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The spread of the exotic conifer *Pseudotsuga menziesii* in *Austrocedrus chilensis* forests and shrublands in northwestern Patagonia, Argentina

Ivonne A. Orellana[1,]* and Estela Raffaele[2]

[1]*Centro de Investigación y Extensión Forestal Andino Patagónico (CIEFAP), Ruta 259 km 2.9, (9200) Esquel, Chubut, Argentina*
[2]*Laboratorio Ecotono, Universidad Nacional del Comahue- INIBIOMA/ CONICET, Quintral 1250, (8400) S. C. de Bariloche, Río Negro, Argentina.*

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*corresponding author: iorellana@correociefap.org.ar

Abstract

Invasive introduced species are among the most severe threats to biodiversity and the functioning of natural ecosystems. In this study we analysed whether *Pseudotsuga menziesii* (Mirb.) Franco is an invader species of two common types of native communities (native *Austrocedrus chilensis* (D.Don) Pic. Serm. & Bizzarri forests and mixed shrublands) of the subantarctic region of Argentina. We determined the density and the age structures of both *P. menziesii* and *A. chilensis* regeneration at the edges of *P. menziesii* plantations adjacent to native forests of *A. chilensis* and mixed shrublands. The invasion of *P. menziesii* was recorded in both types of native communities. In *A. chilensis* forest, the establishment of *P. menziesii* was significantly higher than in the shrublands. Also, *P. menziesii* showed a greater spread than *A. chilensis* inside and outside the plantations. The increased abundance of *P. menziesii* plantations, in addition to its invasive characteristics could lead to the replacement of native communities at a regional scale in the long or medium term.

Keywords: conifer invasions; Douglas-fir; pine plantations; introduced species; subantartic forests.

Introduction

Invasive introduced species are among the most severe threats to biodiversity and the functioning of natural ecosystems (Mooney & Hobbs, 2000; Simberloff, 2000), and they are a significant component of human-caused global change (Vitousek et al., 1997). Some alien trees species used in forestry and agroforestry cause major problems as invaders of natural and seminatural ecosystems (Le Maitre et al., 1998). The magnitude of the problem has increased significantly over the past few decades, with a rapid increase in afforestation and changes in land use (Richardson, 1998; Becerra & Bustamante, 2008).

In the southern hemisphere *Pinus* spp. L. and *Eucalyptus* spp. L´Her are the most important genera used in exotic commercial forestry, and they are widely planted outside their natural ranges in temperate zones (Lavery & Mead, 1998; Richardson, 1998; Richardson & Higgins, 1998). Studies of pine invasions show that the extent of the phenomenon has increased in recent decades and that spread of pines outside plantations is increasing rapidly in South America, New Zealand, and South Africa (Le Maitre, 1998; Richardson & Higgins, 1998; Ledgard, 2002; Ledgard et al., 2005; Richardson et al., 2008).

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In the northwestern Patagonia region of Argentina, plantations of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and various pine species constitute a rapidly growing land use, promoted through a state policy of subsidising plantations. It has been suggested that there are 700 000 to 2 000 000 ha of land that could be converted to plantations (Schlichter & Laclau, 1998). For the year 2005, there were 70 000 ha of such species planted (Gallo et al., 2005), and the rate of plantation increase is estimated at 10 000 ha of new plantations per year (Schlichter & Laclau, 1998). However, it is recognised that there is a lack of knowledge about how to minimise the environmental risks associated with these plantations, such as the invasion of introduced species and the loss of biodiversity in plantations (Frank & Finckh, 1997; Schlichter & Laclau, 1998).

The main species of pine introduced in Patagonia are: *Pinus ponderosa* Dougl. ex Laws & Laws., *Pinus radiata* D.Don., *Pinus contorta* Dougl. ex Loud. These species and *Pseudotsuga menziesii* all have a history of invasion in other countries of the Southern Hemisphere (Richardson et al., 1994; Bustamante et al., 2003; Pauchard et al., 2004; Bustamante & Simonetti, 2005; Peña et al., 2008). Pine plantations in Andean forest are a recent phenomenon, with the first cutting cycle only just being reached. As a result, little is known about the reproductive biology and invasive ability of the introduced species in native vegetation communities. Although it is known that there is a potential risk of invasion in this region (Richardson et al., 2008), few studies have focused on exotic conifer invasion (Simberloff et al., 2002; Nilsson, 2003; Sarasola et al., 2006).

We studied the spread of *Pseudotsuga menziesii* since this is one of the exotic conifer most widely distributed in northwestern Patagonia, Argentina. At present, 170 *P. menziesii* plantations, located between 40º and 44ºS, are known (Gonda et al., 2008; Davel M. personal communication). This species has been introduced after the native vegetation has been removed by clearcutting, especially in two common native communities: *Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri forests and mixed shrublands dominated by *Nothofagus antarctica* (G. Forst.) Oerst. and other woody species such as *Lomatia hirsuta* (Lam.) Diels ex J. F. Macbr., *Schinus patagonica* (Phil.) I. M. Johnst, *Fabiana imbricata* Ruiz & Pav, and several species of *Berberis* spp. L.

Austrocedrus chilensis is the only member of a monospecific genus, endemic to subantarctic forests of South America. Currently there are serious problems with the conservation of *A. chilensis* forests, and this species is included in the Red List of the World Conservation Union (IUCN, 2010). Mixed shrublands are generally found in the boundary zone between forests (e.g. *Nothofagus* spp.-dominated stands, *A. chilensis*-dominated stands), and the patagonian steppe. Shrublands are frequently associated with burnt areas, and they are considered “key” environments in the post-fire dynamics of forests in this region (Veblen et al., 2003). Shrublands are often highly disturbed ecosystems, the principal agents of disturbance being fire, logging and livestock pressure caused by humans (Raffaele & Veblen, 2001). Invasion by *P. menziessi* could contribute to degradation of both *A. chilensis* forest and mixed shrublands. Richardson and Higgins (1998) proposed that susceptibility to invasion varies between different environments, and is highest for bare soil, then progressively lower for sand dunes, grasslands, thickets and finally forests. We proposed to determine whether *P. menziesii* is an invasive species in the forests of *A. chilensis* and mixed shrublands, and which one of these two native environments is more likely to be invaded from *P. menziesii* plantations. However, it is not known whether *A. chilensis* forest or mixed shrubland is the most susceptible to *P. menziessi* invasion.

Within this framework, we propose the following hypotheses:

1. that the native communities of *Austrocedrus chilensis* forest and mixed shrubland show different susceptibility to invasion by *Pseudotsuga menziesii*. We expected to find higher densities of both *P. menziesii* seedlings and saplings in the shrublands than in the forests of *A. chilensis*, based on the previous findings of Richardson & Higgins (1998); and

2. that the edges of *P. menziesii* plantations are more readily colonised by *P. menziesii* than by *A. chilensis* from adjoining native forest.

We tested hypothesis (1) by comparing colonisation of *Austrocedrus chilensis* forest and mixed shrubland by *Pseudotsuga menziesii* saplings. The hypothesis (2) was tested by comparing the number of *A. chilensis* saplings with the number of *P. menziesii* saplings at various distances from the edges of *P. menziesii* plantations.

Methods

Pseudotsuga menziesii plantations in Patagonia are usually established at an initial density of 1000 trees/ha. Planted surfaces range from 0.5 to 12 ha. (Gonda et al., 2008; Davel, 2008; Davel M. personal communication). After 25 years, trees reach a mean basal area of 48 m^2/ha, an average height of 20 m, while canopy cover is 96% (unpublished data).

Mixed shrubland communities have three layers, the top layer is less than 6 – 7 m tall with 60% canopy cover, and comprises many species of shrubs such as: *Lomatia hirsuta*, *Schinus patagonica, Fabiana imbricata, Diostea juncea* (Gillies & Hook.) Miers and *Embothrium coccineum* J. R. Forst . & G. Forst., and some very sparse individuals of trees like: *Austrocedrus chilensis, Nothofagus antarctica*, and *Maytenus boaria* Molina. The second stratum is formed by smaller shrub height, with similar species composition, and with some woody vines as: *Mutisia decurrens* Cav. and *Mutisia spinosa* Ruiz & Pav. The lowest layer is composed by herb species being the dominant species *Alstroemeria aurea* Graham, *Osmorhiza chilensis* Hook. & Arn, and *Agrostis inconspicua* Kunze ex Gay.

Austrocedrus chilensis forest, on the other hand, can be described by a typical three-layer structure. The top layer, with 81% canopy cover, is dominated by *A. chilensis* at a mean density of 840 trees/ha, 44 m^2/ha basal area, and a dominant height average of 20 m (Ferrando et al., 2001; Orellana, unpublished). The shrub layer is comprised of *Lomatia hirsuta*, *Schinus patagonica*, *Mutisia decurrens* and *Mutisia spinosa*. Finally there is a herbaceous layer dominated by Asteraceae and Poaceae (e.g. *Crepis capillaris* (L.) Wallr., *Gnaphalium montevidense* Spreng., and *Agrostis inconspicua* Kunze ex Gay). In humid areas, *A. chilensis* occurs in mixed stands in combination with *Nothofagus dombeyi* (Mirb.) Oerst, while it occurs as pure forests in intermediate rainfall sites. Towards the steppe it is found both as marginal and open forests as well (Dezzotti & Sancholuz, 1991; Veblen et al., 1995; Donoso, 2006).

Study area

The study area was located on the northwest part of Chubut Province and the Southwest part of Río Negro Province, Argentina. The area stretches between the localities of Corcovado 43º 32’ 36.54” S, 71º 26’ 37.5” W and San Carlos de Bariloche 41º 8’ 16,83” S, 71º 17’ 12.09” W (Figure 1). The climate in the study area shows well defined seasonal variations: summers are warm and dry while winters are cold and rainy. Mean annual temperature fluctuates between 10 °C and 15 °C. Annual precipitation declines from 3000 to 800 mm, along a west-east gradient. While Andisols predominate in the most humid areas (3000 to 1000 mm) Alfisols prevail in the intermediate rainfall areas (1000 to 500 mm) (Mazzarino et al., 1998). We selected 4 sites with reproductively mature of *Pseudostuga menziesii* plantations of 25.8 years old established adjacent to shrubland and 11 sites with *P. menziesii* plantation of 25 years old established adjacent to forests of *Austrocedrus chilensis*.

Age structure of *Pseudotsuga menziesii* saplings

To obtain the relationship between age (years) and diameter at breast height, measured at 1.3 m (DBH, in cm) of the *Pseudotsuga menziesii* regeneration on the edges of the plantations, at each site we randomly selected 8 individuals and measured their DBH, and age by counting rings in complete slices taken from the base of the saplings. We obtained the relationship between DBH and age by applying simple linear regression models, where DBH was the dependent variable and age was the independent variable. Using this correlation, we defined three age classes for *P. menziesii*: (a) seedlings; (b) small saplings; and (c) large saplings. Seedlings were individuals less than 10 cm tall without lateral ramifications that were younger than 1 year old (Hermann & Lavender, 1990). Small saplings were individuals taller than 10 cm with a DBH less than 5 cm, and large saplings were individuals taller than 10 cm with a DBH greater than 5 cm. Using these definitions, we analysed the age structure of the *P. menziesii* saplings at the edges of plantation – shrubland and plantation – *Austrocedrus chilensis* forest, in relation to their distance from the plantation edge.

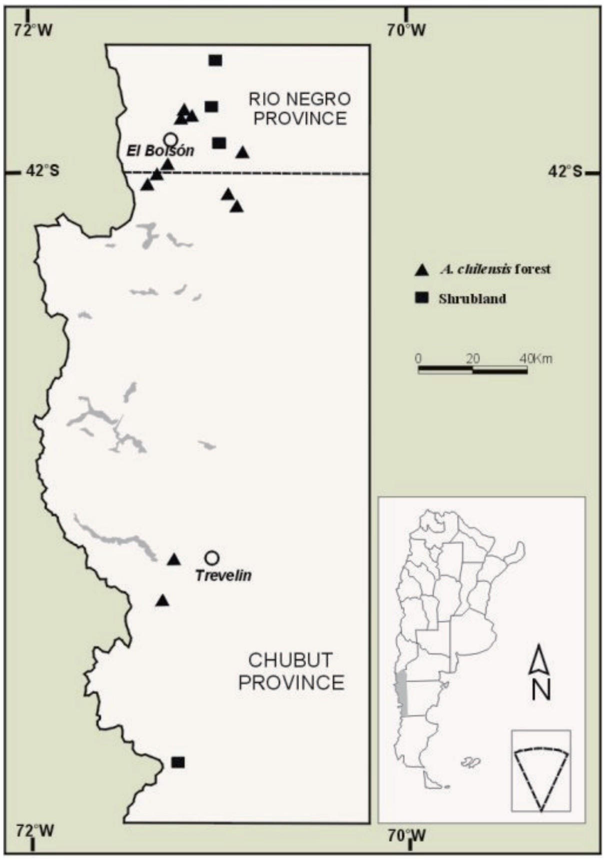

FIGURE 1: Map of the study area and locations of study sites in *Pseudotsuga menziesii* plantations – *Austrocedrus chilensis* forests sites (▲), and *Pseudotsuga menziesii* plantations – shrublands sites (■).

In addition, we estimated the relationship between age (years) and height (in m) of the *Pseudotsuga menziesii* saplings. Age at onset of reproduction was obtained from the difference in age between parent trees and the oldest sapling established in the native environment at each site. Tree age was determined from the parent trees by counting rings in cores taken using increment an increment corer. The increment cores were obtained at 0.3 m in height, the age difference with height was corrected by adding three years. The age of saplings was obtained in complete discs cut across the base of the stem of the larger saplings. On this basis, small saplings were defined as 1 – 10 years old and large saplings were defined as greater than 10 years old.

Age structure of *Austrocedrus chilensis* saplings

Two age classes (seedlings and saplings) of *Austrocedrus chilensis* regeneration were quantified. Seedlings were defined as individuals less than 10 cm tall without lateral ramifications, considered to be younger than 1 year old (Grosfeld, 2002). Saplings were defined as individuals taller than 10 cm, with a DHB of less than 5 cm. Saplings were considered to be between 1 and 20 years old (Rovere, 2000).

Sampling design for Hypothesis 1

We counted the total number of *Pseudotsuga menziesii* individuals (seedlings, small saplings and large saplings) established from the edge of each *P. menziesii* plantation and up to 80 m in the adjoining shrubland or *Austrocedrus chilensis* forest community in one transect placed perpendicularly to each edge of the plantation. All transects were located on undisturbed edges areas (without grazing, pathways, and other species invasions). Each transect was 10 m wide and 110 m long, subdivided into 11 sampling unit (100 m^2 each), three sampling unit inside plantation and eight within the adjoining native community. *P. menziesii* seedlings were counted in four circular plots of 0.5 m^2, randomly selected for each sampling unit. The small saplings of *P. menziesii* were counted on a plot of 25 m^2 chosen at random from each sampling unit. Large saplings were measured in the sampling unit of 100 m^2. From this data, we estimated the density of seedlings, small saplings and large saplings of *P. menziesii* through number of individuals by ha.

Sampling design for Hypothesis 2

We counted the number of *Austrocedrus chilensis* individuals (seedlings and saplings) established in *Pseudotsuga menziesii* plantations and in the adjoining native *A. chilensis* forest along one transect placed perpendicularly to each edge of the plantation, as detailed in Section 2.4. The seedlings of *A. chilensis* were counted in four circular circular plots of 0.5 m^2, randomly selected for each sampling unit. Saplings of *A. chilensis* were counted on a plot of 25 m^2 chosen at random from each sampling unit. From this data, we estimated the density of seedlings, and saplings of *A. chilensis* through number of individuals by ha.

Data analysis for Hypothesis 1

We analysed total density of the *Pseudotsuga menziesii* seedlings and saplings in shrublands and in *Austrocedrus chilensis* forests, according to the distance from the plantation edges by means of a simple linear regression model (Steel & Torrie, 1988). In order to determine whether shrublands or *A. chilensis* forests were more susceptible to *P. menziesii* invasion, we compared regression slopes (Steel & Torrie, 1988). For this analysis, only small and large *P. menziesii* saplings (between 1 and 20 years old) were considered, because seedlings were considered likely to be ephemeral. The dependent variable was estimated small and large *P. menziesii* sapling density and the independent variable was the actual distance from plantation edge.

To determine if seedlings and saplings of *Pseudotsuga menziesii* had established similarly in plantation and both native comunities, we used Friedman's non-parametric tests (Conover, 1980). We analysed the density of seedlings and saplings of *P. menziesii* with the distance from the plantation considering four levels: distance 1 (within plantations: from -30 to 0 m), distance 2 (from 0 to 30 m outside plantations), distance 3 (from 30 to 60 m outside plantations) and distance 4 (from 60 to 80 m outside plantations). Response variables were densities of: (a) *P. menziesii* seedlings; (b) *P. menziesii* small saplings; and (c) *P. menziesii* large saplings.

Data analysis for Hypothesis 2

We analysed the density of *Austrocedrus chilensis* seedlings and saplings on the edges of plantation – *A. chilensis* forest using the same method as in Section 2.6. We also then compared the densities of small and large (1 to 20 year-old) *Pseudotsuga menziesii* saplings and 1 to 20 year-old *A. chilensis* saplings in *A. chilensis* forests to the distance from plantation edges by means of slope-comparison tests.

To determine if seedlings and saplings of *Austrocedrus chilensis* had established similarly in plantation and *A. chilensis* forest, we used Friedman's non-parametric tests. We analysed the density of seedlings and saplings of *A. chilensis* with the distance from the plantation (idem method as in Section 2.6). Response variables were densities of: (a) *A. chilensis* seedlings; and (b) *A. chilensis* saplings.

Results

Hypothesis 1

In both mixed shrublands and *Austrocedrus chilensis* forests, the largest total mean density of *Pseudotsuga menziesii* (seedlings, small saplings and large

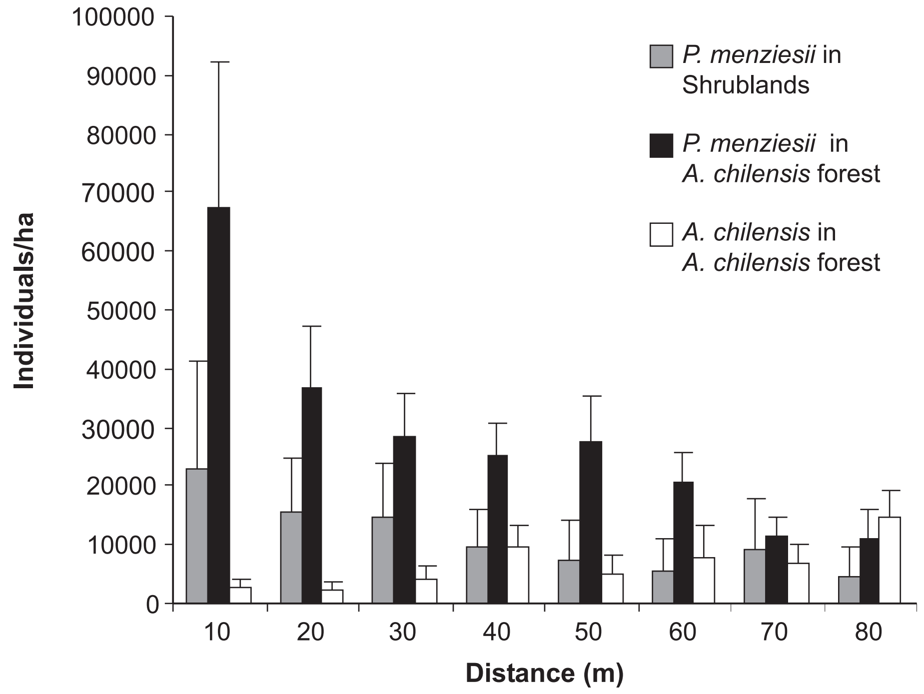

FIGURE 2: Total mean density (± one standard error) of all seedlings and saplings of *Pseudotsuga menziesii* or *Austrocedrus chilensis* at the edges of *P. menziesii* plantations as a function of distance (d).

In shrublands: *P. menziesii* seedlings and saplings/ha = 21 507 - 228 (d), ($F_{1,7}$= 25.5, p = 0.002, R² = 0.77). In *A. chilensis* forests: *P. menziesii* seedlings and saplings/ha = 57 619 - 647 (d), ($F_{1,7}$= 21.36, p = 0.004, R² = 0.74), and *A. chilensis* seedlings and saplings/ha = 568 + 134 (d), ($F_{1,7}$= 11.7, p = 0.014, R² = 0.61).

saplings) was reached at the edge of the plantation, then decreased away from the plantation (Figure 2). In the 80 m from the plantation edge, a total of 11 221 ± 8468 and 28 311 ± 6313 *P. menziesii* individuals/ha (±SE) were recorded in the shrublands and *A. chilensis* forests respectively. As shown in Figure 2, the density of *P. menziesii* regeneration is high near plantations, especially so in *A. chilenis* forest edges, and then it decreases as the distance from the plantation increases.

Pseudotsuga menziesii became reproductively mature at 10.9 ± 1.26 years (±SE). During the first years, *P. menziesii* saplings grew taller and slightly broader in *Austrocedrus chilensis* forests: H = 0.39 (Age), and DBH = 0.54 (Age); than on shrublands: H = 0.33 (Age), and DBH = 0.52 (Age) (Figure 3 a and b). The information gathered about age and DBH enabled the construction of an age structure for *P. menziesii* seedlings, small saplings and large saplings in the edge areas of *P. menziesii* plantation – shrubland (Figure 4 a-c) and *P. menziesii* plantation – *A. chilensis* forest (Figure 4 d-f). The seedling size class (one year old or less) was the most abundant, followed by small saplings (1 to 10 years of age), while the least abundant was large saplings over 10 years of age (Figure 4 a-f). Comparison of the density of large *P. menziesii* saplings in *A. chilensis* forests and shrublands showed that *P. menziessi* sapling mean density was higher in *A. chilensis* forests than in shrublands ($t_{12, 0.001}$ = 4.89), Figures 4 b, c and 4e, f.

A large number of *Pseudotsuga menziesii* seedlings under 1 year of age were recorded in shrubland – plantation edge areas. These had mainly established within the plantation (χ^2 = 9.32, DF = 3, *p* = 0.02, Figure 4a). In contrast, the mean densities for small saplings (between 1 and 10 years of age), within and outside the plantation were more homogeneous (χ^2 = 7.76, DF = 3, *p* = 0.05, Figure 4b). The density pattern for large saplings (over 10 years of age) was different too as these were more abundant in the shrublands than within the plantation (χ^2 = 9.81, DF = 3, *p* = 0.02, Figure 4c).

In the *Austrocedrus chilensis*-plantation edge areas, the *Pseudotsuga menziesii* seedlings were homogenously distributed within and outside the plantation (χ^2 = 2.9, DF = 3, *p* = 0.406, Figure 4d), as were small saplings (χ^2 = 7.56, DF = 3, *p* = 0.05, Figure 4e). Large saplings were more abundant in the adjoining *A. chilensis* forest, however (χ^2 = 17.96, DF = 3, *p* < 0.001, Figure 4f).

Hypothesis 2

The density of *Austrocedrus chilensis* seedlings and saplings is directly related to distance to the

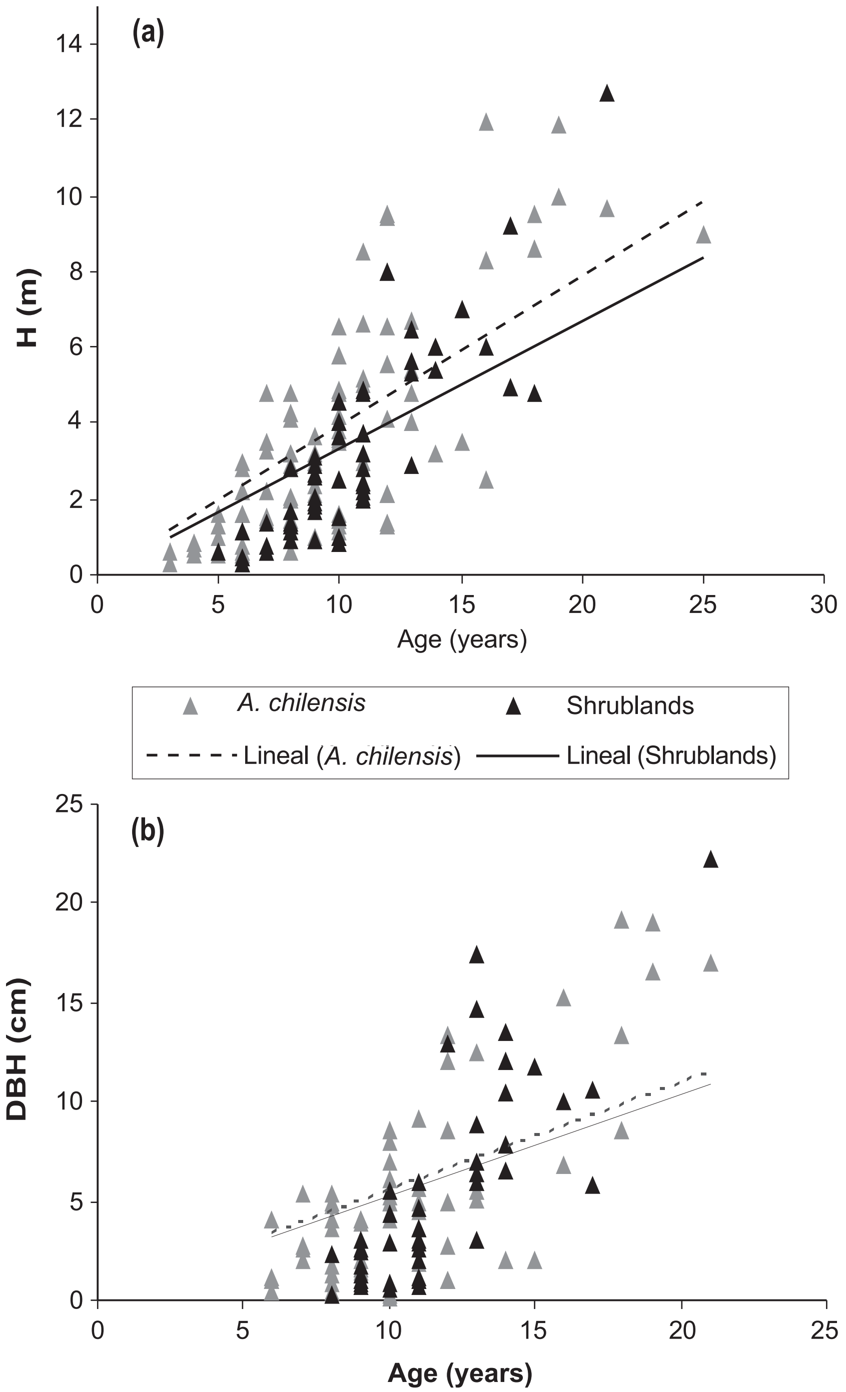

FIGURE 3: (a) Curves of growth in height (m) as a function of age for *Pseudotsuga menziesii* saplings (small and large) in shrublands: H = 0.33 (Age), ($F_{1, 55}$ = 281.4; $p < 0.001$; $R^2 = 0,8$) and *Austrocedrus chilensis* forests: H = 0.39 (Age), ($F_{1, 90}$ = 419.8, $p < 0.001$, $R^2 = 0.8$);
(b) Curves of growth in diameter at breast height (DBH; cm) as a function of age for small and large *P. menziesii* saplings in shrublands: DBH = 0.52 (Age), ($F_{1, 44}$ = 103.7, $p < 0.001$, $R^2 = 0.7$) and *A. chilensis* forests: DBH = 0.54 (Age), ($F_{1, 63}$ = 184.8, $p < 0.001$, $R^2 = 0.7$).

plantation: the larger the distance to the plantation, the higher the density of *A. chilensis* regeneration (Figure 2). On the contrary, the density of *Pseudotsuga menziesii* regeneration is high near plantations and then it decreases as the distance from the plantation increases (Figure 2). The combined density of small and large *P. menziesii* saplings was significantly higher than that of *A. chilensis* saplings of a similar age at the edge of *P. menziesii* plantations ($t_{12,\ 0.001}$ = 7.64). In total, small and large *P. menziesii* saplings reached an average density of 24 118 ± 10 251 saplings/ha (±SE) in *A. chilensis* forests 10 m from the plantation (see

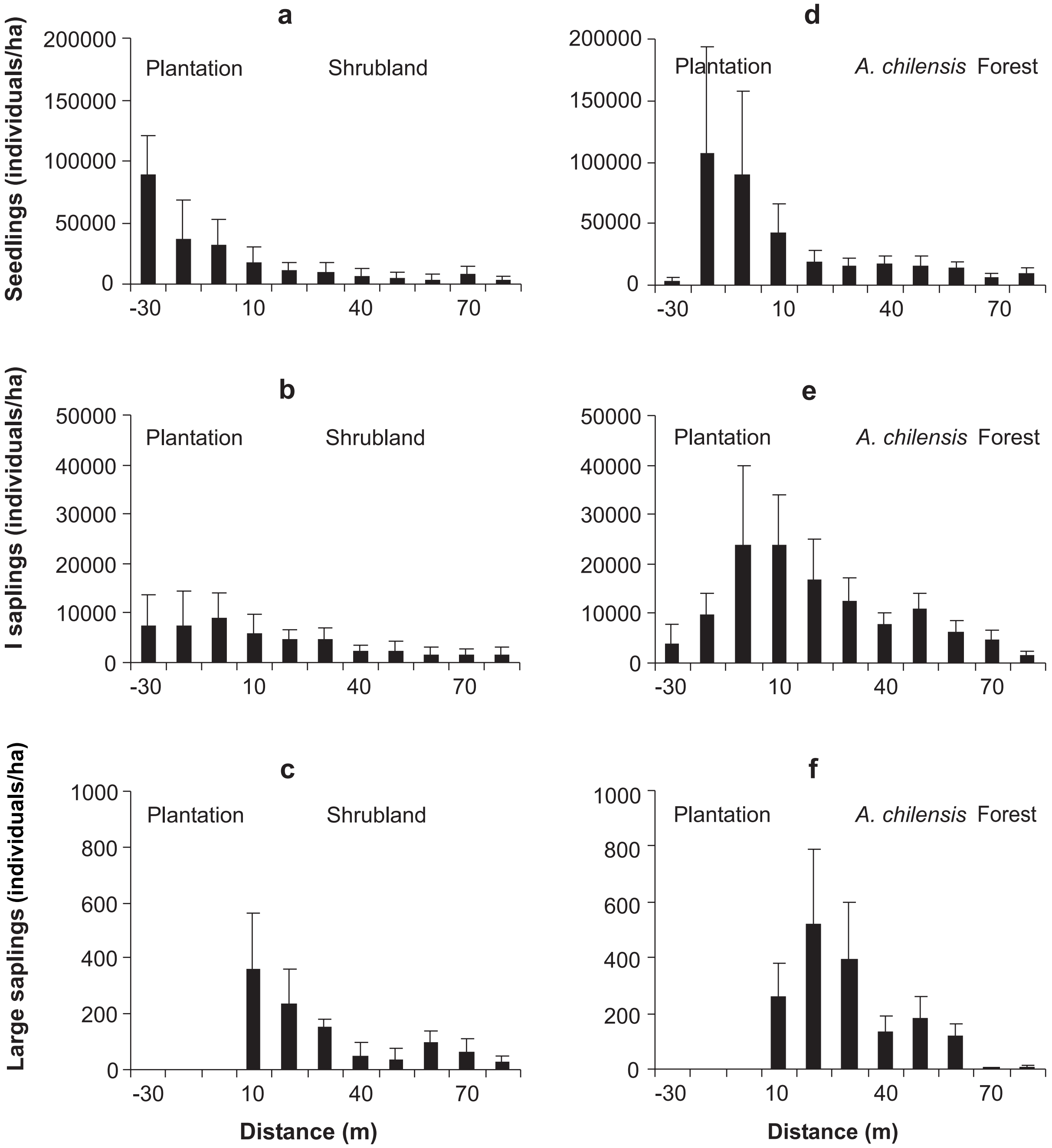

FIGURE 4: Separate mean densities (± one standard error) of seedlings, small saplings and large saplings of *Pseudotsuga menziesii* in *P. menziesii* plantations – shrublands edges areas and *P. menziesii* - *Austrocedrus chilensis* forest edges areas. Seedlings < 1 year (a, d); small saplings between 1 – 10 years (b, e); large saplings > 10 years (c, f). Within plantation (-30 to 0 m), inside native communities (0 to 80 m).

Figures 4e and f), while for the same distance, the *A. chilensis* sapling density was 800 ± 315 saplings/ha (±SE), Figure 5. This situation was reversed at a distance of 80 m away from the plantation, where total *P. menziesii* sapling density was only 1 381 ± 961 saplings/ha (±SE), while *A. chilensis* had increased to 5 400 ± 562 saplings/ha (±SE).

The age structure of *Austrocedrus chilensis* seedlings and saplings in the edge areas of *Pseudotsuga menziesii* plantation – *A. chilensis* forest are shown in Figure 5. The seedlings of *A. chilensis* are more abundant than saplings, However, the *A. chilensis* seedlings density, showed no significant difference within plantations and in the adjacent native forests ($\chi^2 = 6.6$, DF = 3, $p = 0.08$, Figure 5). In contrast, a

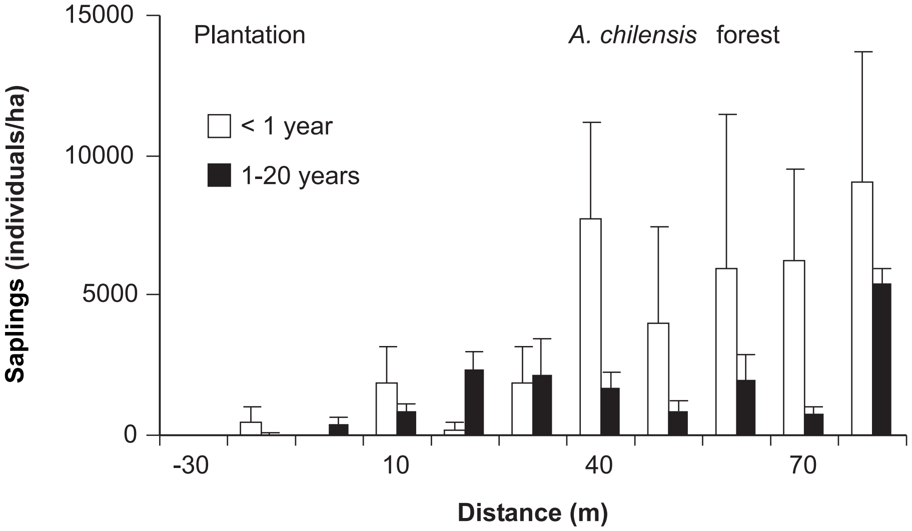

FIGURE 5: Separate mean densities (± one standard error) of *Austrocedrus chilensis* seedlings and saplings in *Pseudotsuga menziesii* plantation – *A. chilensis* forest edges areas. Within plantation (-30 to 0 m), on *A. chilensis* forests (0 to 80m).

significant difference was found between the density of *A. chilensis* saplings within plantations and in the adjacent native forests ($\chi^2 = 11.47$, DF = 3, $p = 0.009$, Figure 5). This suggests that *A. chilensis* individuals are only able to survive long term in the native community.

Discussion

Pseudotsuga menziesii is spreading from plantations into shrublands and *Austrocedrus chilensis* forests which are both very common types of native communities in northwestern Patagonia. *Pseudotsuga menziesii* is able to grow under a wide range of environmental conditions (Ledgard, 2002; Simberloff et al., 2002; Pauchard et al., 2004; Sarasola et al., 2006) and is capable of vigorous regeneration in commercially logged stands. At present, most *P. menziesii* seedlings and saplings still establish within (50 – 200 m) of plantations probably because most of the wind-dispersed seed falls within this zone (Sarasola et al., 2006). Initial establishment of regeneration near the edges of plantations is indeed expected because edge areas are disturbed environments, and are often those that offer the greatest opportunity for exotic species to establish (Ledgard, 2002; Bustamante & Simonettii, 2005; Richardson 2006).

Pinaceae have not proved to be particularly invasive of forest environments (Richardson & Higgins, 1998). However, we found a higher density of *Pseudotsuga menziesii* saplings in *Austrocedrus chilensis* forests than in shrublands. The growth in diameter and height of *P. menziesii* saplings is also higher in the forests of *A. chilensis* than in shrublands. This pattern could be related to light requirement of *P. menziesii*, which during the early stages of its development requires a certain level of shade, but later requires more light (Hermann & Lavender, 1990). We believe that the light conditions in *A. chilensis* forest (80% canopy cover) are more appropriate for the requirements of *P. menziesii*, than those provided by shrublands (60% cover). In Chile, Peña et al. (2008) obtained similar results when comparing the regeneration of *Pinus contorta* in two environments: *Araucaria araucana* (Mol.) C. Koch. forest and *Nothofagus*-dominated shrubland; *Araucaria araucana* forests were more readily invaded. These results suggest that native habitats of subantarctic forests, which are dominated by conifers, are more susceptible to exotic invasions than other environments. The results from Peña et al. (2008) and the study reported here contrast with the findings of Richardson and Higgins (1998) who proposed that susceptibility to invasion was higher for grasslands and thickets than forests.

Although determination of the full impact of the invasion of *Pseudotsuga menziesii* on *Austrocedrus chilensis* forest would require longer-term studies, we suggest that the high vulnerability of the native conifer forest to exotic conifer invasion could produce a replacement of *A. chilensis* trees by exotic conifers in the future. We have found the density of *P. menziesii* saplings to be significantly higher than that for *A. chilensis* in *A. chilensis* forests. Moreover, *P. menziesii* has a faster growth in height and diameter than *A. chilensis* (Davel, 2008; Loguercio et al., 1999) taking over light gaps within the forest more rapidly.

When *Pseudotsuga menziesii* regeneration density within plantation (from -30 to 0 m) was compared to that in shrublands (from 0 to 80 m), differences between seedlings and large saplings (10 years older) were observed. Although seedlings were found mainly within the plantation, density of large saplings is higher within shrublands. In plantation-*Austrocedrus chilensis* forest edge areas, densities of both *P. menziesii* and *A. chilensis* saplings were more abundant within the *A. chilensis* forest (from 0 to 80 m). We believe that seeds of both species germinate successfully, regardless of the environment, but survival rates in plantations and native environments are not the same. Probably, the low light conditions within dense plantations (96% canopy cover), and the lack of light gaps affect the establishment pattern of regeneration within plantations.

Evidence drawn from this paper and several others (Ledgard, 2002; Simberloff et al*.,* 2002; Pauchard et al., 2004; Sarasola et al., 2006; Richardson et al., 2008) emphasises the importance of the invaded environment in determining the success of a given invader. With time, *Pseudotsuga menziesii* will probably invade larger areas since, although the plantations under study had been established less than 25 years before our survey was performed, they show high levels of invasion in surrounding areas. Studies of the processes involved in an invasion where it occurs, as well as on factors preventing it where invasion does not occur, would contribute to our ability or capacity to manage these invasions in the future.

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