Genetic parameters of growth and survival in *Acacia saligna* shrubs

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**Abstract**

F. Mora, S. Perret, C.A. Scapim, and E. Arnhold. 2010. Genetic parameters for growth and survival in *Acacia saligna* shrubs. *Cien. Inv. Agr.* 37(2):5-14. Acacia species have valuable agronomic characteristics, such as the tolerance to unfavorable environmental conditions. In this study, genetic parameters and selection response in *Acacia saligna* shrubs were investigated in two arid environments of northern Chile: Cuz-Cuz and El Tangue. The quantitative traits were assessed in 5 year-old shrubs. A Bayesian approach, implemented using Gibbs sampling algorithm, was used in the data analysis. The tree survival was 87.3% and 81.8% in Cuz-Cuz and El Tangue, respectively, confirming the potential of *A. saligna* in northern Chile. The estimates of posterior mode of the heritability ranged from $h^2=0.13$ (survival) to $h^2=0.25$ (shrub crown diameter). Estimated genetic gain (individual tree selection) ranged from 6 to 14% (selection intensity of 20%). Bayesian credible intervals (p=95%) for genotype-environment correlations included zero, indicating a significant interaction for survival, crown diameter and height. Shrub selection in multipurpose planting will depend on optimizing economical traits by selecting genotypes that perform well on a particular environment.

**Key words**: Drylands, fodder production, *Acacia saligna*, multipurpose trees, Bayesian analysis.

**Introduction**

The species *Acacia saligna* (ex *Acacia cyanophylla*) is considered a tree resource of known aptitude for the establishment of agroforestry systems in arid environments (Hnatiuk and Maslin, 1988; McDonald and Maslin, 2000). Some physiological traits of *A. saligna* have favored the development of some mechanisms for drought tolerance (Nativ *et al.*, 1999; Tiedeman and Johnson, 1992), allowing the settlement of multipurpose plantations under adverse conditions of climate and soil (Degen *et al.*, 1995; Nativ *et al.*, 1999; Midgley and Turnbull, 2003; Mora and Meneses, 2004; George *et al.*, 2006). This species has been planted for forage and wood production, as ornamental plant, and for land rehabilitation and soil conservation (Degen *et al.*, 1995; McDonald and Maslin, 2000). In arid
ecosystems, the settlement of mixed systems of cultivation using trees or shrubs of *A. saligna* is useful for soil protection, allowing nitrogen fixation, providing wood and forage during the dry season (Tiedeman and Johnson, 1992).

In arid zones, primary productivity varies widely from an almost null productivity in extremely arid ecosystems, to values approaching dry tropical deciduous forests (Búrquez et al., 1999). Arid environments have a wide biodiversity of flora and fauna, and a heterogeneous landscape, but they have similar primary productivity due to the wide variation of rain and high rates of evapotranspiration, with abundant periods of drought (Wenninger and Inouye, 2008). These adverse conditions also occur in several countries of South America with continuous periods of drought, increasing soil salinity and desertification (Holmgren et al., 2006).

In Chile, the administrative Region of Coquimbo presents a proved potential for the development of large scale plantations of the species. It corresponds to a Mediterranean type zone with arid tendency, and it is located in the southern part of the Atacama Desert. According to Squeo et al. (2006) this Region presents critical productivity due to the continuous drought periods, which are affecting the social and economic activities of farmers; although previous studies have emphasized the fact that it is an appropriate Region to establish silvopastoral systems, improving the property productivity of agricultural systems (Ormazábal, 1991). Based on this principle, the Chilean Ministries of Agriculture and Economy have financed important projects with this species (Mora and Meneses, 2004; Meneses and Flores, 1999), as well as projects based on other forest alternatives associated to this cultivation (Mora and Perret, 2007; Mora et al., 2007). The Chilean governmental agencies have projected a potential surface of more than a million of hectares for plantations with this species; most of them susceptible to be covered with the Law Decree 701 for forest foster (Mora et al., 2004).

The establishment of provenance and progeny test trials is the first step for improvement programs of forest trees, which allow the identification of the best resources for soil rehabilitation and agroforestry production (Velarde et al., 2003). The genetic variability in genotypes of *A. saligna* is a key factor to improve productivity and survival in drought periods (George et al., 2006; Mora and Meneses, 2004).

The widest genetic diversity of *A. saligna* occurs in the Mediterranean Region in the South West of Australia, with a regime of precipitations varying between 0 (a 250) mm×year$^{-1}$ in the central part, to 1000 mm×year$^{-1}$ in the South Region (Howard et al., 2002). Provenances of forest trees with a wide geographic distribution generally show a significant variation in their anatomic, morphological and physiological traits. This genetic variability among populations may be researched *ex-situ* using agroforestry tests, which allow the identification of superior trees for multiple purposes (Beniwal et al., 1995). The forest plantation programs are usually intended for high biomass productivity, combining acceptable rates of growth and survival. Subsequently, the survival of trees in juvenile states of development has been a trait of interest in different programs of selection and improvement (Coutinho et al., 2004; Mora et al., 2009; Rodovalho et al., 2008).

The analytic objective of the present study was to examine genetic parameters of growth and survival for *Acacia saligna* shrubs, using the Bayesian inference, based on two genetic tests established for agroforestry rehabilitation and production, under the arid conditions in the South of the Atacama Desert, North of Chile.
Materials and methods

Description of the test and sites

This study was carried out in two sites located in Southern Atacama Desert, in the Region of Coquimbo (Figure 1). The site El Tangue is located in the Province of Elqui (30°45’ SL; 71°47’ WL) with an average temperature of 14 °C; on the other hand, the site Cuz-Cuz is located in the Province of Choapa (31°63’ SL; 71°22’ WL), with an average temperature of 15 °C. The sites (Figure 1) were selected based on the climatic conditions and on the previous experience of farmers cultivating A. saligna. The average regime of precipitation is frequently in the range of 100 and 200 mm year -1 in El Tangue and greater than 200 mm year -1 in Cuz-Cuz. The records of precipitation during the experimental period (1999-2004) were: average of 121.6 and 217.6 mm year -1, with minimum levels of 65 and 103 mm year -1, and maximum levels of 192 and 394 mm year -1, for El Tangue and Cuz-Cuz, respectively.

Vegetal material and quantitative traits

The provenances correspond to some of the base population maintained by CSIRO (CSIRO Australian Tree Seed Centre), which are from different localities of Australia (natural distribution of the species). The location of each population is shown in Table 1. The shrubs of A. saligna were measured at five years old considering: canopy diameter (CD), height (H), basal diameter (BD), and survival (measured as a binary response).

Statistical analysis and parameters estimation

The linear model representing the data from the experiment was the following:

\[ y = X\beta + aZ + P_p + \varepsilon \]

This corresponds to a bi-character model, where \( Y_1 \) and \( Y_2 \) are the vectors of observations for a specific trait in the environments 1 and 2, respectively, considering the effect of the genotype-environment interaction. \( X \) is the incidence matrix for the vector \( \beta \), which represents a vector with the Block and Site effects and associated interactions. \( Z \) is the incidence matrix of the vector of additive effects of the individual plants \( a \). \( P \) is the incidence matrix of the effects vector, due to the provenance \( p \). \( \varepsilon \) is the residual vector. The (co)variance components, heritability sensu stricto, and the prediction of the additive effects and provenances were researched by using Bayesian inference, implemented by means of the Gibbs algorithm.
With the Bayesian model, the variance matrices of genetic, provenance and residual effects have the following \textit{a priori} distribution, respectively:

\begin{align*}
G_* & \sim IW(G_0, v_g) \quad P_* \sim IW(P_0, v_p) \quad R_* \sim IW(R_0, v_r) \quad \text{OR:} \\

f(G_* \mid G_0, v_g) & \propto (G)^{-\frac{1}{2}(v + m + 1)} e^{-\frac{1}{2}tr(G^{-1}G_0^{-1})} \\
f(P_* \mid P_0, v_p) & \propto (P)^{-\frac{1}{2}(v + m + 1)} e^{-\frac{1}{2}tr(P^{-1}P_0^{-1})} \\
f(R_* \mid R_0, v_r) & \propto (R)^{-\frac{1}{2}(v + m + 1)} e^{-\frac{1}{2}tr(R^{-1}R_0^{-1})}
\end{align*}

where, $G_0$, $P_0$ and $R_0$ are the matrices with the \textit{a priori} values of the components of (co)variance. $v_*$ is the degree of Bayesian credibility and $m_*$ is the dimension of the scale parameter matrix. The \textit{a priori} distribution of $\beta$ was considered uniform (constant) and the vectors $a$ and $p$ normally distributed:

\begin{align*}
f(\beta) & \sim \text{Uniform} \\
f(a \mid G_*) & \sim N(0, G_*) \quad f(y \mid \beta, a, p, G_*, P_*) \sim N(X\beta + Za + Pp, R_*)
\end{align*}

The synthesized \textit{a posteriori} distribution is:

\begin{align*}
&f(\beta, a, p, G_*, P_*) \propto f(y \mid \beta, a, p, G_*, P_*) \cdot f(G_* \mid G_0, v_g) \cdot f(P_* \mid P_0, v_p) \cdot f(R_* \mid R_0, v_r) \cdot f(\beta) \cdot f(a \mid G_*) \cdot f(p \mid P_*) \\
&f(\beta, a, p, G_*, P_*) \sim N(X\beta + Za + Pp, R_*)
\end{align*}

In the case of survival, the statistical analysis considered the threshold model (Van-Tassell et al., 1998), whose model implemented corresponded to:

\[ \eta = [\eta_1 \quad \eta_2]^T = X\beta + Za + Pp + \varepsilon \]

where $\eta$ is the vector of a continuous randomized variable, normally distributed, non observable (unknown), and corresponding to the variable survival (in this case bi-character).

The program MTGSAM and its \textit{Threshold} version (Van-Tassell and Van-Vleck, 1996) were
used to obtain the further densities of the parameters of interest (Van-Tassell et al., 1998).

The initial size of the chain was determined in 500,000 samples, with withdrawal intervals to each 40 samples and a conservative period of initial discard (burn-in) of 100,000 samples of Gibbs. The seasonability of the Gibbs chains (convergence) was evaluated through the method of Heidelberger and Welch (1983), available in the statistical program R-CODA (Cowles and Carlin, 1995).

The a posteriori heritability or degree of additive genetic control was calculated in each test and for each trait, according to the following relation:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_p^2 + \sigma_e^2}$$

where $\sigma_a^2$, $\sigma_p^2$ and $\sigma_e^2$, correspond to the mode values of the a posteriori distributions of the additive, provenance and residual variances.

The additive genetic association (relation) for the same trait measured in two environments was calculated as:

$$r = \frac{\sigma_{xy}}{\sqrt{\sigma_{ax}^2 \cdot \sigma_{ay}^2}}$$

where $\sigma_{xy}$ the mode of the posterior distribution of the additive covariance is calculated between the characteristics $X$ e $Y$. $\sigma_{ax}^2$ and $\sigma_{ay}^2$ are the mode values of the a posteriori distributions of the additive variances of the traits $X$ and $Y$. An $r$ value close to 1 indicates a scarce genotype-environment interaction, while a value under $r$ (not significantly different from zero) indicates the significant existence of genotype-environment interaction, and the ranking may be different for each site (Sykes et al., 2006).

The predicted genetic gains were estimated using the genetic values of the individual trees (breeding values) according to Mora et al. (2009). Ranking with the genetic values were made and the associations between the rankings of each trait by means of the Spearman correlation coefficient, were measured.

**Results and discussion**

The mode values and the regions of credibility (95% of probability), of the a posteriori distributions of the components of variance and heritability are shown in Table 2. In the Bayesian context, the further distribution of the genetic parameters may be characterized by the median, mean and mode, which are considered as values of central tendency, and are potential point estimators. In the present study, the mode of the distributions of the parameters was considered as point measurement, according to Wright et al. (2000), who recommended this estimator to describe the further distribution. This is the Region of high density, that is, the value maximizing the function $f(h^2|y)$, or the most probable value of $h^2$ (Blasco, 2001).

The magnitude of the values of heritability was moderate. The canopy diameter and the tree height had the highest values of heritability in El Tangue, while the canopy diameter had the highest magnitude in Cuz-Cuz. The heritability values of survival were similar in both sites and presented the lowest magnitudes.

The genetic variability confirms high possibilities to improve traits of growth and forage productivity. That information is important for the start of a small-scale breeding program for the species in southern Atacama Desert. Agroforestry programs in arid zones using *A. saligna*, consider the physiological mechanisms inducing the susceptibility of the plants of water deficit (Nativ et al., 1999; McDonald and Maslin, 2000). Although *A. saligna* is highly tolerant to dry conditions (Nativ et al., 1999), the variability found for survival may be used to improve this tolerance to dry conditions.

The genetic variability found in the present study is coherent with the studies by George et al. (2006), who made a genetic analysis by molecular markers, and they found a large variation in *A. saligna*, although two groups of plants morphologically different had the same genetic
Table 2. Estimates of variance components, additive covariance (σ₁₂) which was estimated between environments, heritability (h₁²: El Tangue, h₂²: Cuz-Cuz), additive genetic correlation (r₁₂) of the same trait measured in different environment and predicted genetic gain in genotypes of Acacia saligna evaluated at the southern part of the Atacama desert.

<table>
<thead>
<tr>
<th></th>
<th>Crown Diameter</th>
<th></th>
<th>Height</th>
<th></th>
<th>Basal Diameter</th>
<th></th>
<th>Survival</th>
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<tr>
<td></td>
<td>Mo</td>
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<td>Mo</td>
<td>IC B</td>
<td>Mo</td>
</tr>
<tr>
<td>σ₁²</td>
<td>507.6</td>
<td>43.3</td>
<td>1521.2</td>
<td>706.6</td>
<td>27.3</td>
<td>1989.5</td>
<td>0.065</td>
</tr>
<tr>
<td>σ₁₁₂</td>
<td>143.9</td>
<td>-963.3</td>
<td>1608.4</td>
<td>422.3</td>
<td>-187.4</td>
<td>2340.2</td>
<td>0.009</td>
</tr>
<tr>
<td>σ₂²</td>
<td>843.0</td>
<td>35.3</td>
<td>3924.2</td>
<td>1095.7</td>
<td>24.0</td>
<td>3965.9</td>
<td>0.072</td>
</tr>
<tr>
<td>σ₁₂</td>
<td>1359.0</td>
<td>354.5</td>
<td>1994.2</td>
<td>1580.4</td>
<td>292.1</td>
<td>2400.0</td>
<td>0.073</td>
</tr>
<tr>
<td>σ₁ε</td>
<td>3876.2</td>
<td>746.7</td>
<td>5322.5</td>
<td>3407.1</td>
<td>446.1</td>
<td>4882.4</td>
<td>0.072</td>
</tr>
<tr>
<td>h₁²</td>
<td>0.25</td>
<td>0.02</td>
<td>0.76</td>
<td>0.25</td>
<td>0.010</td>
<td>0.69</td>
<td>0.013</td>
</tr>
<tr>
<td>h₂²</td>
<td>0.14</td>
<td>0.01</td>
<td>0.67</td>
<td>0.16</td>
<td>0.003</td>
<td>0.58</td>
<td>0.13</td>
</tr>
<tr>
<td>r₁₂</td>
<td>0.21</td>
<td>-0.34</td>
<td>0.81</td>
<td>0.36</td>
<td>-0.14</td>
<td>0.96</td>
<td>0.13</td>
</tr>
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</table>

σ₁² and σ₂² are the additive variances for a determined trait measured in El Tangue and Cuz-Cuz, respectively. σ₁ε and σ₂ε are the residual variances in a determined site. Mo: posterior mode. LI and LS, are the lower and upper cutoffs from the Bayesian credible intervals (ICB).

Survival is an important trait in the agroforestry systems with water deficit (Abebe, 1994). In the present study, the shrubs showed a high survival in both sites, with averages of 87.3 and 81.8% for Cuz-Cuz and El Tangue, respectively. These results are coincident with Abebe (1994), who compared the development of different multipurpose species appropriate for desertic zones, finding that the A. saligna shrubs had the best rates of survival, plant height, and trunk diameter under semiarid conditions in the Southern Ethiopia. In the present study, both sites are under the influence of climatic conditions affecting the competency for water resource and other limiting factors. Not only the plants of A. saligna may be affected by water shortage. According to Jara et al. (2006), in an El Niño southern oscillation event (ENSO; increased precipitation in relation to the average) the seeds from local plants that are dormant may germinate and cause a strong competency for water, nutrients, and light. 2002 was an ENSO year (Montecinos and Aceituno, 2003).
are shown in Table 3. The magnitude of the provenance-environment interaction depended on the trait. The interaction was significant, according to Bayesian credibility intervals, for the canopy diameter, basal diameter and survival. In both sites, the provenances of Murchison River and Greenough River had a high prediction for the canopy diameter; a trait significantly correlated with forage prediction (Mora and Meneses, 2004), although Greenough River presented a low value predicted for survival in El Tangue.

Murchison River in El Tangue presented a high value of prediction for the canopy diameter.

The Spearman correlation coefficients between the ranking of growth characteristics were posi-

<table>
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<tr>
<th>Crown diameter</th>
<th>Height</th>
<th>Basal diameter</th>
<th>Survival</th>
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<tbody>
<tr>
<td></td>
<td>Tangue</td>
<td>Cuz-Cuz</td>
<td>Tangue</td>
</tr>
<tr>
<td>P6-15795</td>
<td>P14-15828</td>
<td>P14-15828</td>
<td>P11-15806</td>
</tr>
<tr>
<td>P4-15791</td>
<td>P13-15822</td>
<td>P6-15795</td>
<td>P13-15822</td>
</tr>
<tr>
<td>P14-15828</td>
<td>P4-15791</td>
<td>P12-15810</td>
<td>P10-15803</td>
</tr>
<tr>
<td>P9-15800</td>
<td>P3-15789</td>
<td>P10-15803</td>
<td>P6-15795</td>
</tr>
<tr>
<td>P3-15789</td>
<td>P9-15800</td>
<td>P1-17971</td>
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</tr>
<tr>
<td>P5-15794</td>
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<td>P13-15822</td>
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$\hat{r}_{12} = 0.19 (-0.27-0.63)$

$\hat{r}_{12}$: intra-class correlation coefficient.

However, the Bayesian credibility interval of the intraclass correlation (provenance level) indicated a significant provenance-site interaction for that trait. The genotype-environment interaction was also evident in the genetic correlations determined at level of individual trees (Table 2). The Bayesian credibility intervals also included the value Zero of the additive genetic correlation (calculated between environments) for the traits of canopy diameter, height and survival.

The values of genetic gain varied between 6% (basal diameter) and 14% (survival) (Table 4), showing that important advances may be obtained in the process of selection. The annual harvest of *A. saligna* shrubs reduces the amount of forage for cattle, wood production, and may also reduce vigour, productivity, and life span of the tree (Tiedeman and Johnson, 1992). These responses may vary between genotypes, which is a significant fact for creating a program of genetic improvement under arid conditions of the Atacama Desert.
Understanding growth and mortality of trees, and how they affect productivity of silvipastoral systems, is fundamental for the success of any program of agroforestry improvement (Chambers et al., 1996). The results of the present study are consistent with the finding of Schneider et al. (2005), who found that mortality of other species of the Acacia genus was highly correlated to the traits of growth, with values of Pearson correlation coefficients varying from 0.49 to 0.73. In the present study, survival had a weak association with growth (measured by the rankings); although high values of prediction for Murchinson River in El Tangue, indicate the possibility of joint selection mechanisms between both traits. This result is relevant for this improvement program with *A. saligna*, as the genetic association between the growth rate and resistance to drought tends to be scarce, according to the studies by Coyle et al. (2006) and Schneider et al. (2005).

The genetic variability existing among these breeding populations may be used for selection and improvement purposes of traits of interest for the arid conditions of the North of Chile. It is suggested that the selection processes are not based only on growth, as it may affect the progress of other features of interest for the genetic program. In this regard, it would also be relevant to consider additional traits, such as the nutritional value of forage, improvement in the capacity of nitrogen fixation, or an increased capacity of capture of carbon dioxide, in order to increase productivity in continuous periods of drought. There is a genotype-environment interaction and it must be considered in the current program, by the selection of individuals (or genotypes) responding well in a particular site.

### Table 4.

Spearman correlation coefficients (N ~ 850 individual trees) calculated among classifications for each trait (Bootstrap confidence intervals between brackets) and predicted genetic gain, which was calculated considering the selection of 100 individual plants of *Acacia saligna* (selection intensity of 20%).

<table>
<thead>
<tr>
<th></th>
<th>Crown diameter</th>
<th>Height</th>
<th>Basal diameter</th>
<th>Survival</th>
</tr>
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<tbody>
<tr>
<td><strong>Spearman correlation</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Crown diameter</td>
<td>1</td>
<td>0.53 (0.46-0.60)</td>
<td>0.62 (0.56-0.68)</td>
<td>-0.06 (-0.16-0.03)</td>
</tr>
<tr>
<td>Height</td>
<td>----</td>
<td>1</td>
<td>0.59 (0.52-0.65)</td>
<td>0.01 (-0.08-0.01)</td>
</tr>
<tr>
<td>Basal diameter</td>
<td>----</td>
<td>----</td>
<td>1</td>
<td>-0.01 (-0.10-0.08)</td>
</tr>
<tr>
<td><strong>Predicted genetic gain (%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>El Tangue</td>
<td>8.48</td>
<td>9.12</td>
<td>6.04</td>
<td>9.92</td>
</tr>
<tr>
<td>Cuz-Cuz</td>
<td>7.93</td>
<td>9.42</td>
<td>7.14</td>
<td>14.25</td>
</tr>
</tbody>
</table>

**Resumen**

F. Mora, S. Perret, C.A. Scapim y E. Arnhold. 2010. Parámetros genéticos del crecimiento y sobrevivencia, en arbustos de *Acacia saligna*. Cien. Inv. Agr. 37(2):5-14. Las especies de acacia poseen características valiosas, como la tolerancia a condiciones ambientales desfavorables. En el presente estudio, se investigaron parámetros genéticos y la respuesta a selección en arbustos de *Acacia saligna*, en dos ambientes áridos del norte de Chile: Cuz-Cuz y El Tangue. Las características cuantitativas se evaluaron en arbustos de 5 años de edad. Para el análisis de datos se utilizó un enfoque Bayesiano, implementado usando el algoritmo de Gibbs. La sobrevivencia fue de 87,3 y 81,8% en Cuz-Cuz y El Tangue, respectivamente, confirmando el potencial de *A. saligna* en el norte de Chile. Las estimaciones de la moda a posteriori de la heredabilidad varió de $h^2=0.13$ (sobrevivencia) a $h^2=0.25$ (diámetro de copa). La ganancia genética (selección de árboles individuales) varió de 6 a 14% (intensidad de selección de 20%). Intervalo de credibilidad Bayesiano (p=95%) de las correlaciones genotipo-ambiente incluyeron...
el valor cero, indicando una significativa interacción para las características de sobrevivencia, diámetro de copa y altura. La selección de arbustos en plantaciones multipropósito, dependerá de la optimización de las características de interés a través de la selección de genotipos que responden bien en un sitio en particular.

**Palabras clave:** Zonas áridas, producción de forraje, *Acacia saligna*, árboles multipropósito, análisis Bayesiano.

**References**


