Ecología Austral 18:27-41. Abril 2008
Asociación Argentina de Ecología

Seedling recruitment of *Austrocedrus chilensis* in relation to cattle use, microsite environment and forest disease

Ludmila La Manna [1, 2, ✉], Marta Collantes [2, 3], José Bava [1] & Mario Rajchenberg [1, 2]

1. *Centro de Investigación y Extensión Forestal Andino Patagónico (CIEFAP), Universidad Nacional de la Patagonia S J Bosco, Esquel, Chubut, Argentina.*
2. *Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.*
3. *Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Argentina.*

Abstract. The forests of *Austrocedrus chilensis* in the Patagonian Andes suffer a disease known as "mal del ciprés". The purpose of this work was to identify the relationship between *A. chilensis* seedling recruitment and disturbances (i.e., disease and cattle grazing), and to identify associations between seedling recruitment and microsite characteristics related to the disturbances. Eighteen sites with "mal del ciprés" were selected for study. In each site, symptomatic and asymptomatic plots were established and characterized. Five control sites, where the disease was totally absent, were also included. Cattle use and disease were negatively associated with *A. chilensis* natural regeneration. Both disturbances seemed to act synergically. In control sites the abundance of seedlings was never null and reached greater values with low cattle use. In symptomatic and asymptomatic plots of diseased forests, seedling abundance tended to be lower than in control forests and was generally null when cattle use was high. The disease was associated with microsite features such as low canopy cover, organic horizon thickness and high understory cover. Although these site conditions were negatively associated with seedling abundance, they could not completely explain the variation found in seedling recruitment.

[Keywords: forest decline, "mal del ciprés", natural regeneration, site effect]

Resumen. Reclutamiento de renovales de *Austrocedrus chilensis* en relación al uso ganadero, los factores de micrositio y la sanidad del bosque: Los bosques de *Austrocedrus chilensis* en los Andes Patagónicos sufren una enfermedad conocida como "mal del ciprés". Los objetivos de este trabajo fueron identificar la relación entre el reclutamiento de renovales de *A. chilensis* y los disturbios (i.e., enfermedad y uso ganadero) e identificar asociaciones entre la abundancia de renovales y características del micrositio relacionadas con los disturbios. Dieciocho sitios con "mal del ciprés" fueron seleccionados para el estudio. En cada sitio, se establecieron y caracterizaron parcelas sintomáticas y asintomáticas. Cinco bosques control, donde la enfermedad estuvo completamente ausente, fueron también incluidos. El uso ganadero y la enfermedad estuvieron negativamente asociados con la regeneración de *A. chilensis*. Ambos disturbios actuarían en forma sinérgica. En los bosques control la abundancia de renovales nunca fue nula y alcanzó valores más altos cuando el uso ganadero era bajo. En las parcelas sintomáticas y asintomáticas de bosques enfermos la abundancia de regeneración tendió a ser menor que en los bosques control y resultó generalmente nula cuando el uso ganadero fue alto. La enfermedad estuvo asociada a ciertas características del micrositio, como baja cobertura del dosel, escaso espesor del horizonte orgánico y alta cobertura del sotobosque. Si bien estas características del micrositio estuvieron negativamente asociadas con la abundancia de renovales, no pueden explicar por sí solas la variación hallada en el reclutamiento de renovales.

[Palabras clave: declinación del bosque, "mal del ciprés", regeneración natural, sitio]

✉ Centro de Investigación y Extensión Forestal Andino Patagónico (CIEFAP) C.C. 14 (9200), Esquel, Chubut, Argentina.
llamanna@ciefap.org.ar

Recibido: 22 de agosto de 2007; Fin de arbitraje: 16 de octubre de 2007; Revisión recibida: 5 de noviembre de 2007; Aceptado: 8 de noviembre de 2007

Introduction

The Cordilleran cypress (*Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri) is an endemic Cupressaceae of the Andean forests of Patagonia. In Argentina it grows between 36º30´and 43º35´ S along a 60–80 km wide strip. It covers ca. 141000 ha including a strong east-west precipitation gradient from 500 to 1700 mm/year (Bran et al. 2002). *Austrocedrus chilensis* forests are an important economic resource for the cordilleran region, their high quality wood being used for construction and woodworking (Díaz-Vaz 1985). Their importance also leans on their environmental and landscape roles, as these forests surround most of the tourist cities and villages in the area.

In mesic habitats the regeneration pattern of *A. chilensis* follows a catastrophic mode in response to stand-devastating disturbances (i.e., fire, earthquakes, landslides) (Veblen & Lorenz 1987; Veblen et al. 1992, 1995). But, as these extensive even-aged stands age, the regeneration pattern becomes one of fine-scale gap phase (Veblen et al. 1995, 1996). *Austrocedrus chilensis* seeds are dispersed by wind. Although most of the seeds fall a few meters from the mother plant (Gobbi 1992), their dispersal range is greater than 200 meters (Schmaltz 1992). It has a transient soil seed bank, since seeds in the soil are not viable for more than a year (Urretavizcaya & Defossé 2004). Litter is important for seed storage (Raffaele & Gobbi 1996), however *A. chilensis* litter represents a poor substrate for germination (Rovere 2000). A high mortality of seedlings in sites with high *A. chilensis* litter was found, suggesting that litter could be the natural habitat for predators (Gobbi & Schlichter 1998) like *Nyctelia* sp. (Coleoptera, Tenebrionidae) as shown by Kitzberger et al. (2000). The abundance of seedlings with embryonic leaves was associated with gaps, open canopy cover, high short understory cover and low levels of litter accumulation. On the other hand, the abundance of seedlings with differentiated leaves was associated with a semi-closed canopy cover and high moss cover (Gobbi 1999a). Microsites in small gaps or even under slight openings in the tree canopy showed high seedling survival (Gobbi & Schlichter 1998), coinciding with a fine-scale gap phase regeneration pattern (Veblen et al. 1995, 1996). Open tree canopy conditions implied brighter and more humid microsites, and were associated with the presence of mosses and herb cover. These variables were also related to high seedling survival (Gobbi & Schlichter 1998).

Two main disturbances threaten forest persistence. One is the anthropic use. *Austrocedrus chilensis* forests are subject to excessive levels of cattle grazing (Veblen et al. 1995) that may affect forest regeneration by trampling and browsing (Loguercio et al. 1999; Relva & Sancholuz 2000). For many years there have been warnings about the negative effect of cattle in the Andean forests of Patagonia (Constantino & Papara 1953). However, grazing licenses are not awarded by forest authorities, but by other organizations that accept cattle grazing of the forest. Browsing was shown to reduce *A. chilensis* growth in height, with saplings targeted by herbivores reaching 0.5 to 1 m high, and to produce deformed individuals (Relva 1999). High browsing occurs beneath canopy gaps, which are also sites of higher sapling densities. Stands that are in the fine-scale gap phase of regeneration are the most susceptible to inhibition of tree regeneration by browsing (Relva & Veblen 1998; Relva 1999). In northern Patagonia it was shown that sites with heavy browsing tended to present a high cover of unpalatable woody species, like *Schinus patagonicus* (Phil.) Johnst., *Lomatia hirsuta* (Lam.) Diels and *Berberis* sp. *Austrocedrus chilensis* was subjected to more browsing in sites where the latter had reduced the abundance of the preferred species, *Schinus patagonicus* (Relva & Veblen 1998).

Widespread mortality due to an illness of *A. chilensis* throughout its range in Argentina also threatens these forests. This illness was detected about 60 years ago and is locally known as "mal del ciprés" (Hranilovic 1988). Symptoms of this disease are progressive withering and defoliation, crown thinning, decay of the main roots and, finally, the death of the tree.

Numerous studies have been done in order to determine the cause of the disease (Havrylenko et al. 1989; Barroetaveña & Rajchenberg 1996; Rajchenberg et al. 1998; Greslebin et al. 2005). It was associated to non-allophanized soils of fine textures (La Manna & Rajchenberg 2004a,b) and sites with high precipitation and moderate altitudes (Baccalá et al. 1998). The onset of the disease was related with climatic and geologic events (Calí 1996). Up to now, "mal del ciprés" has been considered a forest decline disease by many authors (Calí 1996; Filip & Rosso 1999; La Manna & Rajchenberg 2004a,b; La Manna & Greslebin 2005). This type of disease is the result of complex interactions between biotic and abiotic factors (Manion 1991; Manion & Lachance 1992). Site conditions that favour poor internal drainage were shown to act as predisposing factors that enhance the development of the disease (La Manna & Rajchenberg 2004a) and *Phytophthora* species were supposed to be weak pathogens causing chronic root reduction (Greslebin et al. 2005). Forest decline diseases around the world affect trees of reproductive mature populations (Manion 1991), but seedlings are not altered (Mueller-Dombois 1992).

Recently, using molecular techniques, the causal agent of this syndrome has been elucidated. The biotic agent is a fungus of the genus *Phytophthora* (*P. austrocedrae* Gresl. & E. M. Hansen), which has been recently isolated, described, and shown to fulfill Koch's postulates (Greslebin & Hansen 2007; Greslebin et al. 2007). The degree of aggressiveness of *P. austrocedrae* is still unknown (Greslebin & Hansen 2007). This pathogen, which penetrates the plant by its roots, is an aquatic mould which needs water for dispersion and is generally associated to poorly drained soils. Contrary to what happens with decline diseases in other forests around the world where *Phytophthora* species are involved as pathogens, forest seedlings are vulnerable to the attack (Hansen 2000). *Chamaecyparis lawsoniana* [(A. Murray) Parl] forests are affected by *Phytophthora lateralis* (Tucker & Milbrath), which causes a root disease. Symptoms and death occur quicker, within a few weeks, in seedlings and saplings. On the other hand, large trees die much slower, declining over periods of one to four years (Goheen et al. 2005). *Phytophthora cinnamomi* (Rands), which causes a disease in *Pinus occidentalis* (Swartz), attacks mainly mature stands and natural regeneration older than 10 years (Jung & Dobler 2002).

Although natural regeneration might be the key to guarantee the continuity of *A. chilensis* forests, there is no information regarding the way the disease affects regeneration. *Phytophthora austrocedrae* should be able to affect regeneration, since it was isolated from mature trees, saplings and seedlings (Greslebin & Hansen 2007). Beside the possible direct effect on regeneration, the disease could also affect the production of viable seeds and the availability of favourable microsites for germination and survival. The spatial pattern of distribution of "mal del ciprés" [i.e., small diseased patches, mostly less than 400 m^2, surrounded by healthy forest (La Manna & Carabelli 2005)], the seeds dispersal range [i.e., greater than 200 meters (Schmaltz 1992)], the slow progression of symptoms (Calí 1996), and the intensive fructification of trees before dying, suggest that the availability of seeds in the diseased forests should not be limiting. However, no real information exists on the availability of seeds in diseased forests. The progressive defoliation process and the death of trees are disturbances that could modify microsite features such as canopy and understory cover, and affect seedling recruitment (Ling & Ashmore 1999). On the other hand, the disease was found to be associated with particular microsite features. The patches of affected forest tend to develop in poorly drained soils while the asymptomatic patches are associated with allophanic volcanic soils (La Manna & Rajchenberg 2004a,b). Allophane is an amorphous constituent derived from the alteration of volcanic ash. Allophanic soils have good properties for forest development, presenting high porosity, permeability and adequate water availability (Warkentin & Maeda 1980; Colmet Dâage et al. 1995). Stressed edaphic sites could damage or prevent seedling recruitment (Smith et al. 1997).

The anthropic use of *A. chilensis* forests could also affect the development of "mal del ciprés". The spread of *Phytophthora* species could occur by soil clinging to the feet of cattle and humans (Goheen et al. 2005). On the other hand, although no study exists on the understory features of diseased *A. chilensis* forests, it can be expected that the disease affects cover and species composition, and modifies the abundance of palatable species (Ling & Ashmore 1999).

The objectives of the present study were: (i) to identify the relationship between *A. chilensis* seedling recruitment and disturbances (i.e., disease and cattle grazing); and (ii) to identify associations between seedling recruitment and microsite characteristics related with the disturbances. We addressed the following questions: (i) which disturbance-microsite variables are related to the presence/absence of natural regeneration? (ii) do disturbances affect the abundance of seedlings?, and (iii) how are disturbance and microsite variables related?

Materials and Methods

The study was carried out in SW Río Negro Province and NW Chubut Province, Argentina, covering a latitudinal range from 41º53´ to 43º13´ S and a longitudinal range from 71º23´ to 71º43´ W. Eighteen sites with pure *A. chilensis* forests with "mal del ciprés" syndrome were selected covering different soil types, in order to include the wide edaphic variability existing in the area (La Manna 2005). Five control sites, where the disease was totally absent were included (Table 1). All sampled sites were dense forests originated after wildfires, with no history of salvage or logging. Basal area of plots ranged from 30 to 140 m^2/ha, whereas tree density ranged from 400 to 5400 cypress/ha. Values of basal area and number of trees per hectare were associated with soil type (La Manna et al. 2006).

In each diseased forest, a pair of 200 m^2 plots representative of the stand structure and differing in disease symptoms was established: one in a patch of diseased trees, the other in an adjacent patch of trees without disease symptoms. Then, within each diseased forest a plot with an advanced degree of disease (more than 90% of dead trees = diseased plot), and another one without symptoms (asymptomatic plot) were sampled. Both plots within a pair had similar forest structure (according to diameter distribution and heights) and were located 50-100 m apart, within the dispersion range of *A. chilensis* seeds (Schmaltz 1992). At each control site (i.e., healthy forests where the disease was totally absent), one 200 m^2 plot was established, representative of the forest structure. The sampling was done during late spring and summer 2001-2002.

Forest structure

Diameter at breast height (DBH), crown class (i.e., dominant, co-dominant, intermediate, suppressed) and vitality class were recorded for all *A. chilensis* trees ≥ 5 cm in DBH and the total basal area was determined. The vitality class of each tree was assessed visually following the scale of Rajchenberg & Cwielong (1993). This classification scale establishes six categories from 0 (healthy) to 5 (dead), according to percentage of crown defoliation and foliage and bark appearance. The disease condition of each plot was characterized as the percentage of *A. chilensis* diseased basal area (Horsley et al. 2000), which was calculated as the proportion of *A. chilensis* basal area in diseased and dead classes (Rajchenberg & Cwielong 1993) relative to the total stand basal area. Canopy cover was estimated with a concave spherical densiometer following Lemmon (1956).

Understory vegetation

High understory shrub cover (>120 cm height), low understory shrub cover (<120 cm height), herb cover and moss cover were measured by the line interception method with linear subsampling (Matteucci & Colma 1982). Within each plot, cover measurements of all strata were taken in five 10 m long N-S orientated transects, 3 m apart.

Regeneration

The abundance of *A. chilensis* seedlings smaller than 150 cm height was registered. The seedling population was split into five classes: seedlings under 2 years with embryonic leaves (Gobbi 1999b), seedlings with differentiated leaves and smaller than 5 cm height, seedlings 5.1-20 cm high, 20.1-50 cm high and 50.1-150 cm high. In each plot, sub systematic sampling was carried out, establishing 9 subplots of 1 m^2 and 9 of 10 m^2, uniformly distributed, to count seedlings smaller and taller than 20 cm high, respectively. The health condition of each seedling was visually evaluated, according to external symptoms, by registering the presence of chlorotic or dead leaves. No inspections of phloem tissues from main roots, root collar or lower stem were conducted to assess initial damage by *Phytophthora*, because this technique involves killing regeneration. The sampling of seedlings was conducted once within the period of time mentioned above.

Soil features

The organic horizon thickness was measured in two points, not altered by sampling work. A composed clod from A horizon, generated by four subsamples, was collected and its pH in NaF (1:50) was measured (Fieldes & Perrot 1966) in order to detect amorphous constituents (i.e., allophane, imogolite) from

Table 1. Location and climatic and edaphic characteristics of sampling sites.
Tabla 1. Ubicación y características climáticas y edáficas de los sitios de muestreo.

Latitude (S)	Longitude (W)	Precipitation (mm/year)	Soil type*
		Forests expressing "mal del ciprés" disease	
41º53´	71º31´	1000	Humic Udivitrands and Aquic Udivitrands
41º54´	71º32´	1000	Aquic Hapludands
41º55´	71º33´	1000	Humic Udivitrands and Typic Udivitrands
41º57´	71º23´	850	Fluvaquentic Endoaquolls and Aquic Hapludolls
42º17´	71º25´	1200	Humic Udivitrands and Aquic Hapludolls
42º50´	71º39´	1610	Humic Uditrands
43º09´	71º41´	1200	Andic Hapludolls
43º10´	71º30´	690	Vertic Endoaquolls and Endoquerts
43º10´	71º40´	1105	Humic Udivitrands and Aquic Hapludands
43º10´	71º43´	1200	Humic Udivitrands and Fluventic Hapludolls
43º11´	71º29´	690	Endoaquerts
43º11´	71º39´	1105	Humic Udivitrands and Aquandic Endoaquolls
43º12´	71º32´	888	Aquic Hapludolls
43º12´	71º38´	1105	Humic Udivitrands and Lithic Udivitrands
43º12´	71º39´	1105	Lithic Udivitrands
43º13´	71º32´	888	Typic Vitraquands and Typic Hapludolls
43º13´	71º33´	888	Aquic Hapludands and Andic Hapludolls
43º13´	71º38´	1105	Andic Hapludolls and Aquic Hapludolls
		Control forests	
41º58´	71º24´	850	Humic Udivitrands
41º59´	71º29´	1000	Andic Hapludolls
43º02´	71º29´	633	Vitric Hapludands
43º09´	71º39´	1105	Humic Udivitrands
43º12´	71º28´	690	Humic Udivitrands

*According to La Manna (2005b).

*Según La Manna (2005b).

volcanic ash (Irisarri 2000). Two soil cores for bulk density were obtained with a 100 cm^3 soil corer.

Cattle use

Cattle use was estimated by counting faeces and registering browsing symptoms. These included the presence of browsed twigs and deformed stems by loss of apical dominance.

Faeces were counted in two rectangular subsamples of 3 m x 8 m (24 m^2). Each subplot had a N-S direction and was 5 m apart from the other subplot. According to browsing symptoms and the number of faeces, plots were divided into two categories: low cattle use plots (without browsing symptoms and <0.125 feces/m^2) and high cattle use plots (with browsing symptoms and $\geq$0.125 faeces/m^2). Although we had no access to the history of cattle use of each stand, it is known that, in the study area, sites with livestock have suffered from it for at least 40 years.

Data analysis

Discriminant analysis. In order to detect site variables associated with the presence of regeneration, a discriminant analysis was used. Sampled plots were classified into two classes according to their natural regeneration status: with and without regeneration. Independent variables were: microsite features (i.e., canopy cover, high and low understory shrub cover, herb cover, moss cover, organic horizon thickness, bulk density and pH in NaF of the A horizon) and disturbance variables (i.e., percentage of diseased basal area and number of faeces). Variables were transformed in order to reach analysis assumptions (Williams 1983). Equality of group covariance was tested using Box's M-test. A stepwise procedure was used to retain the most significant variables for discrimination. Stepwise discriminant analysis is an efficient procedure for removing redundant variables and selecting the group of variables that produces the greatest discrimination (Afifi & Clark 1984). The classification rates were assessed by means of a cross-validation procedure.

Abundance of seedlings. The abundance of seedlings between control, asymptomatic and diseased plots for each cattle use category was compared using Kruskall Wallis and Kruskall Wallis all-pairwise comparison test (Ramsey & Schafer 1997). Seedling abundance between plots with different level of cattle use was analysed using Mann-Whitney test (Ramsey & Schafer 1997). Non parametric tests were performed since abundance of seedlings did not reach parametric analysis assumptions.

Redundancy Analysis (RDA). In order to study the interrelation between microsite variables and disturbances, a Redundancy Analysis (RDA) was conducted using CANOCO version 4.0 (Ter Braak & Smilauer 1998). RDA allows identification of trends in the scatter of data points that are maximally and linearly related to the set of explanatory variables (Makarenkov & Legendre 2002). RDA was performed with microsite features using the disturbance variables (i.e., percentage of diseased basal area and number of faeces) as explanatory variables (Rao 1973). Monte Carlo permutations were performed in order to determine if the relationship between disturbance variables and measured microsite features was statistically significant. Two tests were performed, one for the first canonical axis and one for both of the extracted canonical axes. Correlations between the RDA canonical axis and seedlings abundance for each seedling class were tested by Spearman coefficient (Ramsey & Schaffer 1997).

Results

Of the sum total, 54% of the plots exhibited *A. chilensis* natural regeneration. The percentage of plots with regeneration varied according to disease condition: 100% for control plots, 56% for asymptomatic plots and 39% for diseased ones. The percentage of plots with regeneration also varied according to cattle use level: 75% for low cattle use plots and 24% for high cattle use ones. The health condition of seedlings was good both in healthy and in diseased plots. The presence of chlorotic or dead seedlings was very rare. Only three and six dead seedlings were registered in the asymptomatic and the diseased plots, respectively, of the same sampling site. Both plots presented high density of trees and high cattle use.

Discriminant analysis

The two disturbance variables (i.e., number of faeces and the percentage of *A. chilensis* diseased basal area) were identified by discriminant analysis as the key variables to differentiate plots without natural regeneration from those with regeneration. These variables produced the best discriminant function and could accurately discriminate between both groups and predict site unit membership at the 0.05 significance level. Plots with regeneration tended to present lower disturbance (i.e., lower number of faeces and percentage of diseased basal area) (Table 2).

Group differentiation was good (Wilks's λ= 0.585, P<0.001). The model had a cross-validation classification success rate of 78%. Ninety-one percent of the original grouped cases were correctly classified as "with regeneration" and 74% of the original grouped cases were correctly classified as "without regeneration".

None of the microsite features (vegetation and soil variables) considered was able to discriminate between plots with and without regeneration.

Seedling abundance

The abundance of *A. chilensis* seedlings in sites with low cattle use was significantly less in diseased plots than in control ones. On the contrary, the abundance of seedlings within asymptomatic plots did not differ from either the control plots or the diseased ones (Figure 1). In sites with high cattle use, the abundance of seedlings was significantly higher in control plots than in asymptomatic and diseased ones (Figure 1). The abundance of regeneration for control plots varied between 1.29 and 7.01 seedlings/m^2 for plots with low cattle use, and between 0.01 and 1.42 for plots with high cattle use, but there were no significant differences comparing both cattle use levels (P=0.248). These results could be biased by the low number of control plots (Figure 1). The abundance of regeneration for asymptomatic plots was significantly greater (P=0.003) in plots with low cattle use (value range: 0-8.45 seedlings/m^2) than in plots with high cattle use (0 seedlings in all cases), being also significantly higher for diseased plots (P=0.049) with low cattle use (value range: 0-3.11 seedlings/m^2) than in plots with high cattle use (mostly 0, and 0.08 seedlings/m^2 in one plot).

In sites with low cattle use, the abundance of seedlings in control and asymptomatic plots tended to be greater than in diseased ones for

Table 2. Discriminant variables for regeneration classes obtained by stepwise procedure. Mean, standard error, range of values (between brackets) and *P* values for One-way ANOVA.

Tabla 2. Variables del Análisis discriminante para parcelas con y sin regeneración obtenidas mediante el procedimiento paso a paso. Promedio, error estándar, rango de valores (entre corchetes) y valor de *P* para un ANOVA de una vía.

Variables	Without Regeneration	With Regeneration	*P*
Number of feces (feces/m^2)	0.22 ± 0.05 [0-0.79]	0.04 ± 0.01 [0-0.23]	<0.001*
Diseased basal area (%)	62.56 ± 10.22 [0-100]	29.89 ± 8.67 [0-100]	0.019

* ANOVA using the log-transformed [ln(x+1)] variable.

* ANOVA realizado con la variable transformada logarítmicamente [ln(x+1)].

each seedling size class, but the differences were not significant ($P>0.05$) (Figure 2a). With high cattle use, the abundance of seedlings in control plots tended to be greater than in asymptomatic and diseased ones, but the differences were also not significant ($P>0.05$) (Figure 2b).

Redundancy analysis

RDA revealed a significant relationship between the disturbance variables and the microsite features on the first canonical axis ($F=10.15$; $P=0.015$) and both canonical axes ($F=6.158$; $P=0.010$) according to the Monte Carlo test (Ter Braak & Smilauer 1998). The disturbance variable explained 21.1 % of the variation in microsite features distribution on the first axis and 24.5 % on the first two axes (Table 3).

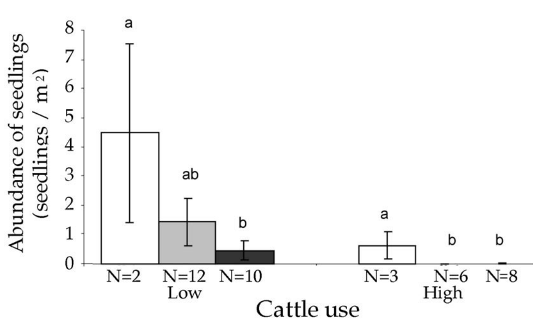
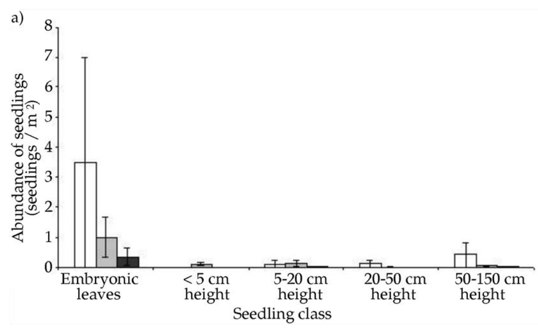


Figure 1. Average abundance of *A. chilensis* seedlings in control (□), asymptomatic (■) and diseased (■) plots, for two cattle use categories: low cattle use (number of faeces <0.125 m²) and high cattle use (number of faeces >0.125m²). Lines upon bars indicate average value ± 1 standard error. Lower case letters indicate significant differences ($P<0.05$).

Figura 1. Abundancia promedio de renovales de *A. chilensis* en parcelas control (□), asintomáticas (■) y enfermas (■), para dos clases de uso ganadero: bajo uso (<0.125 heces/m²) y alto uso ganadero (>0.125 heces/m²). Líneas sobre barras indican valor promedio ± 1 error estándar. Letras distintas indican diferencias significativas ($P<0.05$).

The first RDA axis was highly correlated to the percentage of diseased basal area ($r=0.999$), positively related to herb cover, low understory shrub cover and bulk density of the A horizon, and negatively related to organic horizon thickness and canopy cover (Figure 3). Axis 1 also tended to be negatively related to pH in NaF of the A horizon and moss cover. The second RDA axis was highly correlated to number of faeces ($r=0.999$) but no microsite feature showed a relationship with this axis, except the high understory shrub cover which tended to be negatively related (Figure 3).



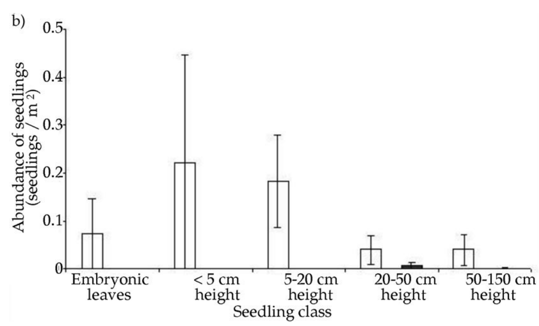


Figure 2. Average abundance of each *A. chilensis* seedling class in control (□), asymptomatic (■) and diseased (■) plots. a) Plots with low cattle use (number of faeces <0.125 m²). b) Plots with high cattle use (number of faeces >0.125m²). Lines upon bars indicate the average value ± 1 standard error. There were no significant differences for non-seedling class ($P>0.05$). The scale of the y-axis differs between Figures 2a and b.

Figura 2. Abundancia promedio de renovales de *A. chilensis* para cada clase de tamaño en parcelas control (□), asintomáticas (■) y enfermas (■). a) Parcelas con bajo uso ganadero (<0.125 heces/m²). b) Parcelas con alto uso ganadero (>0.125 heces/m²). Líneas sobre barras indican valor promedio ± 1 error estándar. No se registraron diferencias significativas para ninguna clase de tamaño de renovales ($P>0.05$).

RDA results showed a positive relation between axis 1 and the disease; the control and asymptomatic plots being placed towards negative values along axis 1 (Figure 3). The total abundance of regeneration and the abundance of regeneration for each seedling size class were also negatively correlated to axis 1 (Table 4). These results show that the abundance of seedlings was greater in sites with high canopy cover, thicker organic horizon, higher pH in NaF, and lower bulk density, herb and low understory shrub cover, which tended to be microsite features associated with healthy plots (Figure 3). The total abundance of regeneration and the abundance of taller seedlings (i.e., seedlings 50.1-150 cm high) were also negatively related with axis 2 (Table 4), presenting lower cattle use and tending to be related to higher shrub cover (Figure 3).

Discussion

Both disturbances evaluated in this study (i.e., forest disease and cattle use) were negatively related to the presence and the abundance of seedlings in *A. chilensis* forests. Cattle use was strongly associated with the absence of *A. chilensis* natural regeneration. Regeneration abundance was greater in sites with lower cattle use, and was low or null in sites with higher cattle use. Cattle not only affects regeneration by trampling but also by browsing. Browsing simulation studies in *A. chilensis* seedlings showed a negative effect on plant biomass and the lack of compensatory growth response (Relva & Sancholuz 2000). Diseased basal area was also negatively associated with the presence and abundance of seedlings. Although health condition of seedlings was good in diseased forests and the abundance reached values up to 3.11 seedlings/m^2, similar to those registered by Gobbi (1999b) in healthy forests, the abundance of seedlings was low compared with the control plots. The few records of plants with disease symptoms might be due to an incomplete study of "mal del ciprés" symptoms, since non-destructive sampling was conducted. Possibly, more seedlings with disease symptoms might have been recorded if the tissues of roots, root collar and lower stem had been analyzed looking for phloem lesions (Greslebin & Hansen 2007). The lack of symptoms in regeneration may also suggest that *P. austrocedreae* could be so aggressive and fast in the case of just-emerged seedlings that there is no evidence of affected seedlings, as happened in *C. lawsoniana* forests attacked by *P. lateralis* (Goheen et al. 2005). If this is the case, the limitation of sampling frequency, done only once in the study period, prevented us to discriminate this situation. Our results are inconclusive on this aspect and further specific studies on pathogenicity and resistance are required.

Table 3. RDA results for site variables in *Austrocedrus chilensis* forests.

Tabla 3. Resultados del RDA para variables de sitio en bosques de *Austrocedrus chilensis*.

	Axis	
	1	2
Eigenvalues	0.211	0.034
Microsite-disturbance correlations	0.664	0.331
Cumulative percentage variance		
of microsite data	21.1	24.5
of microsite-disturbance correlation	86.1	100

The low abundance of regeneration in diseased stands compared with control stands, suggests that there is a greater pool of viable seeds in healthy forests. The spatial pattern of distribution of *A. chilensis* disease (i.e., small patches of diseased trees surrounded by healthy forest) (La Manna & Carabelli 2005) and the dispersion range of *A. chilensis* seeds (i.e., greater than 200 m) (Schmaltz 1992), suggests that the availability of seeds in the diseased forests should not be limiting. However, the abundance of viable seeds could be modified as a consequence of tree death. Moreover, diseased forests appeared to be associated with stressed soils and control forests were associated with good soil conditions (La Manna & Rajchenberg 2004a,b). Favourable conditions of soil and climate for plant growth are associated to frequent and good crops of seed for many forest species (Kozlowski et al. 1991; Smith et al. 1997). The production and viability of seeds in diseased forests should be analyzed in future studies including exclosures in order to remove the influence of cattle. These studies should also include repeated measurements across time because of *A. chilensis* variability in seed production (Urretavizcaya & Defossé 2004).

Disease and cattle use are disturbances negatively related to the abundance of seedlings that seem to act synergically. In control plots, seedling abundance was never null and tended to reach greater values in plots with lower cattle use. Seedlings were generally absent in asymptomatic and diseased plots when cattle use was higher. Cattle could encourage the spread of *Phytophthora* species by clinging to their feet (Goheen et al. 2005). Spread of *P. austrocedrae* occurs primarily in the late fall, winter and early spring when moist environmental conditions favorable for the pathogen prevail. *Austrocedrus chilensis* forests should be restricted to cattle, humans and vehicles at least during this period, as occurs

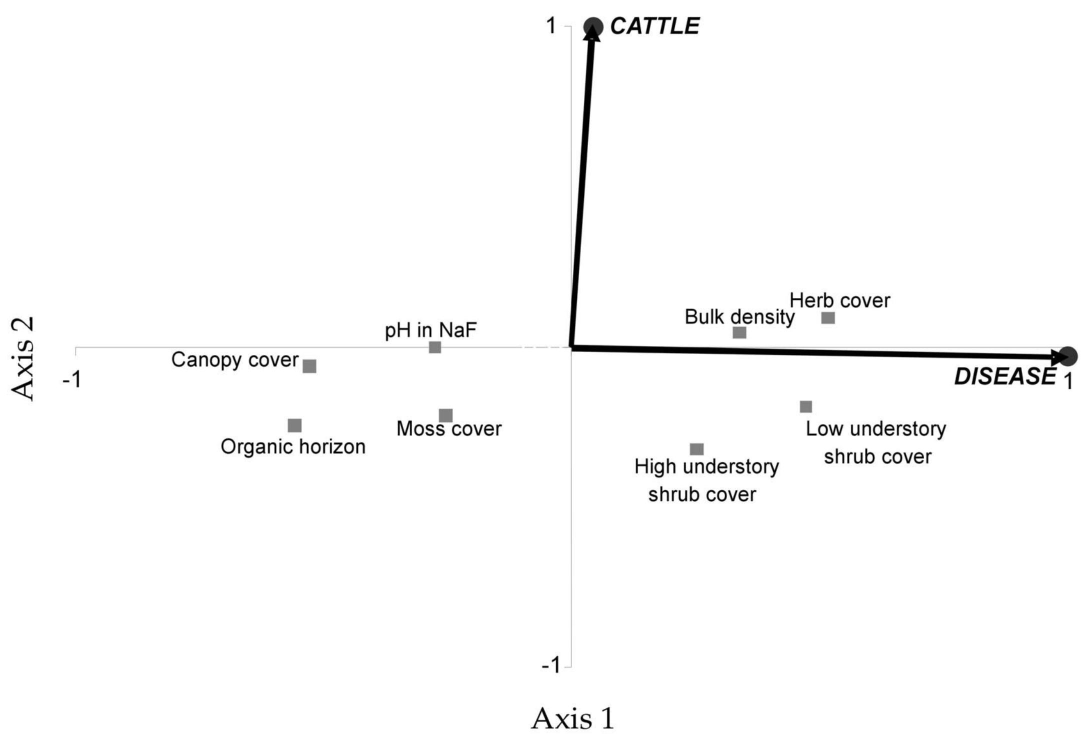


Figure 3. First and second conical axes obtained from redundancy analysis (RDA) of microsite features and disturbance variables. *DISEASE* = percentage of diseased basal area; *CATTLE* = number of faeces/m^2. The longer the arrow, the more important the parameter in explaining microsite variation. Microsite features were represented as points, however they should be interpreted as vectors extending from the origin. Sampled plots were not displayed in order to improve legibility.

Figura 3. Primer y segundo ejes canónicos obtenidos por análisis de redundancia (RDA) de factores de micrositio y variables de disturbio. *DISEASE* = porcentaje de área basal enferma; *CATTLE* = número de heces/m^2. La longitud de la flecha indica el grado de importancia del parámetro para explicar la variación en micrositio. Los factores de micrositio fueron representados como puntos, sin embargo, deberían ser interpretados como vectores que se extienden desde el origen. Las parcelas de muestreo no fueron incluidas en el gráfico a fin de mejorar su legibilidad.

in other forests around the world affected by *Phytophthora* (Goheen et al. 2005). On the other hand, the disease can affect cover and species composition, modifying also palatable species abundance. Although species composition was not evaluated in this study, it has been seen that grasses and palatable shrubs, like the exotic *Rosa eglanteria* L., increase their cover in diseased forests. This situation could generate different effects. The presence of palatable species could attract livestock and worsen trampling on seedlings, but these species could also provide alternative forage to cattle which might therefore decrease herbivory pressure on *A. chilensis* seedlings.

Austrocedrus chilensis disease was shown to modify microsite characteristics related to regeneration and establishment as in many other forest species (Gibson & Good 1987; Keeley 1992; Buckley et al. 1998; Williams et al. 1999; Pearson et al. 2002; Price & Morgan 2003; Palik et al. 2003). Disease was associated with sites of lower canopy cover, organic horizon thickness and pH in NaF, and higher understory strata cover and bulk density, which tended to be microsite features negatively related to seedling abundance. The negatively associated relationship found between *A. chilensis* disease and microsite features with seedling abundance was clear. However, microsite modifications are not enough to completely explain the variation in abundance of seedlings, since asymptomatic and control plots presented similar microsite features but they tended to present different levels of seedling recruitment. In contrast, a relationship between microsite features and cattle use was not found, except for the high understory shrub cover which tended to be negatively related with cattle use.

Table 4. Spearman correlation coefficients between the axis from RDA and seedling abundance (*P* values in brackets).

Tabla 4. Coeficientes de correlación de Spearman entre los ejes del RDA y la abundancia de renovales (valores de *P* están entre paréntesis).

Seedling class	Axis 1	Axis 2
Total abundance	-0,580 (*P*<0.001)	-0.459 (*P*=0.003)
With embryonic leaves	-0.376 (*P*=0.015)	-0.157 (*P*=0.327)
<5 cm height	-0.394 (*P*=0.011)	-0.105 (*P*=0.515)
5-20 cm height	-0.394 (*P*=0.011)	-0.027 (*P*=0.866)
20-50 cm height	-0.295 (*P*=0.061)	-0.267 (*P*=0.092)
50-150 cm height	-0.370 (*P*=0.017)	-0.591 (*P*<0.001)

The abundance of regeneration was positively associated with canopy cover, agreeing with results from previous studies (Gobbi 1999b; Arturi et al. 2001). However, the presence of small gaps and slight openings in the tree canopy showed high seedling survival and abundance (Gobbi & Schlichter 1998). Diseased stands presented more open canopies because of tree death. The positive relation found between canopy cover and abundance of seedlings, may hide the negative relation between the disease and seedling abundance, perhaps because of a lower pool of viable seeds in diseased stands.

The abundance of regeneration was positively associated with organic horizon thickness. In spite of forest defoliation being an important input of dead leaves, this study was centred on forest areas dead for many years. The current input of dead material would be low and, therefore, the organic horizon was thinner in diseased plots. Previous results on the effect of the depth of the organic horizon on *A. chilensis* regeneration are contradictory. Although litter is important for seed storage (Raffaele & Gobbi 1996), it is a poor substrate for germination (Rovere 2000).

The greater abundance of regeneration in sites with lower herb cover and lower understory cover differs from results registered by other authors in post-fire forests or logged forests, where canopy cover was almost absent (Veblen & Lorenz 1987; Gobbi & Sancholuz 1992; Gobbi & Schlichter 1998; Gobbi 1999a; Urretavizcaya et al. 2005). In the present study, diseased forests presented a moderate canopy cover because dead trees were still standing, which could decrease the relevancy of the protective effect of shrubs. Anyway, the negative relationship found between seedling abundance and herb and lower understory cover, may not be due to a direct effect of herbs and shrubs on regeneration, but to an effect of the disease: herb and low shrub cover tended to be greater in diseased plots, probably because there is more light reaching the forest floor as a consequence of tree death. The light reaching the forest floor is not positively related with the abundance of seedlings, as was shown by other studies (Relva & Veblen 1998; Relva 1999), probably as a consequence of a smaller pool of viable seeds in diseased stands.

The abundance of seedlings tended to be greater in sites with high pH in NaF. High values of pH in NaF indicate allophanic soils (Irisarri 2000), which have good water retention and do not present water deficit during the dry season (Colmet Dâage et al. 1995). Seedling abundance also tended to be greater in sites with higher levels of moss cover. Other studies have shown the importance of soil cover, particularly by mosses, in moisture conservation (Gibson & Good 1987). The relationship found between the abundance of seedlings, the pH in NaF and the moss cover could be associated with low water deficit during summer. Gobbi & Schlichter (1998) found that recruitment of *A. chilensis* seedlings and summer survival was greater in soils with more moderate water summer stress.

The relationship found between seedling abundance and lower bulk density could be due to an indirect effect of the allophane; the allophanized soils typically present low apparent densities (Warkentin & Maeda 1980). Results showed that disease was associated with soils with low pH in NaF and greater bulk densities, corroborating the results found by La Manna & Rajchenberg (2004a,b). Soil conditions associated with diseased forests could also negatively affect seedling recruitment. Greater bulk density could also be directly related to cattle use because of the effect cattle has on soil compaction.

In conclusion, this study succeeded in showing that "mal del ciprés" and cattle use disturbances were the main variables related to the absence of natural regeneration. The abundance of seedlings was also affected by disturbances, with low values of regeneration in sites with high disturbance intensity. The disease was related with microsite variables, but this relationship was not enough to explain the variation in seedling abundance. This result suggests that the seed bank would be affected by the disease, diminishing seedling abundance in diseased forests.

This study is the first step towards the characterization of natural regeneration in *A. chilensis* diseased forests. It evidenced the need of evaluating its seed bank, which seems to be a key variable. According to previous studies, crown openings (consequence of the disease) could improve seedling recruitment. However, this is impossible if there is not a proper seed bank in diseased stands. It would also be convenient to carry out experimental studies in order to evaluate and to discriminate the effect of disturbances (disease and/or cattle) and the causes of the microsite pattern that were found in this study. The impact of logging on the level of regeneration should also be investigated, since most of *A. chilensis* stands are logged. Future studies on the pathogenicity and aggressiveness of *Phytophthora austrocedrae* on seedlings are greatly necessary in order to understand the regeneration process. This study showed strong evidence that, in order to guarantee the continuity of *A. chilensis* forests, it is necessary to restrict the areas open to cattle. At present, high cattle use occurs in most of the diseased as well as healthy forests along the distributional range of this species. Forest management should encourage and propitiate the continuity of *A. chilensis* forests, closing diseased forests to cattle. Studies on restoration and planting in diseased forests should also be promoted as has been carried out with success in burned forests (Urretavizcaya 2006).

Acknowledgements

The authors acknowledge Luciano Taladriz, Franco Todone, Agustín Gigli, Carolina Toledo and Celina Escartín for their help in many stages of this study. Pre-submission reviews by Karen Braun, Juan Anchorena and Ana Cingolani provided constructive comments that improved the text and they are gratefully acknowledged. English language was corrected by Andrea Venosa and Karen Santoro. Many thanks to two anonymous reviewers whose comments improved the manuscript. This research was supported by the National Research Council of Argentina (CONICET) through PIP 2166/00 to MR. LLM, MC and MR are CONICET researchers.

References

AFIFI, A & V CLARK. 1984. *Computer-Aided Multivariate Analysis*. Lifetime Learning Publications, Belmont.

ARTURI, M; J FERRANDO; J GOYA; P YAPURA & J FRANGI. 2001. Tendencias espaciales de la regeneración de *Austrocedrus chilensis* en relación con el dosel arbóreo. *Ecol Aust* **11**:31-38.

BACCALÁ, N; P ROSSO & M HAVRYLENKO. 1998. *Austrocedrus chilensis* mortality in the Nahuel Huapi National Park (Argentina). *For Ecol Manage* **109**: 261-269.

BARROETAVEÑA, C & M RAJCHENBERG. 1996. Hongos *Aphyllophorales* (*Basidiomycetes*) que causan pudriciones en *Austrocedrus chilensis* en pie. *Bol Soc Argent Bot* **31**: 201-216.

BUCKLEY, D; T SHARIK & J ISEBRANDS. 1998. Regeneration of northern red oak: positive and negative effects of competitor removal. *Ecology* **79**: 65–78.

BRAN, D; A PÉREZ; D BARRIOS; M PASTORINO & J AYESA. 2002. Eco-región valdiviana: distribución actual de los bosques de "ciprés de la cordillera" (*Austrocedrus chilensis*) – Escala 1:250.000. INTA, APN, FVSA, Bariloche.

CALÍ, S. 1996. *Austrocedrus chilensis*: estudio de los anillos de crecimiento y su relación con la dinámica del "Mal del ciprés" en el P.N. Nahuel Huapi, Argentina. Dissertation, Universidad Nacional del Comahue.

COLMET DÂAGE, F; M LANCIOTTI & A MARCOLÍN. 1995. *Importancia Forestal de los suelos volcánicos de la Patagonia Norte y Central*. INTA, Bariloche.

CONSTANTINO, I & A PAPARA. 1953. *El bosque y la ganadería.* Ministerio de Agricultura y Ganadería, Buenos Aires.

DÍAZ-VAZ, J. 1985. *Austrocedrus chilensis*: descripción anatómica. *Bosque* **6**:49-50.

DONOSO, C. 1982. Reseña ecológica de los bosques mediterráneos de Chile. *Bosque* **4**:117-146.

FIELDES, M & K PERROT. 1966. The nature of allophane in soils Part 3: rapid field and laboratory test for allophane. *N Z J Sci* **9**:623-629.

FILIP, G & P ROSSO. 1999. Cypress mortality (mal del ciprés) in the Patagonian Andes: comparisons with similar forest diseases and declines in North America. *Eur J For Path* **29**:89-96.

GIBSON, D & R GOOD. 1987. The seedling habitat of *Pinus echinata* and *Melampyrum lineare* in oak-pine forest of New Jersey Pinelands. *Oikos* **49**:91-100.

GOBBI, M. 1992. Condiciones para la regeneración natural del ciprés de la cordillera (*Austrocedrus chilensis*) en áreas incendiadas. In: Abstracts II Congreso Latinoamericano de Ecología, Brasil.

GOBBI, M. 1999a. *Austrocedrus chilensis* management: effects on microsites and regeneration. *J Ecol Environ Sci* **25**:71-83.

GOBBI, M. 1999b. Aspectos ecológicos del manejo productivo de bosques puros y densos de *Austrocedrus chilensis*. Dissertation, Universidad Nacional del Comahue.

GOBBI, M & L SANCHOLUZ. 1992. Regeneración post-incendio del ciprés de la cordillera (*Austrocedrus chilensis*) en los primeros años. *Bosque* **13**:25-32.

GOBBI, M & T SCHLICHTER. 1998. Survival of *Austrocedrus chilensis* seedlings in relation to microsite conditions and forest thinning. *For Ecol Manage* **111**:137-146.

GOHEEN, D; P ANGWIN; R SNIEZKO & K MARSHALL. 2005. Port-orford-cedar root disease in southwestern Oregon and northwestern California. In: http://www.fs.fed.us/r6/dorena/documents/publications/pub104.pdf

GRESLEBIN, A; E HANSEN; L WINTON L & M RAJCHENBERG. 2005. *Phytophthora* species from declining *Austrocedrus chilensis* forests in Patagonia, Argentina. *Mycologia* **97**:218-228.

GRESLEBIN, A & E HANSEN. 2007. La causa del "mal del ciprés". *Patagonia Forestal* **13**(1): 5-8.

GRESLEBIN, A; E HANSEN & W SUTTON. 2007. *Phytophthora austrocedrae* sp. nov., a new species associated with *Austrocedrus chilensis* mortality in Patagonia (Argentina). *Mycological Research* **11**(3):308-316.

HANSEN, EM. 2000. *Phytophthora* in the Americas. In: Hansen, EM & W Sutton (Eds.), *First International Meeting on Phytophtoras in Forest and Wildland Ecosystems, Phytophthora Diseases of Forest Trees.* Grant Pass, Oregon, USA, Aug.30-Sep.3, 1997, pp. 23-27.

HAVRYLENKO, M; P ROSSO & S FONTENLA. 1989. *Austrocedrus chilensis*: contribución al estudio de su mortalidad en Argentina. *Bosque* **10**: 29-36.

HORSLEY, S; R LONG; S BAILEY; R HALLET & T HALL. 2000. Factors associated with the decline disease of sugar maple on the Allegheny Plateau. *Can J For Res* **30**:1365-1378.

HRANILOVIC, S. 1988. Informe histórico sobre el mal del ciprés de la cordillera (*Austrocedrus chilensis*).

Rev Asoc For Arg **42**:58-62.

Irisarri, J. 2000. La propuesta de reclasificación de los Andepts de Argentina, de acuerdo al Orden Andisoles. In: *Abstracts of the Workshop Soil Taxonomy*, INTA, AICET, AACS, Buenos Aires.

Jung, T & G Dobler. 2002. First Report of Littleleaf Disease Caused by *Phytophthora cinnamomi* on *Pinus occidentalis* in the Dominican Republic. *Plant disease* **86**(11):1275.

Keeley, J. 1992. Recruitment of Seedlings and Vegetative Sprouts in Unburned Chaparral. *Ecology* **73**:1194–1208.

Kitzberger, T; D Steinaker & T Veblen. 2000. Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology* **81**(7): 1914-1924.

Kozlowski T; P Kramer & S Pallardy. 1991. *The Physiological Ecology of Woody Plants*. Academic Press, San Diego.

La Manna, L. 2005a. Caracterización de los suelos bajo bosque de *Austrocedrus chilensis* a través de un gradiente climático y topográfico en Chubut, Argentina. *Bosque* **26**:137-153.

La Manna, L. 2005b. La declinación de los bosques de *Austrocedrus chilensis*: relación entre el «mal del ciprés» y el sitio. Ph. D. Dissertation, Universidad de Buenos Aires.

La Manna, L & F Carabelli. 2005. Distribución espacial de la declinación de los bosques de *Austrocedrus chilensis* en el Valle 16 de octubre (Chubut, Argentina). In: *Abstracts I Jornadas Argentinas de Ecología de Paisajes*, Buenos Aires.

La Manna, L & A Greslebin. 2005. Estudio de los suelos y de las especies de *Phytophthora* en relación al mal del ciprés. Actas *I Reunión sobre Ecología, Conservación y Uso de los bosques de ciprés de la cordillera*, Esquel, 28 al 30 de Abril de 2005. pp. 95-100.

La Manna, L & M Rajchenberg. 2004a. The decline of *Austrocedrus chilensis* forests in Patagonia, Argentina: soil features as predisposing factors. *For Ecol Manage* **190**:345-357.

La Manna, L & M Rajchenberg. 2004b. Soil properties and *Austrocedrus chilensis* decline in Central Patagonia, Argentina. *Plant and Soil* **263**:29-41.

La Manna, L, J Bava, M Collantes & M Rajchenberg. 2006. Características estructurales de los bosques de *Austrocedrus chilensis* afectados por «mal del ciprés» en Patagonia, Argentina. *Bosque* **27**:135-145.

Lemmon, P. 1956. A spherical densiometer for estimating forest overstory density. *For Sci* **1**:314-320.

Ling, A. & M Ashmore. 1999. Influence of tree health on ground flora in the Chiltern Beechwoods, England. *For Ecol Manage* **119**:77- 88.

Loguercio, G; P Burschel & M Rey. 1999. *El bosque de Ciprés de la Cordillera: su conservación y uso*. Centro Forestal CIEFAP, Esquel.

Makarenkov, V & P Legendre. 2002. Nonlinear redundancy analysis and canonical correspondence analysis based on polynomial regression. *Ecology* **83**:1146–1161.

Manion, P. 1991. *Tree disease concepts*. 2nd ed. Prentice-Hall, New York.

Manion, P & D Lachance. 1992. *Forest Decline Concepts*. APS The American Phytopathological Society Press, St. Paul.

Matteucci, S & A Colma. 1982. *Metodología para el estudio de la vegetación.* The General Secretariat of the Organization of American States, Washington DC.

Mueller-Dombois, D. 1992. A natural dieback theory, cohort senescence as an alternative to the decline disease theory. In: Manion P & D Lachance (eds) *Forest Decline Concepts*. The American Phytopathological Society Press, St. Paul.

Palik, B; RJ Mitchell; S Pecot; M Battaglia & M Pu. 2003. Spatial distribution of overstory retention influences resources and growth of longleaf pine seedlings. *Ecol Appl* 13:674–686.

Pearson, T; D Burslem; C Mullins & J Dalling. 2002. Germination ecology of neotropical pioneers: interacting effects of environmental conditions and seed size. *Ecology* 83:2798–2807.

Price, J & J Morgan. 2003. Mechanisms controlling establishment of the non-bradysporous Banksia integrifolia (Coast Banksia) in an unburnt coastal woodland. *Austral Ecol* **28**:82-92.

Raffaele, E & M Gobbi. 1996. Seed bank composition and variability in *Austrocedrus chilensis* forest sites in Patagonia, Argentina. *Int J Ecol Environ Sci* **22**:59-72.

Rajchenberg, M & P Cwielong. 1993. El mal del ciprés (*Austrocedrus chilensis*): su relación con las pudriciones radiculares y el sitio. In: *Abstracts Congreso Forestal Argentino y Latinoamericano,* Paraná.

Rajchenberg, M; C Barroetaveña; P Cwielong; M Rossini; D Cabral & A Sívori. 1998. Fungal species associated with the decline of *Austrocedrus chilensis* in Patagonia, Argentina: preliminary results. In: Delatour, L; J Guillaumin; B Lung-Escarmant & B Marçais (eds). *Proceedings 9th Int. Congr. on Root and butt Rots*, Carcans, France. Les Colloques **89**:235-244.

Ramsey, F & D Schafer. 1997. *The Statistical Sleuth: a course in methods of data analysis*. Duxbury Press, Belmond.

Rao, C. 1973. *Linear statistical inference and its applications*. 2nd ed. Wiley, New York

Relva, MA. 1999. Efectos del ramoneo sobre la regeneración del bosque de ciprés de la cordillera (*Austrocedrus chilensis*). PhD. Dissertation, Universidad Nacional del Comahue.

Relva, M & L Sancholuz. 2000. Effects of simulated browsing on the growth of *Austrocedrus chilensis* saplings. *Plant Ecol* **151**:121-127.

Relva, M & Veblen, T. 1998. Impacts of introduced large herbivores on *Austrocedrus chilensis* forests in northern Patagonia, Argentina. *For Ecol Manage* **108**:27-40.

Rovere, A. 2000. Condiciones ambientales de la regeneración del ciprés de la cordillera (*Austrocedrus chilensis*). *Bosque* **21**:57-64

Schmaltz, J. 1992. *La reconquista de la estepa por el bosque de ciprés*. Publicación técnica N° 11. CIEFAP, Esquel.

Smith, D; B Larson; M Kelty & P Ashton. 1997. *The practice of silviculture. Applied forest ecology*. 9th ed. John Wiley & Sons, New York.

Ter Braak, CJ & P Smilauer. 1998. *CANOCO reference manual and user´s guide to CANOCO for Windows. Software Canonical community ordination (version 4)*. Microcomputer power, Ithaca.

Urretavizcaya, MF. 2006. Restauración postfuego de bosques de ciprés de la cordillera: comportamiento de distintos plantines a 4 y a 5 años de su plantación. In: *Abstracts II Reunión Patagónica sobre Ecología y Manejo del Fuego*, Esquel, 25-28 April 2006.

Urretavizcaya, MF & GE Defossé. 2004. Soil seed bank of *Austrocedrus chilensis* (D. Don) Pic. Sern. et Bizarri related to different degrees of fire disturbance in two sites of southern Patagonia, Argentina. *For Ecol Manage* **187**:361-372.

Urretavizcaya, MF; GE Defossé & HE Gonda. 2005. Short-term effects of fire on plant cover and soil conditions in two *Austrocedrus chilensis* (cypress) forests in Patagonia, Argentina. *Ann For Sci* **63**:63-71.

Veblen, TT & DC Lorenz. 1987. Post-fire stand development of *Austrocedrus-Nothofagus* forests in Patagonia. *Vegetatio* **73**:113-126.

Veblen, TT; T Kitzberger & A Lara. 1992. Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. *J Veg Sci* **3**:507-520.

Veblen, TT; BR Burns; T Kitzberger; A Lara & R Villalba. 1995. The ecology of the conifers of southern South America. In: Enright N & R Hill (eds) *Ecology of the southern conifers.* Melbourne University Press, Melbourne.

Veblen, TT; T Kitzberger; BR Burns & AJ Rebertus. 1996. Perturbaciones y dinámica de regeneración en bosques andinos del sur de Chile y Argentina. In: Armesto, J; C Villagrán & M Arroyo (eds) *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago de Chile.

Warkentin, BP & T Maeda. 1980. Physical and mechanical characteristics of Andisols. In: Theng, B (ed) *Soil with variable charge.* New Zealand Sociaty of Soil Science.

Williams, B. 1983. Some observations on the use of discriminant analysis in ecology. *Ecology* **64**:1283–1291.

Williams, H; V Burkett & M Craft. 1999. The effect of seedling stock-type and direct-seeding on the early field survival of nuttall oak planted on agricultural land. In: Landis, T & J Barnett (eds) National proceedings: forest and conservation nursery associations Forest Service, USA.