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Heritable leaf traits as indicators of drought tolerance in *Neltuma alba* for genetic improvement and ecological restoration

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Abstract

Climate change-induced droughts are pressing threats to forest species, especially in semi-arid regions like the Chaco, in South America. Developing drought-adapted genetic material for *Neltuma alba*, a keystone species for timber and silvopastoral systems, is crucial for restoration and sustainability. Current breeding often overlooks drought adaptation, and evaluating complex physiological traits is impractical at scale. This study investigated simple, heritable leaf morphological traits as indirect selection criteria for drought tolerance in *Neltuma alba*. We assessed 90 individuals from three natural populations under controlled drought, monitoring senescence and survival. Eleven leaf morphological traits were measured, and their narrow-sense heritability (h^2) was estimated. We then analyzed associations between these traits and drought response (BLUPs for senescence and survival). Results showed that leaf size traits (e.g., leaflet length, width, area) had moderate to high heritabilities (0.40–0.69) and were significantly associated with drought tolerance. Larger leaf sizes correlated with delayed senescence but potentially reduced long-term survival, indicating a functional trade-off between growth-oriented and survival-oriented strategies. These findings demonstrate that easily measurable, heritable leaf morphological traits can serve as reliable, low-cost indicators for drought tolerance in *Neltuma alba*. This provides a practical tool to accelerate early selection in breeding programs and optimize genetic resource management, even using herbarium material. Tailored selection schemes, accounting for the identified trade-offs, are essential for effective restoration and sustainable management of this vital species.

Keywords: Drought tolerance - Tree breeding - Leaf morphology - Ecological restoration - *Neltuma alba*

1. Introduction

Climate change is increasing the frequency and intensity of extreme events, such as prolonged droughts, particularly in semi-arid regions like the Chaco, in South America (IPCC 2023). These adverse conditions threaten the survival and productivity of native forest species, compromising both biodiversity and the ecosystem services they provide (Pörtner et al. 2023). In this context, ecological restoration and the development of genetic material adapted to water deficit have

become strategic priorities to strengthen ecosystem resilience and ensure the sustainability of productive systems.

Neltuma alba (syn. *Prosopis alba*), commonly known as white mesquite, is a keystone species in the ecological and economic systems of the region (Vega et al. 2024). Its importance lies both in the production of timber for industrial uses (sawn wood, carpentry, fence posts, charcoal) and in silvopastoral systems, where it provides shade, forage, and improves soil conditions through biological nitrogen fixation. Despite its ecological and productive relevance, there is a notable lack of propagation material specifically selected for drought stress adaptation, representing a critical gap in restoration and reforestation programs in arid and semi-arid environments. Previous breeding efforts in *Neltuma* (formerly *Prosopis*) have mainly focused on productive traits, such as stem quality or volume yield (López-Lauenstein et al. 2021; López-Lauenstein et al. 2024). However, drought adaptation has rarely been addressed as a selection criterion, limiting the availability of germplasm better suited to the current climatic context.

Forest tree breeding programs face numerous methodological challenges, including long life cycles, extended generation times, and the need to assess adaptive traits under highly variable environmental conditions. These factors hinder accurate estimation of genetic parameters and often lead to low precision and accuracy in field and progeny trials (Grattapaglia et al. 2018). Although several studies have identified physiological mechanisms of drought tolerance in *Prosopis* species (Villagra et al. 2010; Carevic 2014; Carevic et al. 2017) and their hybrids (López-Lauenstein et al. 2013), as well as local adaptive strategies in *Neltuma alba* (López-Lauenstein et al. 2025), their implementation into selection schemes has been limited. Many of these mechanisms, while relevant, are costly to evaluate, require specialized equipment, or are impractical for large-scale screening of extensive populations. Therefore, identifying simple, heritable leaf morphological traits associated with drought tolerance represents an efficient strategy for indirect selection, helping to accelerate breeding processes and reduce evaluation costs.

In a previous study, we demonstrated that *N. alba* exhibits intraspecific variation in traits related to leaf senescence and survival under controlled drought conditions, suggesting the existence of local adaptive strategies to water deficit (López-Lauenstein et al. 2025). From that work, BLUP values for both complex traits were estimated and are used here as indicators of drought adaptation. The present study aims to advance the practical application of these findings in breeding programs by exploring two complementary aspects: (1) the heritability of leaf morphological traits, and (2) their association with BLUPs for senescence and survival. Identifying heritable, predictive leaf traits for drought response would enable indirect selection schemes based on simple, low-cost measurements, including evaluations on preserved material from herbarium collections.

2. Materials and Methods

2.1 Plant material and experimental design

A total of 90 individuals of *Neltuma alba* were evaluated, representing three natural populations distributed along a gradient of mean annual precipitation (500–1100 mm). Leaves and fruits were collected from each sampled individual. The three populations and their geographic origins are described in Table 1.

Table 1 Sampling sites of *N. alba* populations.

Population	Morphotype*	Province	Latitude	Longitude	Altitude (m)	Annual mean precipitation (mm)	Annual mean temperature (°C)
R01	Salta Norte	Salta	22°12′1″S	63°40′33″W	500	1054	21.9
R05	Chaqueño	Formosa	24°15′58″S	61°54′0″W	180	678	22.8
R07	Santiagueño	Santiago del Estero	27°52′44″S	64°9′16″W	176	579	20.7

* Morphotype according to Verga et al. 2009; Verga 2013.

Seeds from each sampled tree were used to establish a progeny trial under controlled greenhouse conditions, where seedlings were subjected to a drought stress treatment. Seeds were sown in 400 cm^3 pots using vermiculite as a substrate, and irrigation was supplied using Hoagland nutrient solution (Hoagland and Arnon 1950). Individual plant responses were recorded by monitoring

leaf senescence and mortality over time, classifying seedlings into five drought stress response classes: Class 5 – plant with no visible drought stress symptoms, all leaves green; Class 4 – approximately 50% of leaves yellowing; Class 3 – approximately 50% of leaves shed; Class 2 – complete leaf shedding (100%); and Class 1 – seedling mortality. This classification was performed every three days from the onset of drought treatment until each plant reached Class 1 (dead). Based on the plant's status at each observation date, the number of days elapsed from the start of the drought treatment until the transition to each class was recorded. This approach transformed the categorical variable (Classes 5, 4, 3, 2, and 1) into four continuous variables: time (days) from drought initiation until reaching Class 4 (Phase_4), Class 3 (Phase_3), Class 2 (Phase_2), and Class 1 (Phase_1). A detailed description of the trial design and methods can be found in López-Lauenstein et al. (2025).

From each sampled tree, five compound leaves were selected for leaf trait measurements. For each leaf, the following morphological variables were recorded: petiole length (PEL), primary rachis (pinna) length (PIL), number of leaflet pairs per pinna (NLP), inter-leaflet distance (DIL), leaflet length (LEL), leaflet width (LEW), leaflet area (LEA), leaflet length-to-width ratio (L/W), leaflet apex area (LAPX), and total leaf area (TOTAR) (Fig. 1). Measurements were performed using the Hoja 3.4 software, specifically developed for morphometric quantification of leaf structures (Verga 2015).

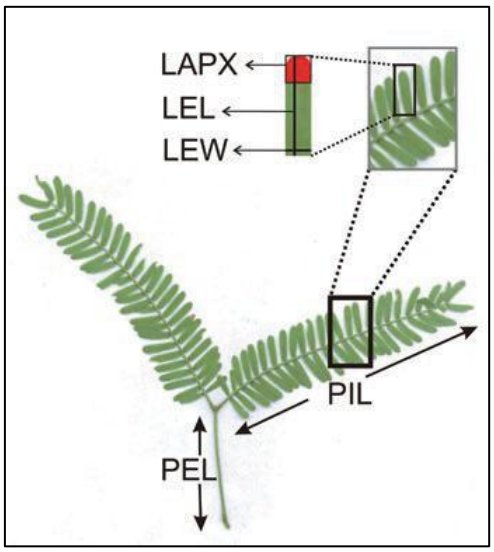


Fig. 1 Leaf morphological traits: petiole length (PEL), pinna length (PIL), leaflet length (LEL), leaflet width (LEW), leaflet area (LEA), leaflet apex area (LAPX). (Taken from Vega et al. 2020).

2.2. Statistical analyses

To explore associations among the evaluated leaf traits, a Pearson correlation matrix was calculated using the GGally package in R (version 4.4.1). A scatterplot matrix was generated, displaying pairwise correlations between variables along with frequency histograms for each trait on the diagonal.

A Principal Component Analysis (PCA) was performed using family mean values for ten morphological leaf traits (PEL, PIL, NLP, DIL, LEL, LEW, LEA, L/W, LAPX, and TOTAR) and two drought-tolerance variables (Phase_1 and Phase_4). The analysis was conducted in **InfoStat** (Di Rienzo et al. 2020). A biplot of the first two principal components (PC1 and PC2) was generated, showing both the contribution of each variable to the principal axes (represented by arrows) and the positioning of each family in the ordination space. Families were grouped by their population of origin: R01 (*), R05 (■), and R07 (▲).

Narrow-sense heritability (h^2) was estimated using linear mixed models fitted with the **ASReml-R** package (VSNi, 2023) in R (v4.3.2):

$$Y_{ijk}=\mu+A_i+R_{j(i)}+e_{ijk}$$

where:

- Y_{ijk} = trait value for the k-th replicate of the j-th individual in the i-th population
- μ = overall mean
- A_i = additive genetic effect of the individual (σ^2_A)
- $R_{j(i)}$ = replication effect (σ^2_R),
- e_{ijk} = residual error (σ^2_E)

Narrow-sense heritability (h^2) was then calculated as:

$$h^2 = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_E^2}$$

where:

- (σ^2_A) = variance among individuals (additive genetic component)
- (σ^2_E) = residual variance (environmental + experimental error)

2.3. Association between leaf traits and drought stress response

Associations between morphological leaf traits and drought stress response were evaluated using Pearson correlation coefficients, based on family mean values for each trait and the BLUP-estimated values for the drought response variables Phase_4, Phase_3, Phase_2, and Phase_1. Correlations were visualized using a heatmap, where the magnitude and direction of the associations are represented by a colour scale (positive values in purple and negative values in red).

For traits showing significant associations, simple linear regression models were fitted between the family mean of the trait and the BLUP values of Phase_1 or Phase_4. The corresponding scatterplots are shown in Figure 5, including the fitted regression line, the 95% confidence interval, and the R^2 and p-values for each model. All analyses were conducted in **R** (R Core Team 2023).

3. Results

3.1. Association among leaf morphological variables

Strong positive correlations were observed among several of the evaluated leaf traits (Figure 2). In particular, leaflet area (LEA) showed a very high correlation with leaflet length (LEL; r = 0.92) and leaflet width (LEW; r = 0.89), reflecting a close association between leaflet size and shape. Likewise, LEA was strongly correlated with total leaf area (TOTAR; r = 0.72), indicating that much of the variability in total leaf area is explained by the size of individual leaflets.

A high correlation was also detected between LEL and the leaflet length/width ratio (L/W; r = 0.72), as well as between L/W and LEA (r = 0.73), suggesting that leaflet shape is closely linked to its size. In contrast, the ratio of leaflet apex area (LAPX) did not show significant associations with other traits, indicating that this characteristic exhibit variability largely independent of the other leaf dimensions.

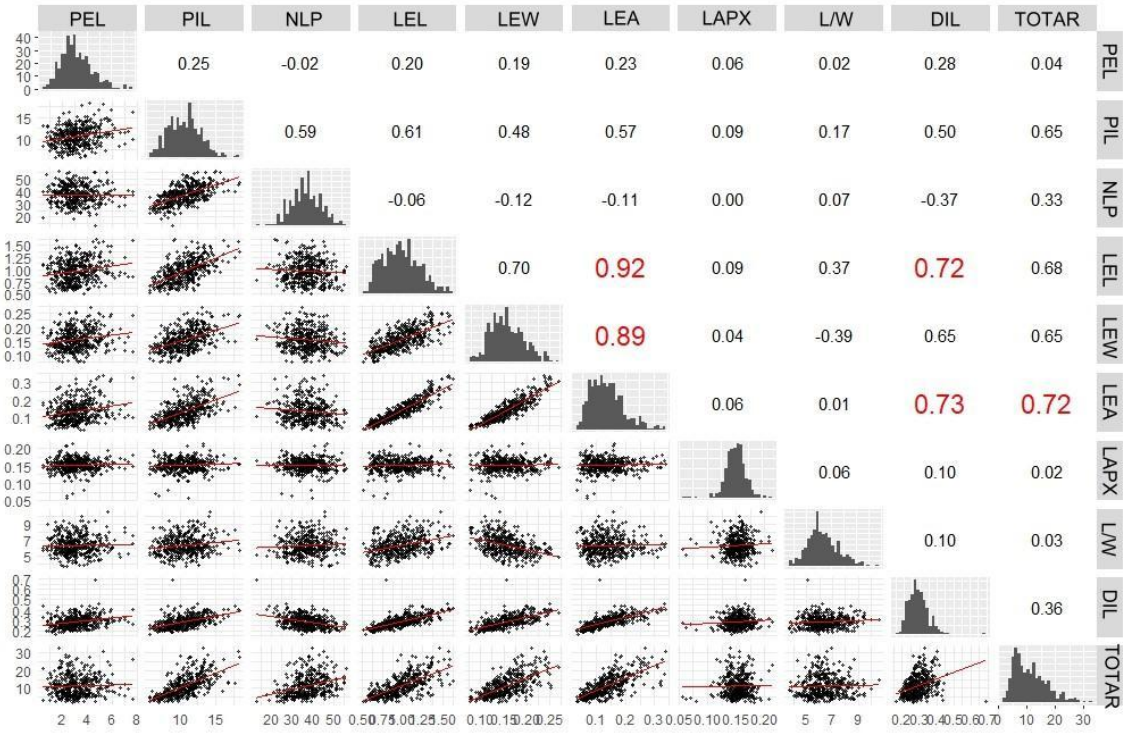


Fig. 2 Scatterplot matrix of leaf traits measured in *Neltuma alba*. Histograms for each variable are shown on the diagonal. Pearson correlation coefficients are presented in the upper panel; values in bold red indicate strong correlations (r > 0.70). Evaluated variables: PEL, PIL, NLP, DIL, LEL, LEW, LEA, L/W, LAPX, TOTAR.

3.2. Principal Component Analysis

The Principal Component Analysis (PCA) performed using family mean values explained 60% of the total variability through the first two components (PC1 = 45.4%, PC2 = 14.6%) (Fig. 3). PC1 was mainly associated with leaf size traits, such as leaflet length (LEL), leaflet width (LEW), leaflet area (LEA), estimated total leaf area (TOTAR), and petiole length (PEL), all oriented in the same direction. In the opposite direction were the number of leaflet pairs (NLP) and the leaflet

length-to-width ratio (L/W), indicating that these traits are relatively independent from size-related variables. The variables *Phase_1* and *Phase_4*, associated with drought stress tolerance, were partially aligned with PC1, suggesting a positive relationship between leaf size and the ability to delay senescence and mortality under drought conditions.

In the multivariate space, families from population R01 tended to cluster on the right side of the plot, associated with larger leaf size and greater drought tolerance. In contrast, populations R05 and R07 showed greater overlap, with smaller leaf sizes and broader variability among families.

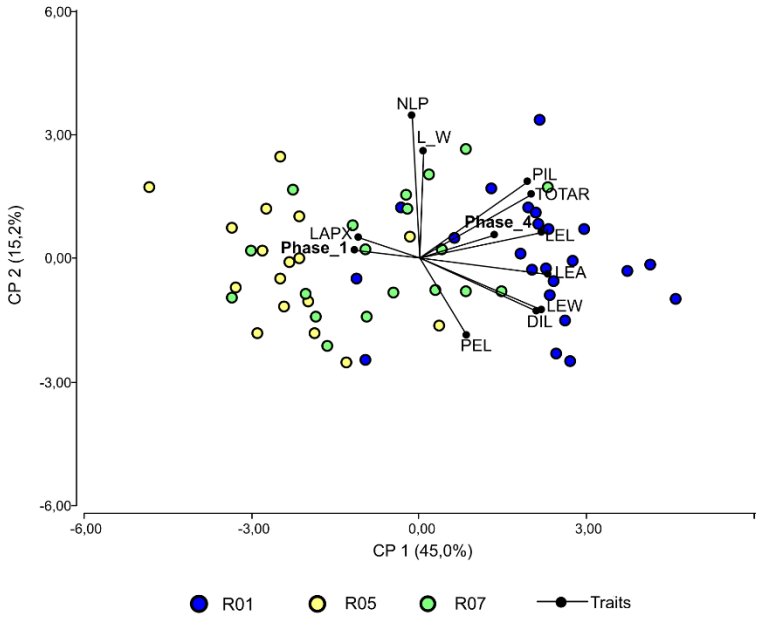


Fig. 3 Biplot of the first two principal components (PC1 and PC2) obtained from a Principal Component Analysis (PCA) based on family mean values of ten leaf morphological traits (PEL, PIL, NLP, DIL, LEL, LEW, LEA, L/W, LAPX, TOTAR) and two variables associated with drought stress tolerance (Phase_1 and Phase_4). Arrows indicate the contribution of each variable to the main axes. Symbols represent families grouped by population of origin: R01 (*), R05 (■), and R07 (▲).

3.3. Heritability of leaf traits

Traits related to leaflet size and area showed the highest narrow-sense heritability (h^2), indicating strong additive genetic control. In this regard, the leaf morphological traits with moderate to high

h^2 were: LEL, LEW, LEA, TOTAR, and L/W. Conversely, the shape of the leaflet apex, measured through the LAPX variable, exhibited very low variation and, therefore, very low heritability (Table 2).

Table 2 Estimates of mean, Standard Deviation (SD), Coefficient of Variation (CV), additive genetic variance (σ^2_A), residual variance (σ^2_E), and narrow-sense heritability (h^2) for leaf morphological traits in *Neltuma alba*.

Trait	Mean	SD	CV	(σ^2_A)	(σ^2_E)	h^2
LEL	0.970	0.230	23.820	0.037	0.017	0.692
LEW	0.160	0.040	24.030	0.001	0.000	0.657
LEA	0.140	0.060	43.590	0.002	0.001	0.649
TOTAR	11.310	5.820	51.510	21.172	12.836	0.623
L_W	6.370	1.190	18.710	0.872	0.551	0.613
DIL	0.290	0.060	20.020	0.002	0.002	0.509
PIL	10.570	2.320	21.920	2.163	3.225	0.401
NLP	37.240	7.210	19.350	19.108	33.038	0.366
PEL	3.130	1.270	40.490	0.576	1.042	0.356
LAPX	0.150	0.020	11.990	0.000	0.000	0.054

PEL (petiole length), PIL (pinna length), NLP (number of pairs of leaflets per pinna), DIL (distance between leaflets), LEL (leaflet length), LEW (leaflet width), LEA (leaflet area), L/W (leaflet length/width ratio), LAPX (leaflet apex area), TOTAR (total area)

3.4. Association with drought stress adaptation

Significant associations were detected between some leaf traits and the BLUPs for the onset of leaf senescence (Phase_4) and survival (Phase_1) (Fig. 4). Pinna length (PIL), distance between leaflets (DIL), leaflet length (LEL), leaflet width (LEW), leaflet area (LEA), and total leaf area

(TOTAR) were positively related to Phase_4 and negatively related to Phase_1. Figure 5 shows the scatterplots of the significant correlations ($p < 0.05$).

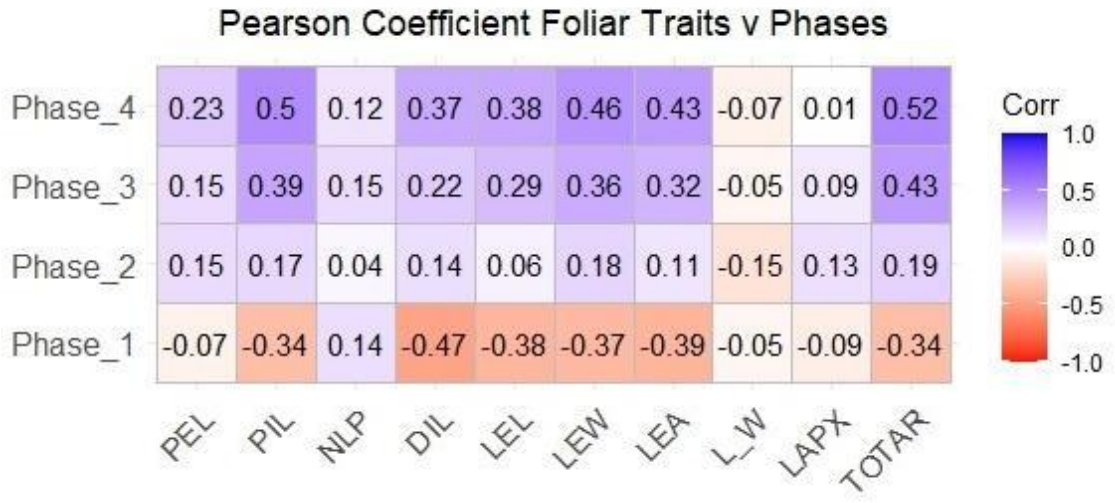
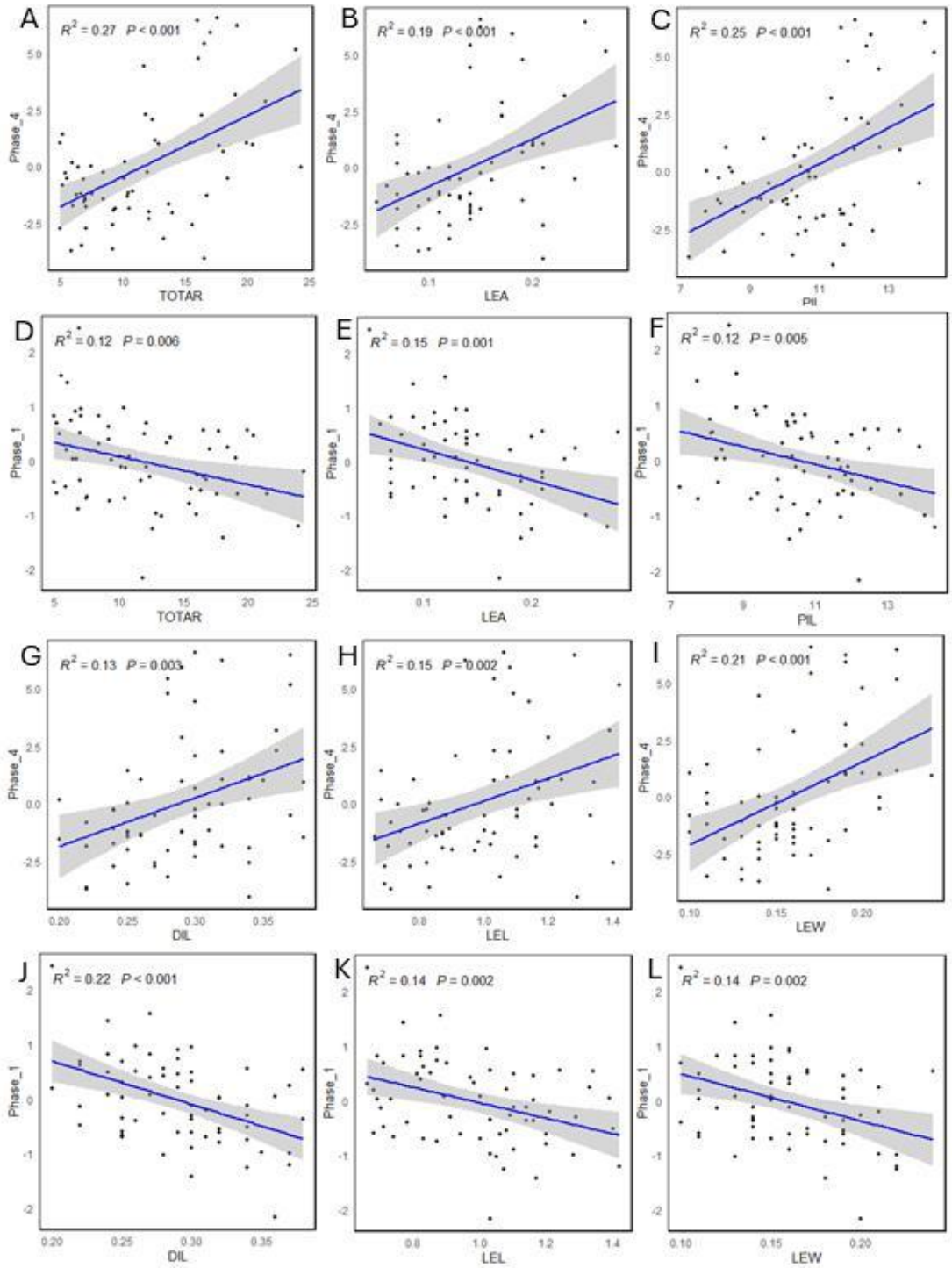


Fig. 4 Heatmap of Pearson correlation coefficients between drought response phases and foliar traits. Colors represent the magnitude and direction of correlations (positive values in purple and negative values in red). PEL (petiole length), PIL (pinna length), NLP (number of pairs of leaflets per pinna), DIL (distance between leaflets), LEL (leaflet length), LEW (leaflet width), LEA (leaflet area), L/W (leaflet length/width ratio), LAPX (leaflet apex area), TOTAR (total area).



221

222 **Fig. 5** Relationship between foliar traits and drought stress response phases. Each panel shows a
223 scatterplot with the fitted linear regression line (blue) and its 95% confidence interval (grey
224 shaded area). The coefficient of determination (R^2) and p value for each model are shown.

225

4. Discussion

Leaf morphological traits have traditionally been used for taxonomic classification. In *Prosopis*, Verga (1995) proposed 13 foliar traits to classify *P. chilensis*, *P. flexuosa* and to identify interspecific hybrids. Since then, these traits have been widely used for the identification and characterization of species, hybrids, and populations of *Prosopis* (Verga and Gregorius 2007; Verga et al. 2009; Bessega et al. 2015; Ferreyra et al. 2013; Joseau et al. 2013, Vega et al. 2020). However, beyond their taxonomic value, our results demonstrate that these traits also have a clear functional and adaptive value in relation to drought stress conditions.

Of the ten foliar traits analyzed, six showed significant associations with key indicators of drought tolerance: onset of leaf senescence (Phase_4) and survival (Phase_1). These traits —pinna length (PIL), distance between leaflets (DIL), leaflet length (LEL) and width (LEW), leaflet area (LEA), and total leaf area (TOTAR)— are directly related to leaf size and exhibited moderate to high heritabilities (0.40–0.69), indicating sufficient genetic control for improvement through selection. These values are consistent with previous studies in the same species, which reported heritabilities ranging from 0.11 for DIL to 0.87 for TOTAR (Camps-Mora et al. 2017), reinforcing their relevance as selection criteria.

The relationship between leaf size and drought stress response suggests the existence of a functional trade-off between survival and growth strategies, as has been widely described in ecological literature (Levitt 1980; Reich 2014). Plants with smaller leaves and reduced transpiring area tend to adopt a water-conservative strategy, showing higher Phase_1 values and thus greater survival under prolonged stress. However, this strategy limits growth potential by restricting the photosynthetic rate due to lower CO_2 uptake. In contrast, plants with larger leaves display a "water-spending" behavior, maintaining their photosynthetic capacity during the early stages of drought (high Phase_4 values) but compromising survival as the drought intensifies. This emerging pattern was evident in the opposite slopes of the correlations between foliar traits and Phase_1 versus Phase_4 (Fig. 4), revealing a clear functional axis synthesizing the divergent plant strategies in response to drought.

Genotype selection must consider the different intended uses. On the one hand, for productive plantations established in controlled environments or with irrigation available during the initial phase, it is desirable to select individuals with traits associated with higher growth rates and the maintenance of leaf area under moderate stress (i.e., high *Phase_4* values). Conversely, for large-scale ecological restoration initiatives in degraded areas, where resources are limited and no subsequent intervention is expected, priority should be given to selecting individuals with high survival capacity, which tend to exhibit early leaf senescence (high *Phase_1* values) and a more conservative water-use strategy. These results indicate that it is not possible to simultaneously optimize both objectives within the same selection program, since the traits that promote growth tend to compromise survival, and vice versa. Therefore, it becomes essential to develop distinct breeding lines or improvement programs according to the intended use and the productive or ecological goals pursued.

Our results further demonstrate that certain leaf morphological traits in *Neltuma alba* are heritable and are associated with greater drought tolerance. Because these variables can be easily measured in the field or even from herbarium material, they represent valuable tools for early selection in breeding programs. These findings complement and reinforce the results reported in our previous study (López-Lauenstein et al. 2025), which documented broad variation in senescence strategies among *N. alba* populations and genotypes. The integration of both approaches—drought-stress trials and morphological evaluation—enables the design of more efficient and cost-effective selection schemes, with direct implications for the genetic improvement and restoration of this key species.

Finally, genetic improvement programs, particularly those targeting forest species, require tools that accelerate and optimize the selection process. This study provides a methodology and the first steps in identifying leaf morphological traits that can assist both breeding and the management of genetic resources in natural populations. The identification of these traits associated with drought tolerance is a critical contribution, as it enables the classification of a much larger number of genotypes at low cost. In this regard, germplasm banks conserving *N. alba*

hold an invaluable resource: extensive herbarium collections that have not yet been characterized in terms of their drought-response behavior, which could be systematically assessed to enhance selection and conservation efforts.

In conclusion, this study demonstrates that simple, low-cost leaf morphological traits can serve as reliable indicators of drought tolerance in *Neltuma alba*, offering a practical and scalable tool for breeding and conservation**.** The clear trade-offs identified between growth-oriented and survival-oriented strategies underscore the need for tailored selection schemes that address distinct ecological and productive goals. By integrating morphological assessments with drought-response trials, we provide a framework to accelerate selection, reduce costs, and expand the range of genotypes evaluated, ultimately strengthening both restoration efforts and the sustainable management of *N. alba* genetic resources.

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