

Stand dynamics, spatial pattern and site quality in *Austrocedrus chilensis* forests in Patagonia, Argentina

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Abstract

Aim of study: The objective of this study was to analyze the stand structure and spatial pattern of two *A. chilensis* stands with contrasting soil conditions and different site qualities in order to explore if these differences lead to patterns similar to the ones observed under different precipitation conditions.

Area of study: The study was carried out in two stands located near the city of El Bolsón (41° 56' S - 71° 33' W), Rio Negro, Argentina.

Material and methods: We evaluated age difference between canopy strata (upper and lower) in two stands with different site qualities by means of a Mann-Whitney test. Dead individuals by diameter class were compared by means of a chi square test. Spatial distribution pattern was analyzed using the pair-correlation function and the mark-correlation function.

Main results: Both sites exhibited a random spatial distribution of *A. chilensis* but different processes seem to underlie the patterns. In the low-quality site facilitation and continuous establishment led to a transient clumped spatial pattern. Mortality mediated by competition occurred mainly on small trees resulting in the current random pattern. On the other hand, spatial pattern in the high-quality site does not reflect a facilitation mediated recruitment. The upper strata established synchronously and subsequent regeneration was episodic.

Research highlights: The results show that the differences in site quality may lead to different establishment spatial patterns, showing the importance of facilitation processes in sites with drier soil conditions and lower quality, although results may be site specific, due to the lack of replications.

Key words: spatial analysis; regeneration; mortality; competition; facilitation.

Introduction

The structure of a stand is the result of the interaction between different factors such as species composition, site quality and disturbance (Oliver and Larson, 1996). These factors have different effects on the establishment, survival and growth of trees in the first stages influencing the subsequent development of the stands (Harper *et al.*, 2006). The spatial pattern of trees determines competitive relationships that are stronger between neighbour trees leading to a decrease in growth of plants located close to each other and in cases where competition is strong enough, an increase in mortality. Species that regenerate in association with

nurse plants, or parent trees, usually present a clumped distribution (Hou *et al.*, 2004) and positive spatial associations. On the other hand, density-dependent mortality may lead to regular spatial patterns (Peet and Christensen, 1987). Depending on the tolerance of species to the shortage of resources, individuals in competitive disadvantage might die or grow slowly. In short, facilitation and competition influence spatial patterns that reflect the interaction between two species or between different cohorts of the same species (Rejmánek and Lepš, 1996).

However, spatial pattern of trees can also be affected by factors other than biotic interactions during stand development. Edaphic factors such as soil moisture

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Abbreviations used: LQ: low-quality site; HQ: high-quality site.

can affect the spatial distribution of plants (Harper *et al.*, 2006) as well as recruitment processes because regeneration patterns might vary depending on site characteristics and associated species (Veblen *et al.*, 1995). The same species, growing under different site conditions might present different spatial patterns and age distributions. Stands developed under the same temperature and precipitation conditions, but on soils with differences in fertility and water retention capacity present different dominant heights interpreted as differences in site quality (Goya *et al.*, 1998). Few studies have compared the effect of site conditions on the spatial pattern (Getzin *et al.*, 2008).

Point pattern analysis of fully mapped plant locations using tree-trunk position has been demonstrated to be a useful approach to explore spatial plant dynamics (Getzin and Wiegand, 2007). The random mortality hypothesis can be used to detect competition, if individuals in a community are equal in death probability, the second-order characteristics of the spatial patterns would remain unchanged (Getzin *et al.*, 2006). Opposite to this hypothesis, elevated death rates among neighbouring trees are expected due to competition.

Austrocedrus chilensis (D. Don) Pic.Serm. & Bizzarri (Cupressaceae) forms dense monospecific or mixed forests in north Patagonia after fires. Most stands originated after fires between 1890 and 1920 (Veblen *et al.*, 2004) in periods of great droughts. In relatively mesic sites, *A. chilensis* seedlings establish rapidly after fires forming dense forests from surviving trees (Veblen and Lorenz, 1987). Seedlings establish near shrubs or parent trees (Arturi *et al.*, 2001) because their partial shade avoids damage due to high temperatures and water stress (Urretavizcaya *et al.*, 2006). Kitzberger *et al.* (2000) suggested that the trend of spatial association between seedlings and other plants might be stronger in moderately dry years while in humid years regeneration does not require nurse plants and in very dry years no regeneration is observed. In humid periods, competitive processes between *A. chilensis* seedlings and shrubs might predominate over facilitation processes (Kitzberger *et al.*, 2000).

A. chilensis forests develop on soils with contrasting textures which determine different water retention capacities and different site qualities. According to the relationship between water availability and incidence of the facilitation proposed by Kitzberger *et al.* (2000), in poorer quality sites and on drier soils, recruitment of *A. chilensis* is expected to be more dependent on nurse plants than on sites of better quality.

In addition, in low quality sites competition processes are expected to be less important and therefore continuous recruitment is expected. In better quality sites, where competition with other species is more important, recruitment is expected to be characterized by small scale gaps and differentiated cohorts (Veblen *et al.*, 2004). Thus, upper and lower tree strata in the high quality site should exhibit greater age differentiation than in the low quality site.

The objective of this study was to analyze the stand structure and spatial pattern of two *A. chilensis* stands with contrasting soil conditions and different site qualities in order to explore if these differences lead to patterns similar to the ones observed under different precipitation conditions. According to previous studies we specifically hypothesize that (1) facilitation processes predominate in low quality sites promoting a more clumped *A. chilensis* spatial pattern than in high quality sites, both in the upper (dominant and codominant trees) and the lower (intermediate and suppressed) strata. (2) Moreover, as a consequence of facilitation, a stronger positive spatial association between the upper and the lower strata is expected in the lower quality site than in the higher quality site. (3) Competition processes also force diameters of nearby trees on high quality sites to be smaller than those expected under a random distribution of tree sizes. This association is expected to be weak or null in the low quality site due to lower competitive interactions. (4) Similarly, dead trees tend to predominate among small and close trees. (5) Another expected consequence of competition induced mortality is a higher frequency of small dead trees in the high quality site. (6) The age class structure in the high quality site is expected to be bimodal due to relatively rapid regeneration followed by a later start of gap phase replacement. In contrast, the age class structure between the upper and lower strata for the low quality site is expected to be more similar due to the relatively continuous recruitment period and continual vertical differentiation because of weaker competition.

Material and methods

Study area

The study was carried out in two stands located in the reserves “Loma del Medio” (high-quality site - HQ) and “El Guadal” (low-quality site - LQ), both near the

city of El Bolsón (41° 56' S-71° 33' W), Rio Negro province, Argentina, with altitudes ranging between 300 and 600 m a.s.l. *A. chilensis* is the dominant species in both stands with more than 70% of basal area (Table 1). Species richness is higher in HQ [*A. chilensis*, *Nothofagus dombeyi* (Mirb.) Blume (coihue), *Nothofagus antarctica* (Forst.) Oerst. (ñire)] than in LQ [*A. chilensis* and *Lomatia hirsuta* (Lam.) Diels]. Density and basal area are higher in LQ while mean annual increment is higher in HQ (Table 1). Sites were selected to allow a contrast of moisture regimes due to soil conditions under the same climatic influences.

The area has a mean annual temperature of 9.38°C and total annual precipitation ranging from 800 to 1,000 mm, concentrated in autumn and winter (April-September) (Cordon *et al.*, 1993). In the growing season (October-March) monthly potential evapotranspiration ranges from 55 to 100 mm month⁻¹, precipitation ranges from 20 to 50 mm month⁻¹ and mean temperature ranges from 10 to 15°C (SMN, 1981). In the dormant season (April-September) monthly potential evapotranspiration ranges from 10 to 35 mm month⁻¹, precipitation ranges from 30 to 190 mm month⁻¹ and mean temperature ranges from 3 to 8.5°C (SMN, 1981), indicating a surplus of precipitation in the dormant season and an important deficit in the growing season.

Soils are derived from holocenic piroclastic deposits classified as Udivitrand (Buamscha *et al.*, 1998). In HQ soils are well drained, with good effective depth and with presence of allophane or imogolite which improve their hydric conditions. These soils reach the end of the dry season with good water availability. In LQ, on the other hand, soils are coarsely textured with high water infiltration rates. These soils enter the

beginning of the dry season with low water contents (Gobbi and Schlichter, 1998, Goya *et al.*, 1998).

This region was strongly affected by fires at the beginning of the twentieth century. These fires were started to open land for grazing and agriculture, so most of the forests of this region were affected by this type of disturbance (Willis, 1914). Since this date fires decreased and allowed current stands to establish (Veblen and Lorenz, 1987).

In each study site stands without signs of recent intervention were selected. In each stand a permanent plot of 2,500 m² (50 × 50 m) was established in the summer of 1994. In each plot all individuals > 5 cm dbh (diameter at breast height or 1.3 m) were marked, measured and stem mapped. For each individual: the species, dbh and crown-class position (dominant or upper strata and suppressed or lower strata) were determined. About 40% of the trees in each plot were randomly selected and cored at 35 cm from the base in order to determine their ages. Samples were conditioned according to Stokes and Smiley (1968), dated and growth ring widths were measured with stereoscopic microscope using equipment to measure increments (TA-System Ring Measurement). Dating and sample measures were verified with computer program COFECHA (Holmes, 1983). Samples were analyzed according to canopy position.

All individuals < 5 cm of dbh were censused in height (m) categories: I = 0.5 – 1.0 m; II = 1.0 – 2.0 m and III > 2.0 m and < 5 cm dbh in 36 circular plots of 360, 540 and 900 m² for the categories I, II and III, respectively. The plots were located on an equally spaced square grid. In addition 100 randomly selected individuals < 5 cm dbh were harvested, height and

Table 1. Forest structure of the low and high quality sites

Structural variables	Low quality site	High quality site
Total Density (trees · ha ⁻¹)	1,428	620
Total Basal Area (m ² · ha ⁻¹)	40.8	23.6
<i>Austrocedrus chilensis</i> relative basal area (%)	95.1	89.8
<i>Nothofagus dombeyi</i> relative basal area (%)	0	3
<i>Nothofagus antarctica</i> relative basal area (%)	0	7.2
<i>Lomatia hirsuta</i> relative basal area (%)	4.9	0
<i>Austrocedrus chilensis</i> Increment (m ³ · ha ⁻¹ · yr)	2	5.1
Mean tree age (years)	67.9	70
Median tree age (years)	67.5	75
Minimum-Maximum tree age	40-90	30-105
Mean tree DBH (cm)	16.3	18.6
Median tree DBH (cm)	9.7	8.6
Minimum-Maximum tree DBH (cm)	5-63.9	5-115

diameter at base were measured and age was determined.

Statistical analysis

Significant differences in several attributes between these two stands were tested. The major driving mechanism is intended to be their site quality differences; however, many other factors may be confounded with site quality due to the lack of replication. So, differences may be due to site quality, but secondarily to other contributing factors.

Testing Hypothesis 1 and 2

Spatial distribution pattern was analyzed using the pair-correlation function $g(r)$, which is a distance-dependent correlation function for completely mapped point patterns (Wiegand and Moloney, 2004). Based on inter-tree distances, the g function describes clumping and regularity of one class of trees (univariate) at a given radius r , using a standardized density. Under complete spatial randomness (CSR), $g(r) = 1$, $g(r) > 1$ indicates aggregation, while $g(r) < 1$ indicates regularity (Getzin *et al.*, 2011). The univariate version can be transformed into a bivariate version in order to analyze the spatial relationship between two different classes of trees; in this case the two patterns were defined according to the canopy position (upper and lower strata). The null model used was complete spatial randomness (CSR).

Testing Hypothesis 3

In order to analyze if there is a density-dependent size reduction, dbh was used as a “mark” in a mark-correlation function (MCF). The MCF is similar to the pair-correlation function $g(r)$ but investigates the size-correlation and not only the distance-correlation at radius r (Getzin *et al.*, 2011). This analysis allows us to detect intra-specific competition processes between individuals of *A. chilensis*. The bivariate version of the MCF was performed using species as patterns in order to study interspecific relationship between *A. chilensis* (pattern 1) and other species (pattern 2). Under competition we would expect that plants which are located close to each other should be on average smaller than the population average (Getzin *et al.*, 2011).

Testing Hypothesis 4

To investigate if mortality is independent of the neighbour trees the random mortality hypothesis was tested. This hypothesis assumes dead trees are independently and randomly distributed relative to live trees. Under strong competition effects we would expect that trees with fewer neighbours would have greater chances of survival (Getzin *et al.*, 2006). The random mortality hypothesis was tested using the univariate random labelling as null model.

Significance departure from the null models was tested using the 5th lowest and 5th highest of 199 Monte Carlo simulations to generate 95% simulation envelopes. We used a moving window with a radius of $R = 10$ m. Hence deviation from the null model can only be interpreted up to 10 meters. For these analyses the software Programita (Wiegand and Moloney, 2004) was used.

Testing Hypothesis 5

Relative frequency of dead individuals by diameter class, defined as lower class (> 5 cm dbh, < 20 cm dbh) and upper class (> 20 cm dbh) were compared by means of a chi-square test. For both sites most trees smaller than 20 cm dbh were younger than 70 yr and belonged to the lower strata which was expected to be more strongly affected by competition.

Testing Hypothesis 6

Median age by strata in each stand was compared by means of a Mann-Whitney test. Upper (ul) and lower (ll) 95% confidence limits of the median age were calculated taking 1000 random samples of equal size as the original sample.

Results

Spatial distribution pattern

Point pattern analysis in both stands (Fig. 1) using the pair-correlation function $g(r)$ (Fig. 2) showed differences in strata. Upper strata showed a random pattern in both stands while lower strata aggregated up to 6 m in LQ and up to 9.5 m in HQ. The null hypothesis of

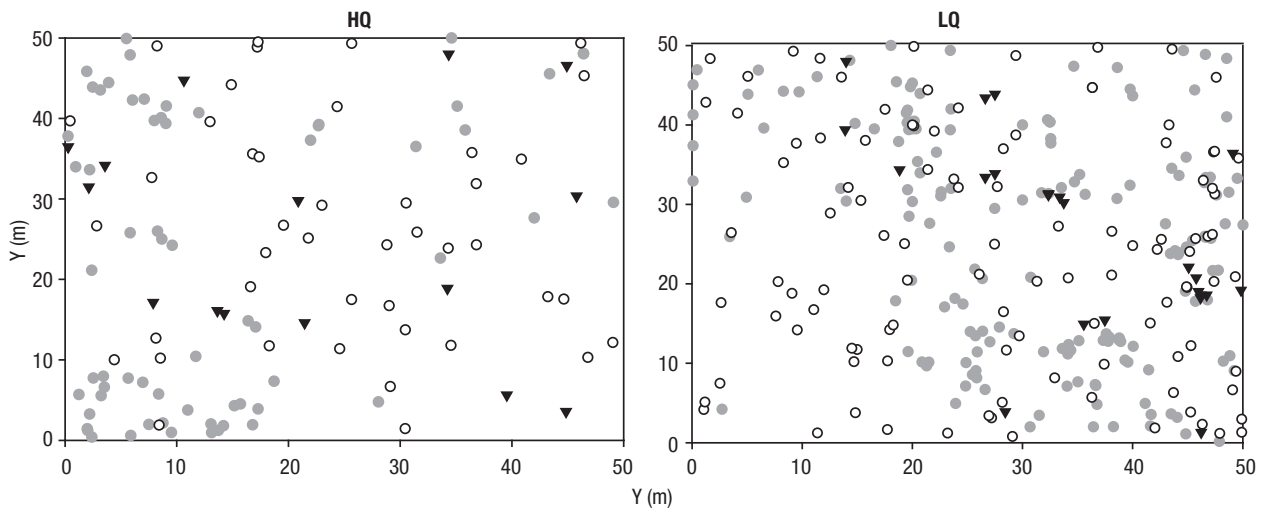


Figure 1. Map of the two study plots showing the spatial distribution of trees differentiated by strata. Upper strata white dots, Lower strata grey dots and Dead trees black triangles.

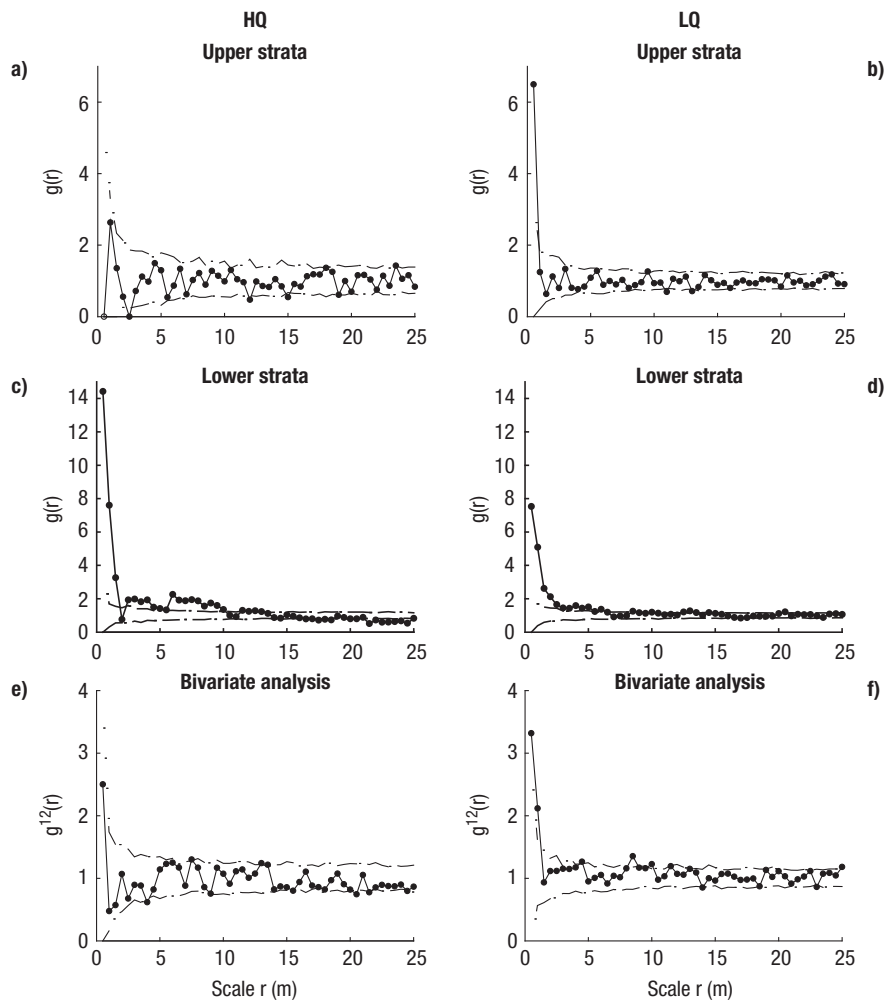


Figure 2. Univariate spatial pattern analyses of the upper strata (a, b), the lower strata (c, d) and bivariate analysis of the lower strata around the upper strata (e, f) in HQ (high-quality) and LQ (low-quality) plots. ($g(r)$ = black dotted line; 95% upper and lower confidence limits = grey dashed lines based on the null hypothesis of complete spatial randomness).

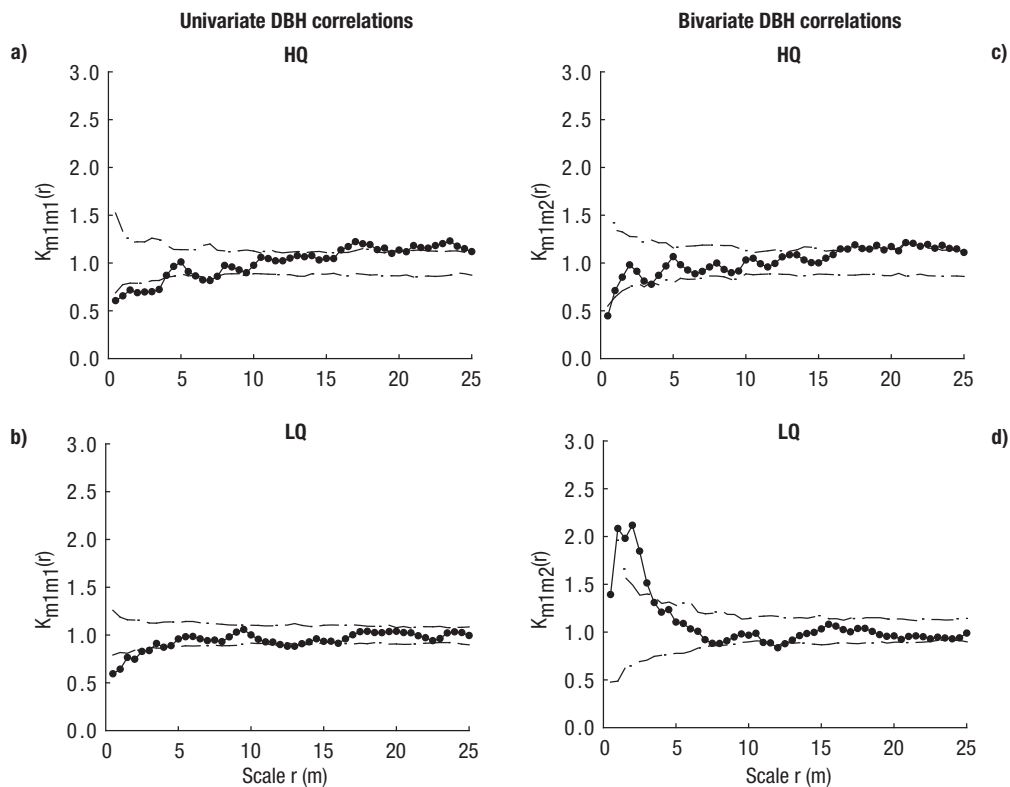


Figure 3. Univariate mark-correlation function with dbh (diameter at breast height) (a, b) and bivariate mark-correlation function with dbh between *A. chilensis* and other arboreal species (c, d) in HQ (high-quality) and LQ (low-quality) plots. 95% upper and lower confidence limits = grey dashed lines based on the null hypothesis of complete spatial randomness.

the bivariate distribution of spatial independence of the lower strata and the upper strata could not be rejected in both sites (Fig. 2).

The mark correlation function using dbh of *A. chilensis* as a mark showed that in HQ intra-specific competition was significant up to 3 m and up to 4 m in LQ. This means that plants located close to each other were on average smaller than the population average. The bivariate analysis showed no relationship between *A. chilensis* and other species in HQ. However, in LQ a strong association of *A. chilensis* with other species was detected up to 3.5 m (Fig. 3).

In LQ the random mortality hypothesis was rejected due to clustering at spatial scales up to 1.5 m while in HQ it could not be rejected (Fig. 4).

Stand structure

The relative frequency distribution of dead individuals was different between sites (Pearson chi-square 17.50, $p < 0.0001$, degrees of freedom: 1). In LQ the greatest frequency of dead individuals was observed

in the lower diameter class (less than 20 cm dbh), while in HQ the frequency of dead trees was similar in the different diameter classes.

Median age of upper and lower strata was 77.5 (ll: 75, ul: 85) and 45 (ll: 45, ul: 55) years respectively in HQ and 75 (ll: 70, ul: 80) and 60 (ll: 55, ul: 65) years respectively in LQ. Age frequency distribution indicated a bimodal irregular structure in HQ ($U = 61.5$, $p < 0.0001$, degrees of freedom: 57) while in LQ the distribution corresponded with a typical inverted j of an irregular stand ($U = 289$, $p < 0.0003$, degrees of freedom: 80) (Fig. 5).

In HQ 70% of individuals < 5 cm dbh belonged to the age classes of less than 40 years while in LQ 72% of the individuals belonged to the age class between 40 and 50 years (Fig. 5).

Discussion

Our results suggest that site quality differences partially resemble the plant patterns expected under contrasting rainfall regimes. However, a warning must

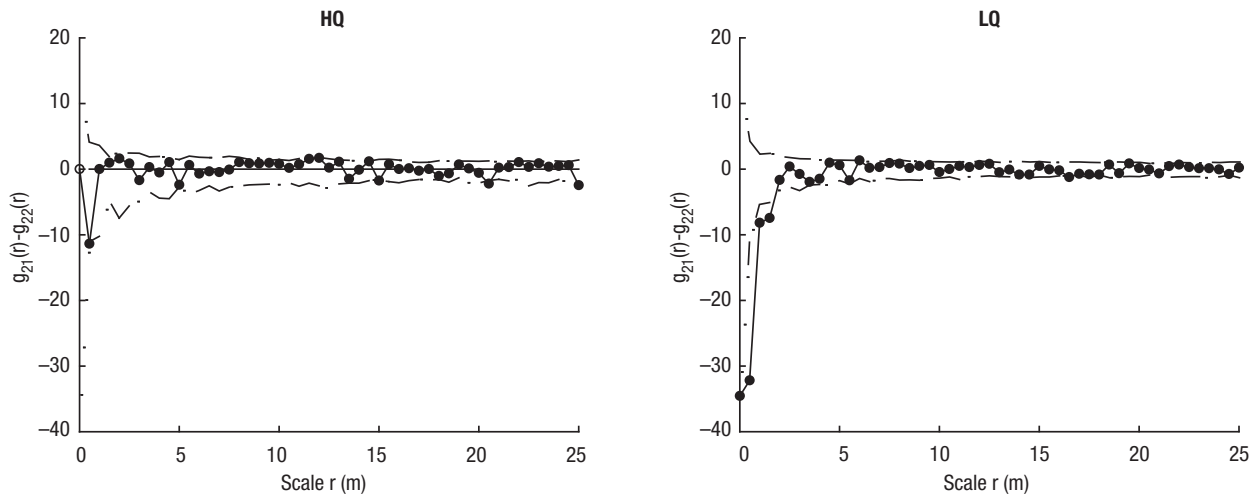


Figure 4. Bivariate random labelling [$g_{21}(r)-g_{22}(r)$] to assess if mortality was a random process in HQ (high-quality) and LQ (low-quality) plots. 95% upper and lower confidence limits = grey dashed lines based on the null hypothesis of random mortality.

be made about the lack of replications so results may be site specific rather than related with site differences. The mark correlation function using dbh as a mark showed intraspecific competition effects in both stands. However when the relationship with other species was analyzed using the bivariate function no association between *A. chilensis* and other species was found in the high-quality site but a positive association up to 3.5 m was detected in the low-quality site. This association could be explained by facilitation processes. Previous studies showed that facilitation processes in this species increased in importance as precipitation decreased along a geographic gradient (Kitzberger *et al.*, 2000).

The pair correlation function showed no departure from complete spatial randomness of the upper strata in both stands; however the lower strata were aggregated up to 9.5 m in the high-quality site and only up to 6 m in the low-quality site. These results differ from the expected patterns of more aggregation in the low-quality site as a consequence of facilitation mediated recruitment. Mortality due to competition may have led to a less aggregated pattern than the expected in the low-quality site. This agrees with the high frequency of dead trees in the lower diameter class which is compatible with a mortality pattern associated with intraspecific competition. On the other hand, in the high-quality site this concentration of dead trees in the lower diameter class

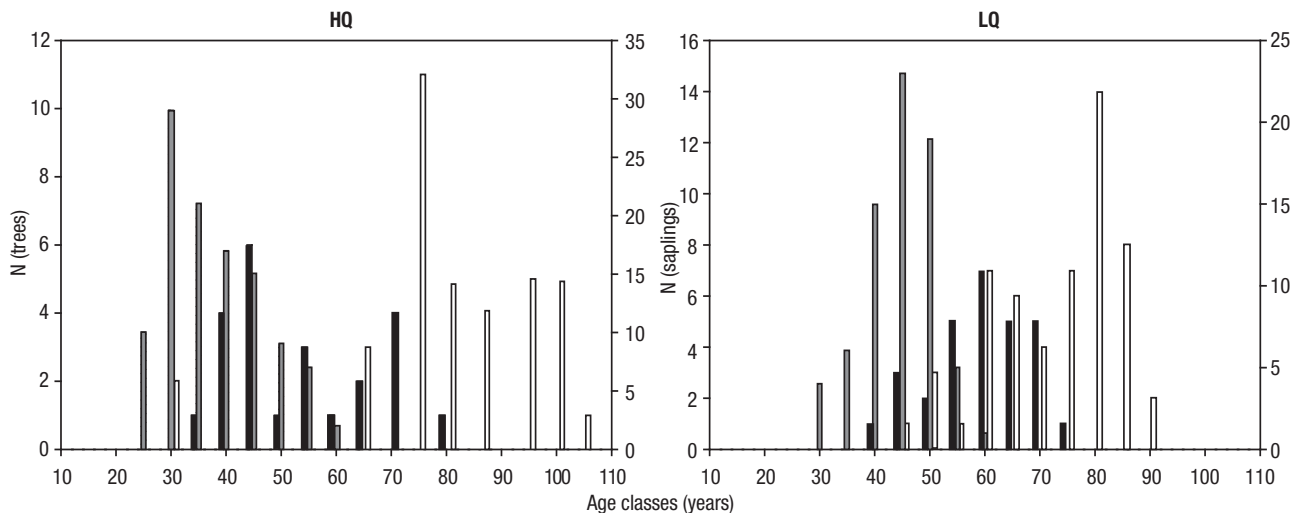


Figure 5. Age class distribution of the upper (white bars) and lower (black bars) strata and saplings (striped bars) (dbh < 5 cm and height > 0.5 m) in HQ (high-quality) and LQ (low-quality) plots

was not detected indicating a weaker relationship between mortality and intraspecific competition than in the low-quality site. This is also shown by the spatial analysis of the random mortality hypothesis which could not be rejected in the high-quality site but indicated non-random mortality of trees up to 1.5 m in the low-quality site.

The analysis of the age structure showed that in the high-quality site the upper strata established in an initial stage after disturbance with discontinuous subsequent recruitment. This process yielded a low density *A. chilensis* stand in which discontinuous regeneration is still observed. In the low-quality site upper and lower strata did not exhibit sharply differentiated age distributions as a consequence of a continuous regeneration. The high density of *A. chilensis* has prevented much of any regeneration over the 40 years prior to sampling. In the high-quality site younger individuals between 0.5 and 1.5 m height established 20 years ago. However, Arturi *et al.* (2001) found that it takes up to 25 years for individuals to reach 0.5 m height suggesting that recruitment is still occurring.

In conclusion, both sites exhibit a random spatial distribution of *A. chilensis* but different processes seem to cause these patterns. In the low-quality site facilitation and continuous establishment led to a transient clumped spatial pattern. Mortality mediated by competition occurred mainly on small trees clustered around larger trees resulting in the current random pattern. On the other hand, stand structure in the high-quality does not reflect a facilitation mediated recruitment of *A. chilensis*. The upper strata established synchronously and subsequent regeneration was episodic, probably due to competition with non arboreal vegetation as found by Veblen *et al.* (1992) in mesic sites. Theories suggest that under more stressful conditions facilitation processes become more important and when conditions are more favourable competition processes predominate (Bertness and Callaway, 1994). Thus, the differences in forest structure between the studied sites resemble those found between stands developed under different moisture regimes. Dry sites are characterized by regeneration patterns mediated by facilitation while interspecific competition could be a more important factor affecting regeneration in mesic sites.

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