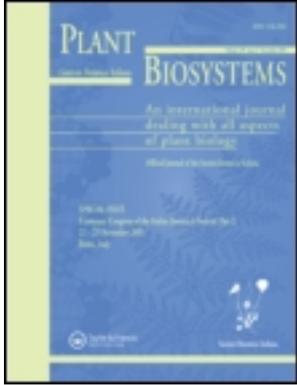


This article was downloaded by: [Vienna University Library]

On: 27 March 2012, At: 10:14

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology: Official Journal of the Societa Botanica Italiana

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tplb20>

Landscape and microenvironmental conditions influence over regeneration dynamics in old-growth *Nothofagus betuloides* Southern Patagonian forests

G. Martínez Pastur^a, C. Jordán^b, R. Soler Esteban^a, M. V. Lencinas^a, H. Ivancich^a & G. Kreps^a

^a Centro Austral de Investigaciones Científicas (CONICET), Ushuaia, Tierra del Fuego, Argentina

^b Facultad de Ciencias Agrarias y Forestales, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina

Available online: 03 Jan 2012

To cite this article: G. Martínez Pastur, C. Jordán, R. Soler Esteban, M. V. Lencinas, H. Ivancich & G. Kreps (2012): Landscape and microenvironmental conditions influence over regeneration dynamics in old-growth *Nothofagus betuloides* Southern Patagonian forests, *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology: Official Journal of the Societa Botanica Italiana*, 146:1, 201-213

To link to this article: <http://dx.doi.org/10.1080/11263504.2011.650725>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

OLD GROWTH FORESTS

Landscape and microenvironmental conditions influence over regeneration dynamics in old-growth *Nothofagus betuloides* Southern Patagonian forests

G. MARTÍNEZ PASTUR¹, C. JORDÁN², R. SOLER ESTEBAN¹, M. V. LENCINAS¹,
H. IVANCICH¹, & G. KREPS¹

¹Centro Austral de Investigaciones Científicas (CONICET), Ushuaia, Tierra del Fuego, Argentina and ²Facultad de Ciencias Agrarias y Forestales, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina.

Abstract

Old-growth forests present a mosaic of different conditions resulting from the natural forest structure of the stands. *Nothofagus betuloides* forests have high spatial variability in regeneration without a clear correlation with overstory, and could be related to location of the stands in the landscape. The objective was to evaluate the influence of macro- and micro-variables over regeneration dynamics in old-growth *N. betuloides* forests, considering the effect of landscape (altitude and influence of the sea) and microenvironment conditions in the forest floor (closeness to trees, pits, understory cover type and bare soil). A total of four sites and 24 stands were sampled including forest structure, regeneration, understory cover and microclimate variables. Macro- (landscape) and micro- (microenvironment conditions in the forest floor) variables influenced over regeneration dynamics. Natural regeneration values (0.17 million ha⁻¹ in the drier site vs. >4.52 million ha⁻¹ in the other sites) not greatly depended on forest structure variables, but they were related to soil moisture (14% vs. 29–36% volumetric soil water content). Microenvironment conditions in the forest floor determined the recruitment as well as regeneration density, age and distribution of seedlings, whereas different soil moisture were related to each microenvironment type, generating positive (bare soil, ferns and mosses growing in turfs) or negative (mosses growing in mats, pits and proximity of the overstory trees) effects over regeneration, according to the soil moisture levels. These findings can be used to understand the functional integrity of the old-growth forest ecosystems and to propose silvicultural prescriptions to ensure regeneration recruitment and maximize growth potential in *N. betuloides* forests.

Keywords: Landscape, forest microenvironments, soil moisture, light availability, recruitment, growth

Introduction

Nothofagus blumei is the main component of Southern Patagonian forests, with a wide range of natural distribution from 36°50' to 55°02' SL. These forests are mainly conformed by evergreen [*N. betuloides* (Mirb.) Oersted] and deciduous species [*N. pumilio* (Poepp. et Endl. Krasser and *N. antarctica* (Forster f.) Oersted] (Moore 1983; Barrera et al. 2000). This region is recognized as one of the world's most pristine wilderness areas (Mittermeier et al. 2002; Rozzi et al. 2006) (e.g., low human population density, highly intact native vegetation cover and well-represented state protected areas). However, some of these forests are used for harvesting, cattle grazing

and tourism, being the objectives of natural ecosystem management primarily economic (Martínez Pastur et al. 2000), and secondarily for conservation purposes (Martínez Pastur et al. 2002, 2006).

Natural *Nothofagus* forests are characterized by a permanent seedling bank in the understory and by the lack of a seed bank in the forest floor, due to seeds lose their viability at the end of one growing season (Cuevas & Arroyo 1999). Seedling bank can survive for long time periods (Cuevas 2000, 2002) awaiting a canopy opening, which can occur by a natural dynamic process (Rebertus & Veblen 1993; Heinemann et al. 2000), human harvesting (Martínez Pastur et al. 2009) or invasive species impacts (e.g., *Castor canadensis* Kuhl, see Martínez Pastur et al. 2006; Anderson et al. 2009).

Old-growth *N. betuloides* forests present a high spatial variability in natural regeneration without a clear tendency or correlation with overstory forest structure or canopy heterogeneity (Cruz et al. 2005, 2007), but quickly react after large canopy disturbances (e.g., gap formation in the canopy overstory) (Promis 2009). However, this variability can be related to macroenvironment variability at landscape level (geographic or topographic location of the stands) or microenvironment variability at stand level (microenvironmental conditions in the forest floor) (Gea et al. 2004; Martínez Pastur et al. 2011). In southern Tierra del Fuego, microclimate of the stands was mostly defined by the location of the stands in the landscape (altitude and influence of the sea). In mountain regions, as altitude increases, so do the stressing environmental conditions for plants. Air and soil temperatures diminish, affecting water availability, and increasing the probability of early frosts and snow impacts (Barrera et al. 2000; Massaccesi et al. 2008). Climate conditions generated in valley zones are usually harder than close to the sea and lakes shores. Another factor is related to light conditions, where in high latitudes of Southern Hemisphere, such as in Tierra del Fuego, the sun path is closer to the horizon, so the influence of topography on spatial light patterning would be higher, producing larger shadows than in lower latitudes (Martínez Pastur et al. 2011).

Old-growth forests have different microenvironments in the forest floor depending on microtopography, understory cover type, abundance of woody debris and the proximity of overstory trees (Chen et al. 1993, 1995; Heithecker & Halpern 2007; Martínez Pastur et al. 2011). These microenvironments increase the diversity of conditions for regeneration at stand level, where light and soil moisture availability are the most important factors determining establishment, growth and eco-physiological performance of *Nothofagus* regeneration (Heinemann et al. 2000; Heinemann & Kitzberger 2006; Lencinas et al. 2007; Martínez Pastur et al. 2007; Peri et al. 2009). Light availability is mainly controlled by canopy of the overstory spatial distribution (Caldentey et al. 2009; Promis et al. 2010a). However, other factors may be more important than overstory structure for modifying soil moisture availability (Heithecker & Halpern 2007; Martínez Pastur et al. 2011). Understory plants and woody debris can act as facilitators or competitors for seedling recruitment, survival and growth (Veblen et al. 1981; Roig et al. 1985; Frangi et al. 2005; Heinemann & Kitzberger 2006). Closeness to overstory trees can generate adverse conditions for regeneration due to water uptake by trees (Wardle 1970, 1974; Martínez Pastur et al. 2011). About microtopography of the forest floor, pits and mounds

(Schmidt et al. 1998) can also influence over soil moisture availability (Heithecker & Halpern 2007).

The integration of knowledge about favourable conditions for natural regeneration and forest management strategies at stand and landscape level is critical for long-term conservation purposes, and give an ecological understanding of forest complexity and dynamics under a multi-scale and multi-disciplinary perspective (Marchetti et al. 2010). Therefore, in this study the objective was to evaluate the influence of macro- and micro-variables over regeneration dynamics in old-growth *N. betuloides* Southern Patagonian forests, considering the effect of environment factors (altitude and influence of the sea) and microenvironment conditions in the forest floor (closeness to trees, pits, understory cover type and bare soil). Tested hypotheses were as follows: (i) locations of the stands in the landscape (altitude and influence of the sea) define environmental values (light and soil moisture availability), and consequently impact over forest regeneration and (ii) microenvironments in the forest floor present different levels of soil moisture, generating positive or negative effects over forest regeneration.

Methods

Study sites

Four study sites (10 to 30 ha) were selected in pure old-growth *N. betuloides* forests along Tierra del Fuego Island (Argentina) without previous impact of harvesting practices. Sites were selected according to their good conservation status and easy field access. The stand age (up to 200 years) corresponded to dominant trees growing in advanced developmental phase (Gutiérrez 1994). *N. betuloides* forests occurred from sea level at Beagle Channel coasts to 350 m.a.s.l. in the hill sides. In the mountain valleys without sea influence, stands occupied the middle height altitude (250 to 350 m.a.s.l.) avoiding the lower part of the valleys due to thermal inversion phenomena that produce lower temperatures. The study sites included two different landscape types: C, coast type with high influence of sea proximity (less than 5 km inland) and V, mountain valley type with low influence of sea proximity (more than 10 km inland); and the natural altitudinal gradient of the species: L, low altitude (< 300 m.a.s.l.) and H, high altitude (> 300 m.a.s.l.). The four study sites were located at (i) Moat (54°54'23" S, 67°05'27" W) at 0.4 km of sea coast and 144 m.a.s.l. (coast in low altitude, CL), (ii) Martial (54°47'48" S, 68°22'03" W) at 3.1 km of sea coast and 324 m.a.s.l. (coast in high altitude, CH), (iii) Vega Café (54°44'06" S, 67°52'00" W) at 13.7 km of sea coast and 251 m.a.s.l. (mountain valley in low altitude, VL)

and (iv) Garibaldi ($54^{\circ}41'19''$ S, $67^{\circ}49'50''$ W) at 19.2 km of sea coast and 337 m.a.s.l. (mountain valley in high altitude, VH) (Figure 1). Regional climate is characterized by short, cool summers and long, snowy winters. Only 3 months per year are free of mean daily air temperatures under 0°C , and the growing season is approximately 5 months. Rainfall, including snowfall, varied from 500 to 1000 mm yr^{-1} according to altitude and sea proximity. Annual average wind speed outside forests is 8 km h^{-1} , reaching up to 100 km h^{-1} during storms (Barrera et al. 2000; Massaccesi et al. 2008; Martínez Pastur et al. 2011).

Forest structure

Six stands (> 1 ha each) were selected in each study site type, where forest structure was characterized by point sampling method (Bitterlich 1984) using a Criterion RD-1000 (Laser Technology, USA) with a variable BAF (basal area factor) between 6 and 9. Diameter at breast height (DBH) (trees > 5 cm) was measured in all trees, while dominant height (DH) was measured in three dominant trees per plot. Tree density (DEN) and basal area (BA) were also obtained from the inventory plots. Selected stands did not present large gap presence in their canopy. To characterize canopy structure and solar radiation transmission we used the methodology and user-supplied input variables proposed by Martínez Pastur et al. (2011). Hemispherical photographs of forest canopy were taken at 1 m above ground level with an 8 mm fish eye lens (Sigma, Japan) mounted on a 35 mm digital camera (Nikon, Japan) with a

tripod levelling head to ensure horizontal lens position. Each photograph was orientated with the upper edge towards the north, and was taken with no direct sunshine (Roxburgh & Kelly 1995). Crown cover (CC), effective leaf area index (LAI) integrated over the zenith angles 0° to 60° , global radiation (GR) at understory level along the growing season (November to March), and percentage of GR (PGR) as the ratio of GR and the amount of incident total radiation above forest canopy were obtained from the photographs using Gap Light Analyzer software version 2.0 (Stenburg et al. 1994; Robison & McCarthy 1999; Frazer et al. 2001).

Regeneration measurements

In each stand, at the same place where forest structure characterization was carried out, number (SAP) and height (H) of saplings (up to 30 cm height and < 5 cm DBH) were measured in a 20 m^2 plot (an average of 11 saplings were found for the selected plot size). Beside this, understory cover and richness were also characterized in each sampling point. Vascular plants (Dicotyledonae, Monocotyledonae and Pteridophyta) were taxonomically classified by species, following Moore (1983) and Correa (1969–1998). Microenvironment variability of the forest floor of each stand was characterized, classifying them in six categories: (i) Ferns: floor covered by Pteridophyta (*Hymenophyllum secundum* or *Blechnum penna-marina*), (ii) Mats: floor or debris covered by mosses with a life form of mats, (iii) Turfs: floor or debris covered by mosses with a life form of turfs (for

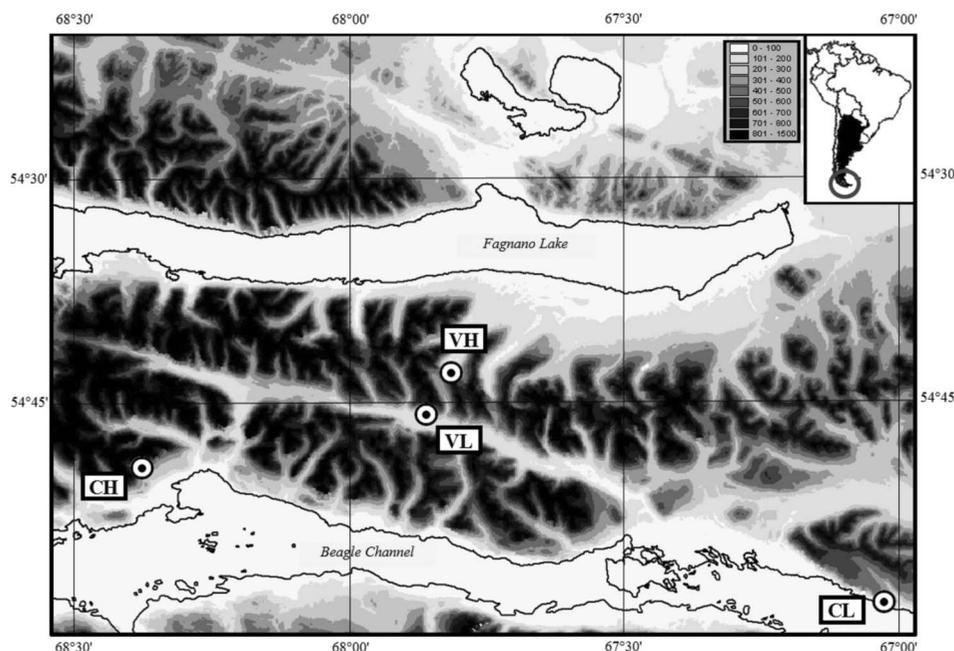


Figure 1. Localization of study sites: CL, coast in low altitude; CH, coast in high altitude; VL, mountain valley in low altitude; VH, mountain valley in high altitude. Gray scale represents the altitude in meters above sea level.

details of mosses life form see Matteri & Schiavone 1988), (iv) Bare floor: when mosses and ferns were absent, and understory or debris cover were less than 50%, (v) Pits: produced by tree throws and with the same vegetation cover characteristics of bare floor treatment and (vi) Trees: bare floor under the influence of large live overstory trees (less than 2 m distance). When category exits, a plot was surveyed (1 m × 0.2 m resulting in a plot of 0.2 m²) considering recruitment (plants with cotyledons and plants of 1-year old) (REC), seedlings (plants ≥2-year old and <30-cm height) (SEED) and total regeneration as REC + SEED (TOT). An average of 47 recruitment plants and 29 seedlings were found in each plot for the selected plot size. For each plant, location inside the plot, height (RH) and age (RA) of each plant were measured. Age was determined in the field from annual growth scars in the stems (Cuevas 2002; Gea et al. 2004; Martínez Pastur et al. 2011), whereas height was measured from the base to the top of the longest extended shoot. Mean annual height growth (RG) of each plant was estimated using individual total height and age. Finally, volumetric soil water content (VSW) (%) using a MP406 moisture probe (ICT, Australia) were also recorded as an average of two measures in each plot. Complementarily, a homogeneity index (HI) was proposed to determine the distribution pattern of recruitment and seedling plants for each plot. This index was defined as follows:

$$HI = \frac{((\sum_{i=1}^n sp_i)/p)}{1.6}$$

where sp = REC + SEED quantity for each i subplot of 20% area; and p = REC + SEED quantity for the entire plot.

This index varied between 0 (maximum homogeneity) when all subplots have the same regeneration number, to 1 (maximum heterogeneity) when all the regeneration occurred in only one subplot.

Statistical analysis

One-way ANOVAs were carried out using study site (considering four levels: CH, CL, VL and VH) as main factor to analyse different variables of forest structure (DH, BA, DEN, DBH, CC and LAI), environmental conditions (GR and PGR), sapling characteristics (SAP and H), total richness for flowering plants (Dicotyledonae and Monocotyledonae) and ferns (Pteridophyta), and floor cover (bare soil, woody debris and understory plants). Complementary, two-way ANOVAs were done using study site (again with four levels: CH, CL, VL and VH) and microenvironment (considering six levels: pits, bare floor, closeness to trees, ferns and mosses in turfs or mats) as main factors to analyse the following variables: VSW, REC, SEED, TOT, RH, RA, RG and HI. In all cases, normality and homoscedasticity of residuals were previously tested, and a post-hoc Tukey test corrected for unequal N was used for all mean comparisons ($p < 0.05$). Cluster analyses were conducted using: (i) study sites (CH, CL, VL, VH) classified by regeneration (recruitment and seedling plants) and density of sapling plants data; and (ii) microenvironments classified by regeneration (recruitment and seedling plants) and VSW data. An analysis for regeneration (recruitment and seedling plants) and values of sapling plant density was performed using a canonical correspondence analysis (CCA) (Ter Braak & Šmilauer 2002) to estimate components of variance contributed by forest structure and environmental data. The significance of direct gradient CCA ordination was tested using Monte Carlo techniques. In the ordination, plots were classified according to study sites (CH, CL, VL and VH). Selected explicatory variables were DH, BA, DEN, DBH, VSW, CC, LAI, GR and PGR. Finally, data of cover from floristic surveys were analysed through a comparison with a detrended correspondence analysis (DCA) for the different study sites.

Table I. One-way ANOVAs with study sites (CL, CH, VL, VH) as main factor, for overstory dominant height (DH) (m), basal area (BA) (m² ha⁻¹), tree density (DEN) (n ha⁻¹), diameter at breast height (DBH) (cm), sapling density (SAP) (n ha⁻¹) and sapling height (H) (cm) in *Nothofagus betuloides* forests.

Treatment	DH	BA	DEN	DBH	SAP	H
CL	19.7 b	75.3 a	486 a	45.1 c	0 a	–
CH	14.2 a	111.8 b	1344 ab	29.8 ab	6960 ab	0.51 b
VL	16.0 ab	92.5 ab	2851 b	21.6 a	11035 b	0.49 ab
VH	15.0 ab	99.3 ab	951 a	40.5 bc	1952 a	0.38 a
$F(p)$	3.70 (0.029)	3.90 (0.024)	5.37 (0.007)	13.00 (<0.001)	6.37 (0.003)	4.40 (0.033)

In each column, letters indicate differences using Tukey test at $p = 0.05$.

CL, coast in low altitude; CH, coast in high altitude; VL, mountain valley in low altitude; VH, mountain valley in high altitude; F , Fisher's test; (p), probability.

Results

Forest structure presented significant differences among the study sites (Table I), where DH and tree diameter (DBH) were lower at higher elevations in the coast, but differences decreased between the valley treatments (low and high altitudes). BA and DEN increased with altitude and into the valley

Table II. One-way ANOVAs with study sites (CL, CH, VL, VH) as main factor, for crown cover (CC) (%), effective leaf area index (LAI), global radiation (GR) (W m^{-2}) and percentage of global radiation (PGR) (%) at understory level transmitted through the canopy in *Nothofagus betuloides* forests.

Treatment	CC	LAI	GR	PGR
CL	81.1	1.82	8.85	22.90
CH	81.4	1.80	9.77	25.40
VL	81.3	1.87	9.06	23.50
VH	80.1	1.67	10.25	26.60
<i>F</i> (<i>p</i>)	0.19 (0.904)	0.96 (0.429)	1.38 (0.278)	1.38 (0.278)

CL, coast in low altitude; CH, coast in high altitude; VL, mountain valley in low altitude; VH, mountain valley in high altitude; *F*, Fisher's test; (*p*), probability.

compared with CL treatment. Saplings were absent in CL, but were abundant in the other study sites (VL > CH > VH) with mean heights of 38–51 cm. Canopy and radiation variables did not present significant differences among study sites, with a complete crown closure (cover > 80%, LAI > 1.7) and low radiation levels (GR < 10 W m^{-2} resulting in PGR < 27%) (Table II).

Total plant understory richness did not vary among study sites (5–8 species). However, significant differences were found when floor cover was assessed (Tables III and IV). Bare soil cover was higher in CL compared with other study sites, and woody debris cover in CL was twofold higher compared with other study sites. Vegetation cover was scarce in CL (flowering plants 17%, lower plants 10%, *N. betuloides* regeneration 3%) compared with other treatments (flowering plants 28–43%, lower plants 28–50%, *N. betuloides* regeneration 13–17%). Other regeneration trees were lower in CH compared with the other study sites, while ferns did not present significant differences among study sites.

When soil water content (VSW) was analysed according to study sites and microenvironments in the forest floor, significant differences were found at

Table III. One-way ANOVAs with study sites (CL, CH, VL, VH) as main factor, for floor cover (%) in *Nothofagus betuloides* forests classified as bare soil, woody debris, flowering plants, ferns and lower plants classified according their life forms (mats or turfs).

Treatment	Bare soil	Woody debris	Flowering plants	Ferns	Lower plants	Mats	Turfs
CL	48.4 b	22.4 b	16.8 a	3.7	9.5 a	74.2	25.8
CH	11.1 a	10.2 a	43.4 b	7.7	27.5 b	65.0	35.0
VL	10.8 a	11.0 ab	27.8 ab	1.2	49.7 b	70.8	29.2
VH	14.2 a	12.2 ab	28.8 ab	0.4	44.5 b	43.3	56.7
<i>F</i> (<i>p</i>)	27.83 (<0.001)	3.61 (0.031)	3.56 (0.033)	1.50 (0.245)	10.81 (<0.001)	2.80 (0.066)	2.80 (0.066)

In each column, letters indicate differences using Tukey test at $p = 0.05$.

CL, coast in low altitude; CH, coast in high altitude; VL, mountain valley in low altitude; VH, mountain valley in high altitude; *F*, Fisher's test; (*p*), probability.

Table IV. One-way ANOVAs with study sites (CL, CH, VL, VH) as main factor, for total richness (flowering plants and ferns) and flowering plant cover (%) in the understory *Nothofagus betuloides* forests, classified as *N. betuloides* regeneration, other tree species regeneration, shrubs, herbs and monocots.

Treatment	Total richness	<i>N. betuloides</i> regeneration cover	Other tree regeneration cover	Shrub cover	Herb cover	Monocot cover
CL	8.0	3.2 a	2.7 b	1.0	9.2	0.7
CH	7.2	15.9 b	0.3 a	18.2	8.8	0.2
VL	5.3	17.5 b	1.3 ab	2.4	5.3	1.2
VH	7.5	12.8 ab	2.5 ab	6.8	6.2	0.4
<i>F</i> (<i>p</i>)	0.97 (0.427)	5.17 (0.008)	3.66 (0.030)	1.68 (0.204)	0.40 (0.755)	0.81 (0.504)

In each column, letters indicate differences using Tukey test at $p = 0.05$.

CL, coast in low altitude; CH, coast in high altitude; VL, mountain valley in low altitude; VH, mountain valley in high altitude; *F*, Fisher's test; (*p*), probability.

Table V. Two-way ANOVAs with study sites (CL, CH, VL, VH) (factor A) and microenvironments (factor B) as main factors for VSW content (%), REC (thousand ha⁻¹), SEED (thousand ha⁻¹), TOT (thousand ha⁻¹), RH (cm), RA (years), RG (cm year⁻¹) and HI in *Nothofagus batuloides* forests.

Type	VSW	REC	SEED	TOT	RH	RA	RG	HI
Factor A	CL	13.7 a	28 a	168 a	5.6 b	4.4 b	1.4 a	0.68 b
	CH	30.2 b	2901 b	6630 c	2.5 a	1.8 a	1.5 ab	0.25 a
	VL	28.8 b	3770 b	4856 bc	2.5 a	1.4 a	1.8 b	0.34 a
	VH	35.8 b	3290 b	4522 b	2.3 a	1.5 a	1.6 ab	0.33 a
Factor B	Pits	50.9 c	2972 ab	4672 bc	3.2	1.9 ab	1.7	0.31 a
	Bare Soil	30.7 b	3555 b	5610 c	2.6	1.6 a	1.6	0.36 a
	Mats	25.2 ab	1560 a	2804 ab	3.1	2.5 ab	1.4	0.39 a
	Turfs	19.8 ab	2701 ab	4185 abc	2.9	2.4 ab	1.5	0.36 a
	Ferns	20.7 ab	2772 ab	4652 abc	4.2	2.4 ab	1.8	0.42 ab
	Trees	15.6 a	1422 a	2341 a	3.2	2.8 b	1.5	0.56 b
<i>F</i> (<i>p</i>)	A	13.01 (<0.001)	15.34 (<0.001)	23.44 (<0.001)	30.21 (<0.001)	26.41 (<0.001)	3.77 (0.014)	25.02 (<0.001)
	B	23.00 (<0.001)	3.82 (0.003)	5.15 (<0.001)	1.74 (0.134)	2.91 (0.018)	1.41 (0.227)	5.22 (<0.001)
	A × B	0.81 (0.665)	1.34 (0.196)	1.19 (0.293)	1.15 (0.328)	0.95 (0.514)	1.10 (0.373)	2.37 (0.007)

In each column and factor, letters indicate differences using Tukey test at $p = 0.05$.

CL, coast in low altitude; CH, coast in high altitude; VL, mountain valley in low altitude; VH, mountain valley in high altitude; VSW, volumetric soil water content; REC, recruitment; SEED, seedling density; TOT, total regeneration density; RH, regeneration mean height; RA, regeneration mean age; RG, regeneration mean height growth; HI, homogeneity index; *F*, Fisher's test; (*p*), probability.

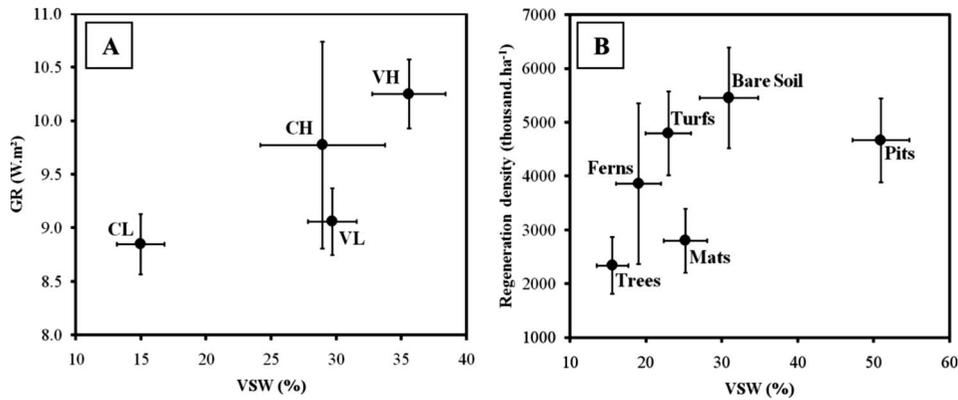


Figure 2. Volumetric soil water content (VSW) gradients comparing (A): global radiation (GR) for study sites (CL, coast in low altitude; CH, coast in high altitude; VL, mountain valley in low altitude; VH, mountain valley in high altitude), and (B) regeneration density for microenvironments in *Nothofagus betuloides* forests. Bars indicate \pm standard error.

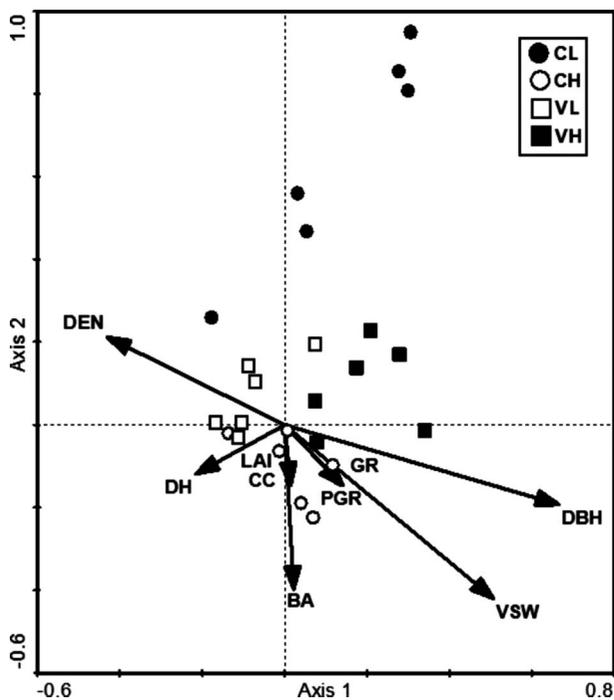


Figure 3. Canonical correspondence analysis (CCA) analysis for regeneration (recruitment and seedlings) and sapling density values for study sites (CL, coast in low altitude; CH, coast in high altitude; VL, mountain valley in low altitude; VH, mountain valley in high altitude) in *Nothofagus betuloides* forests. Explanatory variables were overstory dominant height (DH) (m), basal area (BA) ($m^2 \cdot ha^{-1}$), tree density (DEN) ($n \cdot ha^{-1}$), diameter at breast height (DBH) (cm), volumetric soil water content (VSW) (%), crown cover (CC) (%), effective leaf area index (LAI), global radiation (GR) ($W \cdot m^{-2}$) and percentage of global radiation (PGR) (%).

micro- and macro-level analyses (Table V). VSW was lower at CL than in other study sites, and close to overstory trees than over lower plants than in bare soil than in pits. Regeneration values also varied for study sites and microenvironments (Table V). Regeneration (REC, SEED and TOT) were lower at CL than in other study sites. These lower values in

regeneration numbers in CL resulted in older plants (4.4 years vs. 1.4–1.8 years), higher mean height and more heterogeneous distribution (HI 0.7 vs. 0.3). Overstory trees and mosses forming mats negatively influenced *N. betuloides* plants growing close or over them, producing low REC and TOT values, derived in older plants with more heterogeneous distribution (HI 0.6 close to trees vs. 0.3–0.4 in the other treatments).

When study sites were characterized according to their light and soil moisture availability (GR and VSW), it was observed that CL presented the lower values for both variables, followed by CH and VL, and VH (Figure 2A). These variables influenced regeneration, resulting in a similar clustering of study sites when regeneration values (REC, SEED and SAP) were used into the analysis. Valley sites (VL and VH) were more similar between them (linkage distance of 750), and cluster to CH at a major linkage distance (linkage distance of 3000) than CL (linkage distance of 7250), which is the most dissimilar study site. Ordination analysis (CCA) also separate CL from other study sites (Figure 3). Explanatory variables importance were $DBH > VSW > DEN > BA > DH > LAI > GR > PGR > CC$, where axis 1 (Eigenvalue 0.131) explain 39.1% variance, axis 2 (Eigenvalue 0.059) explain 17.6% variance, and both axes explain 56.7% variance. Monte Carlo analysis for all canonical axes was significant ($F = 2.04$, $p = 0.032$). Clusters of study sites described for the regeneration also were found for understory plant species richness and cover (Figure 4). CL presented the more dissimilar richness and cover with seven exclusive species compared with other study sites (see Appendix 1), and these data were associated with regeneration of accompanying tree species (e.g., *Drymis winteri*, *Maytenus magellanica* and *Embothrium coccineum*) characteristics of mixed evergreen forests, while other study sites ($CH > VL > VH$)

included great shrubs species which are usually characteristics of pure evergreen *N. betuloides* forests.

When microenvironments were characterized according to their soil water content (VSW) and total regeneration (TOT), it was observed that regeneration increased with soil moisture: trees < ferns < turfs < bare soil (Figure 2B). However, there were two exceptions: (i) pits presented higher VSW values but decrease TOT values, and (ii) mosses in mats presented lower TOT values to the expected for the VSW value. These patterns also were found in the cluster analysis (Figure 5) where two main groups were identified: (i) the first group conformed by closeness to trees and mosses in mats, and ferns cluster at major linkage distance and (ii) the second group conformed by pits and mosses in turfs, and bare soil cluster at major linkage distance.

Discussion

In our study, forest structure of the study sites corresponded to old-growth stands without previous management. Forest structure variables, including overstory covers are comparable than those described in other studies of *N. betuloides* primary forests (Gutiérrez 1994; Donoso & Donoso 2006; Cruz et al. 2007; Promis 2009), as well as understory diversity (Cruz et al. 2007). Site quality of the stands belongs to a middle-low class (the studied forests have 14–20 m of DH and some natural stands cited

in the literature can reach up to 35 m height) (Gerding & Thiers 2002; Donoso & Donoso 2006; Cruz et al. 2007). Microclimatic conditions can change according to the location of the stands, e.g., altitude, aspect or topography (Frangi et al. 2005; Kupferschmid & Bugmann 2005). Some differences in forest structure found in this work can be associated to changes in altitude (e.g., BA, DBH), or due to location of the stands into the landscape (distance to the sea coast) which can potentially affect the micro-climate (e.g., lower BA and DEN in the drier studied sites), as was described for other *Nothofagus* forests (Massaccesi et al. 2008). The importance of assessment studies at various scale levels in old-growth forests were previously reported (Corona et al. 2010). In our study area, stands located at lower altitudes have less rainfall than those located at higher altitudes (Massaccesi et al. 2008), as well as stands into the valleys than those close to sea coasts, generating higher availability of soil moisture at the understory level. In the same way, higher altitudes and stands located into the valley presented lower temperatures and more frequent freeze occurrence (Barrera et al. 2000; Frangi et al. 2005). Although detected values of GR among the four studied sites were similar, it is possible to observe a trend of maximum GR levels at higher altitudes, decreasing towards lower elevations, or near to sea coasts, influencing over light availability at stand level.

In our study, understory species (flowering, ferns and lower plants) growing in dried conditions with lower amounts of light availability (GR) develops a scarce vegetation cover on the forest floor. Similarly, Lencinas et al. (2008) described a poorly developed understory in *N. pumilio* stands with a large canopy cover which limit light and water availability at the understory level. However, in our study total richness did not vary at landscape level among the

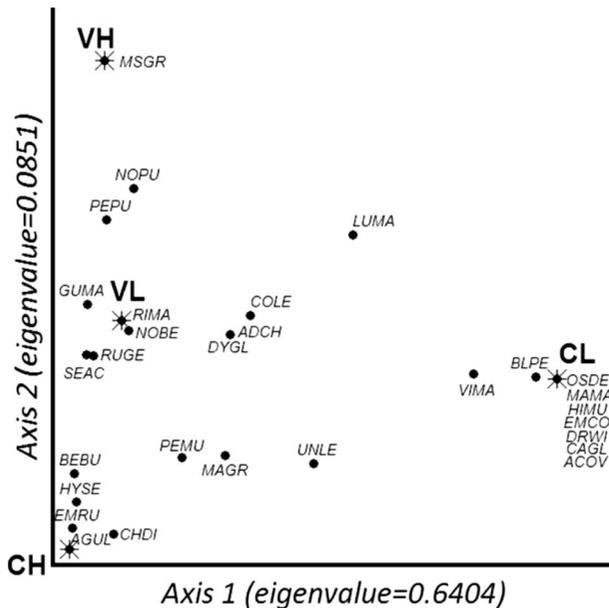


Figure 4. DCA for understory plant species distribution among study sites (CL, coast in low altitude; CH, coast in high altitude; VL, mountain valley in low altitude; VH, mountain valley in high altitude) in *Nothofagus betuloides* forests. Codes for plant species are showed in Appendix 1.

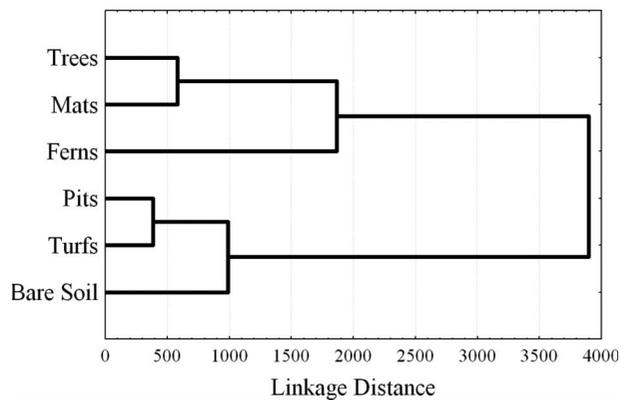


Figure 5. Cluster analysis for microenvironments according to regeneration (recruitment and seedlings) values (density, height and age) and volumetric soil water content (VSW) (%) in *Nothofagus betuloides* forests.

Downloaded by [Vienna University Library] at 10:14 27 March 2012

four study sites, where some differences can be related to the location of the stands: e.g., CL presented some understory species characteristics of the mixed evergreen forests occurring below 180 m.a.s.l. (Gutiérrez 1994), while the understory of the other stands (CH, VL, VH) belongs to pure *N. betuloides* forests (Moore 1983).

N. betuloides is a mid-tolerant tree species due to their colonization abilities and natural dynamics (Gutiérrez 1994). Seedlings and sapling plants exhibited a high shade tolerance, surviving long periods of time under the shaded canopy (Promis et al. 2010b). It is well described that these forests have a permanent seedling bank in the understory (Gutiérrez 1994; Frangi et al. 2005), and most of the studied stands presented large quantities of sapling and seedling plants in the understory. The recruitment and structure of these seedling banks were related to seeding cycles. The amount of seeding varied year-to-year, where these seeding cycles have been described in several forest species (Kelly 1994; Kelly et al. 2000; Koenig & Knops 2000) and have received considerable attention in *Nothofagus* forests (Monk & Kelly 2006) because the level of variation among years is especially high (Kelly 1994; Kelly & Sork 2002). In our study, significant differences found in the regeneration values (recruitment and seedlings) were mostly associated to VSW than overstory canopy variables or location of studied sites, e.g., Kupferschmid and Bugmann (2005) also describe differences along an altitudinal gradient. In our stands, saplings were absent in drier sites, and increase in number in stands with more than 25% VSW. In these forests, *N. betuloides* saplings assume dominance and intermingled with shrubs communities generating a dense understory (Moore 1983; Cruz & Caldenteu 2007). Sapling densities found in this study were comparable with those described for Chile (4000 to 14000 plants ha⁻¹) (Cruz & Caldenteu 2007). Regeneration (recruitment and seedlings) were also related to soil moisture of the stands than canopy cover structure. In fact, most of the rooting systems of these forests were found in the organic layers (Gerding & Thiers 2002), being more vulnerable to the soil moisture changes. In our study, regeneration values of *N. betuloides* (4.5–6.6 million ha⁻¹) at stand level were higher than other reported values for this species (Rebertus & Veblen 1993; Donoso & Donoso 2006; Cruz & Caldenteu 2007; Promis 2009) and other *Nothofagus* species (e.g., 0.185 million ha⁻¹ *N. antarctica*, Bahamonde et al. 2011), but comparable to *N. pumilio* for this region, e.g., maximum values of 6.5 million ha⁻¹ (Cuevas 2000). Beside this, in this work, *N. betuloides* regeneration cover (3% to 17%) was lower than registered by Cruz & Caldenteu (2007) in old-growth unmanaged forests (23% to 31%). In our study,

spatial distribution of regeneration was related to the total regeneration number, where large quantities of regeneration generate homogeneous distribution (e.g., bare soil), and lower amount generates a cluster distribution (e.g., CL stand or sectors close to remnant trees). Keeton & Franklin (2005) concluded that while remnant trees have a seminal influence on regeneration processes, the microenvironments and stand structure variables explain the spatial variability or patchiness in regeneration patterns of *Tsuga heterophylla* and *Thuja plicata* old-growth forests. In our study, the proposed HI clearly reflected the regeneration spatial distribution.

Microenvironments into the old-growth forests offer a wide diversity of conditions for establishment and recruitment of plants, due to the influence of biotic and abiotic factors. Temperature, radiation and soil moisture are the most critical factors (Lieffers et al. 1999) that affect growth and survival of seedlings in these austral forests (Heinemann et al. 2000; Martínez Pastur et al. 2007, 2011). Also, these factors influence decomposition and natural cycles (Barrera et al. 2000; Caldenteu et al. 2001), as well as biodiversity conservation (e.g., forest soil under undisturbed overstory canopies does not freeze during the whole year allowing to survive to several insect and plant species during the winter season) (Spagarino et al. 2001; Martínez Pastur et al. 2002). In our study, soil moisture influenced number of seedling plants when microenvironment conditions in the forest floor were considered. Regeneration values increased with up to 30–40% VSW; however, regeneration decreases with higher VSW values (more than 40%) (e.g., pits). In other *Nothofagus* forests, recruitment, survival and growth also have been related to water availability (Heinemann et al. 2000; Heinemann & Kitzberger 2006), which can affect their biomass compartmentalization (Lencinas et al. 2007) and photosynthetic performance (Sun et al. 1995; Martínez Pastur et al. 2007; Peri et al. 2009). In other temperate forests, the advantages and disadvantages of pits and mounds have been described in relation to the establishment and growth of seedlings (Hörnberg et al. 1997; Schmidt et al. 1998; Blood & Titus 2010; Vodde et al. 2010). In our study, overstory trees negatively influenced regeneration and can be explained by a decrease in the soil moisture availability due to water uptake by the root system of the trees. Also, rainfall interception increases with closeness to the trees and canopy closure, and consequently potentially decreases soil moisture availability (Wardle 1970; 1974; Martínez Pastur et al. 2007). Finally, understory plant species may act as facilitators or competitors, increasing or reducing impacts of stressful environments (Heinemann & Kitzberger 2006; Martínez Pastur et al. 2011). In our study,

understory cover decreased soil moisture and directly influenced over regeneration density (ferns > mosses in turfs). However, mosses growing in mats negatively influenced over regeneration, where the expected regeneration number according to soil moisture was not found. Probably, a competition with regeneration occurred due to the stems of the mats lie flat and forming a closed interwoven (During 1979) over bare soil and woody debris. Most of the dead wood in the forest floor of the studied forests are not a suitable substrate for tree regeneration but were completely colonized by mosses (both turfs and mats), and lichens, with great ecological importance for their conservation in the old-growth forests (Toivanen & Kotiaho 2007; Sabovljevic et al. 2010).

Forest management remarks

Temperate forests of southern Chile and Argentina are recognized as one of the world's most pristine wilderness areas (Mittermeier et al. 2002; Rozzi et al. 2006), where old-growth forests are important sites for biodiversity conservation (Marchetti et al. 2010). Consequently, the integration of effective conservation and forest management strategies, as well as a greater understanding of forest regeneration in these forests is critical for harvesting and conservation purposes. Several regeneration harvesting systems were applied in *Nothofagus* forests to assist regeneration already established or to make the natural regeneration possible, from light selective cuts to clear-cuts (Gea et al. 2004). The current silvicultural prescriptions for *N. betuloides* forests are mainly based on opening the canopy to stimulate natural regeneration by modifying soil moisture and light availability at the understory level, e.g., shelterwood cuts (Cruz & Caldenteu 2007). After harvesting, the survival of the seedling bank and its rapid growth depends on the adaptation to the new micro-climatic conditions (Tognetti et al. 1998) and the availability of favourable sites for establishment (Keeton & Franklin 2005). If new silvicultural approaches intend to manage old-growth *N. betuloides* forests more effectively, it is important to generate knowledge of inter-specific differences in seedling growth, as was showed in the present work. However, the success or failure of silvicultural systems depends on the functional responses of species to different environmental conditions.

Most of the regeneration studies are conducted in harvested forests, without including the study of regeneration ecology in unmanaged old-growth forests. The understanding of differences in the regeneration at macro- (landscape) and micro-scale (microenvironment conditions in the forest floor) can allow to defining specific silvicultural strategies

for each site. A balance between new silvicultural systems that favour timber yield and functional integrity of forest ecosystem is needed to achieve the sustainable management of these natural forests (Messier et al. 1999). Beside this, these findings can allow to define the best variables for survey forest ecosystem attributes evolving into comprehensive environmental inventory and conservation programs (Blasi et al. 2010; Corona et al. 2010).

Conclusions

The proposed hypotheses were verified. Macro- (landscape) and micro- (microenvironment conditions in the forest floor) variables influence over regeneration dynamics in old-growth *N. betuloides* forests. Natural regeneration values do not greatly depend on forest structure variables, but they are related to soil moisture (VSW) at macro- and micro-scale. Microenvironment conditions in the forest floor determines the recruitment as well as regeneration density, age and distribution of seedlings, whereas different soil moisture were related to each microenvironment type, generating positive and negative effects: (i) high soil moisture levels in pits negatively influence over regeneration, (ii) ferns and mosses growing in turfs decrease soil moisture but do not influence over regeneration, (iii) mosses growing in mats negatively influence over regeneration and (iv) soil moisture decrease in the proximity of the overstory trees, where regeneration proportionally decreases. These findings can be used to understand the functional integrity of the old-growth forest ecosystems and to propose silvicultural prescriptions to ensure regeneration recruitment and maximize growth potential.

Acknowledgments

The authors thank the Centro Austral de Investigaciones Científicas and CATIE MIA project for partially funding this work.

References

- Anderson C, Martínez Pastur G, Lencinas MV, Wallem P, Moorman MC. 2009. Do introduced North American beavers engineer differently in southern South America? An overview with implications for restoration. *Mammal Rev* 39: 33–52.
- Bahamonde H, Peri P, Monelos L, Martínez Pastur G. 2011. Aspectos ecológicos de la regeneración por semillas en bosques nativos de *Nothofagus antarctica* en Patagonia Sur, Argentina. *Bosque* 32: 20–29.
- Barrera MD, Frangi JL, Richter L, Perdomo M, Pinedo L. 2000. Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. *J Veg Sci* 11: 179–188.

- Bitterlich W. 1984. The relascope idea. Relative measurements in forestry. London, UK: Commonwealth Agricultural Bureaux.
- Blasi C, Marchetti M, Chiavetta U, Aleffi M, Audisio P, Azzella M, Brunialti G, Capotorti G, Del Vico E, Lattanzi E, Persiani A, Ravera S, Tilia A, Burrascano S. 2010. Multi-taxon and forest structure sampling for identification of indicators and monitoring of old-growth forest. *Plant Biosystems* 144: 160–170.
- Blood LE, Titus JH. 2010. Microsite effects on forest regeneration in a bottomland swamp in western New York. *J Torrey Bot Soc* 137: 88–102.
- Caldentey J, Ibarra M, Hernández J. 2001. Litter fluxes and decomposition in *Nothofagus pumilio* stands in the region of Magallanes, Chile. *For Ecol Manage* 148: 145–157.
- Caldentey J, Mayer H, Ibarra M, Promis A. 2009. The effects of a regeneration felling on photosynthetic photon flux density and regeneration growth in a *Nothofagus pumilio* forest. *Eur J For Res* 128: 75–84.
- Chen J, Franklin JF, Spies TA. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agric For Meteorol* 63: 219–237.
- Chen J, Franklin JF, Spies TA. 1995. Growing-season microclimate gradients from clearcut edges into old-growth Douglas-fir forests. *Ecol Appl* 5: 74–86.
- Corona P, Blasi C, Chirici G, Facioni L, Fattorini L, Ferrari B. 2010. Monitoring and assessing old-growth forest stands by plot sampling. *Plant Biosystems* 144: 171–179.
- Correa MN. 1969–1998. Flora Patagónica. Colección Científica INTA Tomo 8. Parts II, III, IVb, V, VI y VII. Buenos Aires, Argentina.
- Cruz G, Caldentey J. 2007. Caracterización, silvicultura y uso de los bosques de Coihue de Magallanes (*Nothofagus betuloides*) en la XII Región de Chile. CONICYT FONDEF. Santiago, Chile. 126 pp.
- Cruz G, Caprile Navarro R, Promis A, Cabello G. 2007. Structural and biometric characterization of *Nothofagus betuloides* production forests in the Magellan Region, Chile. *J Sustain Forest* 24(2): 123–140.
- Cruz G, Schmidt H, Cabello G, Hidalgo F. 2005. Caracterización estructural y dasométrica de los bosques de producción de coihue de Magallanes. Proyecto FONDEF “Incorporación de los bosques de coihue de Magallanes al manejo forestal para la diversificación e incremento de la producción en la XII Región”. Universidad de Chile. Santiago, Chile. 30 pp.
- Cuevas J. 2000. Tree recruitment at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego, Chile. *Ecology* 88: 840–855.
- Cuevas J. 2002. Episodic regeneration at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego, Chile. *Ecology* 90: 52–60.
- Cuevas J, Arroyo MK. 1999. Ausencia de banco de semillas persistente en *Nothofagus pumilio* (Fagaceae) en Tierra del Fuego, Chile. *Rev Chil Hist Nat* 72: 73–82.
- Donoso C, Donoso P. 2006. *Nothofagus betuloides* (Mirb.) Oersted. In: Donoso C, editor. Las Especies arbóreas de los Bosques Templados de Chile y Argentina: Autoecología. Valdivia, Chile: Marisa Cúneo Ediciones. pp. 411–422.
- During HJ. 1979. Life strategies of bryophytes: A preliminary review. *Lindbergia* 5: 2–18.
- Frangi JL, Barrera MD, Puigdefábregas J, Yapura PF, Arambarri AM, Richter L. 2005. Ecología de los bosques de Tierra del Fuego. In: Arturi MF, Frangi JL, Goya JF, editors. Ecología y manejo de los bosques de la Argentina. La Plata, Argentina: Universidad Nacional de La Plata. pp. 1–88.
- Frazer GW, Fournier RA, Trofymow JA, Gall RJ. 2001. A comparison of digital and film fisheye photography for analysis of forest canopy structure and gap light transmission. *Agric For Meteorol* 109: 249–263.
- Gea G, Martínez Pastur G, Cellini JM, Lencinas MV. 2004. Forty years of silvicultural management in southern *Nothofagus pumilio* (Poepp. et Endl.) Krasser primary forests. *For Ecol Manage* 201: 335–347.
- Gerding V, Thiers O. 2002. Caracterización de los suelos bajo bosques de *Nothofagus betuloides* (Mirb.) Blume, en Tierra del Fuego, Chile. *Rev Chil Hist Nat* 75: 819–833.
- Gutiérrez E. 1994. Els boscos de *Nothofagus* de la Terra del Foc com a paradigma de dinàmica successional del no-equilibri. *Treballs de la SCB* 45: 93–121.
- Heinemann K, Kitzberger Th, Veblen Th. 2000. Influences of gap microheterogeneity on the regeneration of *Nothofagus pumilio* in a xeric old-growth forest of northwestern Patagonia, Argentina. *Can J For Res* 30: 25–31.
- Heinemann K, Kitzberger Th. 2006. Effects of position, understorey vegetation and coarse woody debris on tree regeneration in two environmentally contrasting forests of north-western Patagonia: a manipulative approach. *J Biogeogr* 33: 1357–1367.
- Heithecker TD, Halpern CB. 2007. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. *For Ecol Manage* 248: 163–173.
- Hörnberg G, Ohlson M, Zackrisson O. 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forest. *Can J For Res* 27: 1015–1023.
- Keeton WS, Franklin JF. 2005. Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecol Mon* 75: 103–118.
- Kelly D. 1994. The evolutionary ecology of mast seeding. *Trends Ecol Evol* 9: 465–470.
- Kelly D, Harrison AL, Lee WG, Payton IJ, Wilson PR, Schaub EM. 2000. Predator satiation and extreme mast seeding in 11 species of *Chionochloa* (Poaceae). *Oikos* 90: 477–488.
- Kelly D, Sork VL. 2002. Mast seeding in perennial plants: why, how, where? *Ann Rev Ecol Syst* 33: 427–447.
- Koenig WD, Knops JM. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. *Am Nat* 155: 59–69.
- Kupferschmid AD, Bugmann H. 2005. Effects of microsites, logs and ungulate browsing on *Picea abies* regeneration in a mountain forest. *For Ecol Manage* 205: 251–265.
- Lencinas MV, Martínez Pastur G, Moretto A, Gallo E, Busso C. 2007. Productividad diferencial de plántulas de *Nothofagus pumilio* bajo gradientes de luz y humedad del suelo. *Bosque* 28: 241–248.
- Lencinas MV, Martínez Pastur G, Rivero P, Busso C. 2008. Conservation value of timber quality versus associated non-timber quality stands for understory diversity in *Nothofagus* forests. *Biodiv Conserv* 17: 2579–2597.
- Lieffers V, Messier C, Gendron F, Stadt K, Comeau P. 1999. Predicting and managing light in understory of boreal forests. *Can J For Res* 29: 796–811.
- Marchetti M, Tognetti R, Lombardi F, Chiavetta U, Palumbo G, Sellitto M, Colombo C, Iovieno P, Alfani A, Baldantoni D, Barbati A, Ferrari B, Bonacquisti S, Capotorti G, Copiz R, Blasi C. 2010. Ecological portrayal of old-growth forests and persistent woodlands in the Cilento and Vallo di Diano National Park (southern Italy). *Plant Biosystems* 144: 130–147.
- Martínez Pastur G, Cellini JM, Lencinas MV, Barrera M, Peri PL. 2011. Environmental variables influencing regeneration of *Nothofagus pumilio* in a system with combined aggregated and dispersed retention. *For Ecol Manage* 261: 178–186.
- Martínez Pastur G, Cellini JM, Peri P, Lencinas MV, Gallo E, Soler Esteban R. 2009. Alternative silviculture with variable retention in timber management of South Patagonia. *For Ecol Manage* 258: 436–443.

- Martínez Pastur G, Cellini JM, Peri P, Vukasovic R, Fernández C. 2000. Timber production of *Nothofagus pumilio* forests by a shelterwood system in Tierra del Fuego (Argentina). For Ecol Manage 134: 153–162.
- Martínez Pastur G, Lencinas MV, Escobar J, Quiroga P, Malmierca L, Lizarralde M. 2006. Understorey succession in *Nothofagus* forests in Tierra del Fuego (Argentina) affected by *Castor canadensis*. Appl Veg Sci 9: 143–154.
- Martínez Pastur G, Lencinas MV, Peri P, Arena M. 2007. Photosynthetic plasticity of *Nothofagus pumilio* seedlings to light intensity and soil moisture. For Ecol Manage 243: 274–282.
- Martínez Pastur G, Peri P, Fernández C, Staffieri G, Lencinas MV. 2002. Changes in understory species diversity during the *Nothofagus pumilio* forest management cycle. J For Res 7: 165–174.
- Massaccesi G, Roig F, Martínez Pastur G, Barrera M. 2008. Growth patterns of *Nothofagus pumilio* trees along altitudinal gradients in Tierra del Fuego, Argentina. Trees 22: 245–255.
- Matteri C, Schiavone M. 1988. Comunidades muscinales del suelo de los bosques de *Nothofagus* fueguinos. Monografías de la Academia Nacional de Ciencias Exactas, Físicas y Naturales 4: 25–36.
- Messier C, Doucet R, Ruel J, Claveau Y, Kelly C, Lechowicz J. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can J For Res 29: 812–823.
- Mittermeier R, Mittermeier C, Robles-Gil P, Pilgrim J, Fonseca G, Brooks J, Konstant J. 2002. Wilderness: Earth's last wild places. Washington: EEUU, Cemex and Conservation International. 573 pp.
- Monks A, Kelly D. 2006. Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). Austral Ecol 31: 366–375.
- Moore DM. 1983. Flora of Tierra del Fuego. London, UK: Anthony Nelson – Missouri Botanical Garden.
- Peri P, Martínez Pastur G, Lencinas MV. 2009. Photosynthetic and stomatal conductance responses to different light intensities and water status of two main *Nothofagus* species of south Patagonian forest. For Sci 55: 101–111.
- Promis A. 2009. Natural small-scale disturbances and below-canopy solar radiation effects on the regeneration patterns in a *Nothofagus betuloides* forest: A case study from Tierra del Fuego, Chile. PhD thesis, Faculty of Forest and Environmental Sciences. Freiburg, Germany. 186 pp.
- Promis A, Caldentey J, Ibarra M. 2010a. Microclima en el interior de un bosque de *Nothofagus pumilio* y el efecto de una corta de regeneración. Bosque 31: 129–139.
- Promis A, Gartner S, Reif A, Cruz G. 2010b. Effects of natural small-scale disturbances on below-canopy solar radiation and regeneration patterns in an old-growth *Nothofagus betuloides* forest in Tierra del Fuego, Chile. Allgemeine Forst und Jagdzeitung 181: 53–64.
- Rebertus A, Veblen T. 1993. Structure and tree-fall gap dynamics of old-growth *Nothofagus* forests in Tierra del Fuego, Argentina. J Veg Sci 4: 641–654.
- Robison SA, McCarthy BC. 1999. Potential factors affecting the estimation of light availability using hemispherical photography in oak forest understories. Bull Torrey Bot Club 126: 344–349.
- Roig FA, Anchorena J, Dollenz O, Faggi AM, Mendez E. 1985. Las comunidades vegetales de la Transecta Botánica de la Patagonia Austral. In: Boelcke O, Moore DM, Roig FA, editors. Transecta Botánica de la Patagonia Austral. Buenos Aires, Argentina: CONICET, Royal Society, Instituto de la Patagonia. pp. 350–456.
- Roxburgh JR, Kelly D. 1995. Uses and limitations of hemispherical photography for estimating forest light environments. NZ J Ecol 19: 213–217.
- Rozzi R, Massardo F, Berghoefer A, Anderson CB, Mansilla A, Mansilla M, Plana J. 2006. Reserva de Biósfera Cabo de Hornos. Punta Arenas, Chile: Ediciones de la Universidad de Magallanes. 274 pp.
- Sabovljevic M, Vujicic M, Sabovljevic A. 2010. Diversity of saproxylic bryophytes in old-growth and managed beech forests in the central Balkans. Plant Biosystems 144: 234–240.
- Schmidt MG, Ogden AE, Lertzman KP. 1998. Seasonal comparison of soil temperature and moisture in pits and mounds under vine maple gaps and conifer canopy in a coastal western hemlock forest. Can J Soil Sci 78: 291–300.
- Spagarino C, Martínez Pastur G, Peri P. 2001. Changes in *Nothofagus pumilio* forest biodiversity during the forest management cycle: Insects. Biodiv Conserv 10: 2077–2092.
- Stenburg P, Linder S, Smolander H, Flower-Ellis J. 1994. Performance of the LAI-2000 plant canopy analyzer in estimating leaf area index of some Scots pine stands. Tree Physiol 14: 981–995.
- Sun OJ, Sweet GB, Whitehead D, Buchan GD. 1995. Physiological responses to water stress and waterlogging in *Nothofagus* species. Tree Physiol 15: 629–638.
- Ter Braak CJF, Šmilauer P. 2002. CANOCO reference manual and CanoDraw for Windows User's guide: software for canonical community ordination. Version 4.5. Ithaca, New York: Microcomputer Power.
- Toivanen T, Kotiaho JS. 2007. Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity. Biodiv Conserv 16: 3193–3211.
- Tognetti R, Minotta G, Pinzauti S, Michelozzi M, Borghetti M. 1998. Acclimation to changing light conditions of long-term shade-grown beech (*Fagus sylvatica*) seedlings of different geographic origins. Trees 12: 326–333.
- Veblen T, Donoso C., Schlegel M, Escobar R. 1981. Forest dynamics in south-central Chile. J Biogeog 8: 211–247.
- Vodde F, Jogiste K, Gruson L, Ilisson T, Koster K, Stanturf JA. 2010. Regeneration in windthrow areas in Hemiboreal forests: The influence of microsite on the height growths of different tree species. J For Res 15: 55–64.
- Wardle JA. 1970. The ecology of *Nothofagus solandri*: 3. regeneration. NZ J Bot 8: 571–608.
- Wardle JA. 1974. Ecology and management of south Island beech forests: The life history of mountain beech (*Nothofagus solandri* var. *cliffortioides*). NZ Ecol Soc 21: 21–26.

Table A1. Mean cover (%) of understory plant species in the study sites (CL, CH, VL, VH) in *Nothofagus betuloides* forests.

Species	Type	CL	CH	VL	VH	Code
<i>N. betuloides</i> (Mirb.) Oerst.	T	3.2	15.9	17.5	12.8	NOBE
<i>N. pumilio</i> (Poepp. & Endl.) Krasser	T	0.8	0.5	2.0	2.5	NOPU
<i>Drymis winteri</i> Forster & Forster f.	T	4.0				DRWI
<i>Maytenus magellanica</i> (Lam.) Hooker f.	T	1.7				MAMA
<i>Embothrium coccineum</i> Forster & Forster f.	T	1.0				EMCO
<i>Empetrum rubrum</i> Vahl ex Willd.	S		31.5	2.0	2.0	EMRU
<i>Chiliodotium diffusum</i> (Forster f.) O. Kuntze	S	1.0	10.0			CHDI
<i>Berberis buxifolia</i> Lam.	S		5.5		2.0	BEBU
<i>Pernettya pumila</i> (L. f.) Hooker	S	1.0	3.4	1.9	5.8	PEPU
<i>P. mucronata</i> (L. f.) Gaudich ex G. Don.	S	1.3	2.4		2.0	PEMU
<i>Ribes magellanicum</i> Poiret	S			3.0		RIMA
<i>Acaena ovalifolia</i> Ruiz & Pavón	H	2.0				ACOV
<i>Adenocaulon chilense</i> Less.	H	1.0		3.0		ADCH
<i>Cardamine glacialis</i> (Forster f.) DC.	H	1.3				CAGL
<i>Dysopsis glechomoides</i> (A. Richard) Müller Arg.	H	1.0		3.0		DYGL
<i>Gunnera magellanica</i> Lam.	H		1.0		1.0	GUMA
<i>Hieracium murorum</i> L.	H	1.0				HIMU
<i>Macrachaenium gracile</i> Hooker f.	H	2.0	1.8	1.0	0.1	MAGR
<i>Osmorhiza depauperata</i> Phil.	H	3.2				OSDE
<i>Rubus geoides</i> Sm.	H		6.8	5.0	3.3	RUGE
<i>Senecio acanthifolius</i> Hombrom & Jacquinet	H		4.7	1.0	1.8	SEAC
<i>Viola magellanica</i> Forster f.	H	5.0	0.5	3.0		VIMA
<i>Codonorchis lessonii</i> (D'Urv.) Lindley	M	2.0	0.5	3.5	0.5	COLE
<i>Agrostis uliginosa</i> Phil.	M		0.1			AGUL
<i>Uncinia lechleriana</i> Steudel	M	0.5	0.5			UNLE
<i>Marsippospermum grandiflorum</i> (L. f.) Hooke f.	M				0.5	MSGR
<i>Luzuriaga marginata</i> (Banks & Sol. ex Gaertner) Benth & Hooker f.	M	2.1			2.3	LUMA
<i>Blechnum penna-marina</i> (Poiret) Kuhn	F	7.3	0.1	1.0		BLPE
<i>Hymenophyllum secundum</i> Hooker & Grev.	F		11.5	3.0	0.8	HYSE

CL, coast in low altitude; CH, coast in high altitude; VL, mountain valley in low altitude; VH, mountain valley in high altitude; T, trees; S, shrubs; H, herbs; M, monocots; F, ferns.