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

(With 3 Figures and 6 Tables)

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1. INTRODUCTION

Small-scale canopy disturbances, although less severe than large disturbances in changing forest structure, may be more frequent and affect a larger area over time (SPIES et al., 1990). The severity of such disturbances can stimulate a change in the growth rates of the surviving trees (OLIVER and LARSON, 1996) through increasing the availability of the resources (light, soil moisture, nutrients, microhabitats) and promoting plant growth (DENSLOW, 1980; CANHAM and MARKS, 1985; RUNKLE, 1985; VEBLEN, 1992). The regeneration dynamics are affected by the heterogeneity of resources in forests (CANHAM et al., 1994). Nevertheless, advance regeneration, present and growing slowly beneath a forest canopy, has a potential advantage because they are in a position to respond to the creation of canopy gaps following small-scale disturbances (OLIVER and LARSON, 1996; MESSIER et al., 1999). This has been observed in old-growth *Nothofagus betuloides* forests where an abundance of understorey trees can persist in excess of one hundred years (REBERTUS and VEBLEN, 1993a; VEBLEN et al., 1996) until the creation of a gap when they can grow into the canopy (VEBLEN et al., 1996).

The structure of the *Nothofagus* forests of Tierra del Fuego is principally shaped by wind that acts as an agent of large and small-scale disturbance (REBERTUS et al., 1997; PUIGDEFÁBREGAS et al., 1999). The windthrow of individual trees creates canopy gaps smaller than 200 m^2 (REBERTUS and VEBLEN, 1993a; GUTIÉRREZ, 1994). In pure old-growth *N. betuloides* forests in Tierra del Fuego discrete gaps might not be apparent, as they mostly occur as interwoven gap complexes in the canopy layer (REBERTUS and VEBLEN, 1993a). Small canopy gaps (51 m^2 on average) were observed in a pure uneven-aged *N. betuloides* forest, while somewhat larger gaps (107 m^2) were recorded in a mixed uneven-aged *N. betuloides – Nothofagus pumilio* forest (PROMIS, 2009). Wavelike patterns of gap formation have been documented for pure *N. betuloides*, pure *N. pumilio* and for mixed *N. betuloides – N. pumilio* forests in Tierra del Fuego, in sites predisposed to wind disturbance (REBERTUS and VEBLEN, 1993b; REBERTUS et al., 1993; PUIGDEFÁBREGAS et al., 1999). Moreover, a patch mosaic pattern has been found in these *Nothofagus* forests forming multicohort stands with patches of younger trees alongside larger patches of old-growth forest (GUTIÉRREZ et al., 1991).

The small-scale disturbances mentioned above appear to be important in the regeneration dynamics of southern South American *Nothofagus* forests situated at higher elevations and at higher latitudes where the diversity of tree species is low (VEBLEN et al., 1996; POLLMANN and VEBLEN, 2004), as is the case for forests in Tierra del Fuego. *N. betuloides* is capable of establishing beneath small tree-fall canopy gaps (REBERTUS and VEBLEN, 1993a; GUTIÉRREZ, 1994; ARROYO et al., 1996). Seedlings and saplings present on the ground at the time of gap formation are also released by the creation of these small-scale disturbances in the canopy (VEBLEN et al., 1996; PROMIS, 2009). The successful establishment and growth of young *N. betuloides* can be impeded where the ground cover of understorey trees and shrubs such as *Drymis winteri* and *Maytenus magellanica* is high (REBERTUS et al., 1993a; GUTIÉRREZ et al., 1991; GUTIÉRREZ, 1994; VEBLEN et al., 1996).

There are still knowledge gaps regarding the effects of small-scale disturbances on the regeneration dynamics of old-growth *N. betuloides* forests. It is not known to which degree these small canopy gaps increase the horizontal heterogeneity due to a gradient in below-canopy solar radiation transmittances; and if there are differences in solar radiation transmittances influencing the density and growth rates of the young trees in old-growth forests. The influence of canopy gaps on the browsing habits of *Lama guanicoe* (guanaco) and the age distribution of the young trees in an old-growth *N. betuloides* forest are also unknown.

In Chile today *N. betuloides* forests suitable for timber production can be managed under either a selection or a shelterwood system (DONOSO, 1981), designed to promote natural regeneration after logging. But many stands are hardly managed at all, as regeneration cutting is the only part of the shelterwood system that is implemented (CRUZ et al., 2007), resulting in a homogenisation and simplification of the typically uneven-aged structure of this forest type (CRUZ et al., 2008). Because there are currently plans to intensify the utilisation of *N. betuloides* forests, it is necessary to obtain a better grasp of their natural dynamics. The management of these still very natural forests should be based on an ecological understanding of natural stand development. This includes the role of small scale natural disturbances (MITCHELL et al., 2002), that provide the basis upon which the forest may be managed as a renewable resource while maintaining a functioning biological system in which a high diversity of species is retained (ATTIWILL, 1994 a,b; COATES and BURTON, 1997; FRANKLIN et al., 2002).

The hypothesis central to this study was that the establishment and growth of *N. betuloides* seedlings and saplings are affected by both the occurrence of small-scale gap disturbances and the resulting solar radiation gradient from the centre of a gap to areas

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beneath the undisturbed forest canopy. The objectives of this study were to determine the effects of natural small-scale disturbances (1) on the below-canopy solar radiation conditions, (2) on the regeneration patterns (density and growth rates) of *N. betuloides*, and (3) on the browsing damage caused by by *Lama guanicoe*.

2. MATERIALS AND METHODS

2.1 Study area

The study was conducted in an old-growth, uneven-aged evergreen *N. betuloides* forest (20 ha, 1,362 trees ha^{-1}, 105 m^2 ha^{-1}) with no direct evidence of human impact. The stand belongs to the pure evergreen *N. betuloides* forest type described in PROMIS et al. (2008). Soil conditions varied within the stand ranging from shallow podsols on well-drained sites to deep organic soils under waterlogged conditions. The forest soil is covered by a thick layer of partially decomposed organic matter. The ground vegetation is species poor, most dominant are mosses and liverworts on decaying tree trunks that lie on the forest floor (PROMIS, 2009). The stand is located at the 'Estancia Olguita' on the southeastern side of the Río Cóndor (53°59' S, 69°58' W) and on the southwestern Chilean side of Tierra del Fuego (*Fig. 1*).

The climate of the area belongs to the Northern Antiboreal subzone which has a mean air temperature of 9.0–9.5 °C in the warmest month of the year and remains above zero in the coldest month. The mean annual precipitation is around 500–600 mm, but can reach 900 mm. The wind direction is commonly west to southwest with speeds that average between 14–22 km h^{-1} and with a maximum wind speed of more than 100 km h^{-1} (TUHKANEN, 1992).

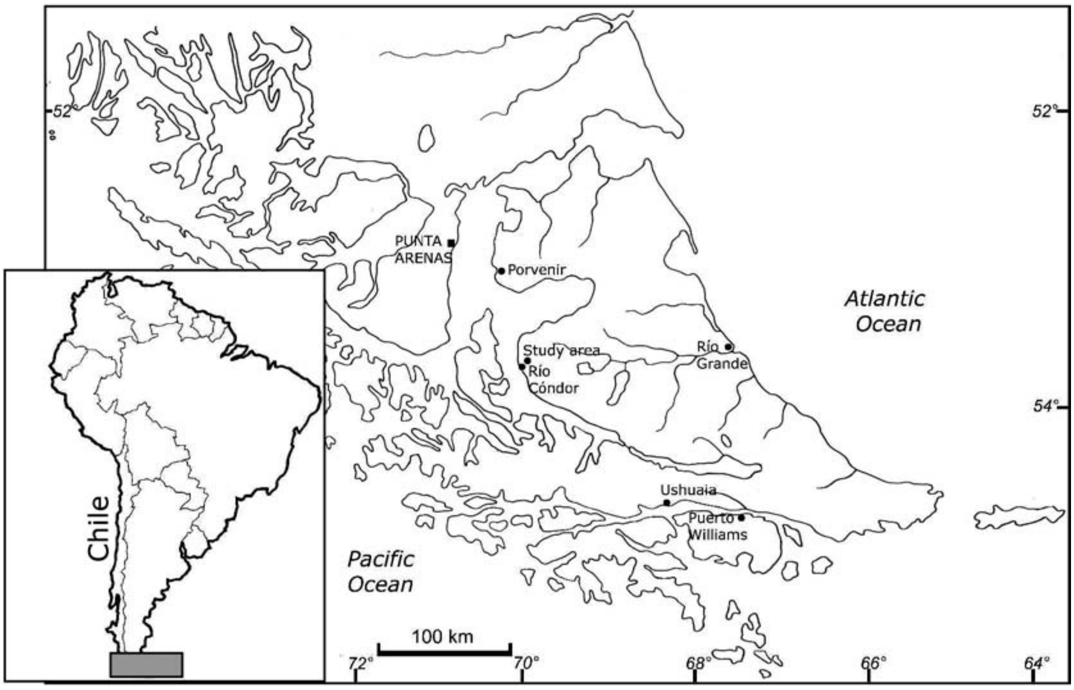

Fig. 1

Map of South America and Tierra del Fuego showing the study area on the Río Cóndor.

Karte von Südamerika und Feuerland mit Lage des Untersuchungsgebietes am Río Cóndor.

Tab. 1

Characteristics of the 13 selected canopy gaps. Mean and range, values in brackets are standard errors.

Beschreibung der 13 Bestandeslücken (Mittelwerte und Wertebereich, Standardfehler in Klammern).

	Canopy gap area (m^2)	Expanded gap* area (m^2)	Gap-makers** per gap
Mean	47 (± 6.3)	167 (± 11.7)	2 (± 0.3)
Range	21-92	110-278	1-5

* The 'expanded gap' was defined as the area formed by the gap in the canopy plus the adjacent area delimited by the bases of the edge trees (RUNKLE, 1982).

** Gap-makers are the trees that whose whole or partial deaths created the gap (RUNKLE, 1992).

2.2 Selection of canopy gaps

A 'gap' was defined as the horizontal projection of a canopy opening to the ground surface (RUNKLE, 1982), larger than or equal to 20 m^2 in area, and was considered to be closed if the vegetation growing below the gap was more than 2 m in height. A total of 25 canopy gaps were found in a *N. betuloides* stand used in a previous study of canopy gaps and disturbance dynamics in Tierra del Fuego (PROMIS, 2009).

For this study 13 canopy gaps (*Tab. 1*) out of the 25 were selected. In order to keep site conditions other than light as constant as possible, only canopy gaps occurring on podsolic, well-drained and shallow soils (< 50 cm) were selected. Canopy gaps on waterlogged sites were not included.

2.3 Seedling and sapling measurements

All seedlings and saplings present in plots measuring 4 m^2 (2 x 2 m) were counted during the summer of 2006. The plots were located along a gradient of expected change in solar radiation conditions for which transects running from areas beneath undisturbed canopy to the centre of canopy gaps were established.

Five plots were established in and around each canopy gap. One plot was located in the centre of the gap, two at the edges of the gap (southeast and northwest of centre), and two more below undisturbed canopy at a distance of half the height of the highest tree in the vicinity of the gap (26 m ± 0.9). This distance was measured from the bases of the trees at the edges of the gap.

The tree seedlings and saplings were counted according to the following classes: germinant and non-lignified, lignified and ≤ 20 cm tall, 21-50 cm tall, 51-100 cm tall, 100-200 cm tall and ≤ 5 cm at dbh. The juvenile trees in each height class browsed by *L. guanicoe* were counted. A sign of browsing was considered as low browsing damage in the foliage to the loss of the apical dominance.

The height of the tallest seedling or sapling in each plot was measured, and its annual height increments over the previous 5 years reconstructed by measuring the lengths between the bud scale scars. These plants were harvested and a stem disc was cut from the root collar in order to measure the diameter, age and the width of the last 10 annual growth increments where this was possible. The diameter at the root collar of the harvested seedlings and saplings ranged from 1.5 to 25 mm and the length from 12 to 248 cm. All discs (n = 65) were dried, sanded and processed at the Department of Silviculture of the University of Chile. Ring widths were recorded to the nearest 0.01 mm using a microscope.

Analysis of absolute height and radius growth for the last complete annual height and radial increment (2005) were conducted, because of the lack of any solar radiation data for the previous years. Absolute growth values were used for further analysis to provide better understandable results compared to relative values (KNEESHAW et al., 2002).

2.4 Measuring below-canopy solar radiation

The transmission of the solar radiation was estimated indirectly using hemispherical photographs. During the summer 2006 a total of 65 hemispherical photographs were taken at 1.3 m above the ground with a Nikon Coolpix 990® digital camera (Nikon Corporation, Tokyo, Japan) fitted with a Nikon FC-E8® fisheye converter (Nikon Corporation, Tokyo, Japan), one at the centre of each sampling plot. The camera was oriented to magnetic north.

The digital images were processed following the method developed by BRUNNER (2002), including the manual setting of a threshold value to separate canopy and sky elements into a binary black and white image (ANDERSON, 1964). All images were analysed using HemiView version 2.1 (Delta-T Devices, Cambridge, UK) (RICH et al., 1999). Using the Coolpix 900 option (HALE and EDWARDS, 2002) the lens distortion was corrected. A universal overcast sky (UOC) model was used to describe the intensity of the diffuse radiation (STEVEN and UNSWORTH, 1980). The model assumes all regions of the sky to be equally bright. As no actual measurements of the diffuse and direct radiation were available for the study area, a relative proportion of direct and diffuse radiation equal to 0.5 was assumed (CANHAM et al., 1990).

Direct, diffuse and global solar radiation transmissions were estimated for the growing season (between October and March). The outputs were non-cosine-corrected, which was desirable for the purposes of measuring solar radiation from all directions (RICH, 1990; BRUNNER, 1998).

2.5 Statistical analysis

In order to contrast the variation in the density of seedlings and saplings (plants m^{-2}), and the numbers of plants browsed by *L. guanicoe*, the values calculated for the centre of the canopy gaps, the two gap edges and beneath the closed canopy were compared using the non-parametric Kruskal-Wallis H-test, and the Mann-Whitney U-test as a post-hoc test, because these variables did not meet the requirements of normality and homogeneity of variances (SOKAL and ROHLF, 2000).The variation of the non-cosine-corrected solar radiation (direct, diffuse and global), and the absolute radial and height growth between areas in disturbed and beneath undisturbed canopies were analysed using a one-way ANOVA, and the Tukey test as a post-hoc test. The hypothesis tested was that the variables mentioned above were derived from the same population. Acceptance of the null hypothesis would mean that there was no difference between the values obtained beneath each of the canopy situations analysed.

Spearman's rank correlation was used to explore the association between the transmission of the non-cosine-corrected solar radiation (direct, diffuse and global) and the density of the regeneration classed by height.

A stepwise multiple linear regression analysis was performed to analyse the effect of the predictor variables age and the size (height or radius) of the plants and the transmission of the direct, diffuse or global solar radiation estimated during the growing season on radius and height growths of the seedlings. Levels of $p \leq 0.05$ and ≥ 0.10 were set for parameters to add or to remove the models, respectively. This procedure was used in order to find the best set of predictor variables (SOKAL and ROHLF, 2000). All statistical analyses were carried out using SPSS 15.0 for Windows (SPSS, Inc.).

3. RESULTS

3.1 Transmission of solar radiation

The transmission of the direct solar radiation into the forest during the growing season ranged between 3.2–19.4% of the above canopy solar radiation. The highest average value (9.5%) was observed under an undisturbed canopy, to the southeast of the gap centre. However, this did not differ significantly (n = 13, $p > 0.05$) from the 8.2% below-canopy direct solar radiation estimated in the gap centre, the 8.0% at the southeastern gap edge and the 8.2% recorded beneath the closed canopy to the northwest of the gap centre. The values estimated for the northwestern edges of the gaps by contrast were significantly lower (average 5.5%) (*Tab. 2*).

The transmission of the below-canopy diffuse solar radiation ranged between 3.2 and 16.7% of the solar radiation above the canopy (*Tab. 2*). The highest values were found in the gap centres (average 8.7%) and at the edges (7.8% to the southeast and 7.1% to the northwest). These values did not differ significantly (n = 13, $p > 0.05$). Lower, albeit not significantly different, diffuse solar

Tab. 2

Descriptive statistics for the transmission of the non-cosine-corrected direct, diffuse and global solar radiation estimated during the growing season in different locations in the forest – in gaps, at gap edges and beneath undisturbed canopies. The standard error is in brackets. Identical letters indicate no significant difference between the different locations in the forest (One-way ANOVA and Tukey test as a post-hoc test, p > 0.05, n = 13).

Deskriptive Statistik für die direkte, diffuse und Gesamteinstrahlung in verschiedenen Bereichen im *N. betuloides*-Wald – in Lücken, am Lückenrand, und im Bestand (Standardfehler in Klammern). Gleiche Buchstaben deuten an, dass keine signifikanten Unterschiede zwischen den Bereichen bestehen (One-way ANOVA und Tukey test als post-hoc test, p > 0.05, n = 13).

Non-cosine-corrected solar radiation transmittances		Gap	Gap edge		Closed canopy	
			SE	NW	SE	NW
Direct	Mean	8.2 ab	8.0 ab	5.5 b	9.5 a	8.2 ab
	(SE)	(1.0)	(0.9)	(0.8)	(0.7)	(1.1)
	Range	4.5-19.4	3.8-15.5	3.2-11.9	5.8-13.8	4.0-17.8
Diffuse	Mean	8.7 a	7.8 ab	7.1 ab	6.1 b	6.3 b
	(SE)	(0.8)	(0.4)	(0.5)	(1.0)	(1.5)
	Range	5.8-16.7	5.4-10.2	3.2-11.0	4.0-7.7	3.1-8.8
Global	Mean	8.6 a	7.9 a	6.6 a	7.2 a	6.9 a
	(SE)	(0.8)	(0.5)	(0.8)	(0.3)	(0.5)
	Range	6.2-17.6	5.2-11.9	3.2-9.9	5.0-8.5	3.6-10.6

radiation transmittances were estimated beneath undisturbed canopies (6.1–6.3%). These were also similar to the values estimated at the edges of the gaps.

The range of the transmission of the global solar radiation lay between 3.2 and 17.6% of the total above canopy solar radiation (*Tab. 2*). Although the transmittances in the gap centre were higher (average 8.6%), there was no significant difference (n = 13, p > 0.05) between this value and the values for the gap edges (7.9% to the southeast and 6.6% to the northwest) or beneath the undisturbed canopy (7.2% to the southeast and 6.9% to the northwest).

3.2 Seedling and sapling density and the influence of solar radiation

Seedlings and saplings were generally present in all of the plots, but with a high degree of variation in density, which ranged between 2 and 93 plants m^{-2}. The total density did not differ significantly between any of the gap situations (n = 13, p > 0.05). The density ranged from an average of 16.9 plants m^{-2} beneath the closed canopy to the southeast of the gap centre and 24.4 plants m^{-2} beneath the closed canopy to the northwest of the gap centre. There was no significant difference in terms of the density of the young trees under the different canopy gap situations in the height classes analysed. The highest numbers of seedlings found were in the height class ≤ 20 cm, with a range of 1 to 86 plants m^{-2} and averages of between 12.2-19.9 plants m^{-2}. The other height classes were characterised by lower plant densities, with ranges between 0 and 6 germinants and non-lignified plants m^{-2}, 0 to 10 seedlings m^{-2} in the class 21–50 cm tall, 0 to 8 plants m^{-2} between 51–100 cm tall, and 0 to 5 plants m^{-2} in the class 101–200 cm tall (*Tab. 3*).

The average rates of browsing by *L. guanicoe* were low (between 0.7 and 2.8% of all seedlings and saplings of *N. betuloides* sampled). *L. guanicoe* did not exhibit any preference as young trees were damaged in both gaps and beneath undisturbed canopy (n = 13, p > 0.05). Seedlings and saplings belonging to the following height classes, ≤ 20 cm tall, 21–50 cm tall and 51–100 cm tall, showed some sign of browsing (*Tab. 3*).

Albeit low, there was a significant correlation between the transmission of the non-cosine-corrected solar radiation and the density of young trees in the height classes 21–50 cm and 51–100 cm (*Tab. 4*). The density of young trees between 21–50 cm revealed a positive correlation with the transmission of the direct (Spearman rank correlation coefficient: 0.319) and global solar radiation (Spearman rank correlation coefficient: 0.405), and also with the transmission of the diffuse solar radiation (Spearman rank correlation coefficient: 0.293). The density of young trees in the height class 51–100 cm was correlated with the transmission of the diffuse and global solar radiation (Spearman rank correlation coefficient: 0.275 and 0.335, respectively). The density of seedlings (germinant and non-lignified, lignified and ≤ 20 cm tall) and saplings (101–200 cm) showed no relation to the transmittances of any type of below-canopy solar radiation. The transmission of the global solar radiation into the forest correlated with the overall young tree density (Spearman rank correlation coefficient: 0.284).

3.3 Height and radial growth of seedlings and saplings and the influence of their size, their age and the transmitted solar radiation

The absolute height growth of seedlings and saplings ranged between 1.5 and 24.0 cm $year^{-1}$ (*Tab. 5*). The highest values were found at the northwestern edge of the gaps (average 11.8 cm $year^{-1}$), followed by the gap centres (9.9 cm $year^{-1}$) and at the southeastern edge of the gaps (8.7 cm $year^{-1}$). Lower absolute height growth was found beneath the undisturbed canopy locations (6.0 and 6.6 cm $year^{-1}$). There was no significant difference between the different locations in the forest. Albeit low, the stepwise multiple linear regression analysis revealed a significant relationship between the

Tab. 3

Density of the young trees (plants m^{-2}) and percentage of plants browsed by *Lama guanicoe* at different locations in the forest – in gaps, at gap edges and beneath undisturbed canopy. The standard error is in brackets. Identical letters indicate no significant difference between the different locations in the forest (Kruskal-Wallis H-test and Mann-Whitney U-test as a post-hoc test, p > 0.05, n = 13).

Dichte der Jungbäume (Individuen m^{-2}) und prozentualer Anteil von durch *Lama guanicoe* verbissenen Pflanzen in den verschiedenen Bestandesbereichen – in Lücken, am Lückenrand, und im Bestand (Standardfehler in Klammern). Gleiche Buchstaben deuten an, dass keine signifikanten Unterschiede zwischen den Bereichen bestehen (Kruskal-Wallis H-test und Mann-Whitney U-test als post-hoc test, p > 0.05, n = 13).

Height classes (cm)		Gap	Gap edge		Closed canopy	
			SE	NW	SE	NW
Germinants and non-lignified	Mean	0.9 a (0.2)	1.6 a (0.5)	0.4 a (0.1)	0.8 a (0.2)	0.9 a (0.3)
	Range	0 – 2	0 – 6	0 – 2	0 – 3	0 – 4
	Browsed (%)	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a
≤ 20 cm tall	Mean	12.5 a (1.6)	15.9 a (3.1)	13.5 a (3.0)	12.2 a (2.2)	19.0 a (5.9)
	Range	4 - 24	1 – 40	4 - 43	1 - 27	3 - 86
	Browsed (%)	0.8 a	0.8 a	0.6 a	2.5 a	2.1 a
21-50 cm tall	Mean	3.3 a (0.7)	2.4 a (0.6)	3.6 a (0.8)	2.5 a (0.5)	2.7 a (0.6)
	Range	0 – 7	0 – 8	0 – 10	0 – 7	0 – 6
	Browsed (%)	1.2 a	3.1 a	1.6 a	2.3 a	8.5 a
51-100 cm tall	Mean	1.8 a (0.6)	1.0 a (0.3)	1.8 a (0.6)	0.5 a (0.1)	1.1 a (0.4)
	Range	0 – 6	0 – 3	0 – 8	0 – 2	0 – 5
	Browsed (%)	0.0 a	3.8 a	0.0 a	7.1 a	5.1 a
101-200 cm tall	Mean	0.4 a (0.2)	0.3 a (0.1)	0.9 a (0.3)	0.9 a (0.4)	0.7 a (0.3)
	Range	0 – 2	0 – 2	0 – 3	0 – 5	0 – 3
	Browsed (%)	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a
Total	Mean	18.9 a (2.3)	21.3 a (3.9)	20.3 a (4.0)	16.9 a (2.6)	24.4 a (5.9)
	Range	4 – 31	2 – 49	6 – 54	4 – 31	12 – 93
	Browsed (%)	0.7 a	1.2 a	0.7 a	2.4 a	2.8 a

Tab. 4

Spearman's rank correlation matrix of the young tree density according to height class in relation to the non-cosine-corrected direct, diffuse and global solar radiation transmittances. * indicates significance at the 5% level, and ** at the 1% level.

Dichte der jungen Südbuchen nach Größenklassen in Relation zur direkten, diffusen und Gesamteinstrahlung (Spearman Rangkorrelation). * = Signifikanz auf dem 5% Niveau, ** auf dem 1% Niveau.

Height class (cm)	Direct	Diffuse	Global	n
Germinants and non-lignified	0.061	0.211	0.154	65
≤ 20 cm tall	0.123	0.129	0.141	65
21-50 cm tall	0.319**	0.293*	0.405**	65
51-100 cm tall	0.209	0.275*	0.335*	65
101-200 cm tall	0.099	0.024	0.107	65
Total	0.222	0.235	0.284*	65

Tab. 5

Descriptive statistics for absolute height growth (AHG) and absolute radial growth (ARG) in different locations in the forest – in gaps, at gap edges and beneath undisturbed canopy. The standard error is in brackets. Identical letters indicate no significant difference between the different locations in the forest (One-way ANOVA and Tukey test as a post-hoc test, p > 0.05, n = 13).

Deskriptive Statistik für den absoluten Höhenzuwachs (AHG) und den absoluten Radialzuwachs (ARG) in verschiedenen Bereichen des *N. betuloides*-Waldes – in Lücken, am Lückenrand, und im Bestand (Standardfehler in Klammern). Gleiche Buchstaben deuten an, dass keine signifikanten Unterschiede zwischen den Bereichen bestehen (One-way ANOVA und Tukey test as a post-hoc test, p > 0.05, n = 13).

Variables		Gap	Gap edge		Closed canopy	
			SE	NW	SE	NW
AHG ($cm\ year^{-1}$)	Mean	9.9 a	8.7 a	11.8 a	6.6 a	6.0 a
	(SE)	(1.8)	(1.6)	(1.5)	(1.1)	(1.)
	Range	3.0-24.0	1.5-16.0	1.5-20.0	2.5-14-0	1.5-17.0
ARG ($mm\ year^{-1}$)	Mean	0.31 a	0.20 ab	0.25 ab	0.20 ab	0.17 b
	(SE)	(0.04)	(0.03)	(0.02)	(0.03)	(0.02)
	Range	0.13-0.48	0.06-0.33	0.13-0.43	0.07-0.51	0.08-0.30

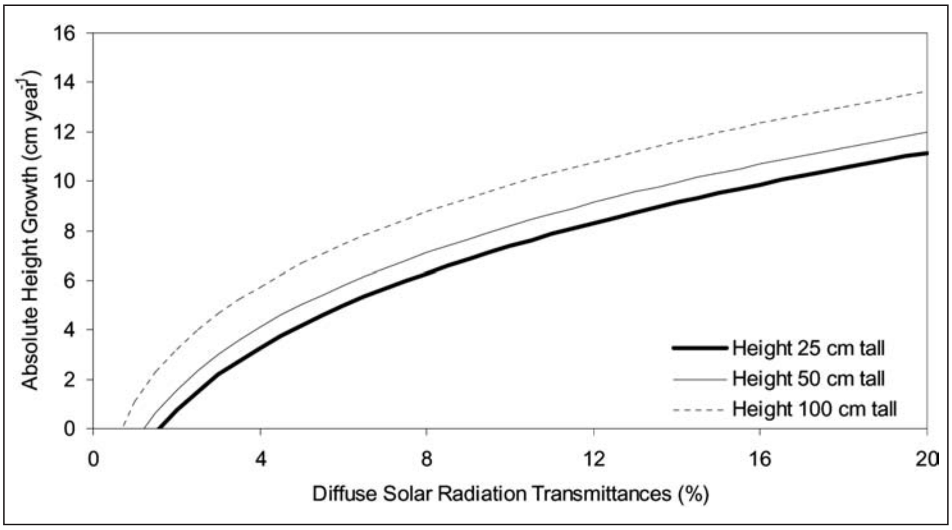

Fig. 2

Estimated absolute height growth functions using model of *Tab. 6*.
Dark solid line corresponds to plants with a height of 25 cm tall, light solid line to a plant 50 cm tall, and dashed line to a plant 100 cm tall before the growing season.

Höhenzuwachsfunktion geschätzt auf der Basis des Models in *Tab. 6*.
Die stärkste duchgezogene Linie steht für den Höhenzuwachs von 25 cm hohen Jungwüchsen, die dünne duchgezogene Linie für 50 cm hohe Jungwüchse und die unterbrochene Linie für 100 cm grosse Pflanzen am Beginn der Vegetationsperiode.

absolute height growth of the seedlings and saplings with the height of the plants and the diffuse solar radiation transmittances (*Tab. 6*, *Fig. 2*). These variables accounted for 23% of the variation in absolute height growth of the regeneration.

The absolute radial growth ranges between 0.06 and 0.051 mm $year^{-1}$ (*Tab. 5*). Although the absolute radial growth in the gap centre was higher (average 0.31 mm $year^{-1}$), there was no significant difference (n = 13, p > 0.05) with the values for the gap edges (0.25 mm $year^{-1}$ to the northwest and 0.20 to the southeast) and beneath the closed canopy at southeastern from the canopy centre (0.20 mm $year^{-1}$). Although, the absolute radial growth was lower beneath the undisturbed canopy at the northwestern location (0.17 mm $year^{-1}$), this value did not differ significantly from the values observed at the southeastern and northwestern edges of the gaps and beneath the closed canopy at southeastern location. The stepwise multiple linear regression analysis revealed that the 35% of the variation in absolute radial growth of the seedlings and saplings could be explained by the effect of the variables of radius of the plants, the diffuse solar radiation transmittances and the age of the plants (*Tab. 6*, *Fig. 3*).

Tab. 6

Results of the stepwise multiple linear regression for the absolute height (AHG) and the absolute radial growth (ARG) based on size of the plants (height or radius at root collar), age and the transmission of the non-cosine-corrected direct (DIR), diffuse (DIF) or global (GLO) solar radiation estimated during the growing season. R^2 is the coefficient of determination. * indicates significance at the 5 % level, and ** at the 1 % level.

Ergebnisse der schrittweisen multiplen Regression für den absoluten Höhen- (AHG) und absoluten Radialzuwachs. Erklärende Variablen sind Gesamthöhe und Wurzelhals-duchmesser der Jungwüchse, Alter, und die transmitierte direkte (DIR), diffuse (DIF) Strahlung oder die Globalstrahlung geschätzt für die Vegetationsperiode. R^2 ist das Bestimmtheitsmaß. * steht für ein Signifikanzniveau von 5 % ** für 1 %.

Dependent variables	Independent variables	Coefficient	R^2	p-value	n	Variables not in equation
AHG (cm year^{-1})	Intercept	-13.454	0.226	<0.001	65	age, DIR, GLO
	Height	0.033**				
	DIF $^{0.25}$	11.247*				
ARG (mm year^{-1})	Intercept	0.054	0.345	<0.001	65	DIR, GLO
	Radius	0.030**				
	DIF	0.014*				
	Age	-0.004*				

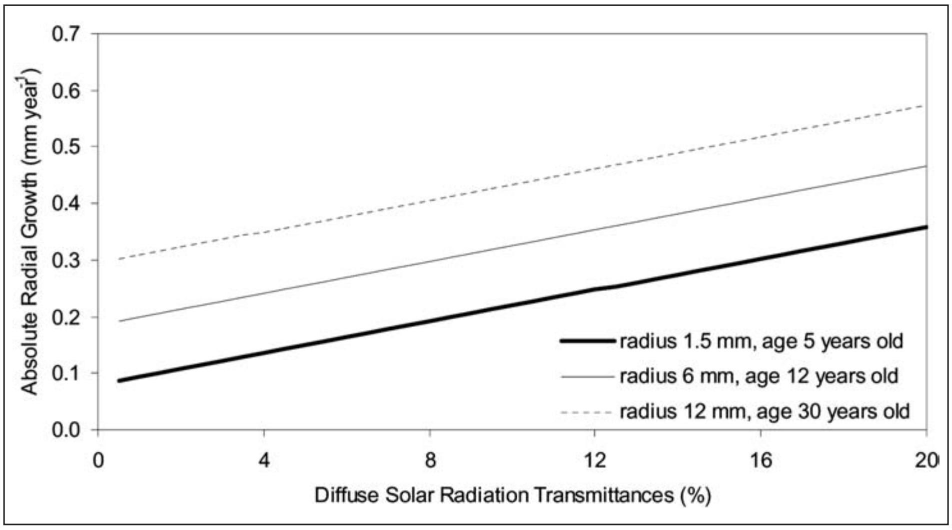

Fig. 3

Estimated absolute radial growth functions using model of *Tab. 6*. Dark solid line corresponds to plants with a radius of 1.5 mm and 5 years old before the growing season, light solid line to a plant with a radius of 6 mm and 12 years old and dashed line to a plant with a radius of 12 mm and 30 years old.

Radialzuwachsfunktion geschätzt auf der Basis des Models in *Tab. 6*. Die stärkste duchgezogene Linie steht für fünfjährige Jungwüchse mit einem Radius von 1.5 mm, die dünne duchgezogene Linie für 12-jährige Jungwüchse mit einem Radius von 6 mm und die unterbrochene Linie für 30 jahre alte Pflanzen mit einem radius von 12 mm am Beginn der Vegetationsperiode.

4. DISCUSSION

4.1 Below-canopy solar radiation conditions

The results indicated that there is a below-canopy solar radiation gradient from the centre of the gap to the undisturbed canopy in old-growth *N. betuloides* forest over the course of a growing season, as described by RICKLEFS (1977), DENSLOW (1980), CANHAM et al. (1990, 1994) and LIEFFERS et al. (1999). The characteristic features of old-growth forest (FRANKLIN and VAN PELT, 2004), such as the presence of small canopy gaps and the heterogeneity of the canopy with a multi-layered vertical distribution and an irregular horizontal distribution of canopy structures result in a more homogenous distribution of the solar radiation in the understorey. In general, a major increase in solar radiation has been found in the centre of gaps (CANHAM et al., 1990). As the studied forest is located in the southern hemisphere, solar radiation was found to be greater at the southeastern edge of gaps rather than the northwestern, i.e. inverse to forests of the northern hemisphere (CANHAM et al., 1990; COMEAU, 1998; LIEFFERS et al., 1999). Higher transmittances of direct solar radiation were measured beneath the closed canopy to the southeast of the gap centre because the effect of canopy gaps on the below-canopy solar radiation extends beyond the edge of the gaps at higher latitudes, where the sun is low in the sky (CANHAM et al., 1990; GRAY et al., 2002).

4.2 Regeneration pattern and the relationship between seedling and sapling growth and the influence of their size, their age and the below-canopy solar radiation

Only minor spatial differences in the natural regeneration processes were found within the old-growth *N. betuloides* forest. The young tree density (*Tab. 3*) was similar beneath gaps and the closed canopy. The seedling and sapling densities were between two and three times those recorded in Tierra del Fuego by REBERTUS and VEBLEN (1993a), with an average of 6.1 plants m^{-2} growing beneath the closed canopy and 8.5 plants m^{-2} in gaps. A large number of seedlings were found in the lower height classes, with fewer in the higher classes. This corresponded with findings from uneven-aged forests dominated by red beech (*Nothofagus fusca*) in New Zealand, where the frequency distribution of the seedlings as a function of height approached a negative exponential (JUNE and OGDEN, 1975; WARDLE, 1984).

The density of plants belonging to the shortest class (≤ 20 cm tall) revealed no influence of below-canopy solar radiation (*Tab. 4*). An explanation for this might be that the young plants are more dependent upon below ground resources than the solar radiation transmitted into the forest (STANCIOIU and O'HARA, 2006; AMMER et al. 2008). For example, seedlings and saplings are susceptible to drought, as has been described for *N. pumilio* (HEINEMANN et al., 2000) and in New Zealand for *Nothofagus* species (WARDLE, 1984). The density of plants 21–100 cm in height, by contrast, was correlated with the transmitted solar radiation (*Tab. 4*). Indeed, the plant density decreased with increasing height, probably as a result of competition for access to solar radiation in this extremely shaded environment.

N. betuloides seedlings are able to establish in the shaded understorey of the old-growth forest, and can survive and grow slowly, as demonstrated by REBERTUS and VEBLEN (1993a) and PROMIS (2009). The death of canopy trees and the creation of small canopy gaps in a small-scale forest texture promote an uneven pattern of regeneration in the old-growth *N. betuloides* forest, with seedling, sapling and pole stage trees growing into the canopy showing a great range of ages and heights (PEET and CHRISTENSEN, 1987; OLIVER and LARSON, 1996; BARNES et al., 1998).

Although the canopy gaps studied were small, both the absolute height and radial growth for the last complete growing season was higher within the gaps (at the centre and at the gap edge), as also has been demonstrated for shade tolerant *Abies balsamea* dominated forests (KNEESHAW et al., 1998). The multiple linear regression analysis revealed that independent variables related to the size of the plants (height and radius) and age seemed to be main factors affecting the absolute height and radius growth, respectively. This was also found by LUSK (2004) and AMMER et al. (2008), who indicated that the size and age might affect the growth response of the plants to resource availabilities. Furthermore, the absolute growth of seedlings and saplings is affected by the effects of the below-canopy diffuse solar radiation, which also has been demonstrated for other *Nothofagus* species in the Patagonia and Tierra del Fuego (MARTÍNEZ PASTUR et al., 2007; CALDENTEY et al., 2009; PERI et al., 2009). However, the effects of other environmental factors (e.g. temperature and moisture) and the availability of soil resources (e.g. nutrients and soil moisture) can affect the seedling and sapling growth (KNEESHAW et al., 2002; MACAHADO et al., 2003; AMMER et al., 2008). Therefore, more research is needed to get a better understanding of the effects of the occurrence of natural small canopy gaps on the availability of other resources (above and below ground) and the regeneration patterns of *N. betuloides*.

4.3 Browsing effects

The levels of browsing damage to young *N. betuloides* by *L. guanicoe* were very low (*Tab. 3*), less than the effect on the deciduous *N. pumilio*. The guanaco feeds on the leaves of the three *Nothofagus* species occurring in Tierra del Fuego, but prefers *N. pumilio* (RAEDEKE, 1980). *L. guanicoe* has become a serious problem for the successful natural regeneration of *N. pumilio*, in both natural canopy gaps (ARROYO et al., 1996; REBERTUS et al., 1997, CAVIERES and FAJARDO, 2005) and in harvested stands (MARTÍNEZ PASTUR et al., 1999; PULIDO et al., 2000). The results of this study did not show any particular preference of *L. guanicoe* for forest conditions, with trees browsed equally in gaps and beneath the closed canopy.

4.4 Silvicultural implications for old-growth *N. betuloides* forest

Historically the canopy layer in the old-growth *N. betuloides* stand has probably been affected mainly by fine-scale disturbances (small gaps), thus the uneven-aged canopy structure has been maintained over time (PROMIS, 2009). Therefore, the competitive pressure exerted upon young trees by the trees in the canopy is great (OLIVER and LARSON, 1996; BARNES et al., 1998). Just as with the regeneration of *Nothofagus* species in New Zealand (WARDLE, 1984), seedlings and saplings of *N. betuloides* progress through the understorey slowly but steadily, often remaining suppressed even after the death of a large canopy tree. Thus, the age of the plants is a better predictor of both their size (height and root collar diameter) and their growth rates than the transmittance of solar radiation into the forest, as young *N. betuloides* may reduce height growth when growing in shade, as is the case with the advance regeneration of boreal forests (MESSIER et al., 1999).

Silvicultural systems have to integrate multiple and often conflicting management objectives (BAUHUS, 1999). In order to maintain the uneven-aged characteristic of the stand, with and abundance of juvenile trees in the understorey, the selection method can be employed to promote regeneration, i.e., the trees are removed as individuals or in small groups (SMITH et al., 1997; LINDENMAYER and FRANKLIN, 2002). This favours the shade tolerant species that typically establish rapidly after harvesting (TAPPEINER et al., 1997). Given the characteristics of a *N. betuloides* stand, with an abundant stock of advance regeneration, the stand development should occur rapidly after harvesting. Different harvesting scenarios tested for temperate rain forest in southern Chile revealed that the structure and composition of old-growth forest can be better maintained using the selection method, although yielding lower harvest volumes (RÜGER et al., 2007).

In order to maintain the unique characteristics of individual old-growth stands, tools for integrating the features of stand structure into management guidelines are needed (O'HARA et al., 2008). This study can serve as a framework for new silvicultural practices to address multifunctional ecosystem management objectives in old-growth *N. betuloides* forests of southern Patagonia and Tierra del Fuego.

5. SUMMARY

Over the last decade a shelterwood system promoting natural regeneration has been applied in the southern Chilean old-growth

Nothofagus forests. However, most of these forests are naturally uneven-aged, and the effect of the application of this silvicultural system has been the homogenisation and simplification of the stand structure. An ecological understanding of natural disturbance processes is necessary to improve the current silvicultural practices.

This study analysed the effects of natural small-scale disturbances on the below-canopy solar radiation conditions, the regeneration patterns (density and growth), and the browsing damage to young trees caused by *Lama guanicoe* in an old-growth *Nothofagus betuloides* forest (*Fig. 1*). The study was carried out in 13 canopy gaps (21–92 m^2) (*Tab. 1*). The regeneration was sampled in 65 plots (4 m^2) in and around the canopy gaps along a solar radiation gradient.

The results revealed that the non-cosine-corrected direct solar radiation ranged from 3.2 to 19.4%, the transmitted diffuse radiation ranged from 3.1 to 16.7% and the global solar radiation ranged from 3.2 to 17.6% (*Tab. 2*). As expected, the transmitted solar radiation was highest in the gaps, and the adjacent southeastern borders.

All *N. betuloides* seedlings and saplings were counted in height classes, together with browsing damage caused by *L. guanicoe* (*Tab. 3*). The height growth and radial increment were measured for the tallest seedling or sapling in each plot (*Tab. 5*). The absolute radial and height growth of seedlings and saplings were affected by the total size and age of the plants and the below-canopy diffuse solar radiation (*Tab. 6*, *Fig. 2* and *3*). The proportions of seedlings browsed by *L. guanicoe* were low (0.7 to 2.8% of the total). Browsing damage to young trees was observed below canopy gaps as well as beneath closed canopy, demonstrating no particular preference (*Tab. 3*).

The seedlings and saplings of *N. betuloides* exhibited a high shade tolerance, apparently not requiring the presence of large gaps to establish. The heterogeneous canopy of old-growth *N. betuloides* stands with only very small canopy gaps produced a variety of mosaics in the understorey, with seedlings and saplings present in a range of ages and heights. It could be shown, that – different to other South American *Nothofagus* species – *N. betuloides* seedlings and saplings can tolerate long periods of dense shade. Similar to some New Zealand *Nothofagus* forests, *N. betuloides* forests are able to regenerate also in a continuous process. This allows to develop perspectives for successful transformations of virgin *N. betuloides* forests into seminatural stands, which could be sustainably managed as selection forests, still having a multi-layered structure and high biodiversity with native species.

6. Zusammenfassung

Titel des Beitrages: *Einfluss von natürlichen kleinflächigen Störungen im Kronendach auf die Strahlungsverhältnisse im Bestandesinneren und die Verjüngungsmuster in einem Nothofagus betuloides Primärwald in Tierra del Fuego (Feuerland), Chile.*

Während des letzten Jahrzehnts wurde in den südchilenischen *Nothofagus*-Naturwäldern ein Schirmschlagverfahren angewendet, um die Naturverjüngung zu fördern. Die Naturwälder jedoch sind in der Regel ungleichaltrig, sodass dieses Waldbauverfahren eine Homogenisierung und Vereinheitlichung der Waldstrukturen zur Folge hatte. Um das bestehende Waldbauverfahren zu verbessern, ist ein tieferes Verständnis der waldökologischen Prozesse nötig.

Die Arbeit untersucht daher den Einfluss natürlicher kleinflächiger Störungen auf die Lichtversorgung im Unterwuchs, die Baumartenverjüngung (Dichte, Zuwachs) und den Verbiss durch Guanaco (*Lama guanicoe*) in *Nothofagus betuloides*-Naturwäldern (*Fig. 1*). Die Studie erfolgte in 13 Kronenlücken (21 bis 92 m^2) (*Tab. 1*). Die Verjüngung wurde auf 65 Probeflächen (jeweils 4 m^2) in einem Lichtgradienten in und um die Lücken erfasst.

Es zeigte sich, dass die direkte Einstrahlung zwischen 3,2 und 19,4%, die diffuse Einstrahlung zwischen 3,1 und 16,7%, und die gesamte Einstrahlung zwischen 3,2 und 17,6% der Freilandstrahlung beträgt (*Tab. 2*). Die Einstrahlung war erwartungsgemäß in den Lücken und am südöstlichen Lückenrand am höchsten.

Alle *N. betuloides* Sämlinge und Jungpflanzen wurden in Größenklassen sowie nach Verbissmerkmalen erfasst (*Tab. 3*). Das Höhen- und Durchmesserwachstum wurde für die jeweils größte Jungpflanze auf jeder Probefläche gemessen (*Tab. 5*). Die Messungen zeigen, dass der Höhen- und Durchmesserzuwachs der Jungpflanzen von der Gesamthöhe, dem Pflanzenalter und dem Anteil der diffusen Einstrahlung bestimmt werden (*Tab. 6*, *Fig. 2* und *3*). Der Verbiss war mit nur 0,7 bis 2,8% der Jungpflanzen überall sehr gering und unterschied sich nicht zwischen den Lücken und dem angrenzenden Bestand (*Tab. 3*).

Die heterogene Struktur des Kronendachs der *N. betuloides*-Naturwälder mit nur sehr kleinen Bestandeslücken hatte ein kleinskaliges Mosaik im Unterwuchs zur Folge, mit Sämlingen und Jungpflanzen in allen Alters- und Größenklassen. Im Unterschied zu den anderen südamerikanischen *Nothofagus*-Arten erwiesen sich die Jungpflanzen von *N. betuloides* als sehr schattentolerant. Sie benötigen keine größeren Lücken zur Etablierung, sie überleben Schattenphasen und verstärken ihr Größenwachstum bereits durch kleine Auflichtungen. Ähnlich wie bei manchen neuseeländischen *Nothofagus*-Arten kann die Waldentwicklung daher kontinuierlich verlaufen. Dies eröffnet Perspektiven für eine erfolgreiche Überführung von *N. betuloides*-Naturwäldern in naturnahe Wirtschaftswälder, die nachhaltig als Dauerwald bewirtschaftet werden könnten. Damit könnte die Strukturvielfalt und Biodiversität der Südbuchenwälder auch bei Holznutzung zu erheblichen Teilen erhalten werden.

7. Résumé

Titre de l'article: *Effets de perturbations naturelles à petite échelle sur le rayonnement solaire sous le couvert et modes de régénération dans une forêt ancienne de Nothofagus betuloïdes de la Tierra del Fuego (Terre de Feu) au Chili.*

Pendant les dernières décennies on a utilisé dans les forêts de *Nothofagus* du Sud du Chili un système de coupe d'abri pour favoriser la régénération naturelle. Mais les forêts naturelles sont en règle générale inéquiennes, si bien que ce procédé sylvicole conduit à une homogénéisation et à une uniformisation des structures forestières. Pour améliorer le procédé sylvicole en cours il est nécessaire d'avoir une connaissance approfondie des processus de l'écologie.

Le travail porte par conséquent sur l'influence de perturbations de faible surface sur la disponibilité en lumière dans le sous-étage, sur la régénération naturelle des essences (densité, accroissement) et l'abroutissement par le Guanaco (*Lama guanicoe*) dans les forêts de *Nothofagus betuloïdes* (*Fig. 1*). L'étude porta sur 13 trouées dans les cimes (21 à 92 m≤) (*Tab. 1*). La régénération a été inventoriée sur 65 placettes (d'environ 4 m≤) sur un gradient de lumière dans et autour des trouées.

Il s'avéra que le rayonnement solaire était compris entre 3,2 et 19,4%, le rayonnement diffus entre 3,1 et 16,7% et le rayonnement total entre 3,2 et 17,6%, ces chiffres étant rapportés au rayonnement en terrain nu (*Tab. 2*). Comme on s'y attendait le rayonnement était à son maximum dans les trouées et les bordures sud-est des trouées.

Tous les semis de *N. betuloïdes* et les jeunes sujets furent inventoriés en classes de hauteur et de diamètre et aussi selon les critères

d'abroutissement (*Tab. 3*). La croissance en hauteur et en diamètre fut mesurée, selon le cas, sur les plus hauts jeunes sujets de chaque placette d'expérience (*Tab. 5*). Les mesures montrent que la croissance en hauteur et en diamètre des jeunes plants sont déterminés par la hauteur totale, l'âge des plants et la proportion du rayonnement diffus (*Tab. 6*, *Fig. 2* et *3*). L'abroutissement, avec seulement 0,7 à 2,8% des jeunes plants concernés était partout très faible et ne se différenciait pas entre les trouées et les peuplements bordants (*Tab. 3*).

La structure hétérogène du couvert forestier des forêts de *N. betuloïdes*, avec seulement de très petites trouées dans les peuplements avait pour conséquence dans le sous-étage la présence d'une mosaïque à petite échelle, avec des semis et des jeunes plants dans toutes les classes d'âge et de dimension. A la différence des autres espèces Sud-américaines de *Nothofagus* les jeunes plants de *N. betuloïdes* apparurent comme très tolérants à l'ombre. Ils n'ont pas besoin de grandes trouées pour s'établir, survivent aux phases d'ombre et renforcent leur croissance en hauteur même dans le cas de faibles éclairements. Comme dans le cas de beaucoup d'espèces de *Nothofagus* néozélandaises le développement de la forêt peut de ce fait se poursuivre continuellement. Ceci ouvre des perspectives pour faire évoluer avec succès les forêts naturelles de *N. betuloïdes* vers des forêts productives proches de la nature, qui peuvent être aménagées selon le principe de la production durable, comme une forêt permanente. De cette façon la diversité de structure et la biodiversité des forêts de «hêtre du Sud» pourrait être maintenue même dans l'hypothèse d'une production de bois sur des surfaces importantes. R.K.

8. Resumen

Efectos de perturbaciones naturales de pequeña escala sobre la radiación solar en el interior del bosque y los patrones de la regeneración en un bosque primario de Nothofagus betuloides en Tierra del Fuego, Chile.

Durante la última década la mayoría de los bosques primarios y adultos de *Nothofagus* ubicados en el sur de Chile han sido intervenidos a través del sistema silvicultural de cortas de protección. Sin embargo, la aplicación de este sistema silvicultural ha conducido a una homogenización y simplificación de la estructura multietánea característica de estos bosques. Como base para el mejoramiento y el desarrollo de nuevos sistemas silviculturales, es necesario comprender la influencia de los procesos de perturbaciones naturales sobre la dinámica natural de los rodales.

El estudio analizó los efectos de las perturbaciones de pequeña escala sobre las condiciones de radiación solar bajo el dosel del bosque, los patrones de la regeneración (densidad y tasas de crecimiento), y el daño provocado por el ramoneo de *Lama guanicoe* sobre la regeneración en un bosque de *Nothofagus betuloides* (*Fig. 1*). El estudio se realizó en 13 claros de dosel (21–92 m^2) (*Tab. 1*). La regeneración fue muestreada en 65 parcelas (4 m^2) localizadas en un gradiente de luz.

Los resultados indicaron que las transmisiones de las radiaciones solares directa, difusa y global (estimadas sin aplicación de ley del coseno) en el interior del bosque fueron entre 3,2 a 19,4%, 3,1 a 16,7%, y 3,2 a 17,6%, respectivamente (*Tab. 2*). La radiación solar transmitida fue mayor en el centro de los claros y en los bordes hacia el sureste del claro.

Se contaron todas las plantas de regeneración de *N. betuloides* de acuerdo a clases de altura, registrándose también el número de ellas ramoneadas por *L. guanicoe* (*Tab. 3*). Se midió el crecimiento en altura y el incremento radial, para la planta de regeneración de mayor altura en cada una de las parcelas (*Tab. 5*). El crecimiento absoluto en radio y en altura de las plantas de regeneración es afectado por el tamaño de las plantas, la edad y la radiación solar difusa transmitida al interior del bosque (*Tab. 6*, *Fig. 2* y *3*). Las proporciones de plantas de regeneración ramoneadas por *L. guanicoe* fueron bajas (entre 0,7 y 2,8% del total). El daño por ramoneo a las plantas de regeneración fue observado tanto en claros de dosel, así como también bajo el dosel del bosque sin perturbación, demostrándose que *L. guanicoe* no presenta un hábitat de preferencia (*Tab. 3*).

Las plantas de regeneración de *N. betuloides* presentaron una alta tolerancia a la sombra, no requiriendo aparentemente de grandes claros de dosel para su establecimiento. El dosel del bosque primario, adulto y multietáneo de *N. betuloides*, que se caracteriza por ser heterogéneo y por presentar claros en el dosel muy pequeños, origina la existencia de una variedad de mosaicos en el interior del bosque, con presencia de plantas de regeneración con un amplio rango de edades y alturas. Se pudo observar que, a diferencia de otras especies de sudamericanas de *Nothofagus*, las plantas de regeneración de *N. betuloides* pueden tolerar largos períodos de sombra. Bosques de *N. betuloides* son capaces de regenerar en un proceso continuo, en forma similar a lo que sucede en algunos bosques de *Nothofagus* de Nueva Zelanda. Esto permite desarrollar perspectivas para una exitosa transformación de los bosques vírgenes de *N. betuloies* en rodales seminaturales, los cuales podrían ser manejados sustentablemente como monte alto irregular, manteniendo sus estructuras multiestratificadas y una alta diversidad de especies nativas.

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