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Seedling density according to structure, dominance and understory cover in old-growth forest stands of the evergreen forest type in the coastal range of Chile

Densidad de plántulas de acuerdo a la estructura, dominancia y cobertura del sotobosque en bosques siempreverdes adultos en la cordillera de la Costa de Chile

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ABSTRACT

Securing timely regeneration is essential in maintaining the long-term ecological or silvicultural functions and values of forests. Its establishment, in turn, depends on many factors, including the structure and composition of the forest itself. Available information shows that seedling density varies greatly across the evergreen forest type in Chile. Yet stand variables that may affect the establishment of advance regeneration have not been studied. To that end, we evaluated seven stands of the coastal range, within the northern part of the evergreen forest type (39°14'-40°16' S). We documented understory cover, tree density and dominance, and stand structure, and used the information to assess their effects over seedling density. Findings indicate that *Laurelia philippiana* was the dominant canopy and regenerating species in these stands. Also, seedling density was significantly greater in stands at lower elevations where shade-tolerant *Aextoxicon punctatum* was important. *Chusquea* spp. and *Lophosoria quadripinnata*, both understory species, had a significant negative effect on seedling density. Basal area and canopy cover, per se, showed little relationship with seedling density. Vertical structure, evaluated through a crown index, had a significant relationship with seedling density, but the direction depended on the species (e.g., *L. philippiana* and *A. punctatum*) and the diameter structure within our plots. Fitted models that included these variables were highly significant, and in most cases their significance increased considerably (14 to 26 %) when we accounted for the diameter structures of the plots.

Key words: *Laurelia philippiana*, *Aextoxicon punctatum*, old-growth forests, vertical structure, *Chusquea* spp.

RESUMEN

La regeneración es esencial para mantener en el largo plazo las funciones y valores ecológicos o silviculturales de los bosques. Su establecimiento depende de varios factores, incluyendo la estructura y composición del bosque. La información disponible indica que existe una gran variabilidad en la densidad de plántulas a través de la distribución del tipo forestal siempreverde en Chile. Sin embargo, las variables de rodal que puedan afectar el establecimiento de regeneración avanzada no se han estudiado. En este estudio se evaluaron siete rodales de la cordillera de la Costa, en la parte norte de la distribución del tipo forestal (39°14'-40°16' S). En ellos se midió la densidad de árboles, plántulas y brinzales, y se estimó la cobertura de copas de los árboles así como del sotobosque, con la finalidad de evaluar los efectos de la dominancia, la estructura y la cobertura del sotobosque sobre la densidad de plántulas de especies forestales. *Laurelia philippiana* fue la especie dominante a nivel arbóreo y de plántulas. El número de plántulas fue en general significativamente más abundante a altitudes menores donde *Aextoxicon punctatum* fue importante. *Chusquea* spp. y *Lophosoria quadripinnata*, ambas especies del sotobosque, tuvieron un efecto negativo significativo en la densidad de plántulas. El área basal y la cobertura de copas mostraron una pobre relación con la densidad de plántulas. La estructura vertical, evaluada a través del índice de copas, tuvo una relación significativa con la densidad de plántulas, pero su dirección dependió de la especie (i.e., *L. philippiana* y *A. punctatum*) y la estructura de diámetros de las parcelas. Los modelos ajustados con estas variables fueron altamente significativos, y en la mayoría de los casos su significancia aumentó considerablemente (14 a 26 %) cuando se ajustaron separadamente para parcelas con distintas estructuras diamétricas.

Palabras clave: *Laurelia philippiana*, *Aextoxicon punctatum*, bosques antiguos, estructura vertical, *Chusquea* spp.

INTRODUCTION

Forest regeneration is the key process that ensures successive generations of trees (Barnes et al. 1998), and a primary requirement for maintaining the ecological or silvicultural functions of a forest. Yet tree seedling establishment depends on many biophysical factors, including the structure and composition of a stand (Crow & Metzger 1987, Nyland 2002), the abundance and distribution of canopy gaps (Veblen 1992, and references therein), and the presence of microsites suited to tree seedling establishment (Lusk 1995, Szewczyk & Szwagrzyk 1996, Chistie & Armesto 2003). Within old-growth forests, tree seedling density also seems related to the availability of propagules of species that can grow in shade or beneath small canopy openings (sensu Oliver & Larson 1996), such as species adapted to the continuous and gap-phase regeneration modes (Veblen 1992). In these forest stands, seedling establishment varies with the degree of shade cast by larger trees (e.g., Leak & Graber 1976, Crow & Metzger 1987, Clark et al. 1999), and by understory species that might oppress tree seedling development by reducing light availability near the ground. In forests with great vertical structure diversity, light levels in the understory are relatively higher than beneath stands with a poorer vertical stratification (Brown & Parker 1994,Van Pelt & Franklin 2000), and this may result in greater understory tree density in areas outside canopy gaps (Van Pelt & Franklin 2000).

In the evergreen (Valdivian) forest type of Chile, several studies have assessed seedling densities in late-successional and old-growth forests, showing dramatic differences in numbers among stands. On the Chiloé Island, for instance, an old-growth forest dominated by *Eucryphia cordifolia* and *Laurelia philippiana* (Donoso et al. 1985) had from 10,000 to 25,000 seedlings (< 2 m tall) ha^{-1}, with Myrtaceae species accounting for > 70 % of them. Stands dominated by *Drimys winteri* associated with *Nothofagus nitida* and conifers of the Podocarpaceae family had from 38,000 to 76,000 seedlings (< 1.3 m tall) ha^{-1}, mostly belonging to *Amomyrtus luma* and *Podocarpus nubigena* (Aravena et al. 2002). By contrast, stands dominated by *L. philippiana* and Myrtaceae species had only 837 seedlings and saplings ha^{-1} (Armesto & Fuentes 1988). Within the coastal range, Donoso (1989) reported that tree seedling densities averaged 318,000 (< 2 m tall) ha^{-1} for old-growth stands (mostly *E. cordifolia, D. winteri,* Podocarpaceae species, and *L. philippiana*). He counted 1,697 thousand tree seedlings (< 2 m tall) ha^{-1} (mostly *Amomyrtus luma*, *L. philippiana* and *D. winteri*) in stands of the Andes.

Aside from these general findings, research has not clearly identified the stand variables that affect the characteristics of advance regeneration within mature and old-growth forest stands of the evergreen forest type. To address this question, we sampled seven stands (> 250 yrs old each) along the coastal range in the Province of Valdivia. We sought to describe differences in abundance and composition of regeneration with reference to overstory and understory characteristics. We hypothesized that tree seedling density would be lower in stands having greater understory and overstory cover, and more abundant in stands having a high degree of vertical structural complexity.

STUDY AREA AND STAND CHARACTERISTICS

Sample stands were located in the Provinces of Valdivia and Cautín, along the Coastal Range and its extension to the Central Depression of Chile, between 39º14' and 40º16' S (Table 1). This region has a temperate maritime climate with high annual precipitation, and an average annual temperature of 11-12 °C over the last 37 yr (Pezoa 2003). It is within a broader macroclimatic region lacking a dry period (Schlatter et al. 1995), except for the stand at Los Boldos on the western slope (Table 1). That area has one dry month per year (Schlatter et al. 1997). Soils on the eastern side of the Coastal Range (Table 1) have old volcanic ash deposited over the mica-schist metamorphic bedrock, are deep (> 60 cm), and have moderate to good drainage. The western side of the coastal range (Table 1) has soils developed *in situ* over the mica-schist bedrock. These have poor drainage, are shallow (< 46 cm) (Schlatter et al. 1995, Schlatter et al. 1997), more acidic, and have a higher bulk density (CIREN 1999).

TABLE 1

General locations of the seven stands studied in evergreen forests of Chile

Ubicación general de los siete rodales estudiados en bosques siempreverdes

Stand	Latitude (South)	Longitude (West)	Elevation (m)	Aspect	Slope range (%)	Location
Los Boldos (LB, cut 1992)	39º14’36”	73º00’19”	500	S/SE	3-20	Western side of coastal range
Llancahue (LL)	39º50’20”	73º07’18”	330	S/SW	5-18	Eastern side of coastal range
La Montaña (LM, cut 1993)	39°57’00”	72°41’15”	330	SW/E	3-25	Eastern side of coastal range
Hueicolla Uncut (HU)	40º10’13”	73º33’02”	540	S/SE/N	5-18	Western side of coastal range
Hueicolla Cut (HC, cut 1983)	40º10’13”	73º33’02”	540	N/SW	10-34	Western side of coastal range
Llancacura Uncut (LU)	40º16’36”	73º23’48”	630	S/SE	5-18	Eastern side of coastal range
Llancacura Cut (LC, cut 1994)	40º16’36”	73º23’48”	630	S	6-15	Eastern side of coastal range

We located four stands on the eastern side of the Coastal Range (two at 330 m, and two at 630 m elevation), and three along the western side (at 500-540 m). Each covered at least 3 ha, with original basal areas ranging from 71 to 111 m^2 ha^{-1}. Of the seven stands, three had been selectively cut 5-7 yr earlier. In another stand, groups of trees were removed 16 yr earlier, with no cutting between the groups (Donoso 1989). Three stands had no cutting history (Table 1). All together, the partial cuttings removed 16 to 26 % of the basal area, and about 10 % of the trees, leaving an average stocking of 64 to 98 m^2 ha^{-1}. The quadratic stand diameters (QSD, diameter of the tree of mean basal area) ranged from 33.6 to 47.1 cm.

None of the cuttings affected the overall composition or the diameter and vertical structures of the stands (Donoso 2002). They were characterized by an upper canopy layer of *E. cordifolia* and *Weinmannia trichosperma*, a subcanopy layer dominated by *L. philippiana*, and an understory of Myrtaceae species with scattered *Raphythamnus spinosum* and *Lomatia ferruginea*. The Llancacura stands also had an emergent layer of scattered *Nothofagus dombeyi* trees. At La Montaña, *Aextoxicon punctatum* shared all diameter classes with *L. philippiana*. In stands on the western slopes, Podocarpaceae species (particularly *Saxegothaea conspicua*) where abundant (Donoso 2002). Overall, the stands correspond to the evergreen-with-shade-intolerant-emergents forest subtype as defined by Donoso (1981).

MATERIAL AND METHODS

Seedlings, saplings, and undergrowth

In each stand, we systematically located five to six square 1,000 m^2 plots, each separated by 50 m. In these plots we measured the diameter at breast height (dbh) of all trees ≥ 5 cm. Each plot was then subdivided into four equal 250 m^2 squares, each having four 2-m^2 circular subplots located at 7.45 m from the corners. This provided a total of 16 subplots (32 m^2) in each 1,000 m^2 plot. In the subplots, tree seedlings were recorded by height class (5- < 50 cm, 50- < 100 cm, and 100-200 cm) and species. The cover (%) of herbs, shrubs, and ferns was also estimated by four height classes (< 50 cm, 50- < 100 cm, 100- < 200 cm, and ≥ 200 cm). Seedlings < 5 cm tall were not tallied because most of them are ephemeral. Saplings (trees < 5 cm dbh and taller than 2 m) were also counted in the 2 m^2 subplots. This systematic sampling allowed us to estimate seedling abundance over average microsite conditions, without bias towards any particular set of conditions within the stands.

Overstory variables

Among overstory variables that could potentially affect regeneration, we evaluated basal area, canopy cover, and vertical structure. Although small gaps were observed in portions of the sample stands, the high average basal areas (50 to 90 m^2 ha^{-1}) indicate that the plots themselves lacked upper-canopy gaps of any appreciable size.

To estimate the actual canopy cover, we measured the dbh and canopy area of all trees ≥ 5 cm dbh in one 250 m^2 subplot within each 1,000 m^2 plot. The widest crown diameter and the one perpendicular to it were recorded for each of these trees. From these measurements, we modelled the relationship between dbh and crown area (based on an ellipse) (Donoso 2002), and used the models to calculate canopy cover across the plots.

To analyze vertical structure, we assigned each plot to a specific structure class based on a modification of the Triangle of Structures (Fig. 1) developed by the French Society of Franche-Comté for irregular (multistrata) forests (SFFC 2000). Their classification recognizes seven possible structures, depending on the proportion of trees in small (10-25 cm dbh), medium (> 25-50 cm dbh), and large (> 50 cm dbh) dbh classes, as follows: S = stand or plot dominated by small trees; SM = stand or plot dominated by a mixture of small and medium trees; SL = stand or plot dominated by a mixture of small and large trees; M = stand or plot dominated by medium trees; L = stand or plot dominated by large trees; ML = stand or plot dominated by a mixture of medium and large trees; IR = stand or plot dominated by a mixture of small, medium, and large trees. Vertical structure was also represented by a Crown Index (CI) (Donoso 2002), based on canopy cover for four broad classes of trees: upper main canopy (UMC; >50 cm), lower main canopy (LMC; 30-50 cm), below main canopy (BMC; 15-< 30 cm), and overtopped (OT; < 15 cm). We calculated CI as:

$$CI = (UMC/UMC+UMC/LMC+UMC/BMC+UMC/OT) / 4$$

Values close to 1.0 indicate a balance in the distribution of crown area among the different tree size classes. Values greater than 1.0 reflect a disproportionate crown area among large trees. A CI of < 1.0 identifies stands with higher concentrations of crown area in small trees.

Analyses

Cover of understory species, and seedling and sapling density by species, was compared among the stands. Data for canopy and non-canopy species were analyzed separately. Variation in seedling density was also compared between plots with different structures: plots where small trees were dominant (S) or codominant (SM and SL) were analysed separately from plots with a more balanced mixture of tree sizes (IR) (see Fig. 1). Tree dominance was evaluated through basal area and canopy cover. Understory variables considered were the overall cover of *Lophosoria quadripinnata* and *Chusquea* spp., and the cover of these two species in the tallest height classes (> 50 cm for *L. quadripinnata*, and >200 cm for *Chusquea* spp.).

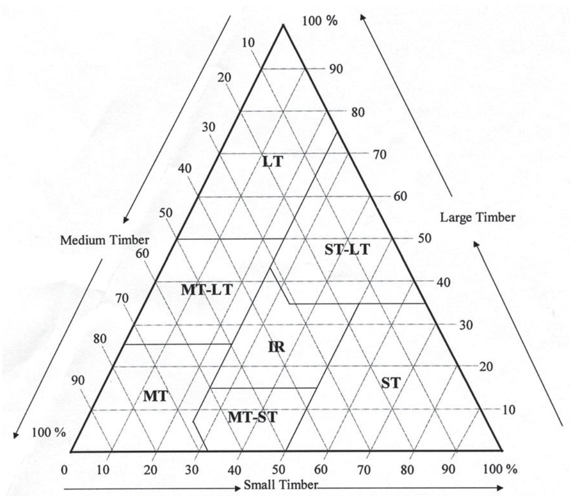

Fig.1: Triangle of structures for irregular forests from the Society of Foresters of the French-Comté in France (SFFC 2000) for classification of irregular forests into one of seven possible diameter structures (see text): T = timber; S = small; M = medium; L = large; IR = irregular.

Triángulo de estructuras para bosques irregulares de la Sociedad de Forestales de French-Comté en Francia (SFFC 2000) para la clasificación de bosques irregulares en una de siete posibles estructuras diamétricas (ver texto): T = timber (Madera); S = small (pequeña); M = medium (mediana); L = large (grande); IR = irregular (irregular).

We used SAS statistical package (SAS 2001) for all statistical analyses. Model development was conducted using the stepwise procedure, after checking the data for normality and homocedasticity. Regression models with the lowest mean square errors, lowest P-values, and highest coefficient of determinations (R^2)

were selected. Transformations were conducted when necessary to improve the models. Possible collinearity between regressor variables were addressed with the COLLIN option in SAS. Individual independent variables were kept in the regression analysis when significant at $\alpha \leq 0.05$ and were not collinear with other variables in the model. Analysis of variance and means separation by the least square difference (LSD) test (α = 0.05) were used to compare seedling densities among stands.

RESULTS

Differences in species composition

Twenty-two species of trees (≥ 5 cm dbh) were sampled across the seven sites. Stands on the eastern slopes had between 10 and 12 tree species each, while those in the west had from 12 to 16 per stand (Table 2). However, in all stands only two or three species dominated, as reflected by their importance values (IV) (Table 2; Cottam & Curtis 1956, Donoso 1993).

TABLE 2

Importance values[a] for species that reached a dbh ≥ 5 cm in each sampled stand (species with a nominal IV: present species: p; absent species: a)

Valor de importancia[a] para las especies que alcanzan un dap ≥ 5 cm en cada rodal muestreado (especies con un IV nominal: presente: p; ausente: a)

	Stand[b]						
Species	LL	LU	LC	LM	LB	HU	HC
Laurelia philippiana	37.6	43.6	24.0	50.3	23.9	29.0	29.7
Eucryphia cordifolia	33.6	12.1	27.5	6.1	10.2	12.8	10.8
Amomyrtus luma/Amomyrtus meli/Myrceugenia planipes	10.2	10.1	10.7	a	3.4	21.7	20.0
Aextoxicon punctatum	6.7	a	a	32.9	9.0	8.3	4.8
Dasyphyllum diacanthoides	1.5	7.8	4.1	a	0.1	9.8	5.0
Saxegothaea conspicua	a	a	a	a	7.3	4.3	14.0
Podocarpus nubigena	a	a	a	a	2.8	0.6	0.8
Nothofagus dombeyi	a	15.0	18.8	a	a	a	a
Weinmannia trichosperma	5.1	9.3	13.8	a	28.8	6.2	a
Gevuina avellana	0.0	a	a	3.0	6.8	1.9	4.1
Drimys winteri	2.7	a	a	A	1.9	1.6	3.9
Laurelia sempervirens	a	a	a	3.2	a	a	a
Persea lingue	a	a	a	1.77	0.13	a	a
Nothofagus obliqua	a	a	a	0.37	a	a	a
Podocarpus salignus	a	a	a	A	p	a	a
Raphythamnus spinosum	p	p	p	P	p	p	p
Lomatia ferruginea	p	p	p	P	p	p	p
Pseudopanax laetevirens	a	p	a	A	a	p	p
Azara lanceolata	a	a	a	A	a	p	a
Aristotelia chilensis	a	a	a	P	a	a	a
Lomatia dentata	p	a	a	P	a	a	a
Caldcluvia paniculata	a	a	a	A	p	p	a
Total number of tree species	11	10	10	12	15	16	12

(a) Importance value: (relative density + relative basal area)/2; (Cottam & Curtis 1956, Donoso 1993);
(b) LL = Llancahue; LU = Llancacura Uncut; LC = Llancacura Cut; LM = La Montana; HU = Hueicolla Uncut; HC = Hueicolla Cut; LB = Los Boldos

We identified more than 60 species in the understory of the seven stands (Donoso 2002). Only 10 species were common to all stands, or had a relatively high cover in at least some stands (Table 3). *Chusquea* spp. (a bamboo) had the highest cover in all stands except for Llancacura Uncut and Llancacura Cut. There *L. quadripinnata,* a 1 to 2 m tall fern, had the highest cover. *Chusquea* spp. accounted for > 42 % cover at Hueicolla, 30 % at Los Boldos, 12 % at La Montaña, and < 5% at Llancahue and the Llancacura stands. Other species with relatively high cover in most stands were *Luzuriaga* spp., *Nertera granadensis*, and the vine *Mitraria coccinea* (Table 3).

Llancahue had the least understory cover (12.6 %) and the lowest average cover in each of the three height categories. Llancacura Uncut had 20 %, and Llancacura Cut 25 % cover. The two cut stands on the western slope (Hueicolla Cut and Los Boldos) had the highest covers (64 and 63 %). Hueicolla Uncut and La Montaña had 52 and 53 % cover (Table 3). For the two tallest understory height classes, Hueicolla Cut had 56 % cover, Hueicolla Uncut 43 %, and Los Boldos 31 % cover. La Montaña and Llancacura Cut ranked intermediate (14.8 % and 15.6 %), and Llancacura Uncut (10.2 %) and Llancahue (5.6 %) had the lowest covers. The relatively high tall understory cover along the western slope was due to *Chusquea* spp.

Seedling density of canopy species

Stands on the eastern slope had more seedlings. In all stands, the 5- < 50 cm height class had the greatest numbers of seedlings per ha (Table 4), and we could distinguish three groups of stands based on stocking in this seedling height class: (1) La Montaña, with 24,583 seedlings ha^{-1} and significantly different from all other stands; (2) Llancahue, Llancacura Uncut, Llancacura Cut, and Los Boldos, with 13,332 seedlings ha^{-1} at Llancahue and 6,000-9,000 seedlings ha^{-1} beneath the other stands; and (3) Hueicolla Cut and Hueicolla Uncut, with the fewest seedlings (3,500 and 1,668 seedlings ha^{-1}, respectively).

For the 50- < 100 cm class, Llancahue, La Montaña, and Llancacura Uncut had > 3,000 seedlings ha^{-1}. Those stands differed significantly from Hueicolla Uncut (968 seedlings ha^{-1}). Llancacura Cut, Hueicolla Cut, and Los Boldos ranked intermediate (1,200 to 2,300 seedlings ha^{-1}). For seedlings 100- < 200

TABLE 3

Mean cover[a] and standard errors for main understory vascular non-tree species in the five or six plots sampled in each stand

Cobertura [a] media y error estándar para las especies vasculares no arbóreas principales del sotobosque en las cinco o seis parcelas muestreadas en cada rodal

Species	Stand[b]						
	LL	LU	LC	LM	LB	HU	HC
Chusquea macrostachya/C. quila	3.5 ± 0.4	0.3 ± 0.1	4.9 ± 1.1	12.2 ± 2.0	29.6 ± 4.1	42.4 ± 2.1	42.5 ± 2.2
Lophosoria quadripinnata	2.4 ± 0.4	4.1 ± 0.7	8.3 ± 1.0	0.7 ± 0.3	5.2 ± 1.1	1.1 ± 0.2	8.5 ± 0.8
Luzuriaga radicans/L. erecta	1.4 ± 0.1	1.8 ± 0.1	3.3 ± 0.2	11.4 ± 1.5	4.0 ± 0.4	1.8 ± 0.01	1.7 ± 0.13
Lapageria rosea	0.7 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	1.5 ± 0.2	2.5 ± 0.3	1.6 ± 0.3	2.4 ± 0.1
Mitraria coccinea	0.4 ± 0.04	4.6 ± 0.7	2.2 ± 0.3	1.8 ± 0.3	1.8 ± 0.1	0.9 ± 0.1	2.9 ± 0.5
Nertera granadiensis	0.9 ± 0.2	2.1 ± 0.5	1.1 ± 0.3	2.3 ± 0.7	17.0 ± 1.7	0.2 ± 0.1	0.04 ± 0.01
Greigia sphaceolata	0.02 ± 0.01	0.2 ± 0.07	0.2 ± 0.07	0.3 ± 0.06	0.02 ± 0.01	0.43 ± 0.09	1.8 ± 0.25
Hydrangea integerrima	0.03 ± 0.01	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.03	1.0 ± 0.01	0.03 ± 0.01
Total cover	12.6 ± 0.5	20.1 ± 1.0	25.1 ± 2.2	51.7 ± 4.1	64.1 ± 5.5	53.3 ± 1.8	62.5 ± 1.5
All non-tree species	32	24	25	36	21	23	18

(a) Cover is percent ground area occupied by the projection of a species' above-ground biomass;
(b) LL = Llancahue; LU = Llancacura Uncut; LC = Llancacura Cut; LM = La Montana; LB = Los Boldos; HU = Hueicolla Uncut; HC = Hueicolla Cut

cm tall, La Montaña, Llancacura Uncut, and Llancahue had > 3,000 seedlings ha^{-1}, and Hueicolla Uncut had the fewest (563 seedlings ha^{-1}). The remaining stands had from 1,438 to 2,396 seedlings ha^{-1} in this height class.

Considering all height classes, La Montaña had significantly more seedlings than the other stands. Llancahue ranked second, and although it had > 20 thousand seedlings/ha, it did not differ significantly from the Llancacura stands that had 14,479 (Cut) and 12,708 (Uncut) seedlings ha^{-1}. Los Boldos, Hueicolla Cut, and Hueicolla Cut, all on the western slope of the Coastal Range, had the fewest seedlings. These stands were significantly different from La Montaña and Llancahue.

TABLE 4

Seedling densities (number ha^{-1}) of canopy species in the seven stands studied in Valdivian forests

Densidad de plántulas (número ha^{-1}) de especies del dosel en los siete rodales estudiados

Species	Height class (cm)	Stand[a]						
		LL	LU	LC	LM	LB	HU	HC
Gevuina avellana	5-< 50	52	0	260	624	1,406	62	0
	50-< 100	0	0	52	156	312	0	62
	100-< 200	52	0	156	260	678	126	0
	Saplings	156	0	156	260	416	188	124
Drimys winteri	5-< 50	260	312	624	0	0	250	1,250
	50-< 100	0	156	156	0	0	125	376
	100-< 200	468	416	52	0	0	250	438
	Saplings	208	52	0	0	0	62	62
Podocarpus	5-< 50	208	0	0	0	1,352	62	626
	50-< 100	52	0	0	0	104	62	0
	100-< 200	0	0	52	0	0	0	252
	Saplings	156	0	0	0	104	0	0
Aextoxicon punctatum	5-< 50	5,000b	208	0	18,698a	1,406b	313b	313b
	50-< 100	990ab	0	0	1,666a	313	0b	63b
	100-< 200	468ab	0	0	990a	364b	62b	0b
	Saplings	208a	0	0	104ab	52ab	0b	0b
Laurelia philippiana	5-< 50	2,708ab	5,104a	5,208a	1,563ab	313	500b	938b
	50-< 100	1,198ab	1,250ab	2,032a	678b	104b	250b	438b
	100-< 200	1,042ab	989ab	1,510a	834ab	208b	62b	188b
	Saplings	1,615a	781b	260bc	417bc	156c	125c	188c
Eucryphia cordifolia	5-< 50	5,104a	886b	1,667b	208b	1,142b	500b	375b
	50-< 100	1,406a	365b	782ab	208b	260b	500ab	188b
	100-< 200	1,042a	1,042a	572ab	208ab	468ab	62b	500ab
	Saplings	313	208a	104a	52a	312a	126a	438a
Total[b]	5-< 50	13,332b	7,031bc	9,010bc	24,583a	5,990bc	1,688c	3,500c
	50-< 100	3,646a	2,292abc	3,073ab	3,125ab	1,198bc	938c	1,250bc
	100-< 200	3,073ab	3,385a	2,396ab	3,594a	1,771ab	563b	1,438ab
	5-< 200	20,052b	12,708bcd	14,479bc	3,1302a	8,958cd	3,188d	6,625cd
	Saplings	2,656a	1,042b	521b	1,815ab	1,042b	500b	938b

(a) LL = Llancahue; LU = Llancacura Uncut; LC = Llancacura Cut; LM = La Montaña; LB = Los Boldos; HU = Hueicolla Uncut; HC = Hueicolla Cut;
(b) Different letters within each row following total numbers of seedlings or saplings denote statistically significant differences in numbers between stands (μ = 0.05)

The high seedling density at La Montaña was due to the abundance of *A. punctatum* in the 5-< 50 cm class, with numbers significantly greater than all other stands. Seedlings at Llancahue were more evenly distributed among *A. punctatum, E. cordifolia*, and *L. philippiana* (Table 4). *E. cordifolia* was most abundant at Llancahue. At Llancacura, *L. philippiana* was the most abundant species, and accounted for 68 % (Llancacura Uncut) and 60 % (Llancacura Cut) of all seedlings.

The density of saplings was also greater in stands on the eastern slope, with significantly greater numbers at Llancahue than elsewhere (2,656 versus an average of < 1,000 saplings ha^{-1} for the other stands), except for La Montaña. Although Hueicolla Uncut and Hueicolla Cut had only limited numbers of seedlings and saplings of upper canopy species, they had the lowest ratio of numbers in the 5-< 50 cm class to those of sapling size, suggesting a better rate of survival for the few seedlings that became established. By stand, these ratios were: Hueicolla Uncut = 3.4, Hueicolla Cut = 4.3, Llancahue = 5.0, Los Boldos = 5.8, Llancacura Uncut = 6.3, Llancacura Cut = 17.3, La Montaña = 22.1.

TABLE 5

Seedling density (number ha^{-1}) of subcanopy tree species in the seven stands

Densidad de plántulas (número ha^{-1}) de especies arbóreas del dosel inferior

Species	Height class (cm)	Stand[a]						
		LL	LU	LC	LM	LB	HU	HC
Raphythamnus spinosum	5-< 50	730	0	416	2,916	468	500	62
	50-< 100	104	0	0	572	0	0	62
	100-< 200	260	0	0	678	52	62	62
	Saplings	312	0	0	208	0	0	0
Aristotelia chilensis	5-< 50	0	0	938	2,708	782	0	0
	50-< 100	0	0	104	364	52	0	0
	100-< 200	0	0	104	1,302	156	0	0
	Saplings	0	0	52	678	416	0	0
Myrtaceas	5-< 50	8,228	6,614	14,634	468	3,542	12,000	22,000
	50-< 100	2,188	1,406	1,198	208	1,302	1,688	4,126
	100-< 200	2,188	2,708	782	156	1,406	1,376	2,938
	Saplings	3,594	1,980	260	52	572	500	1,062
Lomatia ferruginea	5-< 50	312	1,042	1,146	0	2,188	812	4,688
	50-< 100	208	312	520	0	624	750	1,188
	100-< 200	156	730	572	0	624	562	1,376
	Saplings	0	208	105	0	312	376	938
Dasyphyllum diacanthoides	5-< 50	416	572	624	0	52	1,124	312
	50-< 100	260	156	468	0	0	126	62
	100-< 200	104	208	364	0	0	62	126
	Saplings	104	208	104	0	0	126	188
Total[b]	5-< 50	9,844bcd	8,229cd	18,488ab	3,490c	7,240cd	14,500bc	27,126a
	50-< 100	2,760b	1,875bc	2,552bc	885c	2,032bc	2,563bc	5,500a
	100-< 200	2,708bc	33,698ab	1,927cd	938d	2,240cd	2,126cd	4,563a
	5-< 200	15,312bcd	13,802bcd	22,969b	5,313d	11,510cd	19,188bc	37,188a
	Saplings	4,010a	2500b	938cd	312d	1,302bcd	1,000cd	2,250bc

(a) LL = Llancahue; LU = Llancacura Uncut; LC = Llancacura Cut; LM = La Montana; LB = Los Boldos; HU = Hueicolla Uncut; HC = Hueicolla Cut;

(b) Different letters within each row following total numbers of seedlings or saplings denote statistically significant differences in numbers between stands (μ = 0.05)

Seedling density among subcanopy species

Subcanopy tree species included *R. spinosum*, *Aristotelia chilensis*, *L. ferruginea*, species of the Myrtaceae family (mainly *A. luma*, *Amomyrstus meli*, and *Myrceugenia planipes*), and *Dasyphyllum diacanthoides*. The first three are small trees that reach a position below the main canopy, but at Hueicolla Uncut and Hueicolla Cut, some individuals of the Myrtaceae species had grown into the main canopy. *A. chilensis* is a short-lived shade-intolerant species that we found only in the most recently cut stands. Some *D. diacanthoides* also were in the main canopy at Hueicolla Uncut, Hueicolla Cut, Llancacura Uncut, and Llancacura Cut.

Seedlings of the Myrtaceae species were the most abundant subcanopy species, except at La Montaña. There, *R. spinosum* and *A. chilensis* were the dominant species among seedlings (Table 6). The greatest numbers of subcanopy seedlings were in the 5-< 50 cm class.

Hueicolla Cut had the greatest number of subcanopy seedlings (27,126), and this differed significantly from all other stands for each of the height classes. In fact, Hueicolla Cut differed significantly with all other stands, with two-thirds to three times more seedlings than the stands with intermediate numbers (Hueicolla Uncut, Llancacura Cut, Llancacura Uncut, and Llancahue). La Montaña (9,686) and Los Boldos (11,510) had the fewest seedlings ha^{-1} of subcanopy species. For saplings, Llancahue ranked first (4,010 saplings ha^{-1}), with significantly more than all other stands (Table 6).

Regeneration models

The regeneration models developed from these data had R^2 values from 0.344 to 0.828. All were highly significant, with P-values < 0.004 (Table 6). The most significant models were the ones for all canopy species, and for *A. punctatum*. The cover of *Chusquea* spp. was a significant explanatory variable in all models for all plots, for IR plots in the case of *L. philippiana*, and for S plots in the case of *A. punctatum*. Another understory species, *L.*

TABLE 6

Regression models for seedling density (5-200 cm tall ha^{-1}). In multiple regression models, variables with a greater significance are given first

Modelos de regresión para densidad de plántulas (5-200 cm de altura ha^{-1}). En modelos de regresión múltiple primero se entregan las variables de mayor significancia

Plot	Model	R^2	MSE	P-value
All canopy species				
All	$\text{Log(Reg)} = 5.07944 - 0.0005402 * C200^2 - 0.03017 * QSD + 0.04401 * CI$	0.615	0.0674	<0.0001
IR	$\text{Log(Reg)} = 4.08345 - 0.0002833 * C^2$	0.806	0.0261	<0.0001
S	$\text{Log(Reg)} = 4.41035 - 0.02403 * Lq50 - 0.00018376 * C^2$	0.632	0.0420	0.0002
Laureliopsis philippiana				
All	$\text{Reg} = 2962.32 + 652.26 * CI - 116.411 * C200$	0.344	18870857	0.0004
IR	$\text{Reg} = 7{,}408.8 - 1{,}037.39 * \sqrt{C}$	0.486	110607979	0.0039
S	$\text{Reg} = 3021.15 + 67.094 * CI^2$	0.485	11996474	0.0006
Aextoxicon punctatum				
All	$\text{Log(Reg)} = 3.75071 - 0.0177 * C200^2$	0.561	0.5608	<0.0001
IR	$\text{Log(Reg)} = 4.19144 - 0.35364 * CI^2$	0.707	0.32585	0.0012
S	$\text{Log(Reg)} = 3.92972 - 0.00252 * C200^2$	0.828	0.2324	<0.0001

Reg = number of seedlings 5-200 ha^{-1}; CI = Crown Index; LC = crown cover (m^2 ha^{-1}) of large trees (> 45 cm); QSD = quadratic stand diameter (cm); C = cover (%) of *Chusquea* sp.; C 200: cover (%) of *Chusquea* sp., ≥ 200 cm tall; Lq50 = cover (%) of *Lophosoria quadripinnata* ≥ 50cm tall *quadripinnata*, was also negatively related to seedling density in one model (S plots for all canopy species). For both species, in many cases the tall cover in *L. quadripinnata* (> 50 cm) and *Chusquea* spp. (> 200 cm) had a more significant effect than the cover with all height classes combined.

Basal area and canopy cover were not significant explanatory variables in any model. Among structural variables, QSD was negatively related to seedling density in the model for all plots and canopy species. CI was positively related to seedling density in the models for all plots, for all canopy species and *L. philippiana*, and for S plots and *L. philippiana*. It was negatively related to *A. punctatum* in S plots.

Models that were fitted for plots according to their structure (as reflected by proportions of large, medium, and small trees) had, in all cases, greater R^2 values than those without this separation. Except for the model for S plots based on all canopy species, increases in R^2 values were from 14 to 26 %.

DISCUSSION

Effects of diameter structure over seedling densities

Although all plots were dominated by similar species and had a multistoried canopy, those with S or SL structures had greater numbers of seedlings. Stands with an IR structure had intermediate seedling densities (Table 7). Stands with diameter distributions having few large trees, medium numbers of intermediate-sized ones, and a discontinuous upper canopy layer apparently favoured the development of advance regeneration. By contrast, stands with a dense middle canopy layer had the lowest density of regeneration, possibly due to heavy shading from the many intermediate-sized trees of medium heights. For *L. philippiana*, seedling density was greatest among plots having similar numbers of small and large trees (SL plots, Table 7), compared to plots dominated by small trees or a combination of small and medium trees. This suggests that *L. philippiana* regenerates best in plots that have a limited middle canopy layer, and important proportions of large trees. In stands with an important degree of middle story development (i.e., IR and SM plots), seedling densities were lower (Table 7). As with *L. philippiana*, seedling density of *A. punctatum* was lower in IR and SM plots (Table 7).

Effects of understory species over seedling density

Chusquea spp. was the most influential understory species affecting seedling density. These species characterize the understory component of Chilean temperate forests located from 37 to 43° S. Their negative effects on regeneration success have been reported extensively for other temperate forests within Chile, and elsewhere (Veblen 1992, Donoso

TABLE 7

Average and standard deviation of seedling densities of all canopy species, *L. philippiana*, and *A. punctatum* in plots with differing proportions of trees in broad diameter classes, according to Fig. 1

El promedio de desviación normal de densidades de plántulas de todas las especies de dosel, *L. philippiana* y *A punctatum* en las parcelas con diferentes proporciones de árboles en las clases del diámetro anchas, según Fig. 1

Species	Plot structure			
	S-dominated plots			IR plots
	S	SM	SL	IR
All canopy species	23,781 ± 11,774 a	7,578 ± 3,630 bc	17,396 ± 10,695 ab	8,292 ± 5,218 ab
Laurelia philippiana	4,063 ± 3,340 ab	2,109 ± 299 b	7,396 ± 6,987 a	3,167 ± 4,031 ab
Aextoxicon punctatum	14,281 ± 13,356 a	1,355 ± 2,080 b	6,771 ± 7,410 b	1,421 ± 1,656 b

Note: different letters within each row following total numbers of seedlings denote statistically significant differences in numbers (m = 0.05)

1993, González et al. 2002; see also references in these sources). *Chusquea quila*, a shade-intolerant species that grows at relatively low elevations, will prevent or delay regeneration, particularly in open sites (e.g., Donoso 1989, González et al. 2002). *C. machrostachya* is more tolerant to shade (M. González, personal communication) and can survive under relatively dense closed-canopy forests, as evidenced in this study. Such findings suggest that in lower elevation stands having *C. quila* and with basal areas similar to those sampled in this study, *Chusquea* should not impede the development of desirable regeneration.

The fern *L. quadripinnata* had a relatively important effect on tree seedling densities. In fact, tall cover (> 50 cm) of this species was a significant explanatory variable in one of the regeneration models. Similarly, the tall cover of *Chusquea* spp. (> 200 cm), rather than total cover of that species, was a significant explanatory variable of tree seedling density within several regeneration models.

Available information suggests that interference may be caused by rhizomatous ferns (e.g., reported in North America by Horsley 1993, and in New Zealand by Beveridge 1973), by *Chusquea* spp. (Veblen 1992, Donoso 1993, Lusk 1995, Lusk 1996, González et al. 2002; see also references in these sources), or by a generally dense cover of other tall understory vegetation (Lorimer et al. 1994, Clinton 2003). Under appropriate conditions, bamboos and ferns rapidly dominate the understory, preempt resources, and create an unfavourable understory microclimate for other species (Clinton 2003), including trees. This seems the case among our sample stands having the highest cover of *L. quadripinnata* and *Chusquea* spp., which were also the stands with the lowest number of vascular plants and at an elevation > 500 m (*C. machrostachya* at Hueicolla Uncut, Hueicolla Cut, and Los Boldos, and *L. quadripinnata* at Llancacura Uncut and Llancacura Cut). The two lower elevation stands (Llancahue and La Montaña) seem to presently have better regeneration of canopy species. Based on the diameter distributions in these stands, with the interspersion of trees having different diameters and heights (Donoso 2002), this might also have been the situation in the past.

Effects of tree dominance and vertical structure over seedling density

Basal area and canopy cover were used as measures of dominance in this study. In the past, canopy cover has been regarded as a more reliable measure of dominance, because basal area continues to increase at a linear rate even after crown area has approached an asymptote (Cole 1991). Both high basal area (e.g., Leak & Graber 1976, Crow & Metzger 1987) and a dense canopy cover (Clark et al. 1999) reportedly have negative effects on regeneration success. Yet those variables did not explain differences in seedling density in our study. Similarly, Berg & Van Lear (2004) also found little relationship between these factors and regeneration density in other temperate hardwood forests.

We used crown index (CI) and quadratic stand diameter (QSD) as surrogates for stand structure, and entered them as variables in the regression models. QSD was only significant in the model for all plots and all species, and had a negative relationship to seedling density. CI was a significant explanatory variable in several models. While all the sample plots had high vertical structure (sensu Brokaw & Lent 2001), CI reflected the degree of balance among the different tree strata within a plot.

For all canopy species, CI was positively related to seedling density when we lumped all plots. When we separated the plots into S-dominated or IR plots, CI was not a significant explanatory variable. The positive relationship of CI and seedling density for *L. philippiana* in the model for combined plots was very weak (Table 6). The relationship greatly improved when only S-dominated plots were considered. For these plots CI was the only explanatory variable for seedling density. For plots having more balanced numbers of trees across the diameter classes (IR plots) we observed no relationship between seedling density and CI for *L. philippiana*. Understory cover rather than vertical structure seems to more profoundly affect tree seedling density in those cases (Table 6).

With *A. punctatum* we found no relationship between seedling density and CI for all plots combined, or among S-dominated plots. For the latter condition, density was negatively affected by cover of *Chusquea* spp. Density was sensitive to CI only within IR plots, and seedling numbers declined with higher CI values (i.e., plots with a relative high proportion of crown area among large trees).

Although both species seem sensitive to shade by *Chusquea* spp., *A. punctatum* seems more tolerant than *L. philippiana* to conditions beneath a continuous canopy in stands having more balanced numbers of trees across the diameter classes (IR plots). *Laurelia philippiana* appears especially sensitive to shade cast by a middle canopy layer and regenerates better beneath stands with a broken vertical structure. Usually both species have been classified as being very shade tolerant (Donoso 1993, Figueroa & Lusk 2001). Yet, in addition to the present findings that relate the regeneration of these species according to cover and vertical structure, little has been reported on their habitat choices in regions where both species grow and coexist. For regions where *A. punctatum* does not grow, it has been reported that for *L. philippiana* numbers of seedlings established on logs are similar or greater than those established on litter (Lusk 1995, Christie & Armesto 2003). On the contrary, in low-land forests of Valdivia, Neumann (2001) reported that both *L. philippiana* and *A. punctatum* had a small proportion of seedlings growing on logs, although the former had a greater proportion (18 versus 3 %). Thus, in addition to possible microsite preferences, these two species (widely known as shade tolerant) also seem to respond differently to light availability. Analyses of both variables combined could provide a better explanation for plant recruitment, especially considering that regeneration on coarse woody debris may help these tree species to escape understory species interference.

This observational study revealed a wide range of seedling densities among stands of the evergreen forest type in the coastal range of Chile. Findings indicate that within the levels of basal area studied (only one plot having < 40 m^2 ha^{-1}), understory cover of *Chusquea* spp. and *L. quadripinnata*, and stand vertical structure, were the best indicators of seedling density for canopy species in general, as well as that of the two major shade-tolerant species. Neither the degree of canopy cover nor the total stand basal area, alone or in combination, appeared to significantly affect seedling density in stands of this forest community type. Silvicultural experiments that test alternate levels of residual basal area might identify thresholds where those two stand attributes have greater effects on the establishment and development of advance regeneration, and where less shade-tolerant species like *C. quila* begin to importantly interfere with seedling establishment within low elevation stands.

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LITERATURE CITED

ARAVENA, MC CARMONA, CA PÉREZ & JJ ARMESTO (2002) Changes in tree species richness, stand structure and soil properties in a successional chronosequence in northern Chiloé Island, Chile. Revista Chilena de Historia Natural 75: 339-360.

ARMESTO JJ & ER FUENTES (1988) Tree species regeneration in a mid-elevation, temperate rainforest in Isla de Chiloé, Chile. Vegetation 74: 151-159.

BARNES BV, DR ZAK, SR DENTON & SH SPURR (1998) Forest ecology. Fourth Edition. John Wiley & Sons, New York, New York, USA. 774 pp.

BERG EC & DH VAN LEAR (2004) Yellow-poplar and oak seedling density responses to wind-generated gaps. In: Connor CF (ed) Proceedings of the 12th biennial southern silvicultural research conference: 254-259. USDA Forest Service, General Technical Report SRS-71, Ashville, North Carolina, USA.

BEVERIDGE AE (1973) Regeneration of podocarps in a central North Island forest. New Zealand Journal of Forestry 18: 23-35.

BROKAW NV & RA LENT (1999) Vertical structure. In: Hunter M (ed) Maintaining biodiversity in forest ecosystems: 373-399. Cambridge University Press, New York, New York, USA.

CHRISTIE D & J ARMESTO (2003) Regeneration microsites and tree species coexistence in temperate rain forests of Chiloé Island, Chile. Journal of Ecology 91: 776-784.

CIREN (1999) Estudio agrológico de la Provincia de Valdivia-X Región. Descripciones de suelos. Materiales y Símbolos. Santiago, Chile. 178 pp.

CLARK JS, B BECKAGE, P CAMILL, B CLEVELAND, J HIILERISLAMBER, J LICHTER, J MCLACHLAN, J MOHAN & P WYCKOFF (1999) Interpreting recruitment limitations in forests. American Journal of Botany 68: 1-16.

CLINTON BD (2003) Light, temperature, and soil moisture responses to elevation, evergreen understory, and small canopy gaps in the southern Appalachians. Forest Ecology and Management 186: 243-255.

COLE WG (1991) Prediction of tree growth and gap closure rates after selective cutting in second-growth northern hardwood forests. Ph.D. Thesis, University of Wisconsin, Madison, Wisconsin, USA. 141 pp.

COTTAM G & JT CURTIS (1956) The use of distance measures in phytosociological sampling. Ecology 37: 451-460.

CROW TR & FT METZGER (1987) Regeneration under selection cutting. In: Nyland RD (ed) Managing northern hardwoods: 81-94. State University of New York, College of Environmental Science and Forestry, Syracuse, New York, Faculty of Forestry Miscellaneous Publication 13 (ESF 87-002). SAF Publication N° 87-03.

DONOSO C (1981) Tipos forestales de los bosques nativos de Chile. Documento de trabajo 38. Investigación y Desarrollo Forestal (CONAF/PNUD-FAO) (Publicación FAO Chile), Santiago, Chile. 128 pp.

DONOSO C (1989) Regeneración y crecimiento en el tipo forestal siempreverde costero y andino tras distintos tratamientos silviculturales. Bosque (Chile) 10: 69-83.

DONOSO C (1993) Estructura, variación y dinámica de bosques templados de Chile y Argentina. Ecología Forestal. Editorial Universitaria, Santiago, Chile. 484 pp.

DONOSO C, B ESCOBAR & J URRUTIA (1985) Estructura y estrategias regenerativas de un bosque virgen de ulmo (*Eucryphia cordifolia* Cav.)-Tepa (*Laurelia philippiana* Phil.) Looser en Chiloé, Chile. Revista Chilena de Historia Natural 58: 171-186.

DONOSO P (2002) Structure and growth in coastal evergreen forests as the bases for uneven-aged silviculture in Chile. Ph.D. Thesis, State University of New York, College of Environmental Science and Forestry, Syracuse, New York, USA. 256 pp.

FIGUEROA JA & CH LUSK (2001) Germination requirements and seedling shade tolerance are not correlated in a Chilean temperate rainforest. New Phytologist 152: 483-489.

GONZÁLEZ M, TT VEBLEN, C DONOSO & L VALERIA (2002) Tree regeneration responses in a lowland *Nothofagus*-dominated forest alter bamboo dieback in south-central Chile. Plant Ecology 161: 59-73.

HORSLEY SB (1993) Mechanisms of interference between hay-scented fern and black cherry. Canadian Journal of Forest Research 23: 2059-2069.

LEAK WB & RE GRABER (1976) Seedling input, death and growth in uneven-aged northern hardwoods. Canadian Journal of Forest Research 6: 368-374.

LORIMER CG, JW CHAPMAN & WD LAMBERT (1994) Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. Journal of Ecology 82: 227-237.

LUSK CH (1995) Seed size, establishment stands and species coexistence in a Chilean rainforest. Journal of Vegetation Science 6: 249-256.

LUSK CH (1996) Stand dynamics of the shade-tolerant conifers *Podocarpus nubigena* and *Saxegothaea conspicua* in Chilean temperate rain forest. Journal of Vegetation Science 7: 549-558.

NEUMANN RF (2001) Análisis de la estructura y dinámica de un bosque remanente original de roble-laurel-lingue en el fundo San Julián, Comuna de Panguipulli, X Región. Tesis Ingeniería Forestal, Universidad Austral de Chile, Valdivia, Chile. 103 pp.

NYLAND RD (2002) Silviculture: concepts and applications. Second edition. McGraw-Hill, New York, New York, USA. 704 pp.

OLIVER CD & BC LARSON (1996) Forest stand dynamics. Update edition. John Wiley and Sons, Inc., New York, New York, USA. 520 pp.

PEZOA L (2003) Recopilación y análisis de la variación de las temperaturas (período 1965-2001) y las precipitaciones (período 1931-2001) a partir de la información de estaciones meteorológicas de Chile entre los 33 y 53° de latitud Sur. Tesis Ingeniería Forestal, Universidad Austral de Chile, Valdivia, Chile. 99 pp.

SAS INSTITUTE (2001) SAS/STAT user's guide. Release 8.1. SAS Institute, Inc., Cary, North Carolina, USA.

SCHLATTER J, V GERDING & J ADRIAZOLA (1995). Sistema de ordenamiento de la tierra. Herramienta para la planificación forestal aplicado a la X Región. Serie Técnica, Facultad de Ciencias Forestales, Universidad Austral de Chile, Valdivia, Chile. 93 pp.

SCHLATTER J, V GERDING & J ADRIAZOLA (1997) Sistema de ordenamiento de la tierra. Herramienta para la planificación forestal aplicada a las Regiones VII, VIII y IX. Serie Técnica, Facultad de Ciencias Forestales, Universidad Austral de Chile, Valdivia, Chile. 91 pp.

SFFC (Société Forestière de Franche-Comté) (2000) Typologie des pepleuments feuillus irréguliers de Franche-Comté. Thise, France. 32 pp.

SZEWCZYK J & J SZWAGRZYK (1996) Tree regeneration on rotten wood and on soil in old-growth stand. Vegetatio 122: 37-46.

VAN PELT R & JF FRANKLIN (2000) Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. Canadian Journal of Forestry Research 30: 1231-1245.

VEBLEN TT (1992) Regeneration dynamics. In: Glenn-Lewin C, RK Peet & TT Veblen (eds) Plant succession: theory and prediction: 53-187. Chapman and Hall, London, United Kingdom.

VEBLEN TT, DH ASHTON & F SCHLEGEL (1979) Tree regeneration strategies in a lowland *Nothofagus*-dominated forest in south-central Chile. Journal of Biogeography 6: 329-340.

VEBLEN TT, C DONOSO, F SCHLEGEL & B ESCOBAR (1981) Forest dynamics in south-central Chile. Journal of Biogeography 8: 211-247.

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