diameter range and up to 85 cm in dbh (Figure 2c). The residual stand also left an understorey dominated by mid-tolerant species that, together with shade-tolerant species, had a reverse-J shaped or negative exponential diameter distribution. Twelve years after the cut (Figures 2d and 3b), there has been a massive recruitment of trees, mostly of mid-tolerant (*E. cordifolia, D. winteri* and *P. saligna*) and shade-tolerant species, and also a movement of small residual trees of these species into larger diameter classes.

Overall, the tree species composition of the new cohorts following irregular shelterwood cuts in Hueicolla and Llancahue differed from the tree species composition of the canopy residual trees after the cuts, with both forests having rich understories dominated mostly by mid-tolerant tree species.

Diameter growth

Growth in dbh was slow and similar for all five species evaluated in Hueicolla but rapidly started to differentiate among species in the second five-year period evaluated (5-10 years following the cut; Figure 4), when *L. philippiana*, the most shade-tolerant species of the group, had the smallest PAI and remained in this position along the entire period evaluated, with significantly smaller growth rates than all other species. In this second period, *G. avellana* had a PAI significantly greater than all other species and remained among those with the highest growth rates for 20 years, but then had a gradual and continuous decline in growth. *D. winteri, L. ferruginea* and *E. cordifolia* had increasing growth rates until the third 5-years period. By the fourth period, *E. cordifolia* did not increase in PAI anymore and started to have a decline from age 30 onwards;

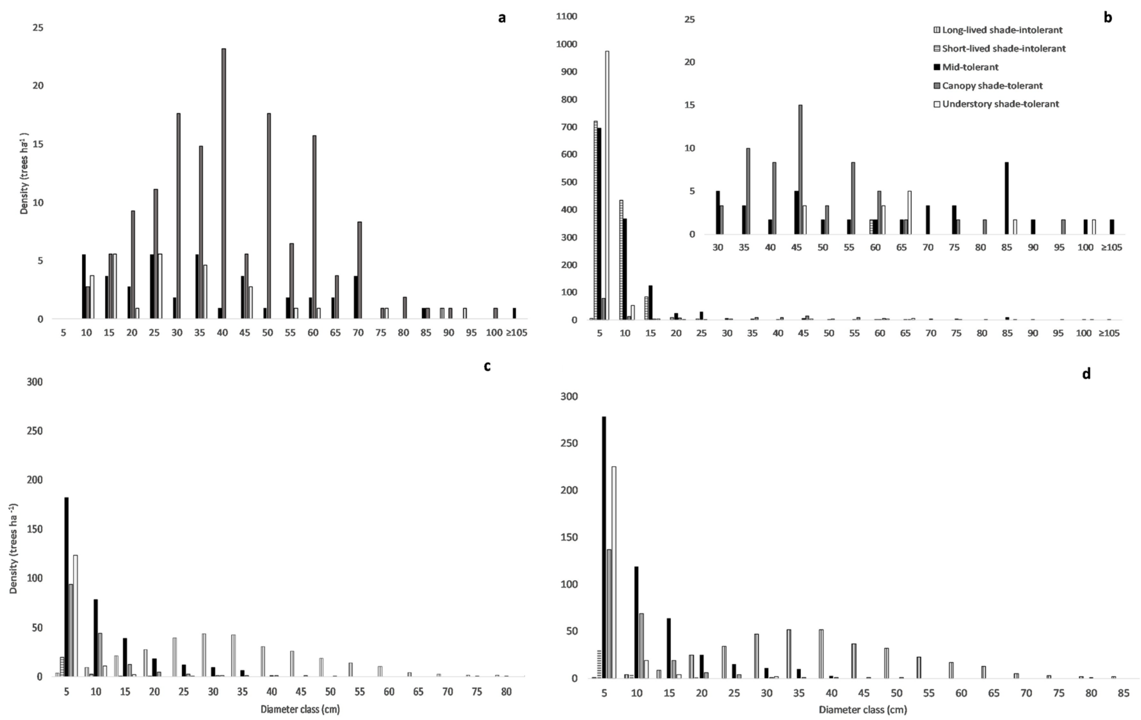

FIGURE 2: Diameter distribution of the trees by functional group (long-lived shade-intolerant species, short-lived shade-intolerant species, mid-tolerant species, canopy shade-tolerant species and understorey shade-tolerant species) after cuttings (left panels) and after the last measurement (right panels) in Hueicolla (a, b) and Llancahue (c, d). The insert in figure b is included for scale reasons since there was a massive increase in tree numbers in the 5 and 10 cm diameter classes in Hueicolla. Note that the axes scales are different for the two sites.

FIGURE 3: (a) A stump from a cut tree and the new cohort (including seedlings, saplings and trees ≤ 25 cm) 39 years after managing an old-growth forest in Hueicolla, and (b) an overview of the managed forest in Llancahue after 12 years following the seed cut, with the overstorey dominated by 30-40 m tall *N. dombeyi* trees and the understorey by a rich mixture of species.

D. winteri continued with increasing growth rates until the end of the evaluation period; *L ferruginea* reached a peak in growth by the fourth period and then had a steep decline. Overall, at the end of the evaluation period (35-40 years), *D. winteri* was the fastest-growing species, *L. philippiana* the slowest, and the other three species ranked in intermediate positions.

At Llancahue, the PAI in dbh was evaluated in small trees (≤ 17 cm in dbh; Table 2) rather than in trees established following the cut (which are likely to be saplings 12 years after the cut). PAI in dbh was greatest during the 5-year period that followed the cut (Figure 4 lower panel). Two species, *D. winteri* and *G. avellana*, maintained the highest growth rates across all the periods evaluated. Growth rates were significantly higher in the 5 years following the cut compared to before although that difference diminished through time across all species. *E. cordifolia* and *P. salignus* generally maintained the lowest growth rates throughout the evaluated period. *L. philippiana* ranked intermediate in growth.

Regeneration

In Hueicolla, seedlings and saplings were dominated by shade-tolerant species, followed by mid-tolerant species. At the same time, ingrowth was a mixture of species of different shade tolerances, although dominated by mid-tolerant species (Figure 5a, b, c). This is likely because, following the shelterwood cut, environmental conditions (especially light) were favourable for the regeneration of shade-intolerant species. However, once a dense understorey developed, there was no further regeneration.

In Llancahue, mid-tolerant and shade-tolerant species were generally similar in abundance among seedlings, saplings and ingrowth. However, in the saplings category, mid-tolerant species had a significantly greater density than all other species (Figure 5 d, e, f). Shade-intolerant species were present in all classes of regeneration and ingrowth and were always significantly lower in density compared with mid-tolerant species. Shade-intolerant species showed a high density among seedlings but low density among saplings and negligible density in ingrowth.

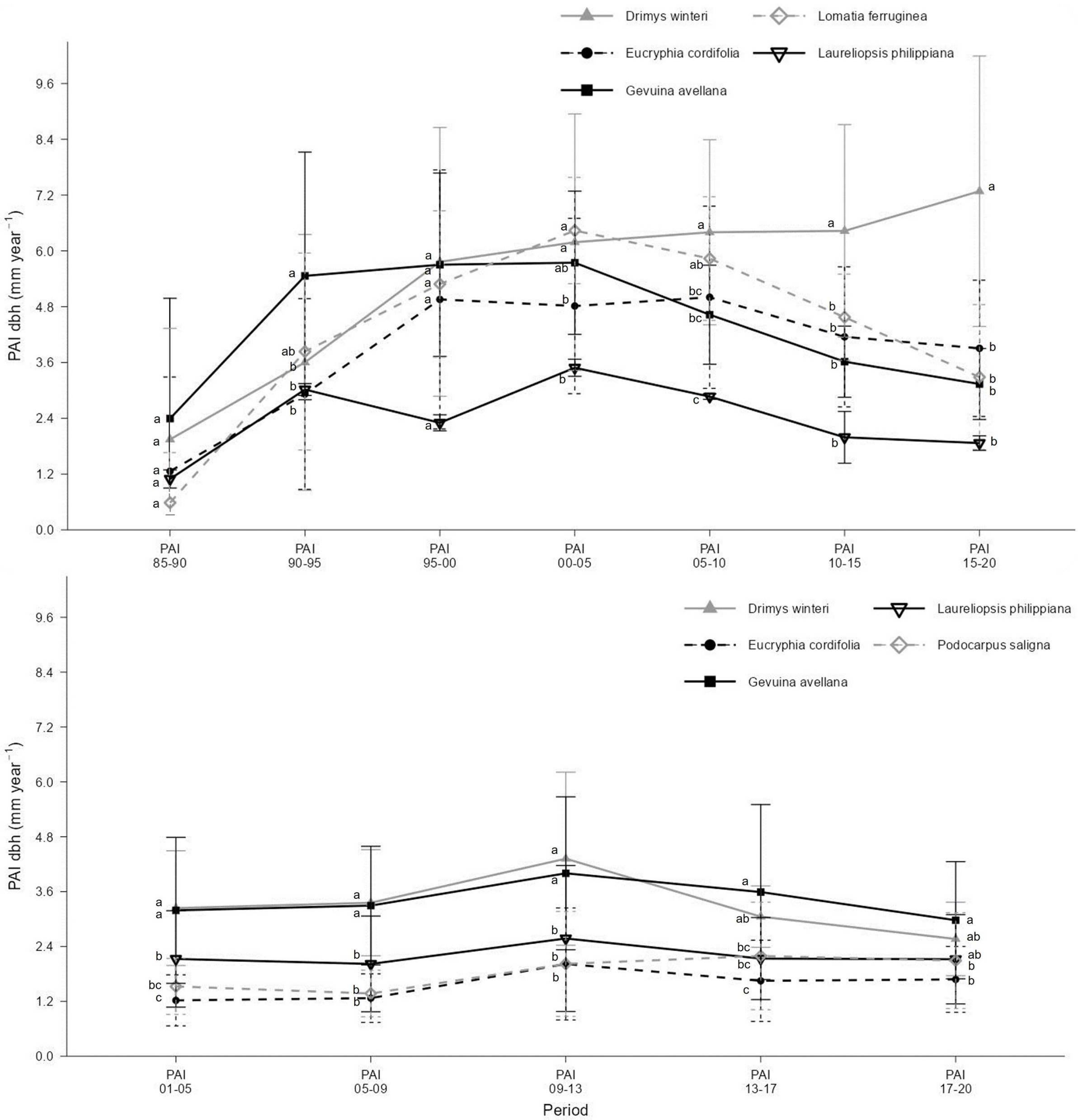

FIGURE 4: Periodic annual increment (PAI) and standard deviation in dbh per species for ingrowth trees in Hueicolla (upper panel; trees 5-30 cm) and Llancahue (lower panel; trees 5-17 cm). On the x axes, numbers for each period evaluated correspond to year ranges, starting in 1985 in Hueicolla (following the cut) and in 2001 in Llancahue (eight years before the cut). Different letters during the same time period indicate significant differences (p-value < 0.05) between species.

In both forests, the shade-intolerant species corresponded to short-lived species, mostly of the Proteaceae family. Therefore, the shelterwood cut did not favour the regeneration of long-lived shade-intolerant species, such as *W. trichosperma* in Hueicolla or *N. dombeyi* in Llancahue.

Vegetation cover

Most non-tree species in the understorey of the forests evaluated had low cover, except for the fern *Lophosoria quadripinnata* (J.F.Gmel.) C.Chr. in Hueicolla and *Chusquea* spp. at both sites (Table 4). The number of these species was similar between both sites (18 in Hueicolla and 21 in Llancahue), with 14 species in common.

Discussion

Development of mixed-species two-storied forests following irregular shelterwood cuts

Considering the relatively low seed cut intensity and the time passed after the cuts, the silvicultural treatments implemented at Hueicolla and Llancahue correspond to the extended irregular shelterwood cuttings (Raymond et al. 2009), particularly at Hueicolla.

If the trees left after the cuts (residual trees) were to be cut at some point soon, these cuts could also be considered extended irregular shelterwood cuts. The cut in Hueicolla was more intense than in Llancahue. The former left mostly shade-tolerant and mid-tolerant

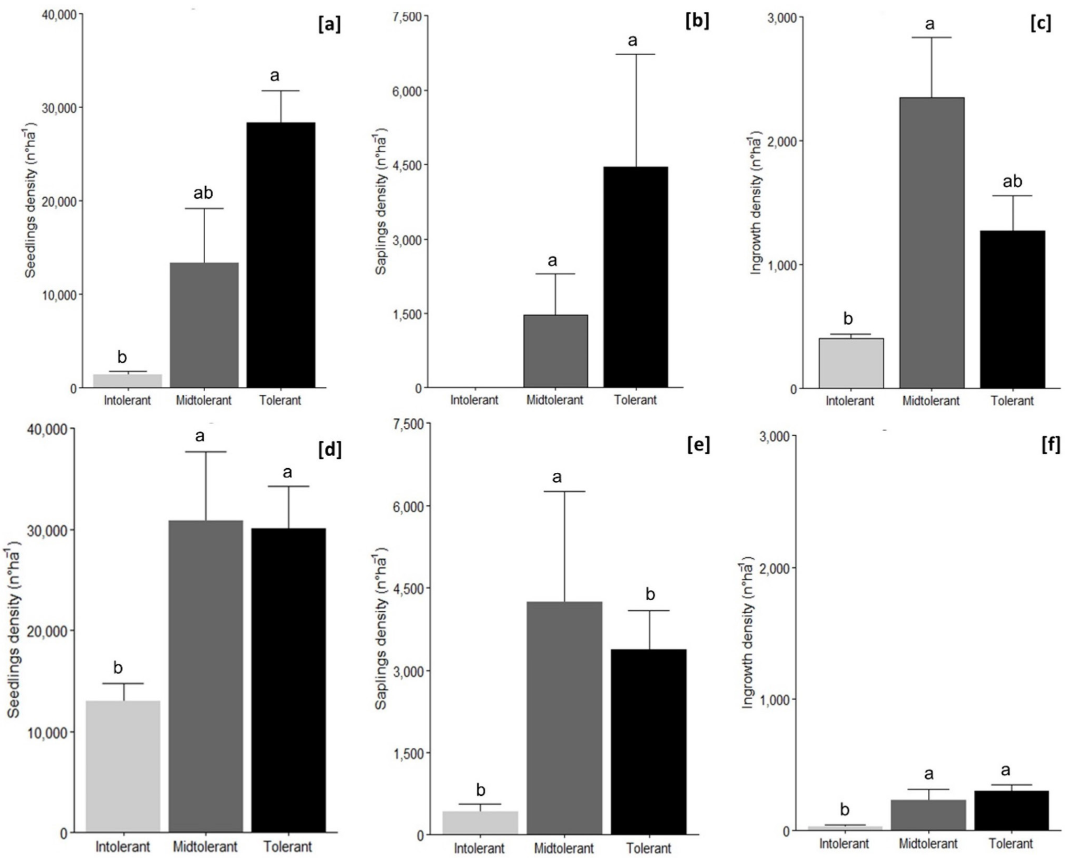

FIGURE 5: Seedlings, saplings and ingrowth density (trees 5-25 cm in Hueicolla, 5-10 cm in Llancahue, i.e., those that have recruited into the 5 cm dbh class and do not belong to residual trees) according to shade tolerance groups by site (Hueicolla: a, b, c; Llancahue: d, e, f), respectively. Different letters in each graph show significant differences (p-value < 0.05). Note that the vertical axes are different in each case. Error bars correspond to standard deviation.

residual trees, while the latter left residual trees corresponding to the shade-intolerant *N. dombeyi.*

The shelterwood cuts evaluated in this study were implemented at different sites but also in different types of forests, i.e., an old-growth (Hueicolla) and a mature secondary (Llancahue) forest. In Hueicolla, the cut old-growth forest was dominated by shade-tolerant species. In contrast, in Llancahue, the cut was conducted in a forest dominated by *N. dombeyi*, which originated from past human disturbances (González et al. 2015). However, these cuts had in common the residual basal area, close to 40 m^2 ha^{-1}. Although elapsed time since the cut is different (almost 40 years in Hueicolla and 12 years in Llancahue), approximately 80% of the residual trees remain alive in both forests and show a clear mixed-species two-storied vertical structure, with relatively large trees in the upper canopy. In addition, neither of the forests now exhibits an understorey and regeneration layer with a tree composition similar to the residual trees. These conditions provide the basis to discuss the implications of the type and intensity of the cuts upon regeneration and growth and the applicability of this type of silvicultural method in the temperate rainforests of South America.

Regeneration and growth

In both forests, regeneration was dominated by mid-tolerant species following the cuts, which must be expected considering the residual basal areas left in each case. Two common mid-tolerant species were *E. cordifolia* and *D. winteri* at both sites, but Llancahue also hosted the conifer *P. salignus* (Podocarpaceae). Other common species at both sites included *G. avellana* and *L. ferruginea*, both short-lived species of the Proteaceae family, which also includes other pioneer species that can have aggressive regeneration following the cuts (Donoso et al. 2019).

Although some shade-intolerant species, such as *G. avellana*, were able to regenerate following the cuts (high ingrowth density in Hueicolla, where 39 years have passed, and among seedlings in Llancahue, where only 12 years have passed), tree species considered highly shade-intolerant, such as *N. dombeyi* and *W. trichosperma*, were unable to regenerate. To succeed with at least some regeneration of these species would require more intense cuts and likely some soil scarification (e.g. Soto & Puettmann 2018). Almost 40 and 12 years after the cuts in Hueicolla and Llancahue, the observed cover of *Chusquea* sp. and the fern *L. quadipinnata* was 15 and 13%, respectively. These

TABLE 4: Mean understorey cover (%) and standard deviation (SD) of non-tree vegetation in Hueicolla and Llancahue following irregular shelterwood cuts.

Species	Understorey cover			
	Hueicolla site		Llancahue site	
	Mean (%)	SD	Mean (%)	SD
Herbs				
Dioscorea auriculata Poepp.	0.01	0.02	-	-
Greigia landbeckii (Lechl. ex Phil.)	2.18	0.32	0.63	1.20
Nertera granadensis (Mutis ex L.f.) Druce	0.04	0.07	2.33	2.93
Uncinia tenuis Poepp. ex Kunth	0.33	0.38	0.67	0.94
Taraxacum officinale F.H.Wigg.	-	-	0.04	0.10
Climbing plants				
Boquila trifoliolata (DC.) Decne.	-	-	0.46	0.75
Campsidium valdivianum (Phil.) Skottsb.	0.14	0.24	0.13	0.31
Cissus striata Ruiz & Pav.	-	-	0.04	0.10
Elytropus chilensis (A. DC.) Müll. Arg.	0.25	0.43	0.13	0.31
Hydrangea serratifolia (Hook. & Arn.) F.Phil.	1.22	1.97	-	-
Lapageria rosea Ruiz & Pav.	6.81	2.85	6.88	3.68
Luzuriaga marginata (Gaertn.) Benth.	0.85	0.79	1.50	1.84
Luzuriaga polyphylla (Hook.) J.F.Macbr.	0.85	1.06	1.75	1.96
Luzuriaga radicans Ruiz & Pav.	2.18	2.47	4.13	2.37
Mitraria coccinea Cav.	3.68	1.24	0.38	0.92
Ferns				
Asplenium dareoides Desv.	0.15	0.20	0.04	0.10
Blechnum blechnoides Keyserl.	0.07	0.12	-	-
Blechnum hastatum Kaulf.	0.60	0.42	0.04	0.10
Hymenophyllum caudiculatum Mart. var. *productum*	0.01	0.02	-	-
Hymenophyllum dentatum Cav. Cavanilles	-	-	0.58	0.98
Lophosoria quadripinnata (J.F.Gmel.) C.Chr.	9.72	8.76	1.67	3.03
Shrubs				
Chusquea spp.	5.61	3.30	11.96	9.92
Gaultheria mucronata (L.f.) Hook. & Arn.	-	-	1.92	2.93
Griselinia racemosa (Phil.) Taub.	-	-	0.63	1.41
Ugni molinae Turcz.	-	-	1.67	3.38

two understorey species may be strong competitors to tree species in the EFT (Donoso & Nyland 2005), suggesting that although they did not have a great cover immediately following the cuts, they became a major factor preventing the regeneration of very shade-intolerant species such as *N. dombeyi* (in Llancahue) and *W. trichosperma* (in Hueicolla).

Trends in diameter growth cannot be fully compared between Hueicolla and Llancahue since sampled trees in the former correspond only to those established following the cuts, while those sampled in Llancahue mostly corresponded to advanced regeneration and not newly established trees following the cut that would take more than 12 years to reach 5 cm in dbh. However, both cases show that: (1) the newly-established or advanced regeneration positively responded to the cuts; (2) eventually, the species that continued to grow faster were the mid-tolerant ones, while (3) the short-lived shade-intolerants declined in growth after the initial period of fast growth; and (4) shade-tolerant species exhibited stable stand density, although slow growth across the periods evaluated.

Overall, results illustrate that these forests regenerated with the irregular shelterwood cuts show abundant regeneration with a mixture of tree species that gradually differentiated in terms of growth rates and positions in the vertical strata. These managed forests have also shown that residual trees continued to increase in size (Donoso et al. 2022a).

Prospects for the implementation of irregular shelterwood cuts in temperate rainforests

The only other case of an irregular shelterwood cut reported in these temperate rainforests of Chile is in an experiment analogous to that of Hueicolla (Donoso 1989b), where 31% residual basal area was left in old-growth forests in the Andes. That experiment was evaluated 26 years after the cut in 2008 (Donoso et al. 2019). The tree density of the new cohorts was similar to Hueicolla but with a much greater density of another highly shade-intolerant Proteaceae species (*Embothrium coccineum* J.R.Forst. & G.Forst.). However, mid-tolerant species had a greater diameter growth than *E. coccineum*, suggesting that they should dominate the new cohort by now. Therefore, all these experiments suggest that moderate-intensity irregular shelterwood cuts favour the development of mid-tolerant tree species, compared with more intense cuttings that promote shade-intolerant species (Nyland et al. 2000).

Results can also be compared with selection cuts implemented in this forest type on two different sites, including one in Llancahue, with similar residual basal areas, where shade-tolerant species have dominated regeneration (Donoso et al. 2020a). Since the differing regeneration results between the two experiments of this study cannot be explained by residual basal area, which was similar, it can be suggested that the difference in regeneration is explained either by the vertical structure left in each case or by soil and environmental conditions of the sites. In the shelterwood cut, the residual forest corresponds mainly to trees in the upper canopy, compared to the selection cut that leaves trees in a range of diameter classes and positions in the vertical strata. A forest with a shelterwood cut eventually allows greater light to reach the understorey, enabling mid-tolerant species to regenerate. To regenerate shade-intolerant species, such as *N. dombeyi* in Llancahue, residual density should have been much lower, and mineral soil should have been exposed through scarification (e.g. Soto & Puettmann 2018).

Irregular shelterwood cuts lead to the formation of multi-aged forests (D'Amato et al. 2011), which can have a greater adaptive capacity to disturbances accumulating higher levels of carbon while also providing high-quality timber (of hardwood species in these temperate rainforests) that will also store carbon. Most temperate rainforests on the west side of the Andes mountains in South America have a great diversity of tree species in terms of shade tolerance. They are, therefore, likely to respond well to irregular shelterwood cuts (Donoso et al. 2022a). However, the development of the more highly valuable shade-intolerant long-lived species seems more difficult to achieve. These species include *Nothofagus dombeyi* (which did not regenerate in Llancahue) or *Nothofagus obliqua* (Mirb.) Oerst. at low elevations or the high-value *Nothofagus alpina* (Poepp. & Endl.) Oerst at intermediate to higher elevations (near 1,000 m a.s.l.)—all occurring within forest types with great management potential in south-central Chile (Donoso et al. 2022b). Succeeding with these species will likely require more intense cuts, some soil scarification, and even planting to enrich sites with target species.

Conclusions

Following four (Hueicolla) or one (Llancahue) decades after a regeneration cut within the shelterwood silvicultural method, but without a final cut (i.e., irregular shelterwood cuts), the resulting forests have a two-storied vertical structure dominated by trees species of intermediate tolerance to shade, although in both cases short-lived shade-intolerant species are also an important part of the new cohorts. Long-lived shade-intolerant species have only marginally regenerated after these cuts, likely due to the relatively high residual basal area and the lack of soil scarification that may be necessary to expose mineral soil to regenerate these species. The irregular shelterwood method results in diverse forests with good growth rates, where mid-tolerant species eventually grow faster. Their future development will be strongly determined by silvicultural treatments implemented for both the old and the new cohorts.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

PJD developed the research projects associated with both study areas, developed the experimental design, and led the writing of the manuscript. TRB developed the figures and tables, as well as the statistical analyses. DPS participated in the study conceptualisation and experimental design for both study sites and supervised the result analyses. All authors read and approved the final manuscript.

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