Forest Ecology and Management xxx (2008) xxx–xxx

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Patterns of spread of *Pinus contorta* Dougl. ex Loud. invasion in a Natural Reserve in southern South America

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ARTICLE INFO

*Article history:*
Received 12 November 2007
Received in revised form 3 June 2008
Accepted 7 June 2008

*Keywords:*
*Araucaria araucana*
Conifer plantations
Pine invasions
Protected areas
Spatial patterns

ABSTRACT

*Pinus* species, which have formed the foundation of commercial forestry industry in many countries, are known to be invasive in natural ecosystems, especially in the Southern Hemisphere. *Pinus contorta* is considered one of the most aggressively invasive plantation species. In this paper we aim to: (a) determine patterns of *P. contorta* invasion in relation to its size and age structure and spatial distribution and (b) determine the effect of vegetation cover on its regeneration. For this purpose, we have chosen the Malalcahuello National Reserve in south-central Chile, which is dominated by *Araucaria araucana* forests. In the three *P. contorta* trial plots, attributes were measured in order to describe its current structure. We selected one of the three *P. contorta* trial plots and set eight 50 m wide and 125 m centrifugal transects starting at the North Azimuth (0°) orientation and then one each 45°. In each transect 25 circular plots of 2.5 m radius were established every 25 m. In each plot, we measured collar diameter (CD) for each *P. contorta* individual and adjusted a diameter–age function. We recorded the presence of cones for each individual *P. contorta* within the plots and the total number of *P. contorta* individuals. In each plot, we measured percent vegetation cover (grass, understory and canopy). The selected parent stand showed a decrease in density from the original plantation spacing, from 2500 to 150 plants ha$^{-1}$. Of all sampled individuals, only a 38% had cones. We found reproductive structures in trees as young as 5-year-old. Regeneration was found in all transects. Mean density for the area was 1600 plants ha$^{-1}$, and the greater plant number was found in the West transect, reaching an average of 6600 plants ha$^{-1}$. Through the interpolation performed with the kriging method, a map of the area with the spatial gradient of plant density was obtained. Naturally regenerated individuals of *P. contorta* occupied an area of 78 ha where the most distant individual is located in the southeast direction at an average distance of 1200 m from the three study plots. We determined that a positive association exists between *P. contorta* and the species *A. araucana* and *Nothofagus antarctica*. The capacity for early and consistent reproduction and the establishment of individuals dispersed at great distances from the original plots allow us to conclude that *P. contorta* has great potential as an invasive species in forests of this area of the Andes of southern South America. Invasion of *P. contorta* has many important implications for the conservation of native forests in our region including diminished regeneration of *A. araucana*.



## 1. Introduction

Non-native *Pinus* spp. have long been used for commercial large-scale afforestation based on their growth attributes and wood properties (Zobel et al., 1987; Richardson, 1998; Le Maitre et al., 2002). Environmental impacts of *Pinus* plantations for many decades were considered low compared to their economic benefits. However, this situation has changed and negative impacts on ecosystems altering natural processes have been documented, leading to a review of environmental, social and economic consequences of plantation forestry (Grez et al., 1998; Richardson, 1998; Mack et al., 2000; Richardson et al., 2008). One of the main impacts of pine plantations is caused by the ability of these exotic trees to regenerate and spread outside the limits where they were originally introduced, invading and thereby changing diverse ecosystems (Kay, 1994; Richardson, 1998; Despain, 2001; Peterken, 2001).

In the Southern Hemisphere, specifically in countries like South Africa, New Zealand and Australia, at least 19 species of *Pinus* have been described as invasive (Kay, 1994; Richardson et al., 1994;

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doi:10.1016/j.foreco.2008.06.020

Richardson, 1998; Higgins and Richardson, 1998; Richardson, 2001; Rouget et al., 2004; Richardson et al., 2008). These species introductions were made considering only viability, growth, and form attributes, and little attention was given to their invasive capacity, which relates to their early seed production (short juvenile period), small seed size, short intervals between high seed crops (Rejmánek and Richardson, 1996) and high seedling growth rates (Grotkopp et al., 2002). In South America, Zalba and Villamil (2002) describe three *Pinus* species being casual or invasive in remnants of Pampean grasslands, including *Pinus halapensis*, *Pinus pinaster* and *Pinus radiata*. They affirm that these species are among the top five invaders in the Southern Hemisphere including Chile and Uruguay. In the Chilean and Argentinean Patagonia, the invasive status of several conifers has been studied, some of them have been found invading patagonian steppe and native forests, *Pinus contorta* and *Pseudotsuga menziesii*, respectively (e.g. Simberloff et al., 2002, 2003; Sarasola et al., 2006; Peña et al., 2007; Richardson et al., 2008).

Among the principal effects derived from the invasion of *Pinus* into natural ecosystems are the alteration of dominant species composition in the community, displacement of native flora and fauna, even causing extinction of some species (Richardson et al., 1994), alteration of nutrient cycles, change in fire regimes, and decreased streamflows (Mack et al., 2000; Peterken, 2001; Richardson, 2001). For example, pine invasions in South Africa have caused a decrease of 6.7% in river flow as a consequence of the high water consumption of these fast-growing species. The cost of control is estimated at 92 million US$ per year, for the next 20 years (Le Maitre et al., 2002).

In Chile, forestry species have been introduced since the European colonization period in the 16th Century but recently they have become one of the major sources of national income. Initially, pines were introduced for ornamental use, and later for erosion control and to stabilize dunes. Some of these species had such a successful development that in a short time they provided timber apt for mill and pulp industries (Peña and Pauchard, 2001; Pauchard et al., 2004). This success motivated the introduction of new species and the establishment of test plots in diverse parts of the country in order to select potential forestry species for determined growth zones. Although, the Chilean forestry industry is based on *P. radiata* and *Eucalyptus globulus*, many other pine species were tested. In 1962, the Forestry Institute (*Instituto Forestal*) developed a species introduction program, establishing trial plots in more than 100 areas located between the Coquimbo Region and Lakes Regions, including protected areas such as National Parks and Reserves (Loewe and Murillo, 2001). One of these zones was the Malalcahuello National Reserve, where more than 10 tree species were introduced between 1969 and 1970. One of them was *P. contorta* Dougl. ex Loud. At that time, however, the invasive capacity of this species and the impact on the natural ecosystem was not recognized.

*P. contorta* is considered one of the most aggressively invasive tree plantation species (Benecke, 1967; Ledgard, 1988; Richardson and Bond, 1991; Kay, 1994; Rejmánek and Richardson, 1996; Higgins and Richardson, 1998; Despain, 2001; Ledgard, 2001). Among the principal traits of this native North American species that are associated with its invasive capacity are seed production at a very early age (5 years), small seed size (one of the smallest *Pinus* seeds) which facilitates wind dispersal, minimal requirements for germination and establishment under adverse edaphoclimatic conditions, and its high juvenile growth rate (Baumgartner et al., 1984; Hunter and Douglas, 1984; Kay, 1994).

Considering the international evidence on the invasive capacity of *P. contorta* and the risk to natural ecosystems, in this paper we aim to: (a) to determine *P. contorta* invasion patterns by studying its size and age structure and its spatial distribution and (b) determine the effect of vegetation cover on *P. contorta* regeneration. We have chosen the Malalcahuello National Reserve as a study case considering its high ecological value as one of the few reserves of the National System of Protected Wilderness Areas (SNASPE) that conserve the *Araucaria araucana* forests.

## 2. Methods

### 2.1. Study area

The study area is located on the Southern side of the Lonquimay Volcano, in the Andes, at 1420 m above sea level in the Malalcahuello National Reserve, Araucanía Region, Chile. Mean annual precipitation is 3083 mm, mostly snow, with an annual dry period of one month and an annual mean temperature of 8.5 °C (INFOR-U. de Chile, 1979). Topographic characteristics of the area are mainly influenced by glaciation and volcanic activity (Becerra and Faúndez, 1999; Peralta, 1980). Wind direction in the area is strongly influenced by topography, being predominantly from the northwest, descending down the volcano's hillsides.

Vegetation is dominated by timberline forest type of *A. araucana* (Mol.) C. Koch. (Monkey puzzle tree) and *Festuca scabriuscula* Phil. (coirón bunchgrass) (Gajardo, 1993). In patches, *Nothofagus antarctica* (Forst.) Oerst. (Ñirre) forms small, dense forests, mainly of regrowth. *Chusquea coleou* Desv. (Coligue – bamboo) also forms monotypic stands, but is less abundant. At lower elevations, combinations of deciduous and evergreen *Nothofagus* species dominate the forest (e.g. *N. obliqua*, *N. dombeyi*, and *N. alpina*) (Donoso, 1993). Non-native pines were introduced as trial plots by the Chilean Forestry Institute (INFOR) in 1970. Eleven experimental plots were located within the study area, three corresponding to *P. contorta*, four to *Pinus sylvestris* L., and four to *Pinus ponderosa* Laws. The plantation design was of 100 plants distanced at 2 m × 2 m, equivalent to an initial density of 2500 plants ha$^{-1}$ (Loewe and Murillo, 2001). In the area there is also a *P. ponderosa* plantation of approximately 2.5 ha, established a couple of years after the study plots.

### 2.2. Sampling

#### 2.2.1. Invasion patterns

In the three *P. contorta* trial plots, attributes were measured in order to describe its current structure, including: density (plants ha$^{-1}$), diameter at breast height (DBH) (cm), and mean height (m).

Using the predominant wind direction (northwest) as the selection criterion (Fig. 1), we selected one of the three *P. contorta* trial plots (from now on E1, E2, and E3). Starting from the edge of the selected trial plot (E1), located at 38°42′ south latitude and 71°53′ West longitude, eight transects (directions: North (N), Northeast (NE), East (E), Southeast (SE), South (S), Southwest (SW), West (W), and Northwest (NW)). Each transect (50 m × 125 m) was divided in five sections 25 m long. In each section, 25 circular plots of 2.5 m radius were randomly distributed. We recorded the distance to the plantation center of each plot, considering the center of E1 as the origin. In each plot, we measured collar diameter (CD) for each *P. contorta* individual. We recorded the presence of cones for each individual of *P. contorta* within the plots. We used a destructive sampling to determine age–diameter relationship with a linear regression model. We used 58 individuals of different CD classes, including 34 years old individuals from the INFOR trial plots. We measured the CD, and determined the age by extracting a cross-section from the stem base for small individuals (CD < 12 cm) or increment cores for larger ones (CD > 12 cm).

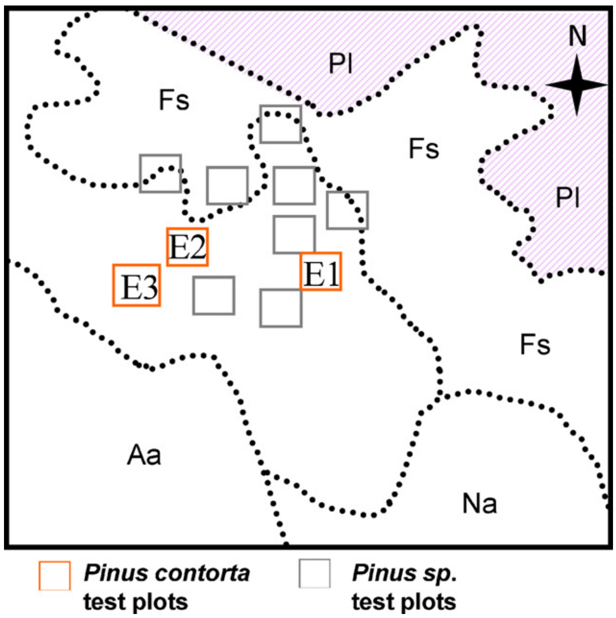


**Fig. 1.** Map of the study area showing the trial plots and native vegetation present in the area. Aa: *A. araucana*, Na: *N. antarctica*, Fs: *F. scabriuscula* and Pl: *P. ponderosa* plantation.

We used geostatistical methods such as semi-variograms and kriging to quantify and model the spatial pattern of pine regeneration. The existence of spatial correlation was evaluated through the variograms (Isaaks and Srivastava, 1989; Grushecky and Fajvan, 1999). A spherical model was adjusted and with the modeled variogram, the interpolation was performed through the ordinary kriging method (Isaaks and Srivastava, 1989). S-plus version 6.0 with the spatial module S+Spatial Stats 1.5 was used for the analyses. Using a Global Positioning System (GPS), we recorded the points where most distant individuals from the parent stands stood (E1). Using Arcview 3.2, we estimated the total surface of *P. contorta* regeneration.

*2.2.2. Vegetation cover and its relationship with Pinus contorta natural regeneration*

In each circular plot, we measured percent vegetation cover (grass, understory and canopy) using the Braun–Blanquet cover classes. We determined species composition of the understory and canopy in order to analyze influence of cover types on natural regeneration of *P. contorta*. To analyze the association of *P. contorta* with *A. araucana* and *N. antarctica*, we used a $2 \times 2$ contingency table using the Chi-square ($\chi^2$) test with a 95% confidence level (Donoso, 1993). We built a multiple regression model for *P. contorta* plant density using the forward stepwise variable selection method. Pine density was transformed using the logarithmic function. The independent variables tested in the model were: percent cover by each vegetation type (grass, understory, and canopy), distance from the study plots to E1, and CD of the largest tree in each plot.

## 3. Results

### 3.1. Transects

The selected *P. contorta* parent stand had a density of 150 plants ha$^{-1}$, showing a steep reduction from the original density (2500 ha$^{-1}$). Stands showed no sign of any type of management, such as pruning or thinning, and dead trees were not observed, suggesting that the reduction in the number of individuals occurred early after planting. Mean DBH was 36.7 cm and mean height of individuals was 15.6 m. Trees were in good conditions; however, some individuals presented deformations at the stem base due to snow damage. Nonetheless, all individuals showed a large number of cones.

We found regeneration of *P. contorta* in a wide range of sizes, forming an inverted-J distribution (Fig. 2). The smallest CD class included the larger number of individuals with a mean of 1043 plants ha$^{-1}$. The regression model between age and CD explains 97.2% of the age variation (S.E. $\pm$1.5 years). Of all sampled individuals, only a 38% of them presented cones, finding reproductive structures in 5-year-old individuals. Individuals between 1 and 5 years did not present reproductive structures (98%). This condition is inverted in the next age range (6–10 years), with 82% of the individuals possessing cones. At 11 years, all trees presented reproductive structures (Fig. 3).

Regeneration was found in all transects. Density, however, was extraordinarily variable. The West transect presented the biggest variation (637–16,603 plants ha$^{-1}$) (Table 1). The highest density values were found in the West, Southwest, and Northwest transects, reaching an average of 6600 plants ha$^{-1}$, probably determined by wind and seed dispersal from other trial plot (E2 and E3). The species spread was lower in the North and Northeast transects, without surpassing 110 plants ha$^{-1}$ (Fig. 4) and individuals present only in the first section. In five of the eight transects we found plants more than 100 m away from the parent trees.

Through the interpolation performed with the kriging variable selection method, a map of the area with the spatial gradient of plant density was obtained (Fig. 5a). In the map, it can be observed

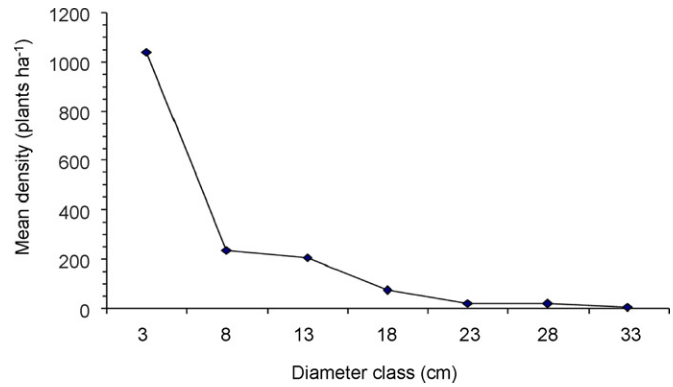


**Fig. 2.** Diametric distribution of *P. contorta* regeneration. Data collected in 192 circular plots.

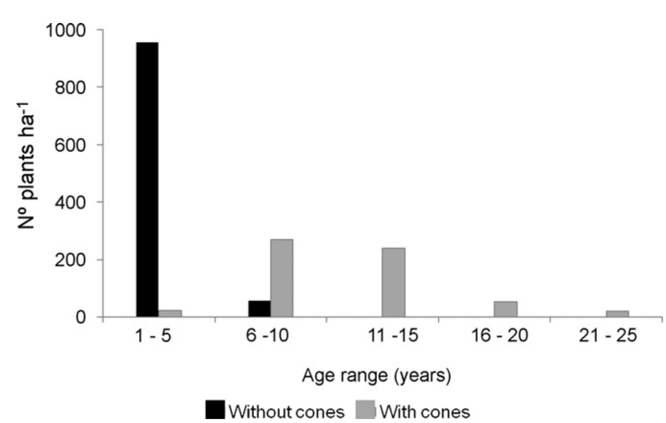


**Fig. 3.** Number of *P. contorta* individuals for all plots ($n = 192$) with and without presence of cones for each age range.

**Table 1**
Plant density for each transect and section

| Section | Transects density (plants ha$^{-1}$) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | N | NE | E | SE | S | SW | W | NW |
| 1 (0–25 m) | 306 | 306 | 2.750 | 1.910 | 1.732 | 849 | 637 | 0 |
| 2(26–50 m) | 0 | 0 | 0 | 2.343 | 1.834 | 815 | 1.019 | 3.565 |
| 3 (51–75 m) | 102 | 0 | 204 | 1.630 | 2.852 | 2.648 | 3.972 | 0 |
| 4 (76–100 m) | 102 | 0 | 0 | 0 | 1.834 | 3.260 | 16.603 | 204 |
| 5 (101–125 m) | 0 | 0 | 102 | 0 | 611 | 1.120 | 9.575 | 1.120 |
| Mean | 102 | 61 | 611 | 1.146 | 1.772 | 1.816 | 6.600 | 994 |

that the species spread towards areas where native *Nothofagus* were absent and areas where *A. araucana* was present. Under the canopy of other *Pinus* spp. (trial plots), the plant density of *P. contorta* decreases or was not present at all. Naturally regenerated individuals of *P. contorta* occupied an area of 78 ha where the most distant individual is located in the Southeast direction at an average distance of 1200 m from the three study plots (E1, E2 and E3; Fig. 5). The regeneration is advancing mainly toward the Southeast, coinciding with the predominant winds of the area (Northwest).

### 3.2. Vegetation cover and its effect on P. contorta natural regeneration

We found grass cover in 68% of the plots, frequently dominated by *F. scabriuscula*. In 42.3% of the plots the understory was absent. The remaining 57.3% plots had an understory composed mainly of *P. sylvestris* and *P. ponderosa* regeneration (44% of total plots), and in a smaller proportion *C. coleu* (13% of total plots) and *N. antarctica* (1% of total plots). Overall, 67.7% of the plots did not have significant overstory canopy cover. The remaining plots (32.3%) included native (*A. araucana* and *N. antarctica*) and non-native (*Pinus* sp.) individuals on the upper stratus. Plots that had non-native species in the canopy corresponded to plots located under the *P. sylvestris* and *P. ponderosa* trial plots mentioned earlier. Most of them had a cover index of 4 (10.4% of total plot). Likewise, when canopy was composed by *N. antarctica*, cover was mainly higher than 75% (6.3% of the plots), since this species grows in the area forming young dense forests. Most plots that had *A. araucana* in the canopy, however, had less than 50% canopy cover.

We found a positive association between *P. contorta* and *A. araucana* (Table 2, $p < 0.05$, $\chi^2$). Additionally, *P. contorta* and *N. antarctica* also show a negative association ($p$-value $<0.05$) (Table 2). The best model for *P. contorta* density includes as independent variables the three cover types (grass, understory and canopy) and CD of the largest tree of each plot (Table 3, DC 65%).

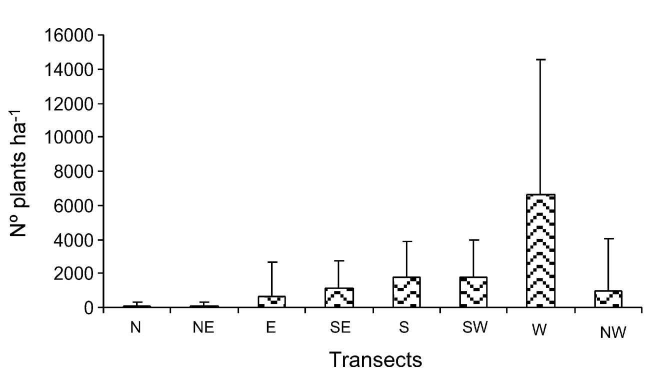


**Fig. 4.** Mean *P. contorta* regeneration density (±standard deviation) for each transect according to orientation.

## 4. Discussion

Patterns of *P. contorta* spread from field trials in the Malalcahuello National Reserve indicate that the species not only is able to survive and establish in natural environments, but it also produces large amounts of propagules at early age which are able to disperse at long distances. The low density of the *P. contorta* planted when the stand was established in 1970 (6% of the original density), and the absence of dead trees indicates a high mortality during juvenile stages of the plantation. However, such mortality does not appear to be occurring in naturally regenerated trees. This could reflect the ending of a lag-phase described by Mack et al. (2000) and Richardson (2001). Therefore, the diameter distribution with the inverted-J form and the age structure dominated by individuals younger than 25 years old reflects that in the last few years, the species is establishing successfully. The total area with of *P. contorta* individuals increased from 0.12 ha (corresponding to the area of the three trial plots) to 78 ha in 33 years (Fig. 5b).

Sexual maturity of naturally regenerated individuals is reached between 6 and 8 years old (Fig. 3). The oldest naturally regenerated individuals were close to 25 years old, 8 years younger than their progenitors (individuals pertaining to the study plots established in 1970). Benecke (1967) indicated that in New Zealand, *P. contorta* individuals growing in open forests could produce cones at ages between 3 and 4 years, but that larger cone production does not begin until ages between 7 and 8 years. Other authors indicate that cone production with viable seeds begins only at 5 years old (Lotan and Critchfield, 1990; Ledgard, 2001). Our results suggest that in the Malalcahuello National Reserve, there has been up to three generations since the species was introduced.

The capacity of *P. contorta* to spread naturally over an extensive area (e.g. individuals at more than one kilometer away from parent trees) allows us to conclude that *P. contorta* is a naturalized and an invasive species in the area (sensu Richardson et al. (2000)). However, despite the rapid appearance of new dispersal points in the area, there are sectors where the species could not be established, limited mainly by dense vegetation cover (Fig. 5, Table 3). As canopy and grass cover increased, the number of individuals decreased. Similar results were reported by Ledgard (2001), who affirmed that successful *P. contorta* establishment decreased when vegetation cover increased, because of its high light requirement and low competition capacity during its first year of life. The species has a radicular root system that only penetrates 10–15 cm deep in the first year, competing for water with grasses (Lotan and Critchfield, 1990; Despain, 2001). During the second year, roots are able to penetrate to deeper horizons, resisting longer drought periods (Despain, 2001).

The fact that *P. contorta* is an invasive species and that higher plant density is concentrated in areas dominated by *A. araucana* could threaten this endemic conifer in the long term. In the short term, both species are probably capable of coexisting. However, in

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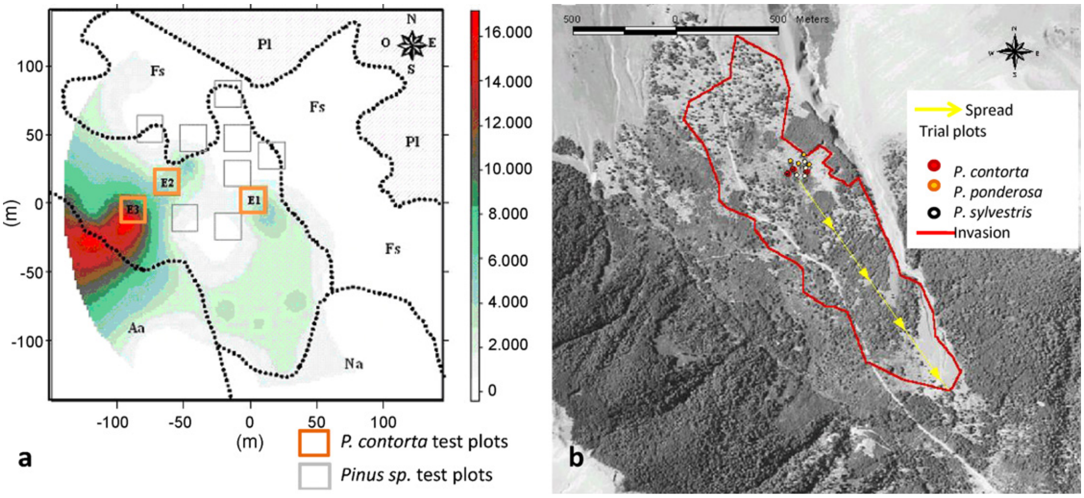


**Fig. 5.** (a) Map of the area showing the *P. contorta* plant density gradient pattern (plants $ha^{-1}$), obtained using ordinary kriging interpolation. The dotted line divides sectors with different vegetation cover, which are identified by the following nomenclature: Aa: *A. araucana*, Na: *N. antarctica*, Fs: *F. scabriuscula* and Pl: *P. ponderosa* plantation. (b) Map of the area with *P. contorta* invasion, including trial plots location (*P. contorta*, *P. ponderosa*, and *P. sylvestris*).

the long term, the establishment of new *A. araucana* individuals will likely decrease, since, despite being shade tolerant and able to establish and survive as suppressed individuals for many years under their own canopy, they require the death of one or several adult individuals and the formation of small gaps for the successful development to the upper layers (Donoso, 1993). The formation of these gaps will be much more difficult with the presence of *P. contorta* in the area due to its growth and reproduction traits, causing a high propagule pressure, rapidly establishing and occupying available sites. An additional disadvantage for *A. araucaria* is its large seed size, which tends to fall to the ground near the mother tree and seed dispersal by birds and mammals is scarce (Donoso, 1993), making its dispersion more difficult than the small seeds of *P. contorta*, easily transported by wind, with greater possibility of acceding to the clearings formed.

*P. contorta* invasion can have long-term effects that are difficult to predict. However, the displacement of native flora and fauna and the alteration of natural processes like nutrient cycling and water dynamics have been reported elsewhere for other non-native conifers (Richardson et al., 2008). These, added to the fact that this is occurring in a state-protected area, whose objective is to conserve Chilean biological patrimony, create the need to plan and execute management procedures in order to control the advance of the *P. contorta* invasion. The results obtained in this study indicate that each year the species has increased its regeneration, a situation that makes its control more complex and costly. Early prevention and control of future invasions is the best way to reduce its economic, social and environmental costs (Pauchard and Alaback, 2002).

**Table 2**
Contingency table presenting the occurrence of *P. contorta* and *A. araucana* and *P. contorta* and *N. antarctica* in 192 plots with the Chi-square value ($\chi^2$) and its probability

| | *P. contorta* | | | $\chi^2$ | *p*-value |
|---|---|---|---|---|---|
| | Presence | Absence | Total | | |
| *A. araucana* | | | | | |
| Presence | 18 | 9 | 27 | | |
| Absence | 64 | 101 | 165 | 7.3703 | 0.0066 |
| Total | 82 | 110 | 192 | | |
| *N. antarctica* | | | | | |
| Presence | 2 | 16 | 18 | | |
| Absence | 80 | 94 | 174 | 8.1044 | 0.0044 |
| Total | 82 | 110 | 192 | | |

**Table 3**
Variables, parameters, and statistical parameters of the selected regression model

| Variation source | $\beta$ | Standard error of $\beta$ | *t* (188) | *p*-value | $R^2$ | EEE[a] | *n* |
|---|---|---|---|---|---|---|---|
| Interceptor | 1.9017 | 0.1391 | 13.6758 | 0.0000 | 0.655 | 0.705 | 192 |
| Maximum CD | 0.0921 | 0.0072 | 12.7635 | 0.0000 | | | |
| Canopy cover | −0.1933 | 0.0439 | −4.4078 | 0.0000 | | | |
| Bare ground cover | −0.1404 | 0.0415 | −3.3802 | 0.0009 | | | |

Log (density) = 1.9017 + 0.0921$a$ − 0.1933$b$ − 0.1404$c$. Where $a$: maximum CD, $b$: canopy cover, and $c$: bare ground cover.
[a] EEE: standard error of estimation.

## 5. Conclusions

In the Malalcahuello National Reserve, *P. contorta* reach sexual maturity at an early age, produce a large number of seeds and are able to disperse and establish over long distances. *P. contorta* in the area will likely occupy areas where *A. araucana* dominates, competing for space and resources with this endemic conifer. This scenario will probably repeat itself in other *P. contorta* plantations. In southern Chile and Argentina, *P. contorta* rotations will, in most cases, be longer than 50 years. Thus, *P. contorta* commercial or trial plantations in the Andes and Patagonian steppe would have a high invasive potential because the species will produce and disperse seeds for more than 40 years. It appears that compared to other *Pinus* spp. with shorter rotations *P. contorta* could have a higher impact on native ecosystems. We believe that controlling propagules coming from *P. contorta* commercial forest stands will be a hard task because of its attributes (e.g. small seed size) and its capacity to produce seed every year and as young as 5 years old. Because of regulations limiting the use of herbicides in protected areas, control of naturalized pines will be mainly by felling and hand pulling (Ledgard, 2001), especially in areas where endemic or endangered species do occur. Until there is a clear understanding of the invasive potential of *P. contorta*, planting of the species should be halted in areas where environmental conditions favor its invasiveness.

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## Acknowledgements

This work was supported by funding from Research Direction of the University of Concepción Grant 202.142.013-1.0. We thank Mauricio Ramirez, Alex Opazo, Paul Alaback and two anonymous reviewers for useful comments on this MS. A. Pauchard is funded by ICM P05–002, PFB-23 Conicyt-Chile, and Fondecyt 1070488. B. Langdon is supported by Conicyt Doctoral Scholarship.

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Please cite this article in press as: Peña, E., et al., Patterns of spread of *Pinus contorta* Dougl. ex Loud. invasion in a Natural Reserve in southern South America, Forest Ecol. Manage. (2008), doi:10.1016/j.foreco.2008.06.020