FUNCTIONAL ECOLOGY OF *Nothofagus pumilio* REGENERATION IN RELATION TO LIGHT AVAILABILITY

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SUMMARY

The silvicultural proposals for *Nothofagus pumilio* forests are mainly based on canopy open to stimulate regeneration growth by modifying water and light availability at understory level. Seedlings and saplings often survive as tolerant species and grow slowly for a long time (up to 20 years) under shaded overstory. However, when canopy is open by harvesting or wind-throws, young trees acting as intolerant species and can quickly colonize the opened areas.

The objective was to make a comparative and functional approach analyzing morphological and physiological characteristics of *N. pumilio* seedlings, growing in a pre-defined light gradient under controlled conditions of irrigation and temperature. Seedlings of 2-3 years were collected in a closed canopy natural stand during September. Then, they were transferred to pots under a greenhouse, where three light levels were assayed (4%-26%-64% of the total natural incident light). Irrigation was made manually, maintaining a soil humidity of 40-60% soil capacity, while temperature was controlled through forced ventilation (less than 24°C). Thirty six plants in 6 clusters per each treatment where measured during January (height, number, size and shape of leaves, branch number and insertion angle), while 6 plants (one per cluster) was selected for physiological parameters measurement (dark respiration rate, light compensation point, photochemical efficiency, light saturation point and chlorophyll content). Photo-respiration was measured using an infra red gas analyzer of CO_2 model S151 of Qubit System Inc. with a leaf chamber of 9 cm^2. Twenty-three variables related with three functional levels (leaf, shoot and crown, whole plant) were analyzed.

At leaf level, most of physiological variables were higher in luminous treatment, while biometric variables were higher in middle light treatment. This last treatment has more chlorophyll a-b (0.033 and 0.011 mg/cm^2), while luminous treatment has more carotenoids (0.010 mg/cm^2). However, dark treatment presented the lower specific leaf mass (0.0007 g/cm^2). At shoot and crown level, no differences were found in branch number and insertion angle, but plants growing in middle light treatment were taller than the others (17 cm compared to 12 cm). At whole plant level, best values were found in middle light treatment. However, the higher leaf area ratio was measured in dark treatment (389 cm^2/g).

Nothofagus pumilio seedlings have morphological and physiological characteristics related to tolerant species, but could quickly change to those adapted to intolerant species when the light availability increases. It is necessary to make comparative and functional models to develop better silvicultural treatments which maximize the seedling potential during the installation and early growth phase.

Key words: *Nothofagus pumilio*, Physiology, light

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ECOLOGÍA FUNCIONAL DE LA REGENERACIÓN DE LENGA (*Nothofagus pumilio*) RESPECTO A LA DISPONIBILIDAD DE LUZ

RESUMEN

Las propuestas silvícolas de los bosques de *Nothofagus pumilio* se basan en la apertura del dosel para estimular el crecimiento de la regeneración, cambiando la disponibilidad de agua y luz. Las plántulas sobreviven como si fueran especies tolerantes y crecen lentamente por largo tiempo (más de 20 años) bajo altas coberturas. Sin embargo, cuando el dosel se abre debido a la cosecha o volteos por viento, la regeneración reacciona como una especie intolerante, colonizando rápidamente los sectores abiertos.

El objetivo del estudio fue efectuar una comparación, analizando las características fisiológicas y morfológicas de plántulas de *N. pumilio*, creciendo en un gradiente de luz bajo condiciones controladas de riego y temperatura. Para ello, En septiembre se colectaron plántulas de 2-3 años del bosque en rodales de alta cobertura, las que fueron transplantadas a macetas en invernadero, ensayando tres niveles de luz (4%-26%-64% de la luz incidente natural). El riego se realizó manualmente, dejando una humedad en el suelo de 40-60% de la capacidad de campo, mientras que la temperatura se controló por ventilación forzada (menor a 24°C). En enero se midieron 36 plantas divididas en seis clusters por tratamiento (altura, número, tamaño y forma de las hojas, número y ángulo de inserción de ramas), mientras que 6 plantas (una por cluster) fue seleccionada para la medición de los parámetros fisiológicos (respiración en oscuridad, punto de compensación lumínico, eficiencia fotoquímica, punto de saturación lumínico y contenido de clorofila). La fotorrespiración fue medida con un *IRGA*[3] de CO_2 modelo S151 de Qubit System Inc. con una cámara de 9 cm^2. Se analizaron 23 variables relacionadas con tres niveles funcionales (hojas, copas, planta entera).

Al nivel de hojas, los mayores valores de variables fisiológicas fueron en el tratamiento con mayor luz, mientras que las variables biométricas fueron mayores en el tratamiento intermedio. Este último presentó mayor clorofila a-b (0,033 y 0,011 mg/cm^2), mientras que el tratamiento con más luz tuvo más carotenoides (0,010 mg/cm^2). Asimismo, el tratamiento mas oscuro tuvo menor masa específica de hojas (0,0007 g/cm^2). A nivel de copas no se encontraron diferencias en número de ramas o ángulo de inserción. Sin embargo, las plantas que crecieron en el tratamiento intermedio fueron más altas (17 cm contra 12 cm). A nivel de planta entera, los valores más adecuados se encontraron en el tratamiento intermedio. Sin embargo, la mayor relación de área foliar se midió en el tratamiento con menor luz (389 cm^2/g).

Las plántulas del bosque de *Nothofagus pumilio* poseen características morfológicas y fisiológicas que las relacionan con las especies tolerantes, pero que pueden cambiar rápidamente a las de una especie intolerante cuando la disponibilidad de luz se incrementa. Es necesario realizar modelos comparativos y funcionales para desarrollar mejores métodos silvícolas que maximicen el potencial de la regeneración durante la instalación y la fase de crecimiento inicial.

Palabras clave: *Nothofagus pumilio*, fisiología, luz

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[3] IRGA: Analizador de gases infrarrojo (*Nota del Editor*)

INTRODUCTION

Seedlings of *Nothofagus* species often survive and grow slowly for very long time periods in the shaded understory (Rebertus and Veblen, 1993), creating a seedling bank (Cuevas and Arroyo, 1999) with a potential advantage in reestablishing canopy disturbances after the opening of gaps due to windstorms, ice damage, timber harvesting or beaver engineering (Veblen, 1989; Rebertus and Veblen, 1993; Gutiérrez 1994; Rebertus *et al.*, 1997; Heinemann *et al.*, 2000; Martinez Pastur *et al.*, 2000; 2006; Anderson *et al.*, 2006). However, while it is generally accepted that these forests regenerate in a gap dynamic from an established seedling bank, the eco-physiological factors that determine the seedling bank itself are much less known. After timber harvest, the survival of the seedling bank and its rapid growth depends on the acclimation to the new micro-climatic conditions (Tognetti *et al.*, 1998). Photosynthesis is one of the most important physiological parameter for all plant growth (Kramer and Kozlowski, 1979). Therefore, in this study the objective was to make a comparative and functional approach analyzing morphological and physiological characteristics of *N. pumilio* seedlings, growing in a pre-defined light gradient under controlled conditions of irrigation and temperature.

MATERIALS AND METHODS

Two to three year old *Nothofagus pumilio* seedlings from 6-7 cm in height were obtained from the understory in natural primary forests (54°06' S, 68°37' W). The seedlings were collected in stands with high canopy cover (94% ± 5% SE) at the beginning of the spring. Seedlings were transplanted into plastic pots with 14 cm diameter and 15 cm height, which were filled with a substrate of peat – sand – humic forest soil (1:1:1). Field capacity was determined gravimetrically with the water content after two days of abundant irrigation. Plants were kept in a greenhouse at Ushuaia city (Tierra del Fuego) (54°46' S, 68°12' W) under three light intensity treatments (4%, 26% and 64% of the natural incident irradiance). Temperature was controlled through forced ventilation avoiding more than 24°C at plant canopy level. Irrigation was done manually, maintaining half of the plants under a soil humidity of 40-60% soil capacity, while the other half was grown under 80-100% soil capacity.

Six treatments were defined (three light intensity levels and two soil water contents), consisting in six repetitions with 20 plastic bags each. During the first week of each month (October to March) one plastic bag per repetition per treatment was randomly chosen for the measurements. The CO_2 gas exchanges were measured using an infra red gas analyzer (Model S151 - Qubit Systems - Canada) with a 9 cm^2 leaf chamber and electronic thermal mass flow-meter. The measurements were taken in controlled laboratory conditions (12-14°C in complete darkness) after an 8 hours acclimatization period of the plants to the new environmental conditions. Leaf chamber temperature was 19.6°C ± 2.9°C SE, and the supplied air humidity was 44.8% ± 7.2% SE, while air CO_2 concentration was 315 ppm ± 43 ppm SE. Air supply was taken from outside and varied according to climatic conditions during the growing season.

Leaf phenology was determined in all treatments along the studied period. Phenological stages were defined as bud sprouting (*S*), leaf aperture (*E1*), leaf expansion (*E2*), leaf reddening (*R*) and leaf fall (*F*). The first open leaf (October) and the newly full expanded leaf (November to March) per plant where selected for the measurements. To develop the photosynthetic light response curves, ten irradiance levels were assayed (0, 25, 50, 75, 100, 200, 300, 500, 750 and 1000 µmol quanta/m^2.s). The leaves were allowed 3-5 min to acclimatize to light intensity changes. CO$_2$ measurements were taken 500 times/min and data were acquired when the concentrations were stabilized at least 150 times with a variation of ± 1 ppm. In each curve, the rate of dark respiration (µmol CO$_2$/m^2.s) (*RDR*), photochemical efficiency (µmol CO$_2$/µE) (*PE*), net assimilation rate (µmol CO$_2$/m^2.s) (*NAR*), light compensation point (µE/m^2.s) (*LCP*) and light saturation point (µE/m^2.s) (*LSP*) were derived. Data were subjected to an analysis of variance, where means were separated through a Tukey multiple range test at $p \leq 0.05$.

RESULTS

The rate of dark respiration significantly varied during the growing season and with light intensity treatments (Table N° 1). It was lower at the beginning and the end of the experiment (-0.7 to -0.8 µmol CO$_2$/m^2.s), compared to the other months (-1.6 to -1.8 µmol CO$_2$/m^2.s). The rate of dark respiration increased with the light intensity treatment from -0.9 to -1.7 µmol CO$_2$/m^2.s. Photochemical efficiency significantly varied over the growing season and with light intensity treatments as well. It increased from the early spring (0.02 µmol CO$_2$/µE) to the mid-summer (0.08 µmol CO$_2$/µE) and decreased before the end of the growing season (0.06 µmol CO$_2$/µE). Photochemical efficiency was significantly different between low light intensity treatment (0.05 µmol CO$_2$/µE) and the others (0.06-0.07 µmol CO$_2$/µE). The net assimilation rate significantly varied among the three studied factors (Table 1). As for photochemical efficiency, values increased from the beginning of the growing season (2.1 µmol CO$_2$/m^2.s) to mid-summer (9.7 µmol CO$_2$/m^2.s) and then decreased in March (7.3 µmol CO$_2$/m^2.s). In the dry soil treatment, the net assimilation rate was significantly higher (7.9 µmol CO$_2$/m^2.s) than the wet treatment (6.7 µmol CO$_2$/m^2.s). As in photochemical efficiency, the net assimilation rate was significantly different among the low light intensity treatment (5.1 µmol CO$_2$/m^2.s) and the others (8.3-8.4 µmol CO$_2$/m^2.s). The light compensation point significantly varied over the growing season and light intensity treatments (Table 1), being highest in the early spring (28.5 µE/m^2.s) and then decreasing up to a minimum at the end of the growing season (12.3 µE/m^2.s). This variable was significantly different between the high light intensity treatment (30.3 µE/m^2.s) and the lower light intensity treatments (12.5-16.5 µE/m^2.s). Also, the light saturation point varied significantly over the growing season and light intensity treatments, with minimum values in the early spring (276 µE/m^2.s) and then increased during the growing season reaching 530 µE/m^2.s. This variable increased with the light intensity treatment from 328 to 549 µE/m^2.s. Significant interactions were found in four variables mainly due to different value increments between main factors (Table 1) and changes in the treatment with the highest values along the growing season, e.g. the low light intensity treatment had higher photosynthetic rate values at low irradiances, while high light intensity treatment had higher photosynthetic rate values at high irradiances.

The lighter treatment has more chlorophyll a-b (0.033 and 0.011 mg/cm^2), while luminous treatment has more carotenoids (0.010 mg/cm^2). However, dark treatment presented the lower specific leaf mass (0.0007 g/cm^2). At shoot and crown level, no differences were found in branch number and insertion angle, but plants growing in middle light treatment were taller than the others (17 cm compared to 12 cm). At whole plant level, best values were found in middle light treatment. However, the higher leaf area ratio was measured in dark treatment (389 cm^2/g) (Table N° 2).

Light intensity and soil water content treatments presented different responses when were compared their photosynthetic light response curves, e.g., during the month with the maximum net assimilation rate. The low light intensity treatment had a higher photosynthetic rate in low irradiance levels (75-100 µmol quanta/m².s) in both soil water content treatments. In the dry treatments, as well as the medium and high light intensity treatments, the photosynthetic rate at high irradiance levels (up to 100 µmol quanta/m².s) was significantly higher than the low light intensity treatment. The photosynthetic rate of the high light intensity treatment was affected by the wet soil water content treatment, decreasing its values and response. The obtained values were intermediate between the medium and low light intensity treatments. Finally, no significant photo-inhibition was observed in the assayed treatments in the highest irradiance levels.

Table N° 1

ANOVA OF CO_2 GAS EXCHANGE OF *Nothofagus pumilio* SEEDLINGS, CONSIDERING SOIL WATER CONTENT, LIGHT INTENSITY AND MONTH AS MAIN FACTORS, AND RATE OF DARK RESPIRATION (µmol CO_2/m².seg) (*RDR*), PHOTOCHEMICAL EFFICIENCY (µmol CO_2/µE) (*PE*), NET ASSIMILATION RATE (µmol CO_2/m².seg) (*NAR*), LIGHT COMPENSATION POINT (µE/m².seg) (*LCP*) AND LIGHT SATURATION POINT (µE/m².seg) (*LSP*) AS DEPENDENT VARIABLES.

Main effects	RDR	PE	NAR	LCP	LSP
Soil water content					
Dry	-1.30a	0.064a	7.89b	19.58a	450.00a
Wet	-1.37a	0.059a	6.68a	19.95a	431.94a
Light intensity					
Low	-0.89c	0.051a	5.11a	12.49a	327.78a
Medium	-1.41b	0.065b	8.34b	16.55a	446.18b
High	-1.72a	0.069b	8.41b	30.25b	548.95c
Month					
October	-0.68b	0.024a	2.08a	28.47c	275.69a
November	-1.84a	0.054b	6.48b	23.71bc	488.19bc
December	-1.60a	0.074cd	8.73cd	15.04a	388.19ab
January	-1.57a	0.083d	9.71d	19.41ab	474.30bc
February	-1.55a	0.072cd	9.45d	19.64ab	488.88bc
March	-0.79b	0.063bc	7.26bc	12.33a	530.55c

Values followed by different letters are significantly different with Tukey multiple range test ($p<0.05$)

Significance of main effects. RDR = Soil water content F: 0.37 p: 0.545, *Light intensity* F: 21.03 p: 0.000, *Month* F: 13.86 p: 0.000, *Soil water content x Light intensity* F: 0.08 p: 0.922, *Soil water content x month* F: 0.72 p: 0.609, *Light intensity x month* F: 3.52 p: 0.001, *Soil water content x Light intensity x month* F: 0.67 p: 0.748. *PE = Soil water content* F: 2.72 p: 0.101, *Light intensity* F: 10.93 p: 0.000, *Month* F: 27.02 p: 0.000, *Soil water content x Light intensity* F: 3.81 p: 0.023, *Soil water content x month* F: 1.40 p: 0.226, *Light intensity x month* F: 4.18 p: 0.000, *Soil water content x Light intensity x month* F: 0.78 p: 0.644. *NAR = Soil water content* F: 11.50 p: 0.001, *Light intensity* F: 37.96 p: 0.000, *Month* F: 42.85 p: 0.000, *Soil water content x Light intensity* F: 9.71 p: 0.001, *Soil water content x month* F: 2.73 p: 0.021, *Light intensity x month* F: 5.46 p: 0.001, *Soil water content x Light intensity x month* F: 2.28 p: 0.015. *LCP = Soil water content* F: 0.05 p: 0.828, *Light intensity* F: 39.55 p: 0.000, *Month* F: 7.73 p: 0.000, *Soil water content x Light intensity* F: 0.51 p: 0.603, *Soil water content x month* F: 0.59 p: 0.704, *Light intensity x month* F: 0.50 p: 0.889, *Soil water content x Light intensity x month* F: 0.92 p: 0.519. *LSP = Soil water content* F: 0.44 p: 0.509, *Light intensity* F: 21.90 p: 0.000, *Month* F: 7.82 p: 0.000, *Soil water content x Light intensity* F: 1.20 p: 0.302, *Soil water content x month* F: 1.73 p: 0.130, *Light intensity x month* F: 2.87 p: 0.002, *Soil water content x Light intensity x month* F: 0.81 p: 0.617.

Table N° 2
ANOVA OF BIOMETRICS AND PHYSIOLOGICAL VARIABLES OF *Nothofagus pumilio* SEEDLINGS, CONSIDERING LIGHT INTENSITY LEVELS.

Variables	Low	Medium	High	F	p
Height (cm)	12.42a	16.87b	12.04a	8.51	0.0034
Leaves number	7.93a	12.00b	11.26b	7.66	0.0051
Leaf size (cm)	2.43b	2.92c	2.12a	16.15	0.0000
Leaf shape (cm/cm)	1.27a	1.35a	1.29a	3.18	0.0706
Leaves biomass (gr/plant)	0,059a	0,164b	0,083a	17.27	0.0001
Foliar area (cm^2/plant)	85.6b	138.1c	39.1a	16.94	0.0001
Specific leaf mass (gr/cm^2)	0.0007a	0.0012b	0.0022c	120.46	0.0000
Foliar area rate (cm^2/gr)	389.5c	294.2b	129.2a	39.73	0.0000
Branch number	0.30a	0.56a	0.66a	2.72	0.0979
Insertion branch angle (°)	42.5a	44.25a	42.5a	0.02	0.9768
Chlorophyll a (mg/cm^2)	0.0215a	0.0331b	0.0291b	9.14	0.0025
Chlorophyll b (mg/cm^2)	0.0088a	0.0112a	0.0109a	1.15	0.3423
Carotenoids (mg/cm^2)	0.0065a	0.0095b	0.0107b	14.79	0.0003

Values followed by different letters are significantly different with Tukey multiple range test ($p<0.05$)

DISCUSSION

Usually, phenology is related to photoperiod, as well as air and soil temperatures (Lechowicz, 1984). The differences observed in the phenology between treatments were due to light intensities and soil water contents. The influence was greater in treatments with a better net assimilation rate, affecting the extent of reddening and leaf aperture. The leaf phenology in the experimental conditions was comparable to the natural growing conditions (Rusch, 1993; Barrera *et al.*, 2000), except for leaf aperture, which was more concentrated at the beginning of the summer in the natural forests.

The light compensation point is known to vary based on species, genetics, leaf type, leaf age, CO_2 air concentration and temperature (Kramer and Kozlowski, 1979). In our experiment, the light compensation point was higher at the beginning of the growing season due to the incomplete development of the photosynthetic structures, and decrease in old tissues. In contrast, the light saturation point increased through the growing season. Leaves do not begin to contribute to the carbon budget of the plant until they are about half expand, which occur earlier in temperate deciduous than in tropical evergreen trees (Hieke *et al.*, 2002).

Water stress influences metabolism, physiology and morphology in plants. Waterlogging causes inadequate aeration in soil, leading to rapid depletion of oxygen, which induces many physiological and morphological changes, affects mineralization and solubility of mineral substances, and leads to the formation of phytotoxic compounds (Sun *et al.*, 1995) that cause drying of leaves and a reduction in photosynthesis (Kramer and Kozlowski, 1979). In our study, phenology was affected by soil water content with leaf aperture lasting longer in the treatments with higher net assimilation rates. For *Nothofagus pumilio*, soils with high humidity were unfavorable compared to drier ones (40-60% soil capacity), decreasing the photosynthetic performance in higher light levels. For several oak species, the effects on seedling performance of a dry or wet summer vary under different light and competition conditions. Although rate of photosynthesis with competitors increase in the shade under dry conditions, it tend to decline in the shade under wet conditions (Davis *et al.*, 1999). In *N. solandri* and *N. menziesii*, the rate of net photosynthesis diminishes about 60-65% in severe water-logged conditions (Sun *et al.*, 1995). Regeneration of *N. pumilio* is produce mainly through gap dynamics (Veblen, 1989) due to the light availability under the overstory. Another limiting factor in this response is the water stress, which could switch the processes from a light- to a water-limited system (Heinemann *et al.*, 2000; Heinemann and Kitzberger, 2006).

In the study, phenology was affected by the light intensities, where leaf aperture was more extended in time in the medium light level. In the higher light level treatments leaf reddening occurs due to the higher carotenoid production or chlorophyll degradation (Larcher, 2003; Hormaetxe *et al.*, 2004). The rate of dark respiration was correlated with light intensities due to the demand of metabolic energy increases in the plant tissues growing in lighted environments. Lichtenthaler *et al.* (1981) report an increase of 3.1x in sun exposed compared to shaded leaves of *Fagus*, while our increase was on the order of 1.9x. Heliophytic tree species have characteristics that favor high-light growth, which include higher relative growth rates and higher respiration under all environmental conditions (Larcher, 2003; Kneeshaw *et al.*, 2006; Niinements, 2006).

The speed of the light reactions is the limiting factor for the photosynthesis process. A steep slope in the light-response curve is an expression of high quantum yield (Larcher, 2003). In this study, the photochemical efficiency and net assimilation rate were related to light availability, as was found in other studies (Tognetti *et al.*, 1998; Larcher, 2003). Seedlings and saplings of *N. pumilio* can grow and survive with low light intensities (Rebertus and Veblen, 1993; Cuevas and Arroyo, 1999), which is the main limiting factor to achieve greater growth rates (Heinemann *et al.*, 2000).

Plants that respire intensely require more light for compensation than those with weaker respiration (Larcher, 2003). The shaded leaves have lower light compensation points than sun-exposed leaves (Kramer and Kozlowski, 1979; Larcher, 2003), as was observed in our study, which was related to the achieved rate of dark respiration. Additionally, the light saturation point was related to light intensities also, due to the photosynthetic structures developed in environments with more light, which are more efficient in light use. In a study of the genus *Fagus*, Lichtenthaler *et al.* (1981) found an increase of 2.5x and 1.9x in sun-exposed compare to shaded leaves for light compensation point and light saturation point respectively, while in our study the values were 2.4x and 1.7x. It is often stated that most plants are light saturated for photosynthesis at one-fourth to one-half of full sunlight (Kramer and Kozlowski, 1979). However, in our experiments it was necessary 14x, 3x and 1.5x more light in the low, medium and high light level treatments, respectively, to saturate photosynthesis, compared to the average available to each treatment type. The photosynthetic rate efficiency was lower in the high light treatment at lower irradiances (<100 µmol quanta/m².s) compared to the other treatments, but it was more efficient at higher irradiances in dry soil water content treatment, and lower in wet.

In forest ecosystems, in both natural and managed stands, acclimation to changing conditions plays a major role in tree recruitment and competition processes. The increase in resource availability can lead to differences in photosynthetic characteristics, leaf anatomy and whole plant growth. The overall response of tree seedlings to canopy opening depends upon their ability to endure sudden exposure to the new conditions in managed forests (Tognetti *et al.*, 1998; Heinemann *et al.*, 2000).

Nothofagus pumilio primary forests have high crown closure, which retains a large percentage of the rainfall (13-25% for interception and 15-50% for evapotranspiration) and diminishes the light availability at the understory level (Frangi and Richter, 1994; Caldentey *et al.*, 2005). Inside the primary forests a great variability of micro-environment conditions can be found, ranging from high shaded sites (such as our low light intensity treatment) to small patches in the canopy with more light availability (comparable to our medium light intensity treatment). The soil water content can reach up to 50-60% of capacity during the late spring and summer (Mormeneo *et al.*, 2004) in better quality sites in southern Patagonian primary forests (Martínez Pastur *et al.*, 1997), which was quite similar to our dry treatment. These primary forests have no long-term seed bank. The seed-fall is produced at the beginning of the autumn before leaf-fall, and seeds germinate during the spring of the same year. So, this creates a seedling bank (Cuevas and Arroyo, 1999), which often survives and grows slowly for a long time in the shaded understory (Rebertus and Veblen, 1993). These seedlings are adapted to this limited light resource environment, developing photosynthetic machinery that allows them to grow and survive waiting for a canopy opening. Generally, in temperate boreal forests shade tolerant tree saplings may survive 7-20 years in deeply shaded understories with 0.2-1 m in height (Niinemets, 2006), while *Nothofagus pumilio* seedlings survive less than 20 years with no more than 0.5 m height (Martínez Pastur *et al.*, 1999; Gea *et al.*, 2004). Due to the low growth rate, the probability of seedling mortality increases with their size, because more energy is allocated to support non-photosynthetic tissue, including greater allocation to fine roots, mechanical support and more complex branch architecture (Kneeshaw *et al.*, 2006).

Information to date suggests that acclimation to a high light environment is species dependent, and likely related to the plants successional stage (Reynolds and Frochot, 2003). If we considered the pure natural *Nothofagus pumilio* forests of southern Patagonia, the seedlings are the main woody component of the understory, constituting the pioneer species after large disturbances and the climax species of the final succession. For this reason, many authors classified it as a shade intolerant species (Richter and Frangi, 1992; Veblen *et al.*, 1997). However, when we analyzed its photosynthesis performance, we determined that the species can be considered as mid-tolerant, due to the shade tolerance in early development stages and for the fact that it reaches the maximum photosynthesis efficiency at relatively low light levels (26% of the natural incident irradiance). *N. pumilio* is not a shade tolerant species, as it is not able to reproduce and survive for long periods of time under closed canopy. Nor is it shade intolerant, due to the fact that its photosynthesis performance is not significantly improved in high light environments. Gutiérrez (1994) suggest that Fuegian *Nothofagus* species are mid-tolerant due to their colonization abilities.

The photosynthesis performance of *N. pumilio* seedlings along light intensity and soil water content gradients has important implications for forest management. In mesic *N. pumilio* forests, small- to moderate-sized gaps typically result in abundant regeneration, while in drier conditions soil moisture is a dominant factor and regeneration only occurs under special conditions (Heinemann *et al*., 2000). According to these results, the established seedlings of *N. pumilio* forests have the capacity to quickly adapt to the new environmental conditions generated by forest management practices. Gradual openings in the canopy of the overstory appears to be the most convenient (e.g., shelterwood cuts in Chile), due to the fact that seedlings in the understory reach their maximum photosynthetic potential. Water availability positively controls seedling survival and growth in the xeric forest, while in the mesic forest, survival and growth are differentially controlled by water and light availability, respectively (Heinemann and Kitzberger, 2006).

CONCLUSIONS

Natural *Nothofagus pumilio* seedlings grow below their optimum photosynthetic potential in the understory, and quickly acclimate to dramatic changes in the forest structure acting as pioneer plants in the succession process that follows. This photosynthesis acclimation allows the adaptation to several silvicultural proposals. However, small apertures in the canopy are enough to attain the maximum photosynthetic performance. These findings must be combined with morphological variables obtained at whole-plant, shoot, crown and leaf levels, e.g., medium and high light intensity treatments presented the same photosynthesis efficiency, but if it is combined with the foliar area, the achieved growth could be different. Finally, it is necessary to compare this results of light and soil water performance with natural regeneration patterns and forest dynamics.

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