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Development of 26-year-old mixed forests following different regeneration cutting treatments in Andean temperate rainforests of south-central Chile

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ABSTRACT

Tree regeneration following even-aged silvicultural methods in the evergreen forest type (EFT) has been scarcely studied in Chile, although this is the largest forest type in a region of highly productive native forests. In 1981/1982 a total of nine 1.44-ha experimental units with old-growth forests of the EFT were subjected to block clearcutting (BCC), strip clearcutting (SCC) and reserve shelterwood cutting (RSC) methods (three replicates in each case) in the Andes range in south-central Chile (41°35′S–72°35′W). The resulting second-growth forest stands following these cuttings were evaluated in terms of composition, density, basal area, mean diameter and height after four and 26 years (432 4 m^2 plots in 1986, and 78 100 m^2 plots in 2008). Four years after cutting, there were > one million tree seedlings per hectare in more than 10 species. In all experimental units one shade-tolerant species (*Amomyrtus luma*), one midtolerant species (*Eucryphia cordifolia*) and two very shade-intolerant species (*Embothrium coccineum* and *Weinmannia trichosperma*) comprised between 69 and 74% of the total density. The SCC favored a greater relative dominance of all the more shade-tolerant species, and the BCC treatment was more favorable for pioneer species (in addition to *E. coccineum* and *W. trichosperma* also *Drimys winteri*, *Caldcluvia paniculata* and *Nothofagus nitida*). At age 26, the short-lived *E. coccineum* dominated in all treatments, and its major coexisting species in terms of tree density were the midtolerants *D. winteri*, *Eucryphia cordifolia* and *N. nitida*, and the shade-tolerants *Laureliopsis philippiana* and *A. luma*. However, the BCC significantly favored the development of *N. nitida* and *D. winteri* (three times more basal area than in the other treatments), which might be explained by increasing soil moisture that occurs in this region following this type of disturbances. While these treatments did not show significant differences in mean diameters and dominant height, the BCC and SCC treatments allowed denser, diverse and well-stocked second-growth forests compared to the RSC method, illustrating the differences between truly even-aged and two-aged silvicultural methods upon these variables. Overall, these forests show a high resilience, rapid reorganization and high productivity following the application of even-aged silvicultural methods.

1. Introduction

Natural large-scale disturbances, land-use changes, or forest regeneration cuttings have favored the development of extensive areas of forests dominated by a single age class, i.e. even-aged forests (Oliver and Larson, 1996; Veblen et al., 1996; Nyland, 2007). The development of even-aged forests in temperate regions has received considerable attention among forest ecologists and silviculturists (e.g., Bormann & Likens, 1979; Oliver, 1980, 1981; Peet and Christensen, 1987; Nyland et al., 2000). Numerous studies have analyzed regeneration and development of even-aged stands following different silvicultural methods or regeneration cuttings that completely or partially remove the forest cover (Kelty, 1987; Walters and Nyland, 1989; Martin and Hornbeck, 1990; McClure and Lee, 1993; Ray et al., 1999; Nyland et al., 2000). These studies show a common temporal pattern in the composition of tree species, initially consisting predominantly (but not exclusively) of early successional shade-intolerant species with a fast initial growth, progressing towards mixed stratified stands containing late-

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successional species (Bormann and Likens, 1979; Oliver, 1980, 1981; Smith and Ashton, 1993; Wang and Nyland, 1996; Liptzin and Ashton, 1999; Allison et al., 2003). When secondary succession follows a large-scale disturbance of an established forest, it is expected that the new community will follow the initial floristic model of succession, including pioneer, seral and climax species (Barbour et al., 1987). Also after the implementation of even-aged silvicultural methods, a combination of species of different shade tolerances may simultaneously establish on the site, i.e. shade-tolerant or shade mid-tolerant (hereafter "midtolerant") species establish alongside shade-intolerant species (e.g., Marquis, 1967; Matthews, 1989; Allison et al., 2003; Yamasaki et al., 2014).

The relative dominance of species with different shade tolerances is highly dependent on the type and intensity of the cut and resulting environmental conditions, ecological characteristics of the local species, and the characteristics of the forest at the time of cut, especially in relation to the type and quantity of advance regeneration and propagule availability (Hibbs, 1983; Swanson et al., 2011). In the cases of strip clearcutting or shelterwood cutting either the adjacent forest (in strips) or the residual overstory (shelterwood) provide some shelter on the cut area, which maintains greater rates of soil moisture and nutrients in the soil compared with clearcuttings (Keenan and Kimmins, 1993). These differences (light, moisture, nutrients) may eventually affect differential patterns of regeneration and growth of seedlings (Matthews, 1989; Hornbeck et al., 1987). These conditions complement with the sprouting capacity of many hardwoods, which further favors regeneration of more shade-tolerant species (Del Tredici, 2001; Swanson et al., 2011).

Among temperate rainforests of Chile, the evergreen forest type is the largest, growing throughout the Coastal and Andean ranges, and is characterized by its multispecific composition dominated by broadleaf evergreen species. In the Andes this forest type is pervasive from 40°–47° S Lat. (Donoso, 2015), and large-scale natural disturbances are common, including earthquakes and associated mass movements, volcanisms and associated fires and landslides, and also massive windthrows (Veblen and Ashton, 1978). These stand-replacing disturbances generate even-aged stands (Veblen et al., 1981), which are originally dominated by pioneer tree species and gradually more shade-tolerant species start to occupy lower strata, a process highly affected by gap dynamics (Veblen, 1985). The frequency of large-scale disturbances is shorter than the longevity of pioneer tree species, and that allows these species to remain as dominant or emergent trees in these Andean forests (Veblen and Ashton, 1978). Among pioneers, *Nothofagus* tree species play a relevant role, especially *N. dombeyi* (Mirb.) Oerst. (shade-intolerant) and south of 40°S *N. nitida* (Phil.) Krasser (midtolerant; Donoso and Soto, 2016). Other pioneer species include the shade-intolerants *Weinmannia trichosperma* Cav., and *Embothrium coccineum* J.R. Forst. & G. Forst., and the midtolerants *Eucryphia cordifolia* Cav. and *Drimys winteri* J.R. Forst. & G. Forst. Both *D. winteri* and *N. nitida* have a competitive advantage in poorly-drained soils or soils with permanent high moisture content (Donoso, 1989a, 2015; Donoso et al., 2007).

In spite of the global importance of the evergreen forest type in Chile (its large extent, valuable hardwood species, and complexity), there are few studies on their silviculture. The Chilean forest law allows the application of the shelterwood and "selective" silvicultural methods since 1979, but later it introduced, through specific regulations, the authorization to use strip clearcuttings (Donoso et al., 1998). Of all these options, through legal or illegal harvests, forest owners mostly high-grade their forests through selective cuttings, which in either case harvest the best and leave the worst (Donoso, 2013). There are no reports of the effects of regeneration cuttings for even-aged forests in the Evergreen Forest Type, except for the one by Donoso (1989b), who reported the regeneration of more than a million tree seedlings (≥3 cm in height) four years after the implementation of block clearcutting (BCC), strip clearcutting (SCC) and shelterwood cutting, where residual trees have never been cut later, so it became a reserve shelterwood cutting (RSC).

In this study we follow this experiment to evaluate the development of these second-growth forests during the first 26 years after cutting. The working hypotheses were: (1) The relative dominance of tree species according to their shade tolerances is a function of the level of cutting and shelter provided by the silvicultural treatments applied, i.e., shade-intolerant species have a greater importance in the BCC and lower in the RSC, and (2) RSC has a slower stand development as reflected in lower basal areas, tree densities and mean tree diameters. This study then becomes the first to report early-successional patterns (past the Stand Initiation Stage and into the Stem Exclusion Stage of forest stand dynamics (*sensu* Oliver and Larson, 1996)) of tree regeneration following even-aged silvicultural cuttings in temperate rainforests of the Southern Hemisphere.

2. Methods

2.1. Study area and experimental design

The study area is located at the foothills of the Andes mountain range in the Llanquihue Forest Reserve, adjacent to the Alerce Andino National Park, south-central Chile (41°31′S-72°39′ W; Fig. 1). A west-coast maritime climate with a mild temperature range dominates the area, with a rainfall range from 2500 to 3500 mm and slight decreases during summer months (Donoso, 1989b; Schlatter et al., 1995). The average monthly temperature in July (winter) is 7 °C, and 15 °C in January (summer) (Schlatter et al., 1995). Soils are deep and are derived from recent volcanic ash layers with a topography dominated by steep hills (CIREN, 2001; Schlatter et al., 1995). Overall, soils are well-drained (CIREN, 2001), although in places with gentle slopes, the internal drainage is moderate to slow, and on occasions there is temporary water saturation (Donoso, 1989b). Soils contain high amounts of organic matter, and have a sandy-silt texture (CIREN, 2001).

Our study area (≈100 ha) is dominated by old-growth multi-layered forests located between 420 and 550 m a.s.l. (Table 1). Prior to applying the regeneration cuttings, tree density, tree basal area, and understory cover were measured (ICSA, 1983). Basal area was dominated by *Laureliopsis philippiana* (Looser) Schodde (34%), the Podocarps *Podocarpus nubigena* Lindl. and *Saxegothaea conspicua* Lindl. (27%), *N. nitida* (10%), *D.winteri* (7%), *E. cordifolia* (6%) and *W.trichosperma* (3%). All these are commercial tree species (Donoso, 1989b). Other species (13% of basal area) in the forest included *Dasyphyllum diacanthoides* (Less.) Cabr., *Caldcluvia paniculata* (Cav.) D. Don, *Lomatia ferruginea* (Cav.) R. Br., *E. coccineum*, and species from the *Mirtaceae* family, such as *Amomyrtus luma* (Mol.) Legrand & Kausel and *Myrceugenia planipes* (Hook. et Arn.) Berg. *Nothofagus nitida* was the tallest tree species with a dominant height of 27 m above a main tree canopy with an average height of 22 m and dominated by *W. trichosperma*, *E. cordifolia*, *L. philippiana* and *S. conspicua*. These are common values for forests of this forest type within the region of Valdivian Temperate Rainforests (*sensu* Donoso and Soto, 2016). Regeneration of commercial tree species was dominated by *L. philippiana* and *D. winteri*. Bamboos (*Chusquea quila* Kunth and *Chusquea macrostachya* Phil.) were the dominant species in the understory, and their cover was especially high in higher elevation experimental units (2, 7, 8 and 9). Some silvical characteristics of these species are given in Table 2.

Nine experimental units covered with these old-growth forests received the three different types of even-aged regeneration cuttings mentioned earlier (block clearcutting (BCC), strip clearcutting (SCC) and reserve shelterwood cutting (RSC)), each having three replicates (Fig. 1 and Table 1). No experimental unit had a south aspect; rather they had mostly NE to NW aspects. We do not think that this is a major limitation of the study since the region is characterized by high rainfalls. However, south-facing slopes may be more favorable for *Podocarpaceae* conifers and less favorable for *E. cordifolia* (P. Donoso personal observation). Each experimental unit was harvested in an area of

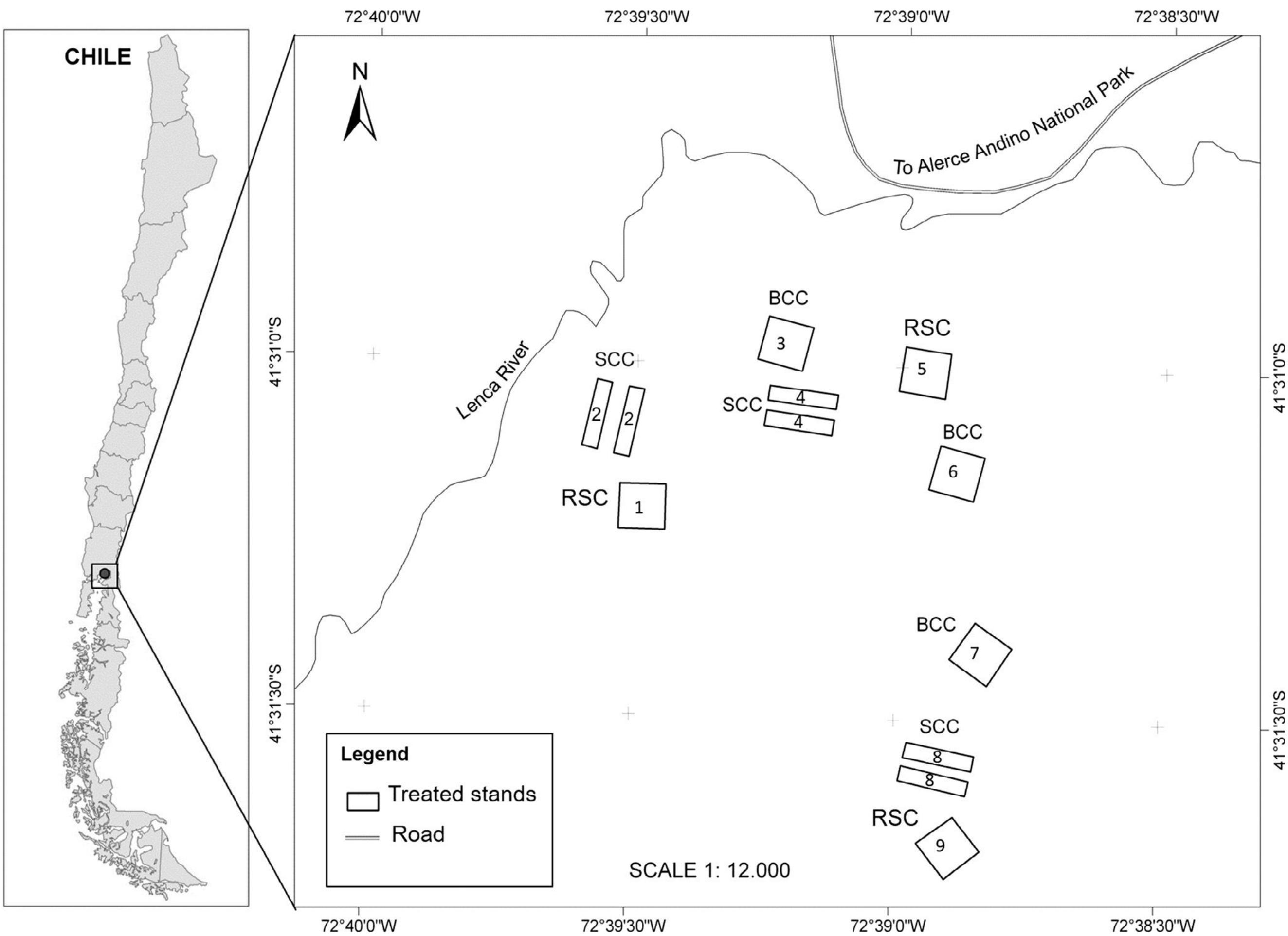

Fig. 1. Study area and the nine experimental units with treatments BCC (block clearcutting), SCC (strip clearcutting) and RSC (reserve shelterwood cutting) repeated three times.

1.44 ha in size: the BCC and RSC treatments were conducted in a square area of 120 × 120 m, and the SCC treatment in two parallel strips of 40 × 180 m (0.72 ha each strip), with a 40 m strip of forests in between. After cutting in 1982, the RSC treatment had residual basal areas between 28.1 and 41.7 $m^2 ha^{-1}$ (≈33% of the original basal area; Table 1), and 40 trees ha^{-1} at least 50 cm in diameter at breast height (dbh) of commercially valuable tree species with different shade tolerances and seed dispersion agents (ICSA, 1983; Table 1). Since these residual trees were never cut, this led to two-aged stands with widely spaced large overstory reserve trees, and an understory of the new cohort. According to Donoso (2002), trees 50–80 cm in diameter in uneven-aged evergreen forests of this forest type have diameter growth rates < 2 mm yr^{-1}, so that the basal area growth for the residual trees in this study has been negligible.

2.2. Field measurements

We considered different measurements to evaluate stand development of the second-growth forests that established following the regeneration cutting treatments. We used regeneration data recorded in 1986 (number and height of seedlings ≥ 3 cm in height per species) in 48 4-m^2 (2 × 2 m) plots systematically distributed in each regeneration cutting unit of the BCC, SCC and RSC treatments (Donoso, 1986). In years 2007/2008 we established nine circular 100 m^2 plots

Table 1
Major characteristics for each experimental unit before and after the implementation of treatments.

Trmt	Experimental unit	Elevation (m a.s.l.)	Aspect	Slope range	N (trees ha^{-1})		BA (m^2 ha^{-1})	
					Before	After	Before	After
BCC	3	420	Flat-N	0–15	960	0	91.5	0
	6	440	NE	5–35	1157	0	98.0	0
	7	480	E	0–35	837	0	77.9	0
SCC	1	400	NW	5–15	763	0	130.5	0
	4	470	N	5–35	752	0	131.5	0
	8	530	E	5–65	436	0	69.2	0
RSC	2	480	W	5–25	549	38	124.0	41.74
	5	415	NE	5–25	949	43	115.0	28.09
	9	550	N	5–25	460	37	95.8	32.78

Table 2
Shade-tolerance, seed dispersion agents and sprouting capacity of regenerating trees in this study.
Source: Donoso (2006).

Species	Family	Shade tolerance	Main seed dispersion agent	Sprouting
Embothrium coccineum	Proteaceae	Intolerant	Wind	Yes
Weinmannia trichosperma	Cunoniaceae	Intolerant	Wind	Yes
Caldcluvia paniculata	Cunoniaceae	Intolerant	Wind	Yes
Drimys winteri	Winteraceae	Midtolerant	Gravity	No
Eucryphia cordifolia	Cunoniaceae	Midtolerant	Wind	Yes
Nothofagus nitida	Nothofagaceae	Midtolerant	Wind	No
Amomyrtus luma	Myrtaceae	Tolerant	Animals	Yes
Laureliopsis philippiana	Monimiaceae	Tolerant	Wind	Yes
Podocarpus nubigena	Podocarpaceae	Tolerant	Animals	No
Saxegothaea conspicua	Podocarpaceae	Tolerant	Animals	No

(radius = 5.64 m) systematically distributed in each BCC and RSC unit, i.e. 27 plots per treatment. These plots were established in a grid with their centers 30 m apart from each other and the central plot in the middle of the 1.44 ha treated unit. In the SCC treatments we established eight circular 100 m^2 plots in each experimental unit, with their centers 20 m apart from the edges of each strip and 40 m apart from a neighboring plot. Overall, we established 78 100 m^2 plots in the nine experimental units. Data from all live and dead individuals was recorded, including species, diameter at breast height (dbh), and sampling of dominant heights. To evaluate the effects of *Chusquea* spp. cover upon tree regeneration we used data recorded by ICSA in 1982 (ICSA, 1983), before the implementation of the cutting treatments (pre-treatment). These data were collected in 40 (2 × 2 m) plots established randomly in each experimental unit of every treatment.

2.3. Data analysis

With data gathered in 1986 we conducted an analysis of variance (ANOVA) for density and height and with data gathered in 2007/2008 for density, height and basal area per treatment and species functional group according to their shade tolerances. In order to take into account the hierarchical structure of the data (plots nested within treatments), we fit a linear mixed-effects model by adding random effects to the plot level. All the models were fitted by maximum likelihood (Pinheiro and Bates, 2000). Differences among treatments were considered significant when the p-value was < 0.05. When significant differences were found, we ran Tukey's HSD to find out which specific groups means were different.

The relationship of stand basal area in 2008 and *Chusquea* spp. variables (e.g., density and mean height) was evaluated through regression analysis (n = 9), checking the assumptions of normality of error terms (Lilliefors test) and homocedasticity of variance (Levene test). The regression model with the lowest mean square errors (MSE) was selected, provided that all its estimated parameters were statistically different from zero.

All statistical analyses were conducted with the R statistical program (R Development Core Team, 2009), and the mixed-effects models using the nlme package (Pinheiro et al., 2017).

3. Results

3.1. Species composition and stand parameters

The regeneration four years following the application of the treatments, was very abundant and diverse, and similarly distributed among species of different shade tolerances (Table 3 and Fig. 2). More than 10 tree species were regenerating and most of these had over 20,000 seedlings per hectare (Table 3). The SCC treatment had significantly higher numbers of seedlings than the RSC treatment, with the BCC ranking in between. Four species of mixed shade tolerances comprised from 69 to 74% of tree density, with near one million seedlings per hectare. The species *A. luma* and *W. trichosperma* were the most abundant, with an average of 46% of tree density, followed by *E. coccineum* and *E. cordifolia*. By species, the SCC treatment had significantly higher densities than one or the two other treatments for all the four shade-tolerant species (*A. luma*, *L. philippiana*, *S. conspicua and P. nubigena*), and also significantly higher densities than the BCC treatment for one midtolerant (*E. cordifolia*) and one shade-intolerant species (*C. paniculata*). This SCC treatment also had a significantly lower density than the other treatments for *D. winteri*. Three species did not differ statistically among treatments, i.e. two shade-intolerants (*E. coccineum* and *W. trichosperma*) and one midtolerant species (*N. nitida*). When pooled by shade tolerances (Table 4 and Fig. 2), the SCC had a significant difference in seedling densities of shade-tolerant species compared with the other two treatments, with twice as many seedlings. There were no statistical differences in tree densities among treatments for pooled shade-intolerant nor for midtolerant species.

Table 3
Number of seedlings (in 1986) and trees (in 2008) by species and treatment. For each year, different letters indicate significantly different means (P < 0.05) among treatments (only significant differences are reported).

Species	Year	Treatment		
		BCC	SCC	RSC
Shade intolerants				
E. coccineum	1986	165,417	203,542	200,417
	2008	1663	1891	1519
C. paniculata	1986	80,833^{b}	86,458^{ab}	28,333^{c}
	2008	733^{a}	479 ^{ab}	189^{b}
W. trichosperma	1986	356,875	277,917	221,875
	2008	126 ^{a}	54^{ab}	19^{b}
Midtolerants				
D. winteri	1986	151,250^{a}	38,958^{b}	87,917^{ab}
	2008	596^{a}	65^{b}	208^{b}
E. cordifolia	1986	99,167^{b}	216,458^{a}	158,750^{ab}
	2008	270	313	177
N. nitida	1986	27,708	4167	51,958
	2008	170 ^{a}	50^{b}	37^{b}
Shade Tolerants				
A. luma	1986	266,667^{b}	554,167^{a}	296,667^{b}
	2008	644	735	373
L. philippiana	1986	31,458^{b}	63,542^{ab}	70,000^{a}
	2008	148	118	131
S. conspicua	1986	77,500^{ab}	139,792^{a}	54,792^{b}
	2008	4	–	–
P. nubigena	1986	24,375^{b}	100,208^{a}	45,833^{b}
	2008	4	4	–
Other	1986	1250	7917	2708
	2008	22	152	38
Total	1986	1,282,500^{ab}	1,693,125^{a}	1,219,250^{b}
	2008	4382	3750	2655

Twenty-six years since the original treatments, and 22 years after the initial evaluation, numbers of trees per hectare ranged between

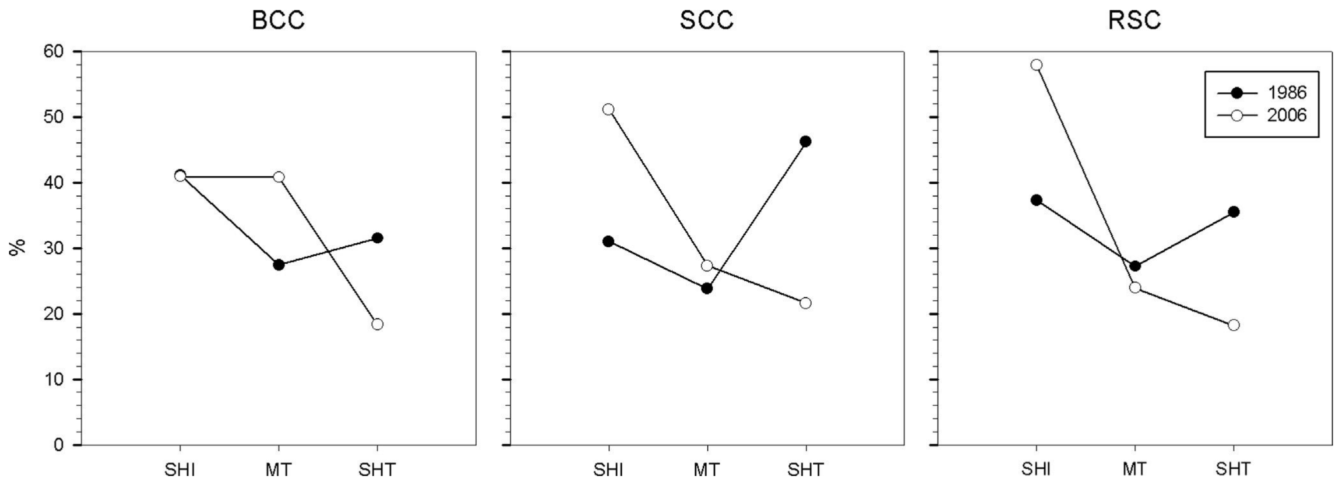

Fig. 2. Changes in the percentage (%) of tree species according to shade-tolerance groups between 1986 (four years) and 2008 (26 years). SHI: shade-intolerant, MT: midtolerant, SHT: shade-tolerant.

Table 4
Density of seedlings (in 1986) and trees (in 2008) by functional group of species (shade tolerance) and treatment four and 26 years since the implementation of silvicultural treatments. Values in parenthesis are the standard errors. For each year, different letters indicate significantly different means ($P < 0.05$) among treatments (only significant differences are reported).

Functional group	Year	Treatment		
		BCC	SCC	RSC
Intolerant	1986	522,292 (± 107,614)	481,458 (± 69,868)	422,292 (± 79,106)
	2008	1789 (± 234)	1946 (± 313)	1537 (± 297)
Midtolerant	1986	358,958 (± 45,849)	346,042 (± 62,741)	326,958 (± 61,619)
	2008	1770 (± 254)	892 (± 159)	596 (± 114)
Tolerant	1986	401,250^{b} (± 61,038)	865,625^{a} (± 93,742)	470,000^{b} (± 68,167)
	2008	822 (± 138)	913 (± 273)	522 (± 165)
Total	1986	1,282,500^{ab} (± 182,396)	1,693,125^{a} (± 142,828)	1,219,250^{b} (± 157,419)
	2008	4381 (± 434)	3750 (± 458)	2656 (± 423)

4382 and 2655, with no significant differences among treatments. By this time tree densities had shifted in favor of shade-intolerant species in comparison with age 4 after treatments (Table 3 and Fig. 2). The resulting second-growth forests were dominated by *E. coccineum* in terms of tree density (38–50%; Table 3), basal area (53–73%; Table 5), and QMD (trees of greater diameter; Table 5). *A. luma* and *C. paniculata* were also very abundant in tree densities, with 14–20% and 7–17% of the total tree density (Table 3), but they, as the other species, comprised a small proportion of the total basal area (Table 5). Tree density was significantly higher in the BCC treatment compared to one or the two other treatments for four pioneer species. For *C. paniculata*, *W. trichosperma*, both shade-intolerants, BCC differed from RSC. Two midtolerant species had significantly higher tree densities in BCC: for *D. winteri* BCC differed from SCC, and for *N. nitida* BCC differed from both SCC and RSC. As with *A. luma*, all other shade-tolerant species did not differ in tree densities among treatments, and the two *Podocarpaceae* conifer species (*S. conspicua* and *P. nubigena*) nearly disappeared (at least among trees ≥5 cm) in all treatments (Table 3). There were no significant differences in tree densities by functional groups (Table 4).

In terms of basal area, *E. coccineum* had significantly greater values in the SCC treatment, *D. winteri* in BCC, and for *N. nitida* basal area in BCC was significantly higher than in RSC. Considering that the two latter species are midtolerants, the basal area of this functional group was higher in BCC compared to SCC and RSC. Quadratic mean diameter (QMD) and dominant height did not differ among treatments for the different species (Table 5) nor by functional groups (Table 6). Height lowered close to one meter from shade-intolerant to midtolerant to

Table 5
Stand basal area and quadratic mean diameter (QMD) for the main species and by treatment after 26 years. Values in parenthesis are the standard errors. For each species, different letters indicate significantly different means ($P < 0.05$) among treatments (only significant differences are reported).

	Treatment					
	BCC		SCC		RSC	
Species	Basal area (m^{2} ha^{-1})	QMD (cm)	Basal area (m^{2} ha^{-1})	QMD (cm)	Basal area (m^{2} ha^{-1})	QMD (cm)
Shade intolerants						
E. coccineum	21.5 (± 2.4)^{b}	14.3 (± 0.8)	31.3 (± 3.1)^{a}	15.2 (± 0.6)	18.8 (± 2.6)^{b}	14.0 (± 0.9)
C. paniculata	4.9 (± 1.2)	9.4 (± 0.5)	4,0 (± 0.9)	9.9 (± 0.4)	1.6 (± 0.6)	9.4 (± 0.7)
Midtolerants						
D. winteri	4.9 (± 1.2)^{a}	10.7 (± 0.8)	1.2 (± 0.8)^{b}	10.8 (± 2.2)	1.7 (± 0.5)^{b}	11.1 (± 1.6)
E. cordifolia	1.5 (± 0.6)	7.4 (± 0.5)	1.6 (± 0.5)	7.9 (± 0.6)	0.9 (± 0.3)	8.0 (± 0.4)
N. nitida	2.5 (± 0.9)^{a}	13.9 (± 1.6)	0.8 (± 0.6)^{ab}	14.6 (± 1.6)	0.3 (± 0.1)^{b}	9.4 (± 0.6)
Shade-tolerants						
A. luma	2.6 (± 0.6)	6.9 (± 0.2)	3.3 (± 0.9)	7.3 (± 0.4)	1.2 (± 0.5)	6.8 (± 0.3)
L. philippiana	1.7 (± 0.6)	11.3 (± 1.5)	0.8 (± 0.4)	8.4 (± 0.9)	1.1 (± 0.3)	10.3 (± 1.2)
Other	0.2 (± 0.1)^{a}	7.2 (± 0.4)	0.6 (± 0.3)^{a}	6.9 (± 0.3)	0.1 (± 0.1)^{b}	7.6 (± 1.0)
Total	40.4 (± 2.6)^{a}	11.9 (± 0.6)	43.6 (± 4.2)^{a}	12.7 (± 0.6)	25.9 (± 2.9)^{b}	12.6 (± 0.8)

Table 6
Basal area and quadratic mean diameter by functional groups (shade tolerance) and treatments, after 26 years. Different letters indicate significantly different means ($P < 0.05$) among treatments (only significant differences are indicated). *BA* is basal area in $m^2\ ha^{-1}$, *QMD* is quadratic mean diameter in cm, and *Hdom* is dominant height in m.

Functional group	Stand variable	Treatment		
		BCC	SCC	RSC
Shade-intolerant	*BA*	22.1 (± 2.1)	31.2 (± 4.0)	18.8(± 2.6)
	QMD	13.9(± 0.8)	14.7(± 0.7)	14.1(± 0.8)
	Hdom	10.1(± 0.3)	10.6(± 0.3)	10.7(± 0.3)
Midtolerant	*BA*	13.8[a] (± 1.8)	7.7[b] ± 1.4)	4.6[b] ± 0.8)
	QMD	10.3(± 0.5)	10.1(± 0.5)	10.2(± 0.5)
	Hdom	9.3(± 0.2)	9.7(± 0.3)	9.5(± 0.2)
Shade-tolerant	*BA*	4.6(± 0.8)	4.7(± 1.4)	2.5(± 0.5)
	QMD	8.5(± 0.8)	7.4(± 0.3)	9.0(± 0.8)
	Hdom	8.2(± 0.3)	7.9(± 0.3)	8.3(± 0.3)
Total	*BA*	40.4[a] (± 2.6)	43.6[a](± 4.3)	25.9[b](± 3.0)
	QMD	12.0(± 0.6)	12.8(± 0.6)	12.6(± 0.8)
	Hdom	9.2(± 0.2)	9.2(± 0.2)	9.3(± 0.2)

shade-tolerant species (Table 6; statistical differences not recorded in this case), but for each group there were no statistical differences in height among treatments (Table 6).

3.2. Effects of Chusquea spp. on tree density

The best regression model to represent stand basal area in 2008 (i.e., 26 years after the cutting) as a function of *Chusquea* sp. variables (prior to cutting), uses both density (*Nq*) and mean height (*Hq*) (Table 7). The experimental units that were located at the highest altitudes (480–550 m, 2, 7, 8 and 9; Table 1) had the largest numbers of *Chusquea sp*. culms before the cuts in 1982 (2: 29,875; 9: 24,000; 7: 17,250; 8: 9438; the remaining experimental units had from 5063 to 10,750 culms per ha; ICSA, 1983), and were also prominently covered by *Chusquea* sp. in 2007/2008 (personal field observation by B. Schlegel).

4. Discussion

4.1. Rapid tree recolonization after stand-replacing disturbances.

Early successional forest ecosystems (ESFEs) correspond to the initial stages post disturbance when vegetation is dominated by herbs and shrubs, i.e. before tree dominance (Swanson et al., 2011). This stage would be part of the stand initiation stage described by Oliver (1981) and Oliver and Larson (1996), which corresponds to the period of time before trees start to compete for light. The high tree densities found in this study at age four suggest that canopy closure had already occurred by then, and illustrate that the ecological stage of ESFEs was already past. This also reflects that these forest ecosystems subjected to even-aged cuttings have a rapid reorganization of their tree cover, a consequence of the high site productivity and resilience to disturbances of these forest ecosystems of south-central Chile (Donoso and Soto, 2016).

This successional pattern of rapid tree recolonization is well-known following stand-replacing disturbances, where the site is reoccupied (or the ecosystem reorganized) by stems from pre-existing stumps and roots, buried or newly dispersed seeds, and advance regeneration (Oliver, 1981; Smith et al., 1997; Nyland, 2002; Swanson et al., 2011). This pattern also occurred in the present study as illustrated by the species that regenerated and their life history traits (Table 2; Donoso, 2006). Initial tree regeneration was dominated by *W. trichosperma*, *A. luma*, *C. paniculata* and *E. coccineum* in all cutting treatments. The species *W. trichosperma*, *E. coccineum and C. paniculata* are light-seeded, wind-dispersed and very shade-intolerant species (Donoso, 2006), and were nearly absent in the original old-growth forests (ICSA, 1983), so that they must have invaded the cut plots through seeds from neighbour forests. In regards to *A. luma*, in these old-growth forests this shade-tolerant species grows in the understory or midstory, with abundant tree densities but little basal area (ICSA, 1983; Donoso and Soto, 2016), and has both a vigorous stump sprouting as well as edible fruits mainly dispersed by birds (Donoso, 2006), so that likely invaded the sites by these two means. Apart from these species, the two midtolerant *E. cordifolia* and *D. winteri* were the main coexisting tree species during initial succession, with both having a similar presence in the original forest. Both can be pioneer species, *E. cordifolia* especially due to its vigorous root sprouting capacity following partial or large disturbances (Escandón et al., 2013), and *D. winteri* due to its high annual seed production and capacity to dominate soils with high moisture or poor drainage conditions (Donoso, 2006; Donoso et al., 2007). The different reproduction strategies of these and other species (Table 2), plus the pioneer character of several of them, provide an insurance basis for ecosystem reorganization following large or stand-replacing disturbances in the Chilean Andes, such as the even-aged cuts of the present study.

4.2. Early patterns of tree development after even-aged regeneration cuts in evergreen rainforests

Initial tree regeneration was greater in the SCC treatments since this treatment especially favored all the shade-tolerant species (Table 3). The BCC treatment tended to favor the shade-intolerant species, and clearly and significantly the midtolerant *D. winteri.*

Therefore, these results illustrate and confirm that more intense silvicultural methods or cuttings favor pioneer species, and in our study suggest that relatively narrow strips (a bit wider than one height of the dominant trees) may provide better conditions for shade-tolerant species compared with a reserve shelterwood cutting that also provides shelter to the new cohort. Overall, initial tree regeneration was consistent with expectations in the sense that the two methods with greater understory shelter (from above in the case of RSC or from the sides in the case of SCC) were more favourable for tree species of greater shade-tolerance. However, after 26 years, the shade-tolerant species had a dramatic decline in their proportion in numbers, and a very low proportion of the basal areas, while it was the group of shade-intolerant species which became dominant in tree densities (40–60%) and basal areas (55–72%), which is consistent with expectations and with literature on the subject (e.g., Marquis, 1967; Keenan and Kimmins, 1993; Wang and Nyland, 1996; Nyland et al., 2000; Allison et al., 2003; Yamasaki et al., 2014). Beyond these general trends, only midtolerant species made a difference among treatments, with significantly greater basal area in the BCC treatment. Again, this is largely explained by *D. winteri*, which in spite of being classified as midtolerant to light, it is a truly pioneer species in this region of high rainfall, i.e. it is midtolerant to light and very tolerant and competitive in conditions of soils of high moisture. Overall, there was a shift in the dominance of shade-tolerance functional groups from the short-term (4 years) to the long-term (26 years) following even-aged silvicultural methods. In the long term, shade-intolerant species had a greater importance in all three methods, thus we could not support our first hypothesis that shade-intolerant species had a greater importance in the BCC and lower in the RSC.

Table 7
Regression model of stand basal area (*BA*, in $m^2\ ha^{-1}$) in 2008 (i.e., 26 years after the cutting) as a function of density (*Nq*, in culms per ha) and mean height (*Hq*, in meters) of *Chusquea* spp.

Equation	R^2	MSE (%)	Overall regression p-value
$BA = 76.60040 - 0.20043\ Hq - 0.05218\ Nq$	0.69	7.17 (19,5)	0.0121

However, the significantly lower basal area in RSC partially supports our second hypothesis, that this method has a slower stand development compared to the others. This was reflected in lower basal areas, but not in tree densities or mean tree diameters.

The rapid decline in numbers of stems as tree canopy competition increases during early stages of succession has been shown in many regions following even-aged silvicultural cuttings (e.g., Martin and Hornbeck, 1990; Ray et al., 1999; Nyland et al., 2000). Patterns of tree composition changed significantly (Fig. 2). While *E. coccineum* became the dominant species in all plots, BCC plots had much greater densities and basal areas of *N. nitida* and *D. winteri* (both midtolerant species) than the other two types of cuttings, which is consistent with previous findings in second-growth forests in this region (e.g., Donoso et al., 2007) that report the dominant co-occurrence of these two mid-tolerant species. Cohort development should tend towards an eventual site dominance by species of longer life spans (Horn, 1975; Bormann and Likens, 1979; Hibbs, 1983; Wang and Nyland, 1996; Arthur et al., 1997). In the region of our study it is expected that long-lived pioneer species will increasingly dominate the BCC plots, while SCC and RSC plots would be dominated by a mixture of mid- and shade-tolerant species characteristic of late successional forests in this region (e.g., Donoso and Soto, 2016).

4.3. The role of Embothrium coccineum and Chusquea sp. during early succession

After 26 years the fast-growing shade-intolerant species *E. coccineum* (Donoso, 1989a; Donoso, 2015; Escobar et al., 2006; Lusk and Contreras, 1999) dominated in all plots, along with other midtolerant and shade-tolerant species in the mid and lower canopies. *Embothrium coccineum* is a short-lived pioneer species (< 100 years) that is well adapted to natural and anthropogenic disturbances and acts as an invader of denuded areas (Donoso, 1989a; Alberdi and Donoso, 2004; Donoso, 2006; Smith-Ramírez et al., 2007; Souto et al., 2009) because of its high annual seed production, efficient mechanism of seed wind dispersion, and a high germination capacity (Escobar et al., 2006). Its resistance to low temperatures also provides this species with the capacity to survive in early successional sites of southern Chile (Alberdi, 1995). These characteristics allowed *E. coccineum* to dominate the cut plots from the very beginning of forest reorganization following the even-aged cuts, and after 26 years the species limited the development of other shade-intolerant species of slower growth rates such as *W. trichosperma*, which had a great tree density at age four and dramatically reduced it by age 26. However, after this time *E. coccineum* has been the tree species with highest rates of mortality (Schlegel, 2014), a phenomenon that is expected to continue. Since this is also a nitrogen-demanding species (Lusk and Contreras, 1999), the expected accelerating rates of mortality of *E. coccineum* will fertilize the system in favor of species adapted to high-fertility sites, such as *L. philippiana* (Lusk et al., 1997). Thus, this *Proteacea* species may play important roles during early succession, as other *Proteacea* species also seem to play farther north, such as *Gevuina avellana* (González et al., 2015).

Early forest succession was also influenced by the cover of *Chusquea* species. The density and height of these species greatly influenced the basal area found 26 years after the cuttings. González et al. (2002) and Donoso and Nyland (2005) also found that high densities and heights of *Chusquea* sp. affect tree regeneration. Similar effects of bamboos upon regeneration have been found in other temperate forests. For instance, the regeneration of the shade-intolerant *Betula albosinensis* after strip clearcutting in China was impeded due to the presence of the bamboo *Fargesia qinlingensis*, thus suggesting the removal of bamboo to improve the competitive status of *B. albosinensis* regeneration following clearcutting (Guo et al., 2013). It is necessary then to search for options to control this *Chusquea* spp. competition when it may become a problem in managed forests. One option may be to gradually open the canopy, or even moving to uneven-aged cuttings in some cases. Another option is deep soil scarification, which has been shown to be a successful measure to reduce *Chusquea* competition and favour tree regeneration in Chilean Andean forests with coarsed-textured soils (Soto et al., 2015). In addition, it would also be interesting to analyze changes in the competitive ability of *Chusquea* in areas with gentle slopes and greater soil moisture, where species such as *N. nitida* and *D. winteri* (Donoso et al., 2007) have aggressive regeneration and growth.

4.4. Management implications

Immediate complete removal of the forest following the implementation of even-aged silvicultural cutting methods seems to allow a more rapid site occupation by trees. This pattern was clearly depicted by Nyland et al. (2000) between clearcut and shelterwood cuttings after 25 years of succession in Northern Hardwoods in North America. In our study, the RSC treatment had lower stockings mainly because of the lower basal area of all species (while having similar diameters and heights), especially of the midtolerant and shade-tolerant species that grew along with *E. coccineum* (Table 5). The large seed trees and basal area (i.e., tree cover; Table 1) that remained in the RSC plots throughout the measurement period seems to be the most plausible explanation for this result. The significantly reduced density in RSC was especially an effect of the lower densities of species different than *E. coccineum* in these plots. Overall, results suggest that truly even-aged silvicultural methods allow for faster rates of site occupancy than a two-aged method (like RSC). It might happen, however, that site occupancy could be greater in the RSC treatment if the residual tree basal area had been lower or if a complete shelterwood cut, including the final cut, had been conducted.

With similar site occupancy at age 26, the BCC had one-third less basal area of *E. coccineum* than the SCC, while it had three times more basal area of the midtolerants *D. winteri* and *N. nitida*. This means that if forest owners want more commercially valuable forests in a shorter time, a density control of *E. coccineum* may be more required in stands treated with more conservative even-aged or two-aged silvicultural treatments (SCC or RSC). Density or cover control of other competitive species, such as *Chusquea* spp., may also be particularly necessary under certain conditions. Since ecological conditions and species composition may change from site to site, forest managers need to carefully assess these interactions of silvicultural treatments and ecological settings to improve regeneration and growth of the most desired species. These decisions would be facilitated if there were homogeneous management zones, and will also depend on whether the landowner prefers an even- or uneven-aged silvicultural system for the forest.

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