Stand structure and regeneration of harvested *Araucaria araucana–Nothofagus* stands in central Chile

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In this study we examined the current structure and regeneration status of mixed *Araucaria araucana–Nothofagus* spp. stands that had been logged 20 years ago. We measured stand density of saplings, juvenile and adult trees, as well as stand basal area of *A. araucana* and *Nothofagus* spp. in 69 plots distributed in five sites in order to characterise diameter distributions using a Weibull function. *Araucaria araucana* represented 23–75% of total stand density (69–197 trees ha−1) and total basal area (17.5–54.9 m2 ha−1), and the remaining tree species were *Nothofagus pumilio*, *N. dombeyi* and *N. obliqua*. Stand density of *A. araucana* juveniles ranged from 106 to 1 422 plants ha−1, whereas juveniles of *Nothofagus* spp. ranged from 4 to 495 plants ha−1. Based on the fitted Weibull distribution function, the shape of the diameter distribution for *A. araucana* individuals ≥10 cm dbh was dominated by the reverse-J (c = 1.0) and mound-shaped (c = 1.26) forms. The Weibull shape parameter of *N. pumilio* indicated that the diameter distributions were positively skewed. These results are indicative of a good regeneration status for *A. araucana* and a medium one for *N. pumilio*. Stand characteristics were used to predict regeneration of *A. araucana* on the study sites using a principal component analysis (PCA). The PCA showed that regeneration, including seedlings and saplings, was higher in those stands including high values of density of *A. araucana*. Stand density of juvenile trees in stands where *A. araucana* had been previously logged suggests that harvesting during the 1980s may have provided occasional recruitment sites where shading may have otherwise precluded regeneration. The results of the study improve our understanding of the ecology, dynamics and succession of mixed *A. araucana–Nothofagus* forests in southern South America.

**Keywords**: forest stand dynamics, forest stand structure, *Nothofagus pumilio*, silviculture, sustainable forest management, Weibull

**Introduction**

*Araucaria araucana* (Molina) K.Koch (Araucariaceae) is an endemic conifer that occurs in the Andean cordillera between 37°27′ S and 40°03′ S, besides two isolated populations in the Cordillera de Nahuelbuta of the Chilean coastal mountains (Donoso 1993). *Araucaria araucana* usually forms mixed stands with the so-called southern beeches, namely *Nothofagus pumilio* (Poepp. & Endl.) Krasser, *Nothofagus dombeyi* (Mirb.) Oerst. and *Nothofagus antarctica* (G.Forst.) Oerst., covering an area of approximately 442 000 ha in Chile and Argentina, of which 194 000 ha are designated as protected areas (Lara et al. 1999). Since 1976, *A. araucana* has been protected in Chile under the status of a Chilean National Monument and the species is also protected internationally under the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES).

The forest dynamics and regeneration strategy of *A. araucana* and *Nothofagus* spp. and their relationship with disturbance regimes has been studied extensively in natural forests (Veblen 1982, Burns 1991, 1993, Donoso 1993, Veblen et al. 1995, Cortés 2003, González et al. 2006). The long-lived, large-seeded southern conifer *A. araucana* has life-history and ecological features that are characteristic of a species with intermittent variable reproduction (Veblen et al. 1995). Although the secondary forest succession of *A. araucana–Nothofagus* forests has been the subject of previous research, understanding how such forest ecosystems recover after disturbances represents a relevant topic of current research (e.g. Veblen et al. 1995, González et al. 2006). However, less attention has been given to the impact of logging on the successional and regeneration status of such forest systems (González et al. 2006, Mujica et al. 2009). Stands typical of secondary *A. araucana–Nothofagus* forests have been well described from an ecological perspective in relation to old-growth forest conditions (Veblen et al. 1995). In contrast, there is a gap in knowledge concerning the structural characteristics and regeneration dynamics during the secondary succession of historically managed *A. araucana–Nothofagus* forests. Therefore, a more detailed insight into the stand dynamics along the development of natural *A. araucana* forests under historical management practices is needed.
Araucaria araucana natural regeneration results from large- and small-scale disturbances such as fire, wind throw, tree falls and anthropogenic factors. Small forest gaps caused by the fall of (normally) senescent trees under the action of wind or snow (Wardle 1984, Donoso 1993), as well as larger gaps caused by massive wind-tree falls (Rebertus and Veblen 1993), allows the establishment of early successional species, in particular Nothofagus spp. (Burns 1993, Veblen et al. 1995). A. araucana–Nothofagus forests typically show a broad and continuous range in adult density and size, with heights of co-occurring species ranging from 1 to 40 m (Donoso 2003). Such variation in tree size within a stand results in a trade-off between tree size at the first reproduction stage and the life-long reproductive output, where the latter is enhanced by prolonged vegetative growth to construct large, elevated crowns that intercept much light and produce large seed crops (Veblen et al. 1995). Forest management removes the existing forest vegetation and may partly replace it with other species when managed stands of altered structure result in a mosaic of forest stands with different characteristics (Burns 1993, Veblen et al. 1995). Therefore, taking into account the past, present and future forest management, and understanding its impact on species and ecosystem dynamics is an important issue in forest ecology.

Recruitment into mature A. araucana forest stands is regulated by a wide variety of factors, such as erratic seed production, fruit consumption, browsing damage, fire occurrence, light conditions under the canopy and climatic variability (González et al. 2006). Many mature A. araucana stands have relatively high densities suggesting that seed production, germination and seedling recruitment were not a problem in the past (Burns 1991, González et al. 2006). However, relating tree regeneration dynamics in A. araucana forests to previous silvicultural treatments has proven more difficult (Mujica et al. 2009). Silvicultural treatments are followed by successive cohorts of early successional Nothofagus species and Chusquea culeou that dominate the forest understory and suppress the recruitment of A. araucana seedlings, which become restricted to multiple tree-fall gaps (Burns 1991). Because of the high longevity and large size of A. araucana adult trees, they remain as dominant components of the forest biomass and structure for long periods of time, although demographically functioning as remnant stands, which lack significant continuous regeneration (González et al. 2006).

In harvested forests, size class distribution has been often used to assess the viability and response of a given stand to harvesting impacts (Wright et al. 2003). Diameter-class distribution models have become a useful tool in forest management, growth and yield modelling, and forest inventory. Various probability density functions (pdf) have been utilised to characterise the diameter frequency distributions of forest stands (e.g. Bailey and Dell 1973, Kangas and Maltamo 2000). A direct application of the Weibull density function is the comparison of conspecific stands at multiple sites for the assessment of stand responses to human activities (Souza 2007).

The major objective of silvicultural treatment of A. araucana–Nothofagus forests traditionally was to produce quality timber, whereas little attention was given to the provision of suitable conditions for the regeneration of dominant species. Forest management based on the seed tree silvicultural system (reserve trees between 30% and 50% of the initial basal area before harvest) has been suggested for A. araucana forests in Chile (Schmidt and Urzáiz 1982) to obtain a successfully regenerated stand prior to the final cut. Consistent with this proposal, the Corporación Nacional Forestal (CONAF) of Chile suggested the extraction of basal area over 30 m² ha⁻¹ in A. araucana–Nothofagus spp. forests, which was applied between 1980 and 1989 in numerous A. araucana forests.

Studies have tended to focus on the response of A. araucana forests to the management practices implemented over time, whereas studies exploring how management factors interact with the regeneration process are scarce (Mujica et al. 2009). In this study, we explored the diameter distribution and regeneration of five natural A. araucana–Nothofagus forests in central Chile. The specific objectives of the study were (1) to quantify the current composition and structure of such forest ecosystems, (2) to determine which stand characteristics are the best to predict A. araucana regeneration, and (3) to investigate the impacts of harvesting disturbances on forest stand dynamics.

Materials and methods

Study area

The study sites were located in Curacautín and Lonquimay provinces (c. 38°09′ S, 78°31′ W) in central Chile (Figure 1). The study area ranges in elevation from 1 372 to 1 781 m above sea level. The average annual precipitation is 2 000 mm with 70% falling between May and August (Hayek and Di Castri 1975). The mean annual temperature is 8.6 °C with an average of 15.1 °C in January and 1.9 °C in July. The bedrock consists of recently deposited volcanic ejecta, tuff and scoria over basaltic deposits (Peralta 1975). The soils in A. araucana–Nothofagus forests are porous with a very low bulk density (0.4–0.6 g cm⁻³) and low levels of fertility due to P fixation, pH c. 6.0, 2.3% organic matter content and a C:N ratio of 24.50 (Peralta 1975).

The forest stands considered in this study contained emergent individuals of A. araucana and N. pumilio, with a few individuals of N. dombeyi and N. obliqua (Mirb.) Oerst. sparsely mixed with Drymis winteri J.R.Forst. & G.Forst., Maytenus magellanica (Lam.) Hook.f. and Embothrium coccineum J.R.Forst. & G.Forst. Evidence of direct human intervention included forest management plans, mostly of A. araucana and N. obliqua (Table 1), and historical records of cattle ranching, which ceased approximately 25 years ago. Aside from fire suppression and prevention activities, no interventions have occurred in the study area compartments since they were cut in the early 1990s. Windthrow occurs rarely in the study area and, since the onset of fire suppression operations around 1980 as part of the CONAF Fire Management Plan, fire was largely excluded from the study sites.

Sampling methodology

After a general reconnaissance of the study area, we selected five A. araucana–Nothofagus stands based on forest management plans (FMPs) prepared by CONAF
between 1980 and 1990 (Table 1, Figure 1). The FMP is a technical document describing forest management objectives, strategies and commitments. It identifies intended methods of cutting, reforesting and managing timber resources within a defined forest (Donoso and Lara 1998). The selected FMPs exhibit large variability in target forest area (between 27 and 592 ha), and their selection was based on the following criteria: (1) maximum unit homogeneity, (2) availability of reliable data of the harvesting year, (3) representative and homogeneous distribution over the area and time, (4) no sign of recent disturbance (e.g. fire and windstorms) other than occasional livestock grazing, and (5) accessibility. In addition, the selected FMPs were mapped and their geographical centres, areas and size were determined (Table 1). Two sites were dominated by *A. araucana* (Hijuela and Pino Huacho), two sites were dominated by *N. pumilio* (El Indio and San Antonio), and one site had relatively even abundances and total basal area of both species (Lolco; Table 1). *Araucaria araucana* and *Nothofagus* spp. had been selectively logged from the study sites in 1989–1990. The logging intensity of *A. araucana* varied across the study sites from 0.7 to 9 m² ha⁻¹ of basal area extracted but there was not any information about the logging intensity of *Nothofagus* (Supplementary Table S1).

Inventory samples, performed sequentially for each site, followed a two-phase scheme known as double sampling for stratification (see Chojnacky 1998). In the first phase, a grid of sample points (200 m × 200 m) on aerial photographs was interpreted, and the area covered by *A. araucana–Nothofagus* forests was calculated. A random sample of the grid points was chosen for field measurement in the second phase. The number of sampled plots falling within each site was weighted according to the total surface area of

### Table 1: Study site, species composition and structural parameters for five *Araucaria araucana* populations in the Melleco province, central Chile. Different letters indicate a significant difference between sites at *P* ≤ 0.05 (ANOVA, Tukey’s test for multiple comparisons). Values are the mean ± SE

| Site      | Species            | Adults ha⁻¹ (dbh > 10 cm) | Basal area (m² ha⁻¹) | Seedlings ha⁻¹ (height < 0.5 m) | Saplings ha⁻¹ (0.5 < height < 1.5 m) | Juveniles ha⁻¹ (height ≥ 1.5 m, dbh < 10 cm) |
|-----------|--------------------|---------------------------|----------------------|-------------------------------|-----------------------------------|-----------------------------------------------|
| Hijuela 12| *Araucaria araucana*| 191 ± 41ab               | 31 ± 14.9ab          | 3 750a                        | 375a                              | 696b                                          |
|           | *Nothofagus pumilio*| 63 ± 17b                 | 10.6 ± 3.6c          |                               |                                   |                                               |
|           | *Nothofagus dombeyi*| 0                         | 0                    |                               |                                   |                                               |
|           | *Nothofagus obliqua*| 0                         | 0                    |                               |                                   |                                               |
| Pino Huacho| *Araucaria araucana*| 169 ± 33ab               | 54.9 ± 11.3ab        | 7 614a                        | 341b                              | 106b                                          |
|           | *Nothofagus pumilio*| 65 ± 18b                 | 17.1 ± 4.5c          |                               |                                   |                                               |
|           | *Nothofagus dombeyi*| 0                         | 0                    |                               |                                   |                                               |
|           | *Nothofagus obliqua*| 0                         | 0                    |                               |                                   |                                               |
| San Antonio| *Araucaria araucana*| 67 ± 17b                 | 25.5 ± 6.2b          | 11 875a                       | 2 250a                           | 1 424b                                        |
|           | *Nothofagus pumilio*| 226 ± 24a                | 45.9 ± 2.7a          |                               |                                   |                                               |
|           | *Nothofagus dombeyi*| 0                         | 0                    |                               |                                   |                                               |
|           | *Nothofagus obliqua*| 0                         | 0                    |                               |                                   |                                               |
| El Indio  | *Araucaria araucana*| 88 ± 25a                 | 17.9 ± 6.2b          | 4 779a                        | 294b                             | 302b                                          |
|           | *Nothofagus pumilio*| 265 ± 38a                | 29.1 ± 4.4bc         |                               |                                   |                                               |
|           | *Nothofagus dombeyi*| 4 ± 3a                   | 3.9 ± 3.8a           |                               |                                   |                                               |
|           | *Nothofagus obliqua*| 0                         | 0                    |                               |                                   |                                               |
| Lolco     | *Araucaria araucana*| 100 ± 26ab               | 17.5 ± 3.2b          | 2 917a                        | 595b                             | 369b                                          |
|           | *Nothofagus pumilio*| 140 ± 32ab               | 16.6 ± 4.2c          |                               |                                   |                                               |
|           | *Nothofagus dombeyi*| 50 ± 19a                 | 11.3 ± 4.2a          |                               |                                   |                                               |
|           | *Nothofagus obliqua*| 14 ± 12                  | 2.3 ± 2.2            |                               |                                   |                                               |

![Figure 1: Distribution map of Araucaria araucana (dark grey-shaded areas) in the Araucania Region, central Chile. The study sites in the Curacautin and Lonquimay provinces (shaded light grey) and management units (stars) are also indicated.](image-url)
A. araucana–Nothofagus forests (Supplementary Table S1). Time and accessibility restrictions resulted in the exclusion of several plots from the sampling area. During January 2009, 69 square sampling plots (1 000 m², 31.6 m × 31.6 m) were established. In each plot, all trees with diameter at breast height (dbh) > 10 cm were measured for diameter and height using a calliper and hypsometer, respectively. We also counted all tree individuals greater than 1.5 m in height and less than 10 cm dbh, hereafter referred to as juveniles, within each plot. To measure regeneration since the last harvest 20 years ago, we counted all tree individuals less than 150 cm tall, hereafter referred to as saplings (0.5 < height < 1.5 m), and seedlings (height < 0.5 m) in four 1 m × 1 m subplots located within each plot.

**Stand structure analysis**

We grouped A. araucana, N. pumilio, N. dombeyi, and N. oblicua into 10-cm diameter classes, using averaged densities across sampling plots, and generated diameter frequency distributions for each species at each site. To quantitatively compare stand structures, we used fitted two-parameter Weibull distribution functions to the data. The three-parameter Weibull probability density function (pdf) is given by [Equation 1]:

\[
f(x) = \frac{c}{b} \left(\frac{x-a}{b}\right)^{c-1} \exp \left[ -\left(\frac{x-a}{b}\right)^c \right]
\]

where \( x \) is the observed variable (i.e. dbh), \( c \) is the shape parameter, \( b \) is the scale parameter and \( a \) is the location parameter. As mentioned above, in this study we used fitted two-parameter Weibull functions with the location parameter set to zero (\( a = 0 \)) with the statistical package Sigmaplot 12.1 (Systat Software, San Jose) using the maximum likelihood method. The value of parameter \( c \) has the following meanings (Shifley and Lentz 1985):

1. For \( 0 < c < 1 \), indicates an exponential distribution. It means that there are abundant young individuals in the stand plot and the regeneration status of the species is very good;

2. For \( 1 < c < 2.6 \), a positively skewed Weibull pdf distribution (i.e. has a right tail) is produced. Such a right-skewed dbh distribution means that there are fewer young individuals compared to the individuals of average size, and that the regeneration status is medium;

3. If \( 2.6 < c < 3.7 \), the coefficient of skewness approaches zero and stands for the Weibull pdf distribution may approximate the normal pdf;

4. For \( c \geq 3.7 \), diameter distributions is negatively skewed distribution and indicates a poor regeneration status.

Diameter distributions between different stands were compared using the Kolmogorov–Smirnov statistical test (nonparametric two-sample test) that has a high power-efficiency for small samples (Zar 1999).

**Statistical analyses**

Prior to statistical analysis we examined dbh and stand density for normality and homoscedasticity using the Kolmogorov–Smirnov test and Levene’s test, respectively. Square-root transformation of dbh was used to stabilise variances. The results in the tables are shown as means with their standard errors for the untransformed variables. Once the basic requirements were found to be met, data were analysed statistically using one-way analysis of variance (ANOVA). In those cases where the stand characteristics proved significant in the ANOVA, Tukey’s test for multiple comparisons of means was used to check for differences (Sokal and Rohlf 1995).

To establish which stand characteristics are the best in predicting A. araucana regeneration, we treated the plots as the unit of replication and calculated a mean value for each stand characteristic. All plots were included in a principal component analysis (PCA) and the stand characteristics examined were: (1) stand density considering all A. araucana individuals, (2) stand density of reproductive A. araucana individuals (dbh ≥ 30 cm), (3) stand basal area of A. araucana, (4) stand basal area of reproductive A. araucana (dbh ≥ 30 cm), (5) mean dbh of A. araucana, (6) mean dbh of reproductive A. araucana (dbh ≥ 30 cm) (González et al. 2006), (7) mean height of A. araucana, (8) ratio of mean height to mean dbh of A. araucana, (9) stand density of N. pumilio, (10) stand density of all Nothofagus spp., (11) stand basal area of N. pumilio, and (12) stand basal area of all Nothofagus spp. To improve normality, we subjected variables 1, 2, 3, 4, 9 and 10 to square-root transformation and variable 6 to logarithmic transformation, and graphically assessed residuals to check for homoscedasticity (Zar 1999). Prior to the PCA, we constructed a correlation matrix to examine possible relationships among forest characteristics. Of the 12 stand characteristics surveyed, six (stand basal area of A. araucana, stand basal area of reproductive A. araucana, mean dbh of A. araucana, mean dbh of reproductive A. araucana, stand basal area of N. pumilio and stand basal area of all Nothofagus spp.) showed significant correlations (\( r > 0.602, P < 0.05 \)) with other stand-associated characteristics variables and were removed from the analysis. Thus, we summarised the other six variables (stand density of A. araucana, stand density of reproductive A. araucana, mean height of A. araucana, ratio of mean height to mean dbh of A. araucana, stand density of N. pumilio, and stand density of Nothofagus spp.), hereafter referred to as stand-associated characteristics, using PCA. We compared PCA axes with eigenvalues > 1 to the abundance of A. araucana saplings, A. araucana juveniles and Nothofagus spp. juveniles using a partial correlation analysis to determine whether regeneration of A. araucana was related to ordination-defined stand characteristics.

Specific correlation between harvesting intensity, expressed as extracted basal area of A. araucana, and saplings and juveniles of A. araucana were determined using a non-parametric Spearman’s rank correlation at a significance level of 5% (\( P \leq 0.05 \)) because the harvesting intensity data did not follow a normal distribution. Null hypotheses were rejected at the \( P < 0.05 \) level and all analyses were run with SPSS® 15.02 (SPSS, Chicago).

**Results**

**Current composition and structure of the Araucaria araucana–Nothofagus forests**

Stem density of A. araucana trees ≥ 10 cm dbh ranged from 69 to 197 ha⁻¹ among study sites, whereas that of
N. pumilio ranged from 63 to 272 trees ha\(^{-1}\) (Table 1). Nothofagus dombeyi and N. obliqua reached a maximum of 50 and 14 trees ha\(^{-1}\) at the same site (Lolco) and were completely absent from three and four sites, respectively. Total basal area of A. araucana ranged from 17.5 to 54.9 m\(^2\) ha\(^{-1}\), whereas that of N. pumilio ranged from 10.6 to 45.9 m\(^2\) ha\(^{-1}\). Two sites were dominated by A. araucana (Hijuela and Pino Huacho), two sites were dominated by N. pumilio (El Indio and San Antonio), and one site had relatively even abundances and total basal area of both species (Lolco; Table 1).

Mean diameters of A. araucana ranged from 37.1 to 96.2 cm. In all stands the frequency of A. araucana trees ≥10 cm dbh progressively decreased with increasing size classes (Figure 2). The shape of the Weibull diameter distribution had an exponential form in Hijuela (c = 1.0), Lolco (c = 1.0), San Antonio (c = 1.0) and El Indio (c = 1.0), and a positively skewed Weibull pdf distribution form in Pino Huacho (c = 1.2). The exponential distributions were the result of a peak in abundance at the smallest and intermediate size classes, and a rapid decline in the number of individuals in larger size classes (Figure 2), which indicates there were abundant young individuals in the stand and the regeneration status of A. araucana was very good. Hijuela was significantly different from the other stands in the distribution of individuals among lower size classes (Kolmogorov–Smirnov two-sample test, \(P = 0.05\)), due to a high number of individuals in the 10–20 cm dbh size class. Compared with the other stands, Hijuela and Pino Huacho had a greater number of individuals of A. araucana in the 10–30 cm dbh size classes. The mean diameter of N. pumilio trees ranged from 32.5 to 53.3 cm among stands, with a high abundance of individuals in the size classes <40 cm (Figure 2). The Weibull shape parameter indicated that the distributions in San Antonio (c = 1.5), Pino Huacho (c = 2.2), Hijuela (c = 2.5) and El Indio (c = 1.4) were a positively skewed Weibull pdf distribution. It indicates a right-skewed distribution of the diameter distribution and means a few small diameter individuals compared to the individuals of average diameter, and also means that the regeneration status was medium. Only in Lolco, N. pumilio distribution (c=1.0) exhibited an exponential form.

Nothofagus obliqua and N. dombeyi were relatively rare and occurred only in one and two stands, respectively. Therefore, the Weibull function was not fitted for these two species because of the small number of stands.

**Araucaria araucana regeneration**

*Araucaria araucana* sapling stand density was significantly higher in San Antonio (2.8 trees ha\(^{-1}\)) than in the other forest stands (\(F = 3.481, P < 0.019\)), which were not significantly different from one another (Table 1). Sapling stand density in San Antonio was more than double than that in El Indio and Hijuela and at least three-times greater than that in Lolco.

Pino Huacho had the lowest density of *A. araucana* juveniles (106 trees ha\(^{-1}\)). In the other stands, juvenile densities ranged from 299 to 1 422 trees ha\(^{-1}\). Juveniles stand densities were significantly greater (\(F = 8.247, P < 0.001\)) in San Antonio than in the other forest stands. The density of *Nothofagus* spp. juveniles ranged from 4 to 495 trees ha\(^{-1}\). El Indio presented the highest value of *Nothofagus* spp. juveniles (\(F = 8.071, P < 0.001\)) with respect to the other forest stands.

**Impacts of harvesting disturbances on the forest dynamics**

Three PCA axes accounted for 71% of the variation between tree size and stand characteristics (Figure 3). The first axis, representing 49.0% of model variance, was positively correlated with stand density and height of *A. araucana* trees. The second axis, representing 22.0% of model variance, was positively correlated with density of *N. pumilio* and of all *Nothofagus* spp., and negatively correlated with stand density of *A. araucana*.

Based on the PCA axes with eigenvalues > 1, the results showed that regeneration of *A. araucana* saplings and juveniles was more abundant in those stands with high density of *A. araucana* (Sqrt_N_AA and Sqrt_N_AA30) and negatively correlated with density of *Nothofagus* spp. (Sqrt_NPpumilio and Sqrt_Nothofagus). Controlling for the UTM coordinates of each plot to account for spatial segregation of plots among sites, the abundance of *A. araucana* saplings (\(r = 0.404, P < 0.001\)) and juveniles (\(r = 0.315, P = 0.008\)) were significantly correlated with the first PCA axis only. Juveniles of *Nothofagus* spp. were not correlated with any PCA axis.

Harvesting intensity, expressed as extracted basal area of *A. araucana*, showed a positive and significant correlation (non-parametric Spearman’s rank correlation, \(P = 0.05\)), with the abundance of saplings (\(r^2 = 0.380, P < 0.001\)), and juveniles (\(r^2 = 0.237, P = 0.050\)) of *A. araucana*.

**Discussion**

**Characteristics of forest stand structure**

*Araucaria araucana* and *Nothofagus pumilio* (Table 1, Figure 2) were the major components of the studied forest stands in terms of stand basal area and density. Veblen (1982) and González (2001) have studied the stand structure of *A. araucana–Nothofagus* communties in similar ecological situations. They suggest that *N. pumilio* probably establishes as a dense cohort following a severe disturbance (e.g. fire) and continues to regenerate in large tree-fall gaps. Current recruitment of *N. pumilio* was apparently greater than that of *A. araucana* at some locations where both species co-occur (Table 1). *Nothofagus pumilio* showed a medium regeneration status, suggesting that *A. araucana* may eventually dominate these forests in the continued absence of disturbance (Hijuela and Pino Huacho).

The reported Weibull shape parameters for *Araucaria* showed an exponential pdf distribution (c = 1.0) and a very good regeneration status, whereas *Nothofagus* had positively skewed mound-shaped distributions (1 < c ≤ 2.6), most likely due to high mortality or growth suppression of individuals in the young size-classes (González et al. 2006). Even though *N. pumilio* is a deciduous broadleaf light-demanding species, it can germinate in deep shade conditions. In such conditions, the percentage of germination is lower than under higher light availability, but seedlings may still be incorporated into the seedling bank.
Figure 2: Histograms for the 10 cm diameter class and the corresponding two-parameter Weibull distributions (solid line) for the five Araucaria araucana–Nothofagus study sites. Sample size (N), mean diameter at breast height and standard deviation (x), and values of the Weibull parameters (b and c) are also included.
Nothofagus codes: Sqrt_N_AA
regeneration according to silvicultural variables. Variables
Sqrt_N_AA30
stand density of
ratio of mean height to mean dbh of
uals, Height_AA
massive regeneration in
canopy at the upper forest layer resulting in an episodic
2002, González et al. 2006). Logging activities open the
where they survive in shade for up to 17 years (Cuevas
2002, González et al. 2006). Logging activities open the
canopy at the upper forest layer resulting in an episodic
regeneration of Araucaria araucana
Recruitment of Araucaria araucana
Araucaria stands in forests and the mechanisms involved
(Veblen et al. 1995, Donoso and Schmidt 1991, González
2001, González et al. 2006, Drake et al. 2012). This study
showed that A. araucana was able to establish in mixed
A. araucana–Nothofagus spp. stands after harvesting.
Seedling and sapling stand densities found in the study
forest sites were similar or greater that those suggested
in the literature for similar growing conditions (González
2001, González et al. 2006, Mujica et al. 2009). The high
density of seedlings and sapling in immature forest stands
may reflect the ability of A. araucana to recruit quickly in
disturbed forests due to the seed input from surviving trees.
In general, all the study areas presented high seedling and
sapling densities. Ratios of seedlings and saplings to juvenile trees suggest that at present A. araucana is
regenerating successfully in forest sites of Central Chile
(Table 1, Figure 2).

The ability of A. araucana to successfully regenerate
below the canopy may depend on factors controlling
growth, such as soil resources, light availability or tempera-
ture, rather than factors associated with fruit production,
germination or seedling mortality (Veblen 1982, González
2001). Because A. araucana saplings were much more
numerous than juveniles, regeneration establishment
does not seem to be a problem in these stands. Since the
study plots were harvested in the late 1980s (Table 1),
the under-representation of A. araucana juveniles could
be interpreted as a consequence of the low abundance
of juveniles compared to seedlings and saplings after the
harvesting conducted 20 years before. The juveniles likely
represent a cohort that established before extraction, under
deep shade, whereas the seedlings and saplings represent
cohorts that established when the canopy was opened by
means of harvesting operations. These juvenile trees seem
to be suppressed and do not move into larger size classes.

The role of harvesting
Harvesting may have played an important role in these
stands by changing the regeneration rate and pattern
(Schmidt et al. 1980, Donoso and Schmidt 1991, Drake
et al. 2005, Mujica et al. 2009). Although in some stands a
bimodal diameter distribution may have been also suitable
to describe the resulting stand structure (e.g. Navarro-
Cerrillo et al. 2013) from applying the seed tree silvicul-
tural system, this was not a systematic trend in the data.
Therefore, unimodal diameter distributions were finally
regarded as more suitable and consistent to describe the
general stand structure of A. araucana–Nothofagus forests
in the study area. In addition, other historical factors such
as recovery time since abandonment or logging are also
expected to influence the proportion of small trees in
a stand (Drake et al. 2005). In this study, A. araucana
structure suggests that logging may have impacted on
seedling, sapling and juvenile tree dynamics (Donoso and
Schmidt 1991, Drake et al. 2005, Mujica et al. 2009).

The regeneration of A. araucana is related to stand
characteristics. The results showed that regeneration,
including seedling and saplings, were more abundant in
those forests including abundant A. araucana and high
values of mean diameter, height and stand basal area of
A. araucana (negatively related to Nothofagus density and

Figure 3: First two axes of PCA ordination of Araucaria araucana
regeneration according to silvicultural variables. Variables
codes: Sqrt_N_AA = stand density of all A. araucana individuals,
Sqrt_N_AA30 = stand density of reproductive A. araucana individ-
uals, Height_AA = mean height of A. araucana, Height_DBH =
ratio of mean height to mean dbh of A. araucana, Sqrt_Npumilio =
stand density of N. pumilio, Sqrt_Nothofagus = stand density of all
Nothofagus spp.

where they survive in shade for up to 17 years (Cuevas
2002, González et al. 2006). Logging activities open the
canopy at the upper forest layer resulting in an episodic
regeneration and promoting seedling growth, given the
massive regeneration in A. araucana–Nothofagus stands
under management. Both seedling and adult stand
structures support this hypothesis (Martínez-Pastur et
al. 1999, Cuevas 2002). In the study area, N. pumilio
dominated the area right after logging, and now is being
gradually substituted by A. araucana. Similar characteris-
tics have been found in other mixed Araucaria–Nothofagus
forests (Veblen et al. 1995, Ogden and Stewart 1995,
Enright and Hill 1995, Enright et al. 1999, Drake et al. 2005,
Souza 2007, Mujica et al. 2009), supporting the hypoth-
esis that silvicultural treatments are followed by success-
eous cohorts of early successional Nothofagus species that
dominate the forest understory and suppress temporarily
the recruitment of A. araucana seedlings. As the stand develops
A. araucana becomes more competitive and Nothofagus
species are gradually substituted by A. araucana.

Old-growth mixed Araucaria–Nothofagus forests are
characterised by the dominance of A. araucana (Veblen
1982, Veblen et al. 1995, González et al. 2006), suggesting
that stands in which large Araucaria individuals were more
abundant (San Antonio and Pino Gaúcho) were the better
conserved ones. This confirms the mature status of these
forests despite the heavy selective logging of A. araucana
during the last decades of the past century.

Recruitment of Araucaria araucana
Regeneration of A. araucana–Nothofagus spp. forests
still requires research as well as the implication of histor-
ical silvicultural practices. Nevertheless, there is much
debate over the level of perturbation necessary to maintain
basal area) (Figure 3). In this situation, determining the suitable remaining and removed stand basal area to ensure the adequate regeneration of _A. araucana_ is a complex task. Although our analysis demonstrated that logging plays a role in structuring _A. araucana_ regeneration, over 36% of variation in relation to regeneration remained unexplained. This suggests that regeneration is possibly driven as well by additional factors other than the parameters measured in the analysed stands (e.g. seed production and dispersal or unmeasured environmental variables).

**Conclusion**

The empirical evidence so far from central Chile suggests that _A. araucana_ regenerates continuously after harvesting, which is clear from the reverse-J shape of the diameter class distributions found in many of the study stands. Logging activities open the canopy at the upper forest layers resulting in an episodic regeneration and promoting seedling growth, given the massive regeneration in _A. araucana–Nothofagus_ forests. This supports the hypothesis that silvicultural treatments are followed by successive cohorts of early successional _Nothofagus_ species that dominate the forest temporarily, which are gradually substituted by _A. araucana_. Forest stands in the study area represent a successional gradient from mature stands dominated by _A. araucana_, to more mixed forests typical of earlier successional stages where _A. araucana_ is less abundant and _N. pumilio_ or mixed _Nothofagus_ species dominate.

**Acknowledgements** — This project was funded through the collaboration between the National Forestry Corporation of Chile (CONAF) and University of Córdoba (Spain). We thank Fernando Drake and Daniel Griffith for their contribution to the initial research proposal, and Jaime Vielma of CONAF for logistic support. Additional thanks are due to project DIVERBOS-CGL2011-30285-C02-02.

**References**

Bailey R, DELL T. 1973. Quantifying diameter distributions with the Weibull function. _Forest Science_ 19: 97–104.

Burns BR. 1993. Fire-induced dynamics of _Araucaria araucana–Nothofagus antarctica_ forest in the southern Andes. _Journal of Biogeography_ 20: 669–685.

Burns BR. 1991 The regeneration dynamics of _Araucaria araucana_. PhD thesis, University of Colorado, Boulder, USA.

Chojnacky DC. 1998. Double sampling for stratification: a forest inventory application in the Interior West. Research Paper RMRS-RP-7. Ogden, Utah: US Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Cortés M. 2003. Dinámica y conservación de _Araucaria araucana_ (Mol.) Koch. En la Coordinilla de la Costa de Chile. PhD thesis, Universidad Austral de Chile, Valdivia, Chile.

Cuevas JG. 2002. Episodic regeneration at the _Nothofagus pumilio_ alpine timberline in Tierra del Fuego, Chile. _Journal of Ecology_ 90: 52–60.

Donoso C. 1993. _Bosques templados de Chile y Argentina: variación, estructura y dinámica_. Santiago: Corporación Nacional Forestal, Editorial Universitaria.

Donoso C, Lara A (eds). 1998. _Silvicultura de los bosques nativos de Chile_. Santiago: Editorial Universitaria.

Donoso S, Schmidt H. 1991. Crecimiento de regeneración de _Araucaria araucana_ (Mol.) Koch con diversas intervenciones silvícolas. _Ciencias Forestales_ 7: 13–19.

Drake F, Herrera MA, Acuña E. 2005. Propuesta de manejo sustentable de _Araucaria araucana_ (Mol. C. Koch). _Bosque_ 26: 23–32.

Drake F, Molina JR, Herrera MÁ. 2012. An ecophysiographic approach for _Araucaria araucana_ regeneration management. _Ciencia e Investigación Agraria_ 39: 159–176.

Enright NJ, Hill RS. 1995. The southern conifers – a synthesis. In: Enright N, Hill RS (eds), _Ecology of the southern conifers_. Washington, DC: Smithsonian Institution Press. pp 271–287.

Enright NJ, Ogden J, Rigg LS. 1999. Dynamics of forests with _Araucaria araucana_ in the western Pacific. _Journal of Vegetation Science_ 10: 793–804.

González A. 2001. Análisis de la densidad y crecimiento de la regeneración en un bosque de _Araucaria araucana_ bajo distintas intensidades de cortas de selección. PhD thesis, Universidad de Chile, Chile.

González M, Cortés M, Izquierdo F, Gallo L, Echevarria C, Bekksey S, Montaldo P. 2006 _Araucaria araucana_ (Mol.) K.Koch. In: Donoso C (ed.), _Las especies arbóreas de los bosques templados de Chile y Argentina_. Autoecología. Santiago: Marisa Cueno Editores. pp 36–53.

Hayek E, Di Castri F. 1975. _Biolimnogratia de Chile_. Santiago: Universidad Católica de Chile.

Kangas A, Maltamo M. 2000. Performance of percentile based diameter distribution prediction and Weibull method in independent data sets. _Silva Fennica_ 34: 381–398.

Lara A, Solari M, Rutherford P, Thiers O, Trecaman R, Prieto R, Montory C. 1999. _Coberturas de la vegetation original de la ecorregión de los bosques valdivianos en Chile hacia 1950_. Informe Técnico. Proyecto FB 49-WWF. Valdivia: Universidad Austral de Chile.

Martínez-Pastur G, Peri PL, Fernández MC, Staffieri G. 1999. Desarrollo de la regeneración a lo largo del ciclo del manejo forestal de un bosque de _Nothofagus pumilio_: 1. Incidencia de la cobertura y el aprovechamiento o cosecha. _Bosque_ 20: 39–46.

Mujica R, Schmidt H, El Kateb H, Mosandl R. 2009. Evaluación de tratamientos silvícolas en bosques de _Araucaria araucana_ en el sur de Chile. Paper presented at the XIII Congreso Forestal Mundial, 18–23 October 2009. Buenos Aires, Argentina.

Navarro-Cerrillo RM, Manzanedo RD, Bohorque J, Sánchez R, Sánchez J, de Miguel S, Solano D, Qarro M, Griffith D, Palacios G. 2013. Structure and spatio-temporal dynamics of cedar forests along a management gradient in the Middle Atlas, Morocco. _Forest Ecology and Management_ 289: 341–353.

Ogden J, Stewart GH. 1995. Community dynamics of the New Zealand conifers. In: Enright N, Hill RS (eds), _Ecology of the southern conifers_. Washington, DC: Smithsonian Institution Press. pp 81–119.

Peralta M. 1975. _Tipificación de los Suelos en la formación forestal Araucaria-Lenga en el Parque Nacional Conguillío_. Santiago: Universidad de Chile.

Rebertus A, Veblen T. 1993. Structure and tree-fall gap dynamic of old growth _Nothofagus_ forests in Tierra del Fuego, Argentina. _Journal of Vegetation Science_ 4: 641–654.

Schmidt H, Urzúa A. 1982. _Transformación y manejo de los bosques de Lenga en Magallanes_. _Ciencia Agrícolas_ 11. Santiago: Facultad de Ciencias Agrarias, Veterinarias y Forestales, Universidad de Chile.

Schmidt H, Toral M, Burgos P. 1980. Aspectos de estructura y de regeneración natural para el manejo silvícola de los bosques de _Araucaria araucana_ en Tierra del Fuego, Argentina. _Transformación y manejo de los bosques de Lenga en Magallanes_. _Ciencia Agrícolas_ 11. Santiago: Facultad de Ciencias Agrarias, Veterinarias y Forestales, Universidad de Chile.
Sokal RR, Rohlf FJ. 1995. *Biometry: the principles and practice of statistics in biological research* (3rd edn). New York: Freeman and Co.
Souza A. 2007. Ecological interpretation of multiple stand size structures in trees: the case of *Araucaria angustifolia* in South America. *Austral Ecology* 32: 524–533.
Veblen T. 1982. Regeneration patterns in *Araucaria araucana* forests in Chile. *Journal of Biogeography* 9: 11–28.
Veblen T. 1998. Influences of large-scale climatic variability on episodic mortality in northern Patagonia. *Ecology* 79: 2624–2640.
Veblen TT, Burns BR, Kitzberger T, Lara A, Villalba R. 1995. The ecology of the conifers in southern South America. In: Enright N, Hill RS (eds), *Ecology of the southern conifers*. Washington, DC: Smithsonian Institution Press. pp 120–155.
Wardle JA. 1984. *The New Zealand beeches: ecology, utilisation, and management*. Wellington: New Zealand Forest Service.
Wright SJ, Muller-Landau HC, Condit R, Hubbell SP. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84: 3174–3185.
Zar JH. 1999. *Biostatistical analysis* (4th edn). Upper Saddle River: Prentice-Hall.