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Developing a breeding strategy for multiple trait selection in *Prosopis alba* Griseb., a native forest species of the Chaco Region in Argentina

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Prosopis alba is a native forest tree growing in arid and semi-arid regions of Argentina. It is a multipurpose species suitable for silvopastoral systems. The breeding programmes of *P. alba* in Argentina started ~25 years ago. Although several important advances have been made, the number of experimental stands is small in comparison with other forest species. In this study genetic parameters in several traits of economic importance were evaluated, including tree form (number of stems), height, diameter and size increments in an experimental stand. These traits exhibit significant heritabilities. The trade-off between genetic gain and increase of average kinship in the selected group was considered. With an elite group of 20 trees, the average group kinship drops from 0.5 to 0.03. An important constraint to selecting multiple traits was that the improvement on height and diameter was associated with a reduction in the form of the trees. The strategy of using a selection index was evaluated giving variable weights to tree form, height and diameter. Although gain at individual trait levels is reduced in comparison with the potential maximum, index selection allows significant gains for all three traits and represents a suitable strategy to improve *P. alba* stands in order to establish clonal seed orchards.

Introduction

Prosopis alba (white mesquite or 'algarrobo blanco') is one of the native species of greatest importance in South America by the quality of their wood and non-wood products and their wide geographic distribution. The species is found in Argentina, Uruguay, Paraguay, Peru, Bolivia and Chile (Burkart, 1976). Its natural populations develop in areas with summer rainfall ranging from 500 to 1200 mm per year, maximum absolute temperatures of 48°C, and absolute minimum of −10°C. They are able to grow in different types of soils, especially in sandy loam, tolerate high salinity and 1–2 months waterlogging (Galera, 2000; Felker, 2009).

The range of natural populations of *P. alba* in Argentina is mainly the Chaco ecoregion, where this species constitutes the most valuable wood resource for furniture and door and window frames because of its extraordinary physical and mechanical properties, ease of drying, fine grain, high resistance to moisture, fungi, and insects and great durability (Pometti *et al.*, 2010; Coronel de Renolfi, 2011; Coronel de Renolfi *et al.*, 2012). However, sawmill yield is only 30–58 per cent due to the predominance of short and crooked logs, or their low health status (Cuadra, 2009; Coronel de Renolfi *et al.*, 2012).

The white mesquite is also appreciated for producing highly nutritious fruits for forage and human food, which have great commercial potential (Fagg and Stwart 1994; Felker *et al.*, 2001). Moreover, its high tolerance to drought and its ability to fix nitrogen in the soil, means that it can be used to mitigate the effects of desertification in degraded environments (Roig, 1993; Cony, 1996; Felker and Guevara, 2003) and it represents one of the best alternatives for afforestation of subtropical arid and semi-arid areas.

Unfortunately this resource is endangered due to the unsustainable use during the last two centuries. Deforestation associated with extractive exploitation as well as agricultural (REDAF, 1999; Paruelo *et al.*, 2004; Adámoli *et al.*, 2011; Cuadra, 2012), and stockbreeding expansion has led to a gradual decrease in the raw material available and the genetic erosion of the species (SADyS, 2012). One way to reduce the pressure on *P. alba* forests remnants and recover their productive role is developing *ex-situ* conservation, domestication and breeding programmes (López, 2005; Verga *et al.*, 2009). The first trials involving *Prosopis* species were established in the 1980s in southern California using half-sib families (Felker *et al.*, 1983, 1989; Duff *et al.*, 1994). In 1990 coordinated activities were started by several public and private Argentine institutions with the purpose of producing improved genetic material of species of *Prosopis* (Cony 1996; Felker *et al.*, 2001). As *P. alba* is a multipurpose resource (Galera, 2000), its domestication process should involve different strategies according to the product to be improved (wood quality, fruit production, etc.). This requires taking into account the genetic material properties, traits selected and the propagation techniques. Nowadays the main natural populations of *Prosopis* are georeferenced, germplasm has been harvested and preserved (BNGP, 2015), and molecular and morphological characterizations of several species, populations, and selected clones are available (López, 2005; Bessega *et al.*, 2009; Darquier *et al.*, 2012; Ferreyra *et al.*, 2013; Roser *et al.*, 2014; Verga, 2014; Bessega *et al.*, 2016). Mesquite provenance trials are established from open-pollinated seeds collected from phenotypically selected individuals in wild populations. Seed orchards with origin certified are available (INASE, 2015) but their genetic quality has not been evaluated. Nurseries able to provide plants with standard quality are indeed scarce and dispersed. The INASE provides provenance but not quality certifications for seeds provided from these orchards. Furthermore, the outcrossing mating system determines high variability within families. As a result, plantations obtained so far are heterogeneous, with the presence of shrub features, thorny trees or slow growth, which do not the features required if better ultilization of the timber is an objective (Bischoff, 2011).

Currently the *P. alba* programme in Argentina is represented by a network of trials consisting of three progeny trials respectively in the provinces of Santiago del Estero, Formosa and Chaco with the final purpose to get improved traits like growth (diameter and height) and tree form (López, 2005). Moreover, clonal orchards have been also established with material improved for different traits: pod production and palatability, resistance to phytophagous insects and fungal pathogens, growth rate under increased salinities (Felker *et al.*, 2001; Ewens and Felker 2010; Ewens *et al.*, 2012).

Breeding programmes usually integrate pathways of agamic and sexual reproduction to provide increasing levels of genetic improvement through a process of selection, conservation and continuous evaluation of materials aimed to preserve most part of genetic variability and generate gain by genetic recombination (White *et al.*, 2007). The selection for high-quality wood requires improving traits like tree form, diameter and height. However, studies conducted so far showed that in *P. alba* tree form is negatively correlated with the other two traits (Salto, 2011). This fact imposes constraints for the breeding programme as trees selected for fast growth would show low quality in terms of tree form and/or wood properties. An efficient strategy to cope with this constraint makes use of the multitrait selection theory based on selection index, with the goal of getting the maximum possible gain in all traits simultaneously (Torres Cuadros and Gezan Pacheco, 1998; Apiolaza and Greaves, 2001; Lee, 2001; Marcó and White, 2002; Bessega *et al.*, 2015).

Although the main focus of breeding is economical important traits, it is also relevant to preserve wide genetic diversity to prevent inbreeding depression in the following generations (Lindgren and Mullin, 1997). Average kinship and breeding value (BV) in the reproductive group may be combined as an optimality criterion for the selected group throughout the breeding programme (Lindgren and Mullin, 1997; Kang *et al.*, 2001; Olsson *et al.*, 2001; Bessega *et al.*, 2015). The actual challenge consists in determining the trade-off between a significant increase in orchard gain together with an acceptable coancestry level.

Following this line, the objective of the present work was to develop an appropriate breeding strategy for multiple trait selection taking into account heritability of individual traits, the genetic correlations between traits and the increase of selected group kinship inherent to the selection process. The criterion applied was to search for an acceptable simultaneous improvement of all traits compatible with preserving genetic diversity in the selected group. Applying the selection index method (Hazel, 1943), we explored a high number of scenarios considering: (1) the effect of different relative weights to each trait in the selection index and (2) the effect of group size on average group kinship.

Materials and methods

Material of study

A progeny trial with 201 open-pollinated families from 10 natural populations (provenances) of *P. alba* established in 2008 was used in this study. Candidate trees were phenotypically selected in the wild by ‘good shape and development’ (Verga *et al.*, 2009). Each provenance was considered as representing a different genetic group. The average family size (number of progeny per mother tree) was 15, ranging from 6 to 22. The trial is located at Vivero San Martín (latitude 27°56′44″S, longitude 64°13′10″W, 174 m asl), ~16 km South of Santiago del Estero City. The soil was formed from loessical silt with scarce development; its profile is characterized by A-AC-C horizons (Galizzi *et al.*, 1999). The experimental design was a randomized complete block, with three replicates of 1–10 multiple-tree non-contiguous plots, and the spacing was 4 × 4 m.

For the present work a random sample of 387 individuals of the trial was taken. This sample was stratified in order to have all origins represented. Approximately seven families were randomly chosen from each origin and the number of trees per family analysed ranged from 4 to 6. All statistics were based on these individuals.

Morphometric data

The height (H), diameter at breast height (DBH) and stem number (SN) of each sampled individual were measured directly in the experimental field. Two herbarium vouchers were obtained from each individual (in June 2011), one from the top and the other from the lowest third of the canopy. Spine lengths (SLs) were measured from these specimens after drying the vouchers.

Height was measured with a rod of height with a minimum graduation of 1 cm. DBH was measured at a height of 1.30 m from ground level at the nearest 1 mm, using a diametrical measuring tape, following the methodology indicated by the First National Inventory of Forests Native (Primer Inventario Nacional de Bosques Nativos, 2007). H and DBH were measured twice in each individual at the ages of 3 and 5 years (in June 2011 and 2013, respectively). The acronyms for the first measurements were H1 and DBH1, and for the second ones were H2 and DBH2. Increments for H (HG) and DBH (DBHG) were respectively estimated as H2-H1 and DBH2-DBH1.

SN was recorded as recommended by Primer Inventario Nacional de Bosques Nativos (2007) in June 2013 as the number of stems below the height of 1.30 m over ground level. This trait was considered as a parameter negatively related to tree form quality: the best tree form corresponds to SN = 1, and quality is reduced with increasing SN values.

SL was measured with a scale ruler with precision of 1 mm. A total of six spines were measured from each individual (three on each voucher), which were averaged to obtain the individual value. In cases where specimens showed no spine (unarmed individuals) SL was considered 0 mm. Although this criterion may invalidate, the normal distribution assumptions, excluding unarmed individuals from the analysis of SLs, prevent the inclusion of such individuals in the multivariate analysis conducted with 'MCMCglmm' (see below). In order to test the possible bias attributable to the inclusion of unarmed individuals, univariate analysis including and excluding unarmed individuals was run.

Data analysis

Pairwise phenotypic correlations between traits were estimated using Pearson's product moment coefficient with the package 'stats' of the programme R (R Core Team, 2016). Significance was corrected for multiple comparisons using the method of Benjamini and Hochberg (1995).

The sample was treated as a half-sib design where pairwise kinships can take only three values, 0.5 for an individual with itself, 0.125 for a pair of individuals of the same family (half sibs) and 0 for individuals of different families. This assumption was applied in previous analysis of variance components in experimental stands of *P. alba* (Bessega *et al.*, 2011) and it is supported by genetic studies that suggest that *P. alba* is predominantly outcrosser (Bessega *et al.*, 2012).

H1, DBH1, H2, DBH2, HG, DBHG and SL were treated as continuous variables with normal distribution, whereas NS was considered as a meristic variable following a Poisson distribution whose minimum corresponds to one stem.

Block and origin effects were estimated with the package 'lme4' (Bates *et al.*, 2015) of R (R Core Team, 2016) by applying the following generalized mixed linear model:

$$y_{ijkl} = \mu + p_i + f_{ij} + b_k + \epsilon_{ijkl}$$

where y_{ijkl} is the observation of the trait in the individual tree l of family j from population i in the block k, μ is the overall mean, f_{ij} represents random family effects, b_k is the (fixed) block effect and ε_{ijkl} is the random residual error. Predictions of BVs were obtained applying the generalized mixed model according to the general expression:

$$Y = X\beta + Z\,g + e \tag{1}$$

where Y is a vector of observations on all individuals, β is a vector of fixed effects, X represents a design matrix (of 0 and 1 s) relating the appropriate fixed effects to each individual, g is a vector of random effects (BV), Z is a design matrix relating the appropriate random effects to each individual and e is a vector of residual errors (Kruuk, 2004). In our case, fixed effect is represented by blocks and the random effect is represented by the individual.

According to equation (1) the vector of g (BV) can be obtained as:

$$\hat{g} = AZ'\sigma_A^2 V^{-1}(Y - X\beta)$$

In this equation A represents the relatedness matrix, Z' is the transposed Z, σ_A^2 is the additive genetic variance and V^{-1} is the inverse of the phenotypic variance. The product $\sigma_A^2\, V^{-1}$ is by definition the trait heritability (h^2).

BV predictions were obtained by ridge regression. This method is equivalent to the best linear unbiased prediction (BLUP) in the context of mixed models (Whittaker *et al.*, 2000; Meuwissen *et al.*, 2001) and can be applied with relatedness matrices either derived from pedigree information or estimated from molecular markers. BV calculations were conducted using the package 'rrBLUP' (Endelman, 2011; Endelman and Jannink, 2012) of R (R Core Team, 2016). The command used was 'kin.blup', which requires the vector of phenotypes (trait) measured in each individual and the kinship matrix A, which in this case corresponds to the expected for a half-sib design (with values 0.5, 0.125 and 0 as indicated above). The command calculates BV and the prediction error variance (PEV) (using the option PEV = TRUE) of each estimated BV as the square of the standard error of the BLUPs. The expected accuracy of BLUP predictions (r_i) was estimated according to (Clark *et al.*, 2012):

$$r_i = \sqrt{1 - \frac{\mathrm{PEV}}{V_g \times K_{ii}}},$$

where K_{ii} is the diagonal of the relatedness matrix for individual i.
The output from kin.blup also gives an REML estimate of V_A (\$$V_g$), from which we obtained an estimate of the heritability by applying the basic expression $h^2 = V_A/V_P$.

Variance components were estimated applying a generalized multivariate linear mixed model. We used the R package MCMCglmm (Hadfield, 2010) because it uses Bayesian inference, which is a useful approach to way around some difficulties and uncertainties associated with both parameter estimation and hypothesis testing for non-Gaussian traits, which represent drawbacks for REML approaches (Wilson *et al.*, 2009). The package MCMCglmm uses Markov chain Monte Carlo techniques and supports normal and Poisson distributions. The command used was MCMCglmm, which requires specification of prior distributions for three elements: the R-structure (residual variance), G-structure (genetic variance) and the fixed effects. In large informative datasets the prior has little impact on parameter estimates. In our case, we assumed as a prior that total variance is equally distributed between V_A and V_E components. That is, we defined a matrix V whose diagonal elements are the estimated variance of each trait and off diagonal are zeros. Initially, both R and G structures were assumed as equal to $V/2$. The fixed effect in time corresponded to the blocks. The distribution of traits was defined with the parameter 'family' within the command as Gaussian (traits H1, DBH1, H2, DBH2, HG and DBHG) or Poisson (SL).

The estimates were based on 200 000 iterations, with a thinning 200, and burning of 30 000. A thorough description of the use of this package can be found in Supplementary File S5 accompanying the paper by Wilson *et al.* (2009).

From this analysis we also obtained an estimate of the variance/covariance components with the command 'posterior.mode'. Heritability was estimated by applying the basic formula $h^2 = V_A/V_P$ to each sample of the posterior distribution. The final estimate and 95 per cent Bayesian confidence interval of heritability were obtained from the posterior distribution of h^2 with the functions posterior.mode and HPD interval, respectively.

The pairwise genetic correlation (r_g) between traits was estimated for each iteration from the usual ratio of genetic covariance over the square root of the product of genetic variances of each trait. The final estimate and 95 per cent confidence interval of r_g were obtained with the same procedure as that applied for h^2.

The estimates of h^2 obtained from the analyses conducted with the packages rrBLUP and MCMCglmm were compared by the Spearman's rank correlation test.

For each trait, the individuals were ranked according to decreasing BV from 1 to 387. We considered the effects of selecting a variable number of individuals (N) in terms of the relative gain and the average group kinship. As the number of selected individuals (N) increases, individuals with lower BV are included in the selected group and consequently the relative gain decreases. In parallel, pairwise kinship decreases. We considered 387 situations, involving breeding groups constituted by 1, 2, 3 and so up to 387 individuals. In the first case only the best ranked individual is selected (N = 1) and a single kinship estimate is 0.5 (the selected individual with itself). In the last case all individuals are included, corresponding to the cases where no selection is applied, with no gain and no change in average kinship respect to the original population.

Estimated gains of groups composed of different number of selected individuals were expressed as a percentage of the group average BV relative to absolute population phenotypic mean.

Effect of selection by index on the gains of three traits

A selection mixed index was proposed by Hazel (1943) that considers relative contribution of three traits as follows:

$$I = w_1g_1 + w_2g_2 + w_3g_3$$

where g_i are the BLUP predicted BVs for each trait and w_i are the relative weights given to each trait. A difficult issue is determining the appropriate weight on each trait (White and Neale, 2007).

In the present work we applied this approach to develop an index for H, DBH and SN, the three economical most important traits in the case of *P. alba*:

$$I = w_1 \times Hg + w_2 \times DBHg + w_3 \times SNg$$

where *Hg*, *DBHg* and *SNg* are the BLUP predicted BVs for traits considered.

In the present case the restrictions applied to the relative weights to each trait were

- $0 \le w_i \le 1$ for all traits and
- $w_1 + w_2 + w_3 = 1$.

Individuals were ranked according to decreasing values of I, and the gains obtained for each trait with the 20 top ranked trees were expressed as a percentage of the maximum value possible if the trees would have been selected solely on the basis of the corresponding trait.

Relative gains were evaluated for varying w_1, w_2 and w_3 values, considering the range 0–1 at intervals of 0.1 for each coefficient. With the restriction applied a total of 66 combinations of coefficients were tested.

Relative gain surface trend plots to represent the effect of different weights in the selection index were obtained for each trait using the package 'spatial' (Venables and Ripley, 2002) of R. The surface trend was estimated by generalized least-squares for a polynomial surface of degree 3 and the graph was obtained with the package 'graphics' of R (R Core Team, 2016).

Results

Basic statistics and phenotypic correlations between traits

The basic statistics of the measured traits (Table 1) shows a trend of higher tree growth in Block 3. The trait SLs are not affected by block effect and highly significant differences were recorded among origins. These results were consistent for ANOVA conducted for the whole sample ($F_{\text{orig}} = 5.8$, $P < 10^{-3}$; $F_{\text{block}} = 0.47$, $P = 0.62$) or excluding unarmed individuals ($F_{\text{orig}} = 4.1$, $P < 10^{-3}$; $F_{\text{block}} = 2.1$, $P = 0.13$). Hereafter, all reference to SL analyses correspond to the results based on the whole sample.

The block effect on traits related to tree growth is probably due to different access to irrigation because this block is the nearest to the irrigation canal, see Figure 1; increased tree growth is observed in the trees close to the canal. All traits but HG and DBHG differ significantly among provenances (Table 1). In most cases the phenotypical correlation between traits related with tree growth is significant or highly significant after correction for multiple comparisons (Table 2). Interestingly, H1 and DBH1 are both negatively correlated with HG and DBHG, respectively. This result might be explained assuming that tree growth is asymptotic and so, HG and DBHG are inversely proportional to tree size. Namely, seedlings with fast growth during the first stage reach higher values for H1 and DBH1, but their increment in size is lower during the second stage as compared with seedlings that exhibited lower growth during the first period. From this result further analysis of the consequences of selection on productive traits was based on the measures of H and DBH taken at the age of 5 years (H2 and DBH2).

SL in all cases but DBHG is not significantly correlated with the remaining traits. By contrast, the tree form parameter (SN) is also significantly correlated with height and diameter. This implies that selecting for trees with lower number of stems represents a trade-off with the improvement of growth traits.

BV predictions

According to estimates obtained using the package rrBLUP the genetic variance is relatively high for all traits but DBHG (Table 3). The trait with the highest heritability was SL, with a value close to 1. The average accuracy of BLUP predictions (r_i) ranged from 0.71 to 1.

The variance components for each trait were estimated using the package MCMCglmm (Table 3). In each case the deviance information content (DIC) was used to compare two models, one assuming $V_g = 0$ (null hypothesis) and the other assuming $V_g > 0$. In all cases the model with the lowest DIC was the second one, supporting the assumption that the genetic variance is significant for all studied traits. In most cases the h^2 estimate obtained with rrBLUP is within the Bayesian confidence interval of those retrieved with MCMCglmm. Furthermore, h^2 and CVA estimates obtained from rrBLUP are significantly correlated with the corresponding estimates from MCMCglmm ($r = 0.94$ and 0.93, respectively, $P < 0.04$ according to Spearman's rank correlation test).

The multivariate analysis conducted with MCMCglmm allowed us to estimate the genetic correlations between traits (Table 4). The trend observed for genetic correlations was similar to those observed phenotypically. HG and DBHG are negatively correlated with H1 and DBH1, although only the correlation between DBHG and DBH1 is significant (because its 95 per cent confidence interval does not contain the zero). Diameter and height measures are positively and significantly correlated to each other. SN is also positively correlated with height and diameter, although only the values for H1 and H2 are significant whereas the correlations with DBH1 and DBH2 are borderline significant.

BV and kinship

As indicated above, this analysis is based on H2 and DBH2. The individuals were ranked in decreasing order according to predicted BVs and the effects of sampling size on the genetic gain and the group average pairwise kinship was evaluated (Figure 2a). The BV of the best individual for H2 and DBH2 is 14.68 and 49.42 per cent, respectively, higher than the population mean. As the kinship of an individual with itself is 0.5, this value represents the average kinship of a hypothetical 'breeding group' constituted by a single top individual. In a realistic situation, as the number of individuals in the selected group is increased the average kinship diminishes. In the present case, we observe a dramatic drop of kinship from 0.5 to 0.03 when the number of individuals in the breeding group is increased from 1 to ~20 and then the reduction of kinship is virtually

Table 1 Basic statistics of the traits measured in the *P. alba* progeny trial considering the 10 origins and 3 blocks included in the orchard

Code	Province	H1 (m)	SD	H2 (m)	SD	HG (m)	SD	DBH1 (cm)	SD	DBH2 (cm)	SD	DBHG (cm)	SD	SN	SD	SL (mm)	SD
1	Salta	3.349	1.036	4.581	1.142	0.272	0.194	4.391	2.178	7.682	2.897	0.528	0.362	5.000	2.636	0.252	0.210
2	Salta	2.693	0.902	4.073	1.391	0.524	0.335	2.799	1.930	5.616	2.701	1.346	1.326	4.405	2.142	0.575	0.455
3	Salta	2.618	0.747	3.677	1.159	0.396	0.381	2.527	1.517	5.004	2.484	0.980	1.039	4.111	1.737	0.124	0.220
4	Formosa	2.665	1.025	3.853	1.523	0.447	0.403	2.649	1.762	5.336	3.008	0.999	1.080	3.829	2.135	0.578	0.384
5	Chaco-Formosa	3.162	0.810	4.527	1.268	0.422	0.226	3.702	1.680	6.980	2.795	1.022	0.8650	3.540	1.538	0.450	0.377
6	Santiago del Estero	2.649	0.846	3.830	1.352	0.490	0.446	2.434	1.451	5.337	2.842	1.464	1.209	3.794	2.508	0.457	0.558
7	Santiago del Estero	2.364	0.859	3.457	1.370	0.442	0.333	2.213	1.694	5.037	3.252	1.442	1.382	2.757	1.571	0.243	0.392
8	Santiago del Estero	2.658	0.844	3.866	1.054	0.406	0.231	2.597	1.645	5.853	2.663	1.171	0.976	3.600	1.355	0.195	0.325
9	Chaco	2.721	1.020	4.068	1.509	0.469	0.3330	3.001	1.795	5.968	3.282	0.945	0.939	3.364	1.950	0.284	0.281
10	Entre Ríos	2.250	0.726	2.704	1.160	0.261	0.404	2.099	1.678	3.092	2.691	0.837	1.183	2.889	1.537	0.821	0.480
–	Average	2.713	0.327	3.864	0.536	0.413	0.086	2.841	0.705	5.591	1.227	1.074	0.290	3.729	0.673	0.398	0.217
–	Block1	2.472^{a}	0.974	3.198^{a}	−1.204	0.278^{a}	0.289	2.430^{a}	−1.867	4.160^{a}	−2.557	0.898^{a}	−1.198	3.185^{a}	−1.766	0.388^{a}	0.455
–	Block2	2.511^{a}	0.773	3.616^{b}	0.982	0.468^{b}	0.321	2.484^{a}	−1.644	4.955^{b}	−2.280	1.124^{a}	−1.173	3.376^{a}	−1.386	0.386^{a}	0.425
–	Block 3	3.167^{b}	0.842	4.849^{c}	−1.316	0.540^{c}	0.356	3.540^{b}	−1.675	7.737^{c}	−2.845	1.335^{b}	0.914	4.538^{b}	−2.387	0.340^{a}	0.371
–	Global	2.710	0.919	3.906	−1.364	0.433	0.341	2.807	−1.798	5.649	−2.985	1.125	−1.112	3.748	−2.001	0.372	0.418

SL = spine length; H1 and H2 = first (2011) and second (2013) height measures; HG = height growth; DBH1 and DBH2 = 2011 and 2013 breast height diameter measures; DBHG = diameter growth; SN = stem number; SD = standard deviation. Different index letters indicate significant ($P < 0.05$) differences.

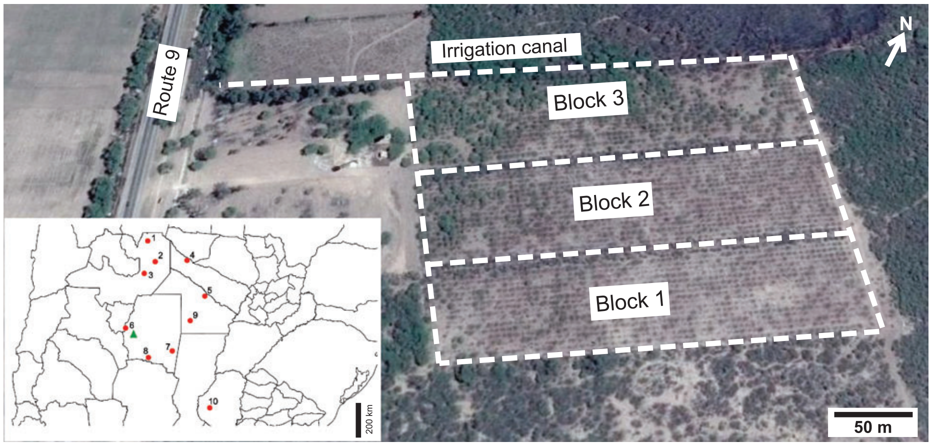


Figure 1 Map with the localization of the 10 natural populations sampled (bottom left) and block design in the provenance trial of *P. alba* in Santiago del Estero. Populations are represented by circles and the trial site by a triangle in the bottom left map. Codes for populations correspond to the list in Table 1.

Table 2 Pairwise phenotypic correlations (below diagonal) between traits measured in a progeny trial of *P. alba* together with their corresponding statistical signification (above the diagonal) after correction for multiple comparisons using the method of Benjamini and Hochberg (1995)

	SL	H1	H2	HG	DBH1	DBH2	DBHG	SN
SL		0.74	0.99	0.35	0.89	0.54	0.01	0.53
H1	−0.02		0.00	0.00	0.00	0.00	0.00	0.00
H2	<0.01	**0.82**		0.00	0.00	0.00	0.35	0.00
HG	0.06	**−0.19**	**0.35**		0.00	0.00	0.00	0.99
DBH1	−0.06	**0.90**	**0.73**	**−0.20**		0.00	0.00	0.00
DBH2	−0.04	**0.81**	**0.92**	**0.23**	**0.70**		0.26	0.00
DBHG	**0.14**	**−0.25**	0.06	**0.58**	**−0.46**	0.07		< 0.01
SN	−0.04	**0.41**	**0.40**	<0.01	**0.29**	**0.34**	**−0.15**	

Bold type indicates significant correlations.

Table 3 Variance components and heritability (h^2) estimations obtained with the packages rrBLUP and MCMCglmm for eight traits measured in a progeny trial *of P. alba*

Trait	rrBLUP						MCMCglmm			
	V_g	V_e	h^2	r_i	CVA	V_g	V_e	h^2	BCI	CVA
SL	0.34	<0.01	>0.99	1.00	1.47	0.13	0.03	0.88	(0.65/0.96)	0.91
H1	0.33	0.68	0.32	0.78	0.21	0.23	0.51	0.37	(0.10/0.70)*	0.18
H2	0.44	1.64	0.21	0.75	0.17	0.52	0.74	0.37	(0.09/0.74)*	0.19
HG	0.01	0.11	0.11	0.73	0.24	0.02	0.09	0.22	(0.07/0.50)*	0.34
DBH1	2.16	2.16	0.50	0.83	0.52	0.97	1.50	0.44	(0.12/0.78)*	0.35
DBH2	4.31	6.76	0.39	0.79	0.37	3.36	3.71	0.50	(0.21/0.84)*	0.33
DBHG	<0.01	1.24	<0.01	0.71	0.09	0.16	1.03	0.11	(0.03/0.34)	0.37
SN	2.81	2.60	0.52	0.81	0.45	1.88	2.79	0.36	(0.15/0.80)*	0.37

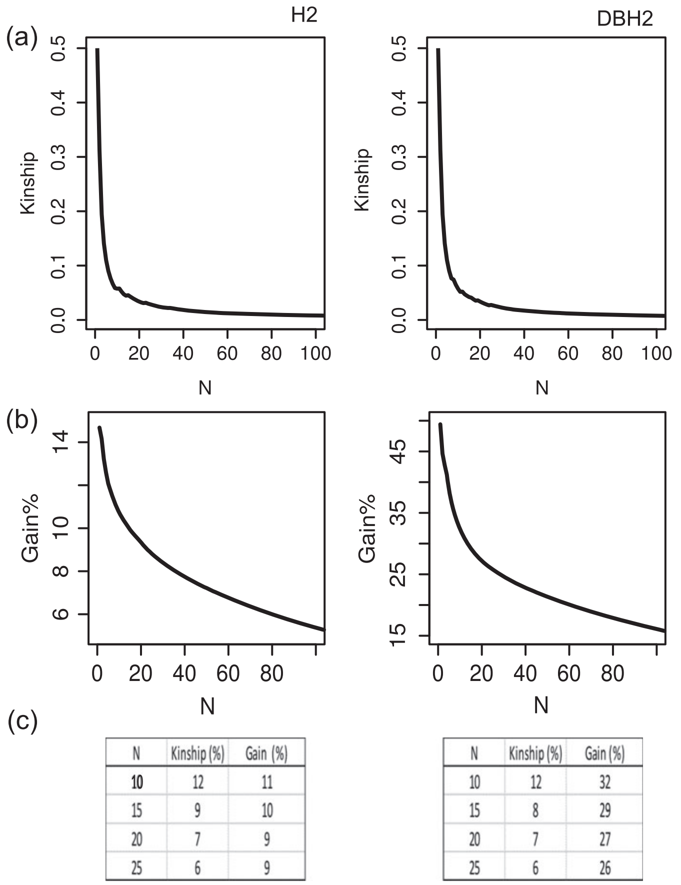
Acronyms for traits are described in the text. V_g = genetic variance; V_e = error variance, r_i = expected accuracy of BLUP predictions; CVA = additive variation coefficient; BCI = Bayesian confidence intervals; * = significant h^2 estimate.

negligible for larger groups. The genetic gain is reduced with increasing breeding population size and for 20 individuals the observed values were 9.34 and 27.21 per cent for H2 and DBH2 relative to population mean (Figure 2b). In the present case, 20 individuals seem to be a good compromise between kinship and gain loss for both traits. The cost of including 20 individuals in the selected group is 36 and 45 per cent of maximum gain respectively for H2 and DBH2 (Figure 2c). By contrast the

Table 4 Pairwise genetic correlations (below diagonal) between traits measured in a progeny trial of *P. alba* together with their corresponding 95 per cent confidence intervals (above the diagonal) estimated with the package MCMCglmm.

	SL	H1	H2	DBH1	DBH2	HG	DBHG	SN
SL		−0.43/0.24	−0.41/0.26	−0.47/0.22	−0.51/0.17	−0.26/0.35	−0.19/0.50	−0.13/0.24
H1	−0.10		0.53/0.92	0.66/0.93	0.46/0.89	−0.68/0.13	−0.73/0.09	0.08/0.88
H2	−0.10	**0.79**		0.42/0.90	0.63/0.92	−0.25/0.64	−0.54/0.39	0.02/0.81
DBH1	−0.10	**0.86**	**0.78**		0.46/0.89	−0.62/0.21	−0.78 /−0.08	−0.03/0.83
DBH2	−0.16	**0.81**	**0.87**	**0.81**		−0.43/0.46	−0.52/0.39	−0.07/0.82
HG	0.01	−0.35	0.33	−0.31	0.15		0.01/0.69	−0.72/0.43
DBHG	0.28	−0.41	−0.27	**−0.49**	−0.163	**0.50**		−0.21/0.19
SN	0.03	**0.79**	**0.75**	0.78	0.75	0.22	−0.01	

Bold type indicates significant correlations.



N	Kinship (%)	Gain (%)
10	12	11
15	9	10
20	7	9
25	6	9

N	Kinship (%)	Gain (%)
10	12	32
15	8	29
20	7	27
25	6	26

Figure 2 Effect of increasing numbers in the selected group (*N*) on the average group kinship (a) and relative gain per cent (b) for tree height (H2) and trunk diameter (DBH2) in a trial of *P. alba*. (c) Detail of average group kinship and relative gain per cent for *N* = 10, 15, 20 and 25.

average kinship is reduced 93 per cent. Including a higher number of individuals in the selected group is no improvement in terms of kinship but involves significant reduction in terms of genetic gain. Indeed, expressed in percentages, average kinship drops only 1 per cent when the breeding group size is increased from 20 to 25. In contrast, the gain drops 4 per cent for H2 and 3 per cent for DBH2 (Figure 2c) for the same interval. These results support the use of selected groups composed of 20 individuals, which in the present case empirically involved 12–13 families.

Selection indices and gain of individual traits

From the results of the former section, we estimated the relative gain of each trait based on individual selection of the 20 elite individuals for each of three traits: H2, DBH2 and SN (Table 5 rows 1–3). In the case of SN top trees are those with the lowest values. According to these results, the selection based on only H2 or DBH2 produces a negative gain of SN. Conversely, selecting by SN only has negative effect on H2 gain and virtually no gain in DBH2.

Table 5 Expected gains obtained for each trait selecting the top 20 individuals according to different criteria, expressed as percentage relative to the population mean in a progeny trial of *P. alba*

Selection criterion	H2	DBH2	SN
H2 only	9.34	22.54	−9.78
DBH2 only	7.76	27.21	−7.38
SN only	−1.35	0.18	29.26
Selection index	5.65	16.99	18.12

The selection index is described in the text ($w_1 = 0.6$, $w_2 = 0.1$, $w_3 = 0.3$).

The consequence of applying a selection index criterion was explored to rank individuals, giving variable weights to each trait. The total number of scenarios considered was 66, but the main results of this analysis may be summarized in Figures 3 and 4. In Figure 3a, w_1 is fixed at 0, w_2 varies from 0 to 1 and $w_3 = 1–w_2$ (that means that the selection criteria are only on DBH2 and SN, whereas H2 is excluded). As the weight of DBH2 increases (higher w_2 values), the gain in DBH2 grows, and, due to the positive genetic correlation, H2 gain also increases. By contrast, the gain in SN is reduced (that is, trees show higher number of stems). In Figure 3b selection criteria excluded DBH2 (w_2 is fixed in 0), and the selection is based on H2 and SN. The trend was similar to that observed in the previous figure. As w_1 increases, there is a parallel increase in gain of DBH2 and H2, and a loss in SN. In both plots the curves of SN show an important decrease for values of w_2 or $w_1 > 0.7$, that is, $w_3 < 0.3$. This

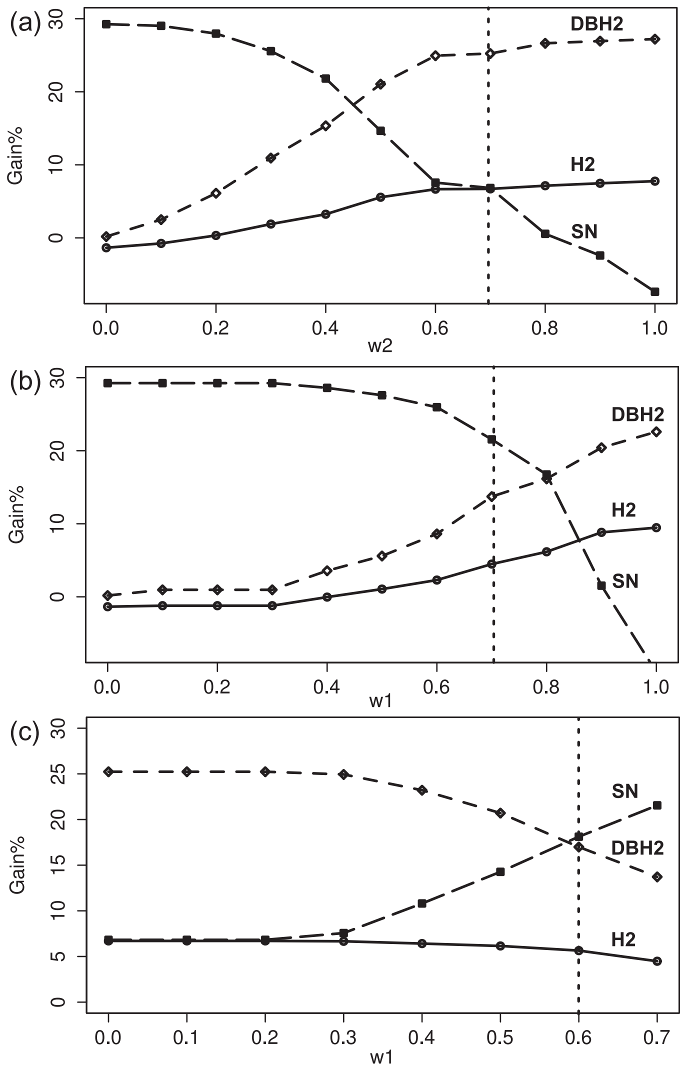


Figure 3 Effect of index multitrait selection on individual trait gain (per cent) in *P. alba*. The relative weight of height (H2), diameter (DBH2) and number of stems (SN) are quantified respectively by the coefficients w_1, w_2 and w_3. The plots represent different selection scenarios: (a) $w_3 = 0$ and $w_1 = 1–w_2$, (b) $w_2 = 0$ and $w_3 = 1–w_1$ and (c) $w_3 = 0.3$ and $w_2 = 1–w_1$.

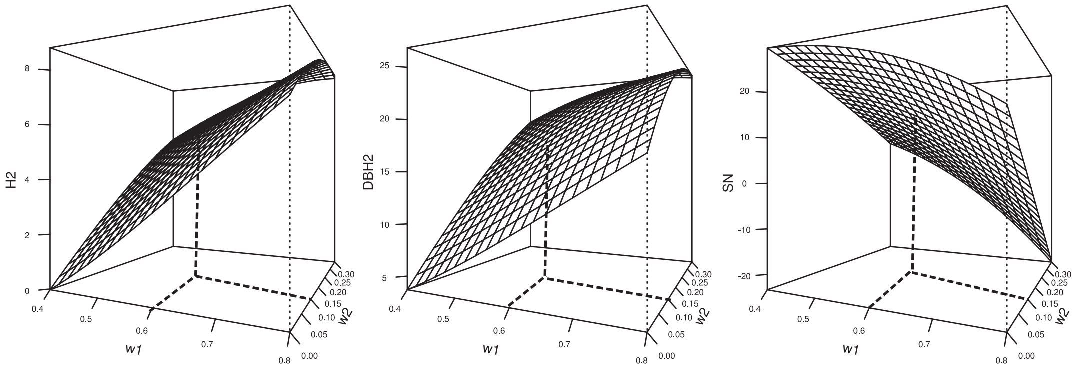


Figure 4 Tri-dimensional plots representing H2, DBH2 and SN gains as a function of trait weights in the selection index around the optimal condition. w_1 and w_2 are represented in the axes *x* and *y*, and w_3 can be obtained by difference ($1 - w_1 - w_2$).

means that $w_3 = 0.3$ represents a compromise between the gain in DBH2 or H2 and the loss in SN. In the Figure 3c w_3 was fixed in 0.3, and the effect of giving variable weights to H2 (w_1) or DBH2 (w_2) was evaluated. In this case the gain of H2 remains almost constant in the entire range, while a reduction in DBH2 and an increase in SN gain are observed for w_1 values higher than 0.3. According to these results the best compromise to obtain acceptable gains when selecting simultaneously for the three traits is using $w_1 = 0.6$, $w_2 = 0.1$ and $w_3 = 0.3$. In Figure 4 the relative gain surface trend of each trait is plotted as a function of the weights of all three traits in the interval around the optimal condition described in Figure 3. With $w_1 = 0.6$, $w_2 = 0.1$ and $w_3 = 0.3$ the expected gains for DBH2, SN and H2 are 17, 18 and 6 per cent, respectively (Table 5 row 4, Figures 3 and 4).

Discussion

Analysis of the components of the phenotypic variance showed that the spines are virtually not affected by environmental conditions within the orchard. This trait exhibited a high heritability and was the only trait not affected by block effect. Moreover, it is neither correlated phenotypic nor genetically with any of the other traits. This suggests that SL can be selected independently of the others and that could respond quickly to the selection.

One of the problems presented in the use of wood for the industry is related to the form of the mesquite tree rather than with growth (Salto, 2011); however, this is a trait that is difficult to quantify. An applicable criterion is to use a visual score representing a phenotype expression in a predefined scale. However, as pointed in Cappa and Varona (2013), the scale is usually arbitrary and subjective, and the output could lead to a strong departure from the Gaussian distribution (Gianola and Foulley, 1983). Therefore, statistical genetic analyses based on these mixed models are generally unsuitable for such traits (Gianola, 1980). A more objective rating scheme was devised by Lee *et al.* (1992), based on the angle of the main stem and/or stems with the ground. These authors rated trees in three categories: 1 for the most upright stems (60°–90°), 2 for intermediate (30°–60°) and 3 for the most prostrate (0°–30°). However, this criterion does not solve the issues related to the expected distribution and it is difficult to apply when several stems are present. To solve this issue we used as a simple and objective criterion for individual tree form the number of stems. Although this is not an exhaustive description, it is easy to get and it may be related with a known theoretical distribution (Poisson).

H, DBH and SN traits are positively correlated phenotypically and genetically. However, both growth parameters (HG and DBHG) are negatively correlated with the first measurements (H1 and DBH1).

This indicates that while H2 and H1 are correlated with each other, as well as DBH1 and DBH2, it is not recommended to select on the basis of the first measurements because a high proportion of individuals with relatively low values of H1 and DBH1 achieves superior phenotypes in the second measurement (and vice versa). In summary, although earlier measurements may reduce the time from orchard installation to harvesting superior genotypes, it seems more relevant for breeding programmes to select trees on the basis of growth after 5 years rather than growth after 3 years. This is consistent with Danusevicius and Lindgren (2002) who recommend selecting in later stages and suggest that the opportune moment is when the trial reaches the state canopy-closure, that is, when juvenile-mature stages for the characters of growth are correlated.

As discussed in Bessega *et al.* (2015), the increase in average kinship of the selected group associated to sample size should be considered as a quality criterion for the propagation material. In the present work we found that, although selection on single traits (H2 or DBH2) was not conducted within families, average pairwise kinship in the sample of 20 top individuals was only 0.03. This low value of kinship is a consequence of the mating system of *P. alba,* which is mostly outcrossing, which determines that the variation within families is high and the selected group included individuals from several families. Empirically in the orchard under analysis we found that the group of 20 elite individuals for H2 and DBH2 includes individuals from 12 to 13 families. This result is consistent with the work of Bessega *et al.* (2015), who observed that by selecting from a natural population, applying a penalty to the average group BV by the kinship, the sample of 20 individuals could be reduced to 10 without increasing inbreeding and with minimal effect on the gain. In our case, in particular, this would be achieved by selecting an individual of each family.

When the best phenotype is defined on the basis of multiple traits, correlations between them should be considered (Sánchez *et al.*, 2008). In other species selection for H and DBH simultaneously is achieved by selecting trunk volume (Lee, 2001; Marcó and White, 2002). In *P. alba* this approach is not suitable because the tree form is usually very irregular and cannot be approximated to a cylinder (Cienciala *et al.*, 2013). For this reason the use of a selection index seems to be more appropriate. Negative correlations may imply serious constraints, which involve a compromise between gains at individual trait levels (Sánchez *et al.*, 2008). In the case analysed here H and DB proved to be phenotypically and genetically positively correlated, hence the selection for one trait indirectly selects for the other. Both are also positively correlated with SN, but this trait should be selected in the opposite direction (the lower is SN, the higher is the ranking of an individual tree). In fact, the ideal tree should have a single, high and thick stem. Salto (2011) also analysed the problem of selecting for height, diameter and tree form in the same trial, although applying different measurement methods. She used a similar approach to define a selection index, considering only two scenarios: (1) $w_1 = w_2 = w_3 = 0.33$ (for height, diameter and tree form, respectively), (2) $w_1 = 0.25$, $w_2 = 0.25$ and $w_3 = 0.5$. Salto (2011) considered that index (2) would be the most appropriate given the economic importance of tree form.

We explored a higher number of scenarios searching for the condition that ensures near-maximum gain in all three traits rather than economic considerations. Our conclusion is that the best condition is $w_1 = 0.6$, $w_2 = 0.1$ and $w_3 = 0.3$, a relation that results from the relative gain of each trait and the correlation between them. With this strategy the expected gains of each trait are positive and the reductions in individual gains seem acceptable (~40 per cent compared with the maximum expected from selection on individual traits).

The significant heritability estimates of these traits indicate that they may be readily improved. The strategy to be applied depends on the relation among the expected gain on each trait, the number of selected individuals, the increase of inbreeding of the selected group and the relative weight of each trait in defining the best genotypes.

The outcrossing system in *P. alba* has an advantage in terms of diversity in the elite group, but it comes with a shortcoming if propagation material is obtained from open-pollinated seeds of top trees. As the progeny is sired by non-selected trees from inside and outside the orchard, extensive variation might be expected in the progeny as observed by Felker *et al.* (1983). The alternative strategies might involve controlled crosses or clonal propagation. Up to now, to our knowledge, only preliminary assays of controlled crossed have been conducted with *P. alba*, but the results are not communicated formally. By contrast, several clonal field trials for pod production and salinity tolerance have been successfully established (Felker *et al.*, 2001; Ewens and Felker 2010; Ewens *et al.*, 2012). Therefore, clonal propagation may be proposed as an efficient strategy to preserve improved characteristics without the risk of reduction in productivity due to segregation in the progeny of elite trees. Additionally more experiments on controlled crosses are required despite the technical difficulties associated with the small flower size and tight inflorescences, which prevent emasculation.

The relative weight given to each trait in order to rank individuals by applying a selection index based on BVs may affect the economic success of the breeding programme and adjustments may be applied on this criterion to include economic considerations.

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Conflict of interest statement

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