Ciencia e Investigación AGRARIA

Cien. Inv. Agr. 38(3):441-452. 2011
www.rcia.uc.cl

PLANT BREEDING, GENETICS AND GENETIC RESOURCES

RESEARCH PAPER

Heterogeneous genetic structure in a natural population of Raulí (*Nothofagus nervosa)*

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Abstract

B. Carrasco, L. Eaton, L. Letelier, C. Díaz, and R. García-Gonzáles. 2011. Heterogeneous genetic structure in a natural population of Raulí (*Nothofagus nervosa*). Cien. Inv. Agr. 38(3): 441-452. Heterozygote deficiencies in natural populations of outbreeding tree species are common and thought to be due mainly to biparental inbreeding. Inbreeding is believed to be caused by family structure within populations, a product of limited seed dispersal and probably limited pollen dispersal. Although both theory and simulation studies predict that structure should be apparent where trees are isolated by distance, most studies of structure in natural populations have detected only a weak spatial genetic structuring. In this contribution, we compare the use of spatial autocorrelation methodology and F statistics with the concept of relatedness to examine the spatial genetic structure in the natural population of a native southern beech and to explore the discrepancy between theory and observations. Autocorrelation detected structure in only a few of the nine enzyme loci tested in an estimated patch size of approximately 10 m. By successively eliminating the largest distances in the Gabriel map, the population was separated into groups or patches of neighbors, which were then tested for relatedness. Three groups of relatives were found interspersed with seven groups of unrelated individuals. The F statistics for these groups also showed weak genetic structure. We suggest that heterogeneity of family structure within natural populations may be one reason why more spatial genetic structure has not been detected.

Key words: Genetic structure, spatial structure, Raulí, spatial autocorrelation.

Introduction

Most temperate and tropical trees have reproductive systems that favor outcrossing (Seltman *et al*., 2009; Muona, 1990; Bawa *et al*., 1985). Surprisingly, many tree species with these characteristics show a deficiency of heterozygotes for allozyme loci in their natural populations (Brown, 1979). Hypotheses to explain this phenomenon, which make up half of Brown's (1979) "heterozygosity paradox," postulate a genetic structure within populations caused by a limited dispersion of pollen and/or seeds.

The limited movement of pollen restricts neighborhood size, while limited seed dispersal

Received June 29, 2010. Accepted January 15, 2011.
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produces a family or kinship structure (Wright, 1943; Malecót, 1948; Levin and Kerster, 1974). Especially if both processes operate, the continuous model of isolation by distance (Wright, 1943; Malecót, 1948) predicts that neighboring individuals should tend to be relatives and should be more similar genetically than a random pair from the population.

It is generally accepted that most plant species do not form panmictic populations (Levin and Kerster, 1974; Brown, 1979) even when their distribution is continuous. There has been considerable interest in methods to document and measure genetic structure within populations, concentrated in spatial autocorrelation analysis (Sokal and Oden, 1991; Hyewood, 1991; Epperson, 1993; Epperson, 2000; Epperson, 2003) but also including F statistics (Slatkin and Arter, 1991; Merzeau *et al.,* 1994; Hardy and Veckemans, 2002, Suarez *et al.,* 2008) and multiple regressions (Furnier *et al.,* 1987). Although there has been some controversy about the efficiency of spatial autocorrelation for detecting structure (Slatkin and Arter, 1991; Sokal and Oden, 1991; Bruno *et al.,* 2008), it has been indicated that both join-counts and Moran's I should accurately detect small-scale structure under an isolation-by-distance model (Sokal and Jacquez, 1978; Epperson and Li, 1996, 1997; Bruno *et al*., 2008).

Quite a few northern-hemisphere species of the Fagaceae have been examined for spatial structure. In most cases, although the studied populations present a deficiency of heterozygotes, only a weak spatial genetic structure has been detected. A number of explanations have been proposed for the lack of structure, including the effects of neutral and selected loci (Bacilieri *et al*., 1994; Gapare and Aitken, 2005), "low heterozygosity alleles" (Leonardi and Menozzi, 1996; Belletti *et al*., 2005), null alleles and allele frequencies (Bacilieri *et al*., 1994; Aldrich *et al.,* 2005), a small number of generations, stochastic effects (Bacilieri *et al*., 1994; Lopez-Aljorna *et al*., 2007), local differences in flowering times (Gregorius *et al*., 1986; Sampson *et al*., 1990; Hendry and Day, 2005; Sampson and Byrne, 2008) and seed dispersal (Berg and Hamrick, 1994; Kuss *et al.,* 2008; Sethi *et al.,* 2009).

Raulí (*Nothofagus nervosa*) show a considerable heterozygote deficit within its natural populations, more so than the majority of the species of Fagaceae (Carrasco, 1998; Marchelli and Gallo, 2000). Thus, we should expect spatial genetic structure to be particularly evident within the populations of this southern beech. In this contribution, we use spatial autocorrelation, F statistics and relatedness coefficients to examine the nature of the spatial genetic structure of a small population of *N. nervosa* with an inbreeding coefficient of almost 0.2. We will argue that the heterogeneity of family structure within populations may be an important reason why more spatial genetic structure is not detected in natural populations of plant species.

Materials and methods

Nothofagus nervosa grows in Chile on the lower slopes of the Andes from 36°S to 40°S and in the Coast Range from 38°S to 41°S at altitudes from 100 m to 1200 m (Donoso, 1995). We mapped the locations of all 110 adult individuals (dbh > 25 cm, height > 5 cm) of a population of *N. nervosa* located 4 km west of Recinto, in the Bio-Bio Region of Chile (71° 41'W, 36° 49'S, 750 m altitude). In contrast to its Northern Hemisphere counterpart *Fagus sylvatica* L., Raulí is never found in pure stands; this population was mixed with Roble [*N. obliqua* (Mirb.) Oerst.], *Geviuna avellana* Molina and *Sophora microphylla* Meyen (Pollman, 2003, 2005). The stand is second growth; we estimated that it was cut 30-40 years ago. The majority of the individuals originated from stump sprouts, but perhaps one third were less than 40 years of age.

We collected a terminal lateral branch including at least 6 leaves from each individual. The bases of the branches were wrapped in wet paper towels

and kept on ice in a cooler until returned to the laboratory, after which the branches were kept at 4°C with the bases in water until processed.

We ground 3-5 of the newest leaves that had been stripped of their main veins, along with scrapings of the cortex, in approximately 2 ml of an extraction buffer, pH 7.5, containing Trizma base 6.5 g, citric acid 1.5 g, cisteine 1.0 g, ascorbic acid 1.0 g, polyethylene glycol 5.0 g, 2-mercaptoethanol 2 drops, soluble Polyvinylpyrrolidone (PVP)13 g in 1 L of water. The resultant slurry was centrifuged at 5000 rpm for 4 min, and then the supernatant was poured into Eppendorf tubes in duplicate and stored at -80°C until used for electrophoresis.

The electrophoretic and staining procedures followed the methods of Conkle *et al.* (1982). We used their System D ("morpholine citrate") for malic dehydrogenase (MDH, EC 1.1.1.37), menadione reductase (MNR, EC 1.6.99.2) and shikimate dehydrogenase (SKDH, EC.1.1.1.25); their System A (Lithium Borate) for alanine amino peptidase (AAP, EC 3.4.11.1), alanine amino transferase (AAT, EC 2.6.1.1), acid phosphatase (ACP, EC 3.1.3.2) and phosphoglucoisomerase (PGI, EC 5.3.1.9); and histidine, pH 8.0, for leucine amino peptidase (LAP, EC 3.4.11.1), peroxidase (PER, EC 1.11.1.6) and fluorescent esterase (Fl-EST, EC 3.1.1.1). These chemical products were purchased from SIGMA.

The zymograms were given a Mendelian interpretation, and the loci were called "variable isozymes *loci*" instead of "putative *loci*." Adequate results were not obtained for 6 of the trees or three of the staining systems; these were eliminated from consideration, and the analyses were based upon 104 individuals and seven systems that provided nine variable loci.

Autocorrelation was performed using the methods and formulas of Sokal and Oden (1978). Nominal data were tested using join-counts based upon Gabriel maps. Because each locus proved to have one allele with a frequency higher than 0.6, we compared homozygotes for the common allele to other genotypes. We also tested the total number of unlike joins. We quantified the number of the most common alleles as 1, 0.5 or 0 depending upon whether 2, 1 or 0 copies of this allele were present in an individual respectively (Dewey and Heywood, 1988). For construction of the correlograms, the distances between all pairs of individuals were calculated, and these were divided into 20 size classes. Moran's I was calculated for each class.

Moran's I is calculated using standardized variables, $Z_i = X_i$-.X. If p is the frequency of the most common allele (A_1) at a locus, then under our quantification scheme, it is also the mean of X, and the values of Z_1 will be 1 – p for A_1A_1, ½ - p for A_1A_j, and –p for A_jA_j, where j represents any of the other alleles. In the present case, where P>0.6 for each locus, the homozygotes for the most common allele will have positive values, while the other genotypes will have negative values. We summed the values of Z_i over the loci for each individual, producing an index that will have positive values for the genotypes that are mostly homozygous for the most common alleles and negative values for the less common genotypes. We then calculated Moran's I for all the pairs of individuals with these values.

We calculated F statistics according to the methods of Weir and Cockerham (1984) and Hamilton's kinship coefficients according to equation 6 from the work of Queller and Goodnight (1989). The variances of the estimators were estimated by jack-knifing over the loci and over the groups. We prefer to call the kinship coefficients "Hamilton's *relatedness*," to avoid possible confusion with Malecot's coefficient of kinship and Wright's coefficient of relationship. The critical values for relatedness were estimated by randomly assigning the individuals to groups, and calculating r values for 10,000 replicates. Genetic diversity and spatial structure were determined using GeneAlex 6.0 (Peakall and Smouse, 2006) and

GS+TM5 (Gamma Design Software, Plainwell, MI, USA) (Chen *et al*., 2008) and SPAGeDi 1.3 (Hardy and Vekemans, 2002).

Results

The nine resolved loci all presented three or four alleles (Table 1). In each case, one allele had a frequency of at least 0.6. The values of F were positive and significant ($P \leq 0.05$) for all the loci except PER_4, for which we found no homozygotes for the uncommon alleles. The average of F over the loci was 0.197. Fast-running allele 1 of PER_2 is found in other populations of Raulí (Table 1).

Autocorrelation analysis

Nominal data. The physical distribution of the 104 analyzed individuals is shown in Figure 1. The numbers assigned to the individuals in the field run roughly from the bottom to the top of Figure 1. Because each locus had one high-frequency allele, the homozygotes for the most common allele were designated as A and compared with the other genotypes (B) using join-counts of the Gabriel map. A few individuals could not be scored for all loci, so we constructed the corresponding Gabriel map for each locus according to the individuals scored.

Five of the nine analyzed loci showed an excess of like join-counts, but only PGI had a standard normal greater than 2.0 (Table 2). The total number of unlike joins was fewer than expected for five loci but was significant only for PGI (Table 2). Thus, join-counts did not provide clear evidence for the spatial genetic structure, contrary to our original expectations.

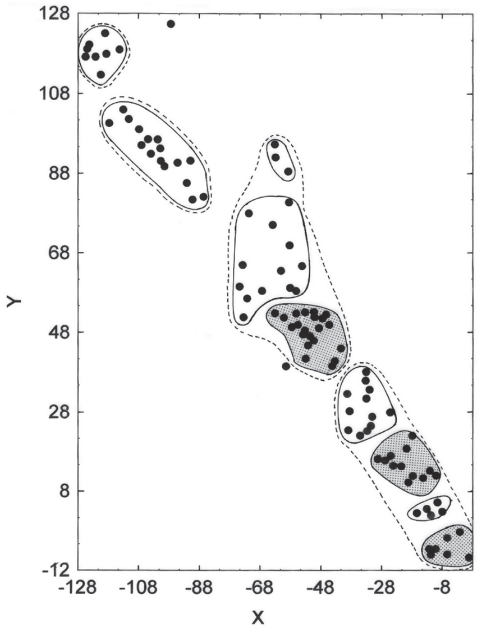

Figure 1. Representation of the locations of 104 individuals of *Nothofagus nervosa* in a population located 4 km west of Recinto, Bío-Bío Region, Chile. The scales are in meters (m). Dotted and solid circles are groups of neighboring trees determined by successively eliminating the largest distances in the Gabriel map. The shaded areas indicate trees with significant relatedness (Hamilton's r) values.

Table 1. Summary statistics for the 9 enzyme loci studied in 104 individuals of *Nothofagus nervosa* from near Recinto, Bío-Bío Region, Chile.

Enzyme	Number of subunits	Allele Frequencies				Fixation Index F
		1	2	3	4	
MNR	4	0.017	0.605	0.209	0.169	0.193
MDH	2	0.031	0.143	0.801	0.026	0.211
PER_2	1	0	0.828	0.162	0.010	0.228
PER_3	1	0.020	0.900	0.080	0	0.127
PER_4	1	0.026	0.896	0.073	0.005	0.021
LAP	1	0.011	0.747	0.242	0	0.139
AAT	1	0.007	0.966	0.027	0	0.382
SKDH	1	0.079	0.916	0.005	0	0.169
PGI	2	0.049	0.238	0.723	0	0.316

Table 2. Join-counts for phosphoglucoisomerase using the Gabriel map for 101 individuals of *Nothofagus nervosa* from near Recinto, Chile. SND means standard normal deviation.

Genotypes compared	Expected	Observed	SND
22 and 22	52.855	61	2.118
22 and others	76.548	66	-1.741
Others and others	26.597	29	0.696
Total unlike joins	88.324	74	-2.201

Interval data. The value of Moran's I, calculated using pairs of individuals connected in the Gabriel maps, was positive for the most common allele in five of the nine loci, but only two were significant, PGI and ACP (data not shown). The correlograms using all the pairwise distances divided into 20 groups showed significant (positive) values of I for the smallest distance class (Figure 2) only for MDH, PER_2 and PGI, and for the second smallest class for PER_3 and SKDH. This indicates that there is some tendency for neighboring trees to be more similar, but this shows only a weak genetic structure.

Moran's I for the Z sums was significant and positive for the first two distance classes (Figure 2). This overall measure confirms that there is some genetic structure in the population and indicates a tendency for the more common genotypes to be neighbors, and the same is true for the less common genotypes.

The range of values in the smallest distance class was 0.8-5.1 m and for the second class approximately 5-12 m (the ranges varied somewhat for the different loci because of the different numbers of individuals). Using Sokal's criterion of the distance at which a correlogram first intercepts the abscissa (Figure 2), we should conclude that for *N. nervosa,* more similar individuals tend to be found within approximately 10 m of one another.

Relatedness of groups within the population

To use F statistics or relatedness, one must first define the groups to be compared. Previous studies have used agglomerative methods, defining quadrants that are then combined. A divisive method to delimit the subgroups within the population was used by successively eliminating the largest distances in the Gabriel map of the 104 individuals. This procedure first separated the last individual sampled (at the top of Figure 1), which was not further considered. Next, the largest distances were eliminated, producing 2, 3 and up to 10 groups. The r values measure the relatedness of the individuals in a group relative to the whole population. Note that the r value of

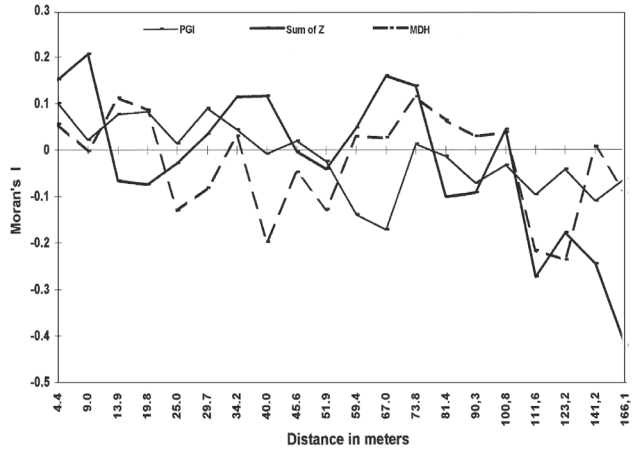

Figure 2. Correlograms for two enzymes and a summary of individuals in a population of *Nothofagus nervosa* located 4 km west of Recinto, Bío-Bío Region, Chile. The physical distances between all pairs of individuals were divided into 20 sizes classes, and Moran´s I was calculated for each class. PGI, phosphoglucoisomerase; MDH, malic dehydrogenase.

a group does not change when other groups are subdivided. We also calculated F statistics for 2, 4, 6 and 10 groups.

The first division separates a group of 24 more-isolated individuals, including the two circles at the upper left of Figure 1, which are relatively unrelated compared with the larger group of 79 (Figure 3). Further division of the smaller group also revealed unrelated individuals. Subdivision of the larger group (Figure 3) first produced two groups whose relatedness values, although positive, were not significant. Further subdivisions revealed three physical groups of significantly related individuals interspersed with groups of unrelated individuals (Figures 1 and 3).

To determine the significance of the observed relatedness values, we divided the individuals randomly into groups of the observed sizes and calculated r for each group. Table 3 presents the results of 10,000 replicates of this procedure, for six groups and 10 groups. Note that standard deviations are appropriated because the observed values are not means. Because there was an allele at high frequency for each locus, a number of genotypes presented few differences, thus critical values are large for the small groups. The 5% level for a group of 6 (0.342, Table 3) is greater than the expected value for a group of half sibs; for this reason, we did not continue to produce larger numbers of smaller groups.

The main increase in F_{ST} was produced between the values for two groups and for four groups (Table 4). Specifically, the group of 36 trees (the dotted circle at the bottom of Figure 1) has allele frequencies somewhat different than the rest of the population. The F_{ST} values were significant for four or more groups (Table 4). We used jack-knife values over the loci because jack-knifing over the groups produced a larger variance. The F_{IS} values for the groups slowly decreased as the number of groups increased; however, the F_{IS} for the 10 groups is only 9% less than for the entire population (Table 4). The F statistics would allow us to conclude that there is some genetic structure in the population but only discovers the group of 36 as different. Note that this group includes two groups of related individuals and two groups of unrelated individuals (Figures 1 and 3).

Discussion

What is known of the reproductive biology of *Nothofagus nervosa* led us to expect that within the population, genetic structure should be detected. Although Raulí is monoecious, anemochorous and anemophilous, most seeds fall near the mother tree,

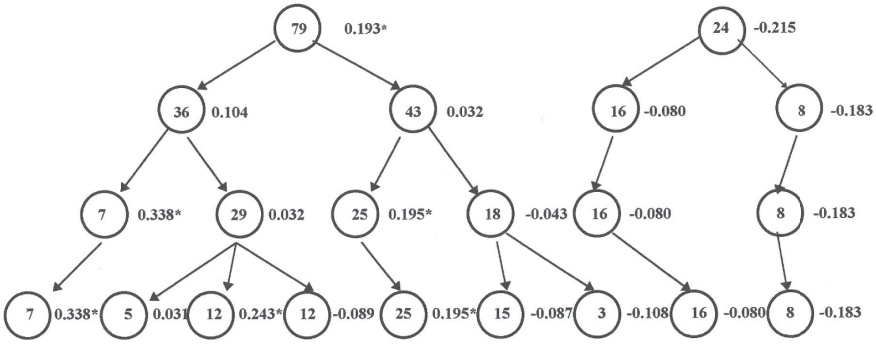

Figure 3. Schematic representation of neighboring groups of individuals by successive elimination of the largest distances in the Gabriel map in a *Nothofagus nervosa* population. The numbers inside the circles indicate the number of individuals in a group. The numbers to the right of the circles are the values of Hamilton's (relatedness) for each group, relative to the other groups on the same horizontal line, for 2, 4, 6, and 9 groups. The asterisks indicate relatedness values significant at the 0.05 level using a randomization test.

Table 3. Relatedness values of six and 10 groups of Raulí trees from near Recinto, Chile compared with values obtained by 10,000 replicates of random assignment of individuals to groups of the observed sizes. The groups were determined by successive elimination of the largest distances in the Gabriel map of these individuals.

6 Groups						10 Groups					
Group			Simulation			Group			Simulation		
N°	Size	Observed r	mean	σ	5%	N°	Size	Observed r	mean	σ	5%
1	7	0.338*	0.0162	0.1780	0.314	1	7	0.338*	0.0095	0.1782	0.313
2	29	0.032	0.0048	0.0936	0.158	2	5	0.031	0.0167	0.2182	0.387
3	25	0.195*	0.0029	0.0998	0.164	3	12	0.243*	0.0102	0.1339	0.238
4	18	-0.043	0.0017	0.1154	0.194	4	12	-0.089	0.1132	0.1326	0.231
5	16	-0.080	-0.0013	0.1206	0.199	5	25	0.195*	-0.0014	0.0989	0.160
6	8	-0.183	0.0330	0.1700	0.286	6	6	-0.026	0.0075	0.1985	0.342
						7	9	-0.044	0.0093	0.1550	0.270
						8	3	0.108	0.0247	0.3119	0.553
						9	16	-0.080	0.0036	0.1190	0.198
						10	8	-0.183	0.0010	0.1582	0.289

Table 4. F-statistics for different subdivisions of a population of *Nothofagus nervosa* from near Recinto, Chile based on 9 polymorphic enzyme loci. The groupings were produced by successively eliminating the largest distances from the Gabriel map of the individuals. Asterisks indicate F_{ST} values significant at the 0.05 level using jackknife values over the *loci*.

Number of group	F_{IS}	F_{ST}
2	0.193	0.009
4	0.190	0.022*
6	0.185	0.025*
10	0.183	0.029*

and pollen production is rather limited (Riveros *et al*., 1995). While Raulí has not been tested for self-compatibility, other species of the genus are self-incompatible or almost completely so (Riveros *et al*., 1995), as is the case for *Fagus sylvatica* (Merzeau *et al*., 1994). The average F_{IS} for 20 populations of Raulí was 0.186 (Carrasco, 1998; Carrasco and Eaton, 2002), whereas the F for this population was 0.197, which represents a considerable level of inbreeding and suggests that there might be some selfing.

Under these conditions, it is rather surprising that spatial autocorrelation methods did not detect more structure. Autocorrelation statistics revealed a weak spatial genetic structure in the population, which was better detected by Moran´s I than by join-counts. However, only three loci had significant I values for the two smallest distance classes, and two were significant using the Gabriel map.

Some simulation studies of isolation by distance have "sampled" every individual in the virtual populations and concur that both join-counts (Epperson and Li, 1997; Geng *et al*., 2009) and Moran´s I for the smallest distance classes (Epperson and Li, 1996; Chung *et al*., 2000) should accurately detect spatial genetic structure as long as the neighborhood size is not too large. In marked contrast, a number of field studies using species of Fagaceae have found only a weak structure using spatial autocorrelation statistics (Sork *et al*., 1993; Houston and Houston. 1994; Merzeau *et al.,* 1994; Leonardi and Manozzi. 1996; Tero *et al*., 2005). It is worthwhile to consider the possible causes for this discrepancy.

One possibility is that the assumptions of the model of isolation by distance are not met in the natural populations, in particular where pollen and/or seed dispersion is not very limited (Tero *et al.,* 2005; Epperson, 2005). There is some evidence that this may be the case in *Silene tatarica,* where seed dispersal seems to be the limiting factor (Tero *et al*., 2005), and in *Quercus* for both seeds (Houston and Houston 1994) and pollen (Dow

and Ashley, 1996). For *C. tepejilote*, nonrandom genetic distribution among the nearest neighbors was detected even from small spatial values, and this distribution seems to be consistent with the neighborhood size (of approximately 300 individuals). For this species, seed dispersal, mortality among life cycle stages, overlapping generations and contrasting traits of mating and reproduction could have influenced the standing spatial genetic structure within populations (Luns *et al.,* 2007).

The model of isolation by distance also requires that enough time has elapsed so that a "quasi-equilibrium" state has been reached (Epperson, 1993; Epperson, 2005). In simulation studies, approximately 50 generations after a random start are needed to reach this stage, at which point, estimations such as Moran´s I have stabilized (Epperson and Li, 1997; Epperson, 2005; Chen *et al*., 2008). Although this assumption may be reasonable for many species, it may not be valid for long-lived temperate forest trees whose ranges have changed considerably due to the last glacial cycle (Yacine and Lumaret, 1989; Leonardi and Menozzi, 1995; Villagrán, 1991; Aldrich *et al*., 2005). The current distribution range for *N. nervosa* on the Chilean side is considered a plant refugia in the last glacial period (Villagran, 1991; Carrasco and Eaton, 2002; Pastorino and Gallo, 2002; Premoli *et al*., 2002). Long-living tree species in the southern temperate forests in Chile show a genetic fragmentation that could be a consequence of their geographic fragmentation during that ice period (Torres-Diaz *et al*., 2007) and the re-colonization process after the glacial periods (Marchelli and Gallo, 2004). For *N. nervosa,* it was suggested that genetic diversity was different between the eastern populations located in Argentina and the western populations located on the Chilean side (Marchelli and Gallo, 2004), and these differences could be related to the existence of glacial refugia. However, it could also reflect low levels of gene flow given the eastward unidirectional winds that limit pollen dispersal or by the low seed dispersal alongside the eastern populations.

The simulations of isolation by distance have all used a "saturated" environment, a 100 x 100 matrix always filled with "individuals." This simulates species that form monospecific stands, such as *Fagus sylvatica*, but may not be appropriate to judge species such as *Nothofagus nervosa* that occur in multi-specific assemblages and whose density is variable within a stand.

Finally, both the model of isolation by distance and the simulations assume that dispersion of gametes and offspring is homogeneous over the whole population, which eventually produces a given level of structure. This kind of spatial genetic structure, which consists of patches of homozygotes with relatively few heterozygotes in between, is well measured by spatial autocorrelation methods. These "patches" or neighborhoods were smaller than the 25 and 28 m estimated for *Quercus laevis* Walter (Berg and Hamrick, 1994) and *Glycine soja* (Zhao *et al*., 2009) and the 40 m estimated for *Dipteryx alata* (Suarez *et al*., 2008). However, they were similar in size to the 10 m estimated for *Quercus petraea* (Matt.) Liebl. (Bacilieri *et al.,* 1994) and mangrove (Geng *et al*., 2009) and larger than the 5 m estimated for *Fumana thymifolia* (Jump *et al.,* 2008). However, a heterogeneous genetic structure in a population would not give such clear results because neighbors would be relatives only in parts of the population.

These findings show that the studied population of *N. nervosa* is a mosaic composed of groups of related individuals mixed with groups of unrelated individuals. A heterogeneous structure is not expected under the model of isolation by distance and must be accounted by other models. Seed dispersion and/or seedling establishment must have been irregular in this population, very limited at some times and much less limited in others because it is hard to imagine a model of selection at the microhabitat level that would produce adjacent groups of related and unrelated individuals. As in many temperate trees, *N. nervosa* tends to reproduce in clearings or gaps (Veblin and Donoso, 1987; Carrasco and Eatton,

2002; Pollman, 2003, 2005), which together with the limited seed dispersion may produce "family patches" (Houston and Houston, 1994). Seed dispersion may not be exponential, thus colonization may occur in jumps rather than an advancing wave (Nichols and Hewitt, 1994). Marchelli and Gallo (2004) found that the genetic diversity of *N. nervosa* did not relate to the geographic distance. This supports the idea that the heterogeneous composition of individuals should be related to seed dispersion and/or recruitment inside the stands.

We suggest that an equilibrium theory of population structure could not be an appropriate model for *N. nervosa* nor for many species whose populations do not persist for many generations or have not occupied their present locations for a long time. We propose that many species may have heterogeneous genetic structure within their populations, and this may explain why spatial autocorrelation methods have not detected more structure. More simulations of non-equilibrium populations are needed to predict the conditions under which structure will be produced, what forms it will take and how long it will last.

Mitton (1992) predicted that the coefficient of relationship would "allow direct examination of the degree relatedness within stands of forest trees." Relatedness makes use of data for all the variable loci, which are summarized in a single estimator r. Because kinship structuring affects all the neutral loci equally and independently (Malecót, 1948; Lewontin and Krakauer, 1973), relatedness should be an adequate estimator to detect structure within populations. However, in more or less continuous populations, we need criteria to determine the groups of individuals that will be compared. Successively removing the largest distances of the Gabriel map produced adequate results in the present case, but other exploratory methods could detect related groups. In those cases in which enough family groups may be determined within a population, it should be possible to test whether a locus is subject to selection because its pattern of variation should differ only from subject to kinship structuring.

Acknowledgements

We thank Dionisia Sepúlveda for her electrophoresis skill and Oscar Chandía for able assistance in the field and laboratory. This work was financed by European Community Project N° CI-CT 930043 and Fondo de Investigación del Bosque Nativo de CONAF, Project 025/2010.

Resumen

B. Carrasco, L. Eaton, L. Letelier, C. Díaz y R. García-Gonzáles. 2011. Heterogeneidad de la estructura genética, en una población natural de Raulí (*Nothofagus nervosa).* Cien.Inv. Agr. 38(3): 441-452. Es común encontrar deficiencias de heterocigotos en poblaciones naturales de especies forestales alógamas, lo cual se explicaría por un aumento del nivel de consanguinidad. Se ha postulado que la consanguinidad es causada por la presencia de estructuras de individuos emparentados dentro de las poblaciones, como producto de la limitada dispersión de polen y semillas. Si bien, antecedentes teóricos y estudios de simulaciones predicen que la estructura debería ser aparente cuando existe aislamiento por distancia, muchos estudios de estructura en poblaciones naturales, han detectado sólo un débil estructuración espacial. En este artículo se compara el uso de la metodología de autocorrelación espacial, estadísticos F y estimadores de parentesco. El objetivo es examinar la estructura genética espacial de una especial nativa de *Nothofagus* y explorar la discrepancia entre teoría y observaciones experimentales. El análisis de autocorrelación detectó estructura sólo para algunas de las nueve enzimas analizadas. Se

estimaron tamaños de vecindades de alrededor de 10 m. Al eliminar sucesivamente las distancias más grandes, en el mapa de Gabriel, las poblaciones se separaron en vecindades, las que fueron analizadas para su nivel de parentesco. Se detectaron tres grupos de individuos emparentados, mezclados con siete grupos de individuos relativamente no emparentados. El estadístico F para los grupos identificados también mostró una débil estructura genética. Se sugiere que la heterogeneidad de la estructura familiar dentro de las poblaciones naturales puede ser una de las razones que explica la escasa estructura genética espacial observada en *Nothofagus nervosa*.

Palabras clave: Autocorrelación espacial, estructura especial, estructura genética, raulí.

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