Diversity and selection of superior algarrobos (*Neltuma pallida*) phenotypes in the natural dry forests of Peru for sustainable conservation and genetic improvement

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ABSTRACT

Neltuma pallida (algarrobo) is a keystone species of the dry forest, faces threats that compromise its persistence, making its conservation and genetic improvement essential. This study aimed to identify outstanding phenotypes of algarrobo in localities of Piura and Tumbes through phenotypic characterization. A stratified random sampling was applied, and forest plots were established to evaluate individual trees. Dendrometric and phenotypic variables were recorded, complemented with physiographic, climatic, and edaphic information obtained through soil sampling and geographic information systems. Individuals were classified as superior when they exhibited outstanding characteristics in height, diameter, stem form, and fruit production, without unfavorable traits. High morphological variability was observed among populations, with notable differences in height, diameter, trunk form, and fruit production. Soil fertility significantly influenced phenotypic expression. Heritability coefficients were estimated for key traits, identifying those with higher genetic control and potential response to selection. As a result, eight outstanding individuals were identified that could be incorporated into a germplasm bank to initiate genetic improvement programs aimed at the ecological restoration and conservation of *N. pallida* in the Peruvian dry forest. This study provides a foundation for sustainable management strategies based on local genetic variability and the ecological knowledge of the Peruvian dry forest.

Keywords: biometry; conservation; genetic improvement; heritability; soil characterization

INTRODUCTION

Neltuma pallida, commonly known as algarrobo, belongs to the genus *Neltuma,* previously classified within *Prosopis* [1]. It is recognized as a valuable forest resource in arid and semi-arid regions [2] due to its ability to fix atmospheric nitrogen in soils [3], its longevity, and its durable hardwood of high economic value [4]. From an ecological perspective, algarrobo enhances soil fertility and moisture retention, moderates extreme conditions by creating microclimates beneath its canopy [5], and contributes to the stabilization of fragile desert ecosystems through processes of desalination and microclimatic amelioration [4]. In addition, the species plays a role in climate change mitigation through atmospheric carbon sequestration [6].

In Peru, it is mainly distributed within the Equatorial Dry Forest, which occupies approximately 3.45% of the national territory and represents about 61% of the vegetation cover of dry ecosystems [7]. This biome extends primarily across the departments of La Libertad, Lambayeque, Piura, and Tumbes [8], where the species constitutes an essential structural and functional component. However, these northern Peruvian regions have been severely affected by deforestation and land-use change processes [9], resulting in pronounced habitat fragmentation and a reduction of natural populations of *Neltuma pallida* (algarrobo). Given this scenario, monitoring and conservation actions have become imperative [9], especially since algarrobo has been declared a priority species for research, conservation, and protection by the Peruvian government [10]. In this context, genetic and morphological characterization studies are critical, as they allow for the precise distinction of species or local ecotypes and the design of conservation strategies focused on populations with higher adaptive value or greater risk of extinction [11]. Achieving adequate characterization requires the evaluation of both quantitative and qualitative attributes. Beseega [12] emphasized that individual selection has major implications for genetic resource management and that adaptive phenotypic traits, as well as population origin, should be carefully considered before initiating any selection program. In this regard, phenotypic evaluation is a key step in identifying superior trees [13] - individuals with superior phenotypes in one or more economically important traits that may serve as progenitors in genetic improvement and conservation programs [14–16]. In general, traits selected for breeding should (a) exhibit strong genetic control, (b) display high genetic variation, and (c) preferably be easy to measure [17].

The effectiveness of phenotypic characterization and tree selection is supported by numerous studies, where phenotypically outstanding trees for one or more economically valuable traits [15] have been successfully used for both conservation and genetic improvement [18,19]. Heritability is a population - and site - dependent parameter, with estimates varying according to the families included in the assessment, tree age, and the testing environment. This parameter expresses the proportion of variance attributable to genetic transmission from parents to offspring, with values ranging from 0 to 1 [20]. For *Neltuma chilensis,* Chequer [21] reported moderate heritability for traits such as biomass ($h^2 = 0.28$) and spine length ($h^2 = 0.22$), emphasizing the importance of considering both provenance and intrafamily variability to maximize genetic gain. Complementary work by López [22] on *Neltuma alba* under drought stress demonstrated the relevance of functional intraspecific diversity and local adaptation, identifying distinct physiological strategies of drought tolerance linked to leaf morphological traits and genetic variation. These findings reinforce the need to prioritize provenances adapted to changing environmental conditions. Likewise, in species such as *Swietenia macrophylla* [23] and *Cedrela odorata* [24], heritability estimates have been used to prioritize genotypes of high genetic value.

Despite its ecological and productive significance, *Neltuma pallida* (Humb. & Bonpl. ex Willd.) Hughes & G.P. Lewis [1] still lacks integrated studies addressing phenotypic characterization, local adaptation, and identification of superior trees in natural populations. To address this gap, the present study aims to characterize algarrobo (*Neltuma pallida*) in populations from Piura and Tumbes, through the evaluation of phenotypic traits, edaphoclimatic conditions, and heritability estimates, with the objective of identifying trees with potential for inclusion in future genetic improvement and conservation programs.

MATERIALS AND METHODS

Study Area

The evaluations of qualitative and quantitative traits of *Neltuma pallida* were conducted in 13 localities distributed across the departments of Piura and Tumbes, in northwestern Peru (Figure 1). In Tumbes, sampling was carried out in the districts of Zorritos (Contralmirante Villar Province), San Jacinto, and Corrales (Tumbes Province), encompassing the localities ISA REP, Pedregal, and Bosque Marginal (Zorritos), Rica Playa (San Jacinto), and INIA (Corrales). In Piura, the evaluations were performed in the districts of Marcavelica and Sullana (Sullana Province), La Matanza and Chulucanas (Morropón Province), and Veintiséis de Octubre (Piura Province). The localities considered were Fundo Valdez (Sullana), Saman Chico (Marcavelica), SENASA and CC Ignacio Távara (Chulucanas), Kurt Beer (Veintiséis de Octubre), and Km 190, Chamchape, and Monte Azul (La Matanza).

Both departments are located within the tropical dry forest ecoregion [7], the natural habitat of *N. pallida.* Piura lies between 4°05′ and 6°22′ S latitude and 79°00′ and 81°07′ W longitude. In the study sites of this department, the average maximum temperature reaches 38.1 °C, while the mean minimum temperature is 15.7 °C. Rainfall is seasonal and scarce, with an annual average of 226.7 mm [25]. Tumbes is situated further north, between 3°22′56.81″ and 4°19′3.48″ S latitude and 80°2′46.90″ and 80°7′37.43″ W longitude. Study sites in this region recorded an average maximum temperature of 37.5 °C and a mean minimum of 17.7 °C. As in Piura, rainfall is seasonal, but with higher accumulation, reaching an annual mean of 324.5 mm [25].
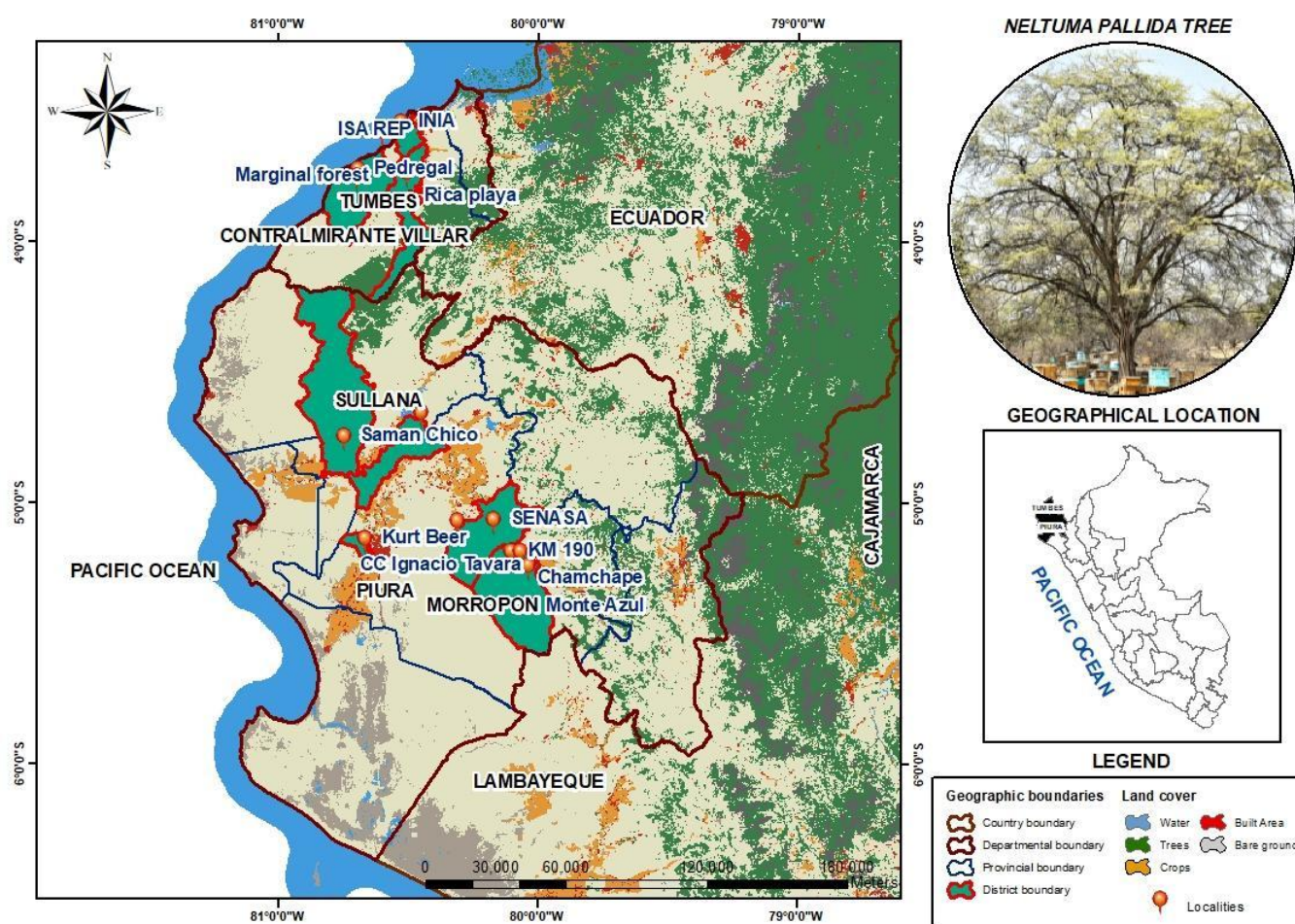

Figure 1: Geographic distribution of the 13 study sites where *Neltuma pallida* was evaluated in Piura and Tumbes, northwestern Peru.

Tree sampling methodology

A stratified random sampling design was employed, establishing plots in each study locality that exhibited relatively homogeneous habitat conditions. Within these areas, sampling units were randomly selected, prioritizing zones with higher individual density and greater canopy cover. Areas were considered when they contained trees taller than 5 meters and a canopy cover greater than 10%, or when they included individuals with the potential to reach these parameters under in situ conditions [26].

The sampling unit consisted of a 0.5 ha forest plot (5,000 m²), which corresponds to the area recommended for forest inventories in dry forests of Peru's coastal region [27] . Each plot measured 250 m × 20 m, following established technical criteria. Within each plot, 10 subplots of 50 m × 10 m were delineated, where all individuals with a diameter at breast height (DBH) ≥ 10 cm were recorded [28]. The evaluation included both adult trees and saplings, and their main morphological and phenotypic characteristics were recorded. In total, 631 individuals were evaluated.

Edaphoclimatic data collection

Soil variables were collected directly in the field. Prior to soil sampling, an exploratory survey was conducted in each study area to identify homogeneous zones in terms of relief, surface color, texture, and land-use type. Based on this preliminary characterization, a random sampling design was applied following a zigzag pattern. At each sampling point (every 15–30 steps), a subsample was extracted with a shovel at a uniform depth of 20–30 cm according to the root depth. For each hectare, between 20 and 30 subsamples were collected and deposited in a clean plastic bucket, mixed thoroughly, and homogenized to form a composite sample [29]. The mixture was subsequently quartered until an approximate volume of 1 kg was obtained. During this process, visible residues of fresh organic matter, stones, and gravel were removed. The final sample was stored in a double clean plastic bag, properly labeled with essential information (identification code, geographic location, sampling date) and hermetically sealed. Samples were then transported to the laboratory for subsequent physicochemical analysis.

Climatic variables were obtained from NASA's Prediction Of Worldwide Energy Resources [25] database, accessed on 22 July 2025. The geographic centroid of each locality was used as a reference point for data extraction, considering the period 2015–2024 for analysis. Physiographic variables were derived from Geographic Information Systems (GIS): slope and elevation were extracted from a Digital Elevation Model (DEM) with a spatial resolution of 12.5 m, while distance to water bodies was estimated using Euclidean distance from Peru's official hydrographic network.

Table 1: Description of the edaphoclimatic characteristics of the study localities distributed across the departments of Piura and Tumbes. CaCO$_3$: calcium carbonates; EC: electrical conductivity; P: phosphorus; OM: organic matter; N: nitrogen; K: potassium; pH: hydrogen potential; CS: incoming solar radiation; pp: precipitation; RH: relative humidity; Tmean: mean temperature; WS: wind speed; Tmax: maximum temperature; Tmin: minimum temperature; SLI: elevation above sea level; Slope: slope; DW: Euclidean distance to water bodies.

	Variable	Minimum	Maximum	Mean	Deviation
Edaphic	CaCO$_3$ (%)	0.09	2.1	1.03	0.7
	EC (dS/m)	0.03	7.69	0.78	2.08
	P (ppm)	8.42	250.1	84.88	94.85
	OM (%)	0.19	6.7	2.29	2.31
	N (%)	0.03	0.2	0.09	0.04
	K (ppm)	11.1	1321.13	415	396.57
	pH	5.59	8.68	7.37	1.01
Climatic	CS (MJ/m²/day)	11.2	11.4	11.32	0.09
	pp (mm/day)	190.8	495.6	264.31	86.83
	RH (%)	60.4	73.1	62.59	3.33
	Tmean (°C)	22.9	26.3	25.25	0.97
	WS (m/s)	2.1	4	3.18	0.66
	Tmax (°C)	31.4	39.3	37.85	2.15
	Tmin (°C)	14	20.4	16.45	1.49
Physiographic	SLI (m)	5	180	71.08	50.16
	Slope (%)	0.33	5.13	2.61	1.49
	DW (m)	14.17	2817.37	751.48	894.24

Phenotypic evaluation

Each evaluated tree was assigned a sequential identification number based on the order of registration within the plot. This number was recorded in the field form and served as a unique code for all subsequent measurements. Following an adaptation of the criteria established by Alban [30], data were collected on dendrometric and phenotypic variables. Tree heights were measured using hypsometers, while DBH and crown diameters were measured with metric tapes. The recorded variables included: total tree height (m); height of the first branching (m); diameter at breast height (DBH, cm), measured at 1.30 m above ground level with adjustments for tree morphology (e.g., bifurcations, sloping terrain); and crown diameter (m), calculated from the average of the longest and shortest crown diameters. In addition, qualitative traits were evaluated, including tree form, stem quality, branching pattern, fruit production, fruit quality, and foliage quality. Fruit quality was evaluated using pods at a uniform stage of physiological maturity, collected during the same phenological period. This approach minimized variation associated with sampling time. In addition, Brix degrees were determined in the laboratory under standardized conditions, ensuring comparability among samples.

Table 2: Qualitative evaluation scale of morphological and functional traits in *Neltuma pallida* individuals, following the criteria of Alban [30].

Variable	Evaluation criteria
Tree form	1 = Multi-stemmed (<1.2 m) with branches >30°
	2 = Intermediate
	3 = Single stem (<1.2 m) with branches ≤30°
Trunk quality	1 = Defective
	2 = Fair with defects
	3 = No defects or only minor defects
Forking	1 = Below DBH
	2 = At DBH
	3 = No branching
Fruit production	0 = No fruits
	1 = Up to 25% of the branches
	2 = Up to 50%
	3 = Up to 75%
	4 = Up to 100%
Fruit quality	0 = Very bitter
	1 = Bitter
	2 = Sweet
	3 = Very sweet
Foliage quality	1 = Foliage on up to 1/3 of the branches
	2 = Up to 2/3 of the branches
	3 = Full foliage on all branches

Identification of superior trees

The selection of superior trees was based on an integrative approach that considered both quantitative and qualitative attributes. A scoring system was established using rank ranges for each type of variable in order to identify individuals with outstanding phenotypic traits. For qualitative variables, individuals that scored greater than or equal to three on the evaluation scale (Table 2) were selected. For quantitative variables, individuals with the highest values were prioritized (Table 3). Any tree that exhibited at least one unfavorable characteristic (scores ≤ 1) was excluded from the selection process, as it did not meet the minimum criteria for consideration as superior genetic material.

The selection objective for *Neltuma pallida* focuses on pod production, in contrast to timber species, where a straight, unbranched stem is prioritized [30]. In *N. pallida* broad and well-branched crowns are valued, as they promote greater fruit production. This type of selection is more complex due to the trade-off between vegetative growth and pod yield. Therefore, traditional dasometric measurements were combined with a visual assessment based on verifiable criteria to identify individuals with the highest productive potential [30] .

Younger trees were not considered, as their development is strongly influenced by other growth variables. Consequently, juvenile individuals were not classified as suitable for this selection process [15].

Table 3: Scoring ranges for quantitative variables used in the selection of *Neltuma pallida* superior tree candidates.

Variable	Score Ranges
Diameter at breast height (DBH) (cm)	1 = 10–35 cm
	2 = 36–60 cm
	3 = 61–85 cm
	4 = >86 cm
Total height (m)	1 = 4.0–9.0 m
	2 = 9.1–14.0 m
	3 = 14.1–19.0 m
	4 = 19.1–24.0 m
	5 = 24.1–29.0 m
Branch height (m)	1 = 0–2.0 m
	2 = 2.1–4.0 m
	3 = 4.1–6.0 m
	4 = 6.1–8.0 m
	5 = >8.1 m
Crown diameter (m)	1 = 0–5.0 m
	2 = 6.0–10.0 m
	3 = 11.0–15.0 m
	4 = 16.0–20.0 m
	5 = >21 m

Heritability

Broad-sense heritability (H²) and the variance components of phenotypic variation were estimated for *Neltuma pallida* populations according to the Cullis [31] approach. Where a linear mixed model was implemented proposed by [32]. To calculate the Best Linear Unbiased Estimators (BLUEs) a linear mixed model was implemented including locality as fixed effects, which is appropriate for hierarchical structures and unbalanced data [33]. The model implemented was the following (Supplementary File 1):

Random model:

$$y_{ijk} = \mu + \left(1|\text{province}_k\right) + \left(1|\text{locality}_j\right) + \varepsilon_{ijk}$$

Fixed model:

$$y_{ijk} = \mu + \left(1|\text{province}_k\right) + \text{locality}_j + \varepsilon_{ijk}$$

Where y_{ijk} represents the observation of trait i in locality j and province k, and ε_{ijk} is the residual error term. The number of replicates was set at eight, corresponding to the maximum number of evaluated localities. To evaluate the balance between genetic signal and environmental noise in the locations we used the ratio index normalized with respect to (V.g):

$$\text{Ratio} = V_g : V_p : V_e$$

Where: V.g represent genetic variance, V.p the total phenotypic variance and V.e as environmental or error variance.

Data processing and statistical analysis

All statistical analyses and graphical outputs were conducted in R software, version 4.5.0 [34]. The coding workflow, data analysis, and computational environment were implemented in Quarto [35], an integrated system for scientific writing and data analysis (Supplementary Material 1).

For multivariate analyses, data were standardized (mean = 0; variance = 1) to homogenize variable scales and reduce bias from differing units of measurement [36]. Principal component analysis (PCA) was employed to explore multivariate relationships among edaphoclimatic variables and localities, as well as among phenotypic variables, localities, and individuals. PCA was performed using the packages *FactoMineR* [37] and *factoextra* [38].

Phenotypic diversity of qualitative variables was quantified using the Shannon–Weaver diversity index (H′), implemented with the *vegan* package [39]. Quantitative variables were analyzed using one-way analysis of variance (ANOVA), and group mean comparisons were conducted with Tukey's HSD test at a significance level of α = 0.05, implemented through the *emmeans* package **[40].** To identify patterns in the multivariate data and visualize similarity structures among localities, hierarchical heatmaps were generated using the *heatmaply* package [41]. Prior to visualization, data were column-normalized, and hierarchical dendrograms were constructed using Euclidean distance matrices.

Genetic parameters and broad-sense heritability (H²) were calculated using the *H2cal()* function implemented in the *inti* package [42], which integrates fixed and random effects through the *lme4* package [43]. Outlier removal was performed (*outliers.rm* = TRUE), and diagnostic plots were generated (*plot_diag* = TRUE).

RESULTS

Edaphoclimatic characterization

The principal component analysis (PCA) showed that the first two components jointly explained 59.40% of the total variability of the system, with 39.90% corresponding to the first component (Dim 1) and 19.50% to the second component (Dim 2). In Dim 1, the variables with the highest contribution were Hydrogen potential (pH) (12.40%), Calcium carbonate ($CaCO_3$) (11.22%), and Phosphorus (P) (11.12%). In Dim 2, the greatest contributions came from Maximum temperature (Tmax) (23.67%), Precipitation (pp) (21.54%), and Relative humidity (RH) (20.37%).

In the factorial plane, the edaphic variables Nitrogen (N), Phosphorus (P), Potassium (K), and Organic matter (OM) exhibited a positive association with each other and were projected toward the positive quadrant of Dim 1. In contrast, pH and Calcium carbonate ($CaCO_3$) were oriented in the opposite direction, indicating a negative relationship with the former variables. Among the climatic variables, Minimum temperature (Tmin), Precipitation (pp), and Relative humidity (RH) shared a common orientation, whereas Incident solar radiation (CS) was aligned toward the opposite region. Regarding the physiographic variables, no clear pattern of association was observed.

The spatial distribution of localities reflected distinct environmental gradients. Monte Azul and Chanchape clustered in the region associated with higher contents of N, P, K, and OM. Conversely, Rica Playa, Pedregal, and Marginal forest were located near the vectors of pH and $CaCO_3$, suggesting soils with greater alkalinity and carbonate content. Along the climatic gradient, Rica Playa, Pedregal, and Marginal forest were associated with higher values of precipitation (pp), Tmax, Tmin, and (Mean temperature) Tmean. Relative humidity (RH) was lowest in Rica Playa, Pedregal, and Marginal forest, while Monte Azul and Chanchape displayed intermediate values. The CS was higher in Monte Azul and Chanchape but lower in Rica Playa, Pedregal, and Marginal forest.

Regarding physiographic characteristics, Pedregal, KM 190, and Fundo Valdez were located closer to water bodies (DW), whereas Kurt Beer, Chanchape, and SENASA were situated at greater distances. The highest elevations (SLI) were recorded at CC Ignacio Távara, KM 190, and Monte Azul, in contrast to Pedregal and INIA, which were positioned at lower elevations.
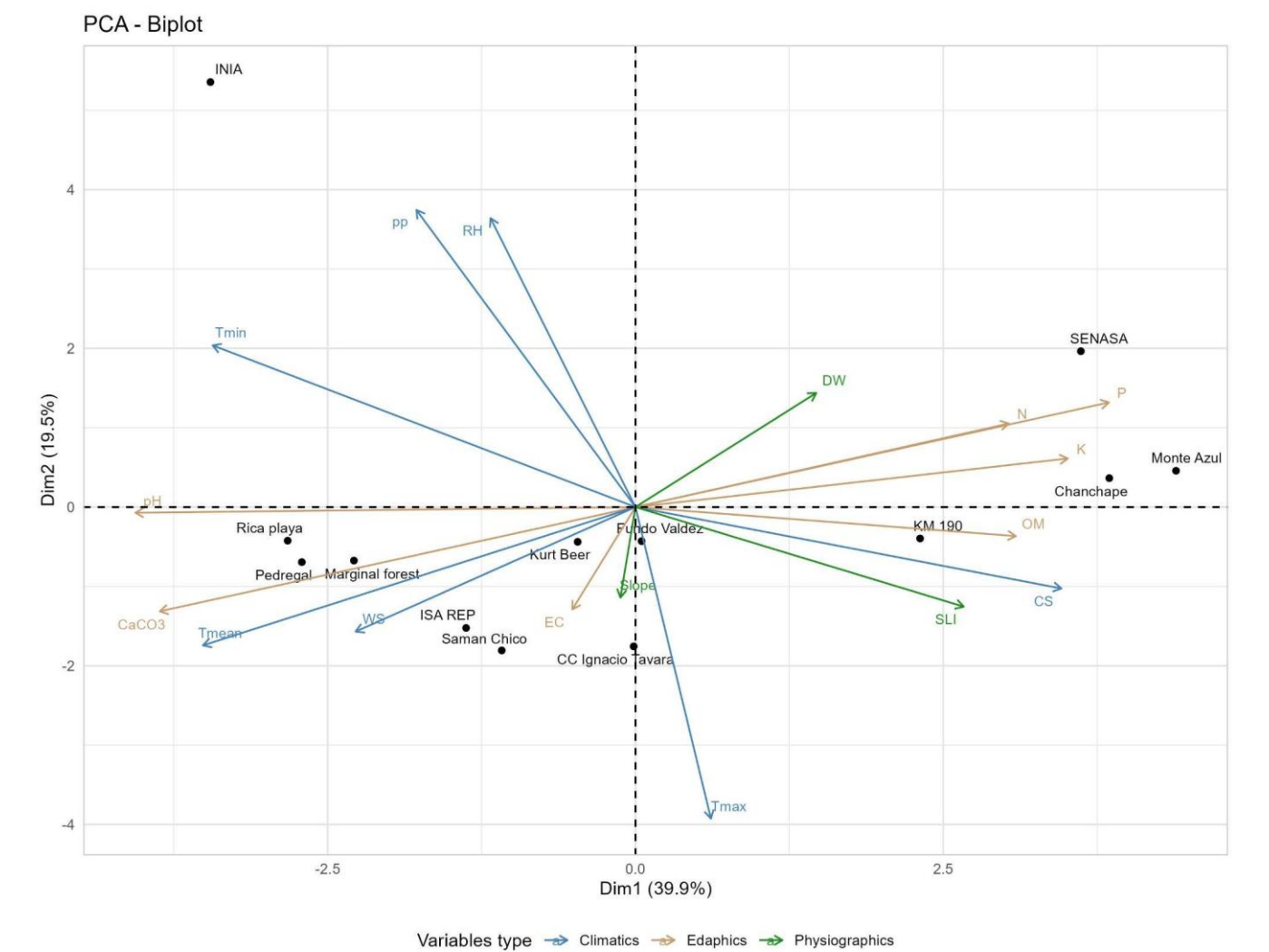
Figure 2: Principal component analysis (PCA) of edaphoclimatic properties in *Neltuma pallida* populations evaluated in the departments of Piura and Tumbes. Projection of edaphoclimatic variables and study localities onto the first two principal components, which together explain the largest proportion of total system variance (n = 631). Description of environmental variables: Calcium carbonate (CaCO₃, %), Electrical conductivity (EC, dS/m), Phosphorus (P, ppm), Organic matter (OM, %), Nitrogen (N, %), Potassium (K, ppm), Potential of hydrogen (pH), Solar radiation (CS, MJ/m²/day), Precipitation (PP, mm/day), Relative humidity (RH, %), Mean temperature (Tmean, °C), Wind speed (WS, m/s), Maximum temperature (Tmax, °C), Minimum temperature (Tmin, °C), Elevation above sea level (SLI, m), Slope (Slope, %), and Euclidean distance to water bodies (DW, m).

Morphological diversity

The phenotypic states, relative frequencies, and Shannon–Weaver diversity index (H′) values for the qualitative traits evaluated are presented in [Table 4](#). Considerable polymorphism was observed across qualitative traits, revealing notable phenotypic variability within *Neltuma pallida* populations. H′ values ranged from 0.55 to 1.30, with an overall mean of 1.01, indicating a high level of phenotypic diversity among the evaluated traits. This index reflects both the richness and evenness of phenotypic classes within each character.

The traits with the greatest diversity were fruit production (H′ = 1.30), tree form (H′ = 1.09), stem quality (H′ = 1.09), foliage quality (H′ = 1.07), and fruit quality (H′ = 1.00). All of these exceeded 1.0, suggesting a relatively even distribution

across their phenotypic categories. In contrast, branching exhibited moderate phenotypic diversity, with a value of H' = 0.55.

In terms of frequency distributions, tree form was dominated by individuals with intermediate morphology (37.88%), defined as trees with traits between a single stem with narrow branch angles (≤30°) and multistemmed forms with wider branching angles (>30°). For stem quality, the "moderate" class predominated (39.30%), representing trees with defects affecting 10–40% of the bole. Regarding fruit production, more than half of the trees evaluated (52.61%) did not produce fruits, while in fruit quality the "bitter" category was most frequent (53.41%). In foliage quality, the largest proportion of individuals (42.00%) exhibited foliage covering up to two-thirds of branches. Finally, branching showed a clear trend toward absence, with 83.04% of individuals lacking bifurcation.

Table 4: Phenotypic diversity of qualitative traits in *Neltuma pallida* populations from Piura and Tumbes. Observed states of qualitative descriptors and Shannon–Weaver diversity index (H′) values are presented for each trait. Diversity levels were categorized as low (H′ = 0.10–0.40), intermediate (H′ = 0.40–0.60), and high (H′ > 0.60). The analysis was based on 631 observations (n = 631).

SN	Qualitative traits	Shannon-Weaver index	Descriptor's states	Frequency	Proportion (%)
1	Tree form	1.09	1 = Multi-stemmed (<1.2 m) with branches >30°	195	30.9
			2 = Intermediate	239	37.88
			3 = Single stem (<1.2 m) with branches ≤30°	197	31.22
2	Trunk quality	1.09	1 = Defective	195	30.9
			2 = Fair with defects	248	39.3
			3 = No defects or only minor defects	188	29.79
3	Forking	0.55	1 = Below DBH	25	3.96
			2 = At DBH	82	13
			3 = No forking	524	83.04
4	Fruit production	1.3	0 = No fruits	332	52.61
			1 = Up to 25 % of the branches	93	14.74
4	Fruit quality	1	2 = Up to 50 %	117	18.54
			3 = Up to 75 %	52	8.24
			4 = Up to 100 %	37	5.86
5	Fruit quality	1	0 = Very bitter	337	53.41
5	Foliage quality	1.07	1 = Bitter	14	2.22
			2 = Sweet	223	35.34
			3 = Very sweet	57	9.03
6	Foliage quality	1.07	1 = Foliage on up to 1/3 of the branches	139	22.03
			2 = Up to 2/3 of the branches	265	42
			3 = Full foliage on all branches	227	35.97

Phenotypic diversity in quantitative traits

To evaluate phenotypic diversity in quantitative traits, variability was analyzed across localities. The results revealed pronounced heterogeneity in the performance of the dendrometric traits assessed, highlighting significant structural differences among *Neltuma pallida* populations (Figure 3).

Analysis of diameter at breast height (DBH) showed significant differences among localities ($p < 0.001$). Fundo Valdez (50.07 cm), Monte Azul (46.62 cm), and KM 190 (45.77 cm) exhibited the highest mean values, indicating individuals with greater stem diameter development. In contrast, ISA REP (15.59 cm) and Rica Playa (16.06 cm) displayed the lowest values, reflecting populations with reduced bole thickness (Figure 3a).

For total tree height, statistically significant differences were also detected among localities ($p < 0.001$). The tallest individuals were recorded at Monte Azul (14.44 m), Fundo Valdez (12.33 m), and Saman Chico (11.40 m), while ISA REP (4.67 m) and Rica Playa (7.95 m) presented the shortest trees (Figure 3b).

Crown diameter likewise exhibited significant variability across localities ($p < 0.001$). Monte Azul (14.42 m), Saman Chico (14.25 m), and CC Ignacio Távara (14.02 m) had the largest average crown diameters, reflecting individuals with broader architectures and potentially greater dominance. Conversely, ISA REP (6.04 m) and SENASA (6.68 m) displayed the smallest crowns (Figure 3c).

Finally, for height to the first branching, significant differences were observed among localities ($p < 0.001$). Fundo Valdez (4.08 m), SENASA (3.21 m), and Monte Azul (3.20 m) recorded the greatest branching heights, suggesting trees with cleaner boles. In contrast, ISA REP (1.32 m) and Chanchape (1.71 m) exhibited the lowest values (Figure 3d).
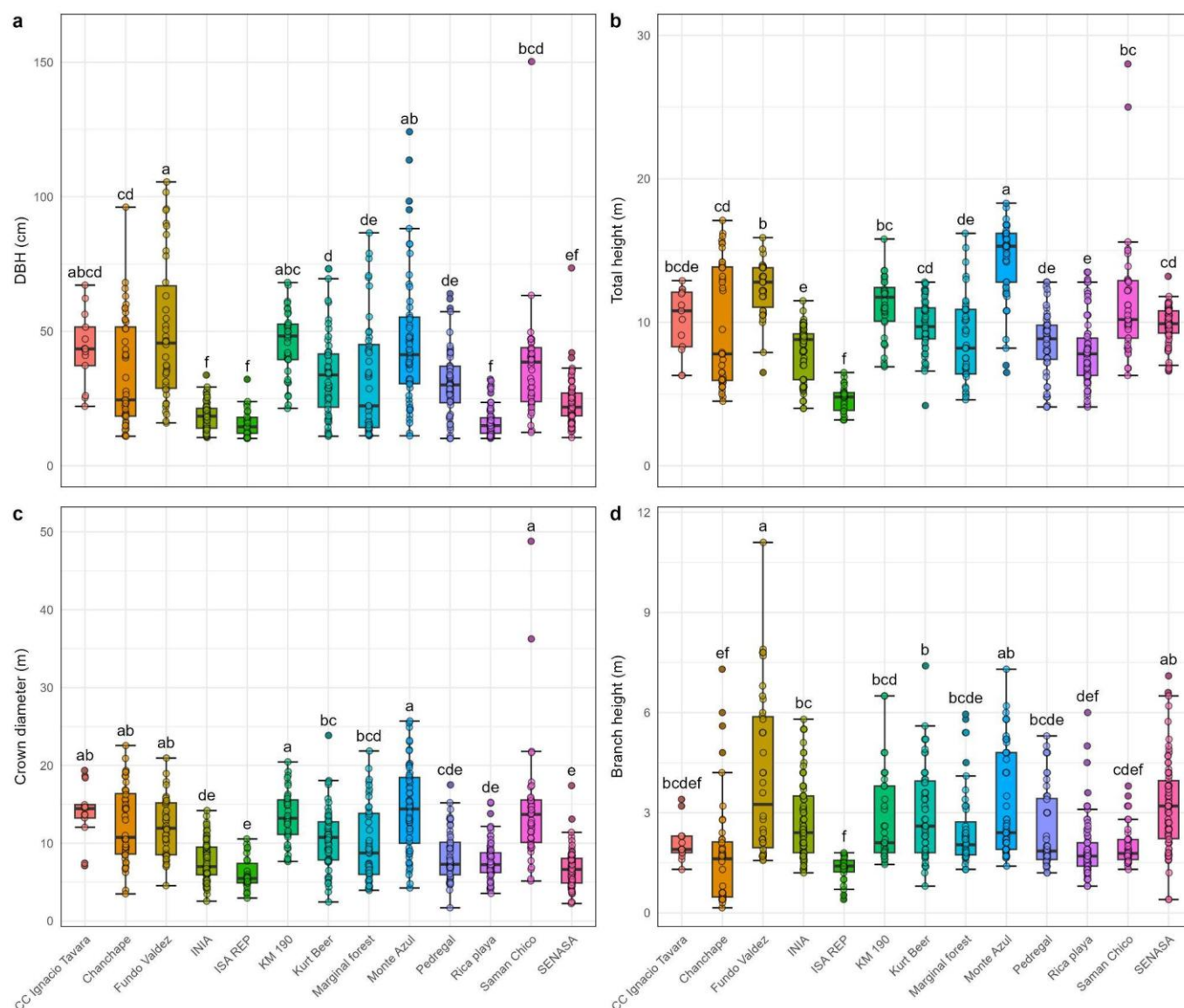
Figure 3: Distribution of quantitative morphological traits in *Neltuma pallida* populations evaluated across 13 locali-
ties in the departments of Piura and Tumbes. (a) Diameter at breast height (cm, DBH). (b) Total height (m). (c)
Crown diameter (m). (d) Height to the first branching (m). Distributions are based on the evaluation of 631 individ-
uals, allowing the characterization of phenotypic variability among localities and providing inputs for germplasm
conservation and selection. Different letters indicate statistically significant differences according to Tukey's multi-
ple comparison test (p < 0.05).

Hierarchical cluster analysis, based on the combination of qualitative and quantitative traits previously evaluated,
grouped the 13 study localities into four distinct clusters. This classification reflects patterns of phenotypic variation in
Neltuma pallida populations, highlighting relationships between structural and functional traits of individuals and their
geographic origin. This clustering reflects patterns in the phenotypic variation of *Neltuma pallida* populations. (Figure
4).

Cluster I included the localities Saman Chico and Monte Azul, distinguished by individuals with the highest average
values of DBH (37.33 cm and 46.62 cm, respectively), total height (11.40 m and 14.44 m), and crown diameter (14.25 m

and 14.42 m). These trees also exhibited high fruit production, with very sweet fruits, and dense foliage providing full   258
branch coverage.   259

Cluster II comprised the localities Kurt Beer, Chanchape, and Fundo Valdez. This group displayed intermediate DBH   260
values (33.63 cm, 34.20 cm, and 50.07 cm, respectively), total heights ranging from 9.77 m to 12.33 m, and crown diam-   261
eters between 10.50 m and 12.40 m. Qualitatively, trees in this group bore fruits distributed across up to 75% of branches,   262
accompanied by dense foliage covering two-thirds to the entirety of branches.   263

Cluster III was formed by the localities Marginal Forest, Pedregal, CC Ignacio Távara, and KM 190. This group was   264
characterized by individuals with relatively high DBH values, ranging from 30.81 cm (Pedregal) to 45.77 cm (KM 190).   265
Total heights remained intermediate (8.49–11.13 m), while crown diameters varied between 8.30 m and 14.02 m. Qual-   266
itatively, trees presented fruits distributed across 25–50% of branches, with flavors ranging from sour to sweet, and   267
partial foliage coverage limited to two-thirds of branches.   268

Cluster IV included the localities INIA, Rica Playa, ISA REP, and SENASA, which grouped individuals with the lowest   269
average values for all evaluated traits. DBH ranged from 15.59 cm (ISA REP) to 23.59 cm (SENASA), total height varied   270
between 4.67 m and 9.80 m, and crown diameter between 6.04 m and 7.66 m. These localities were also characterized   271
by low fruit production, frequent stem defects, sparse or low-quality foliage, and a predominance of bitter-tasting fruits.   272
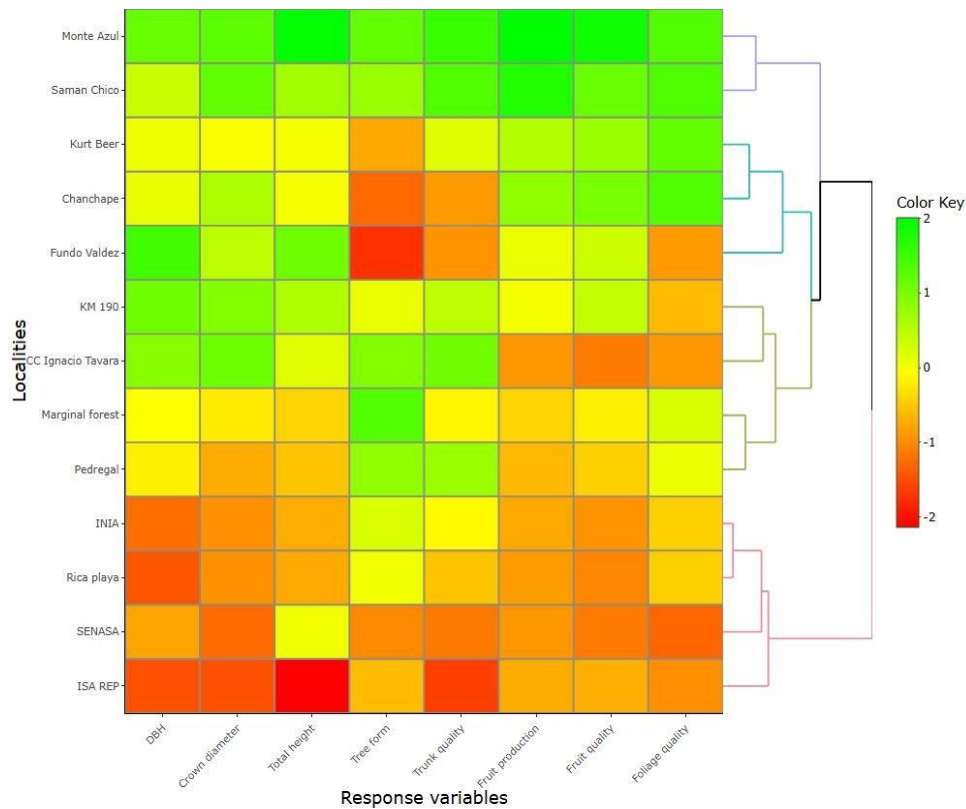

Figure 4: Cluster analysis of 13 *Neltuma pallida* localities evaluated in the departments of Piura and Tumbes. Clus-
tering was performed using Euclidean distance as the dissimilarity measure and the Weighted Pair Group Method
using Centroids (WPGMC). The optimal number of clusters was determined using the average silhouette coeffi-
cient, allowing the identification of locality groups with similar morphological and phenotypic characteristics. De-
scription variables evaluated: Diameter at breast height (cm, DBH), Crown diameter (m), Total height (m), Tree
form (1-3 scale), Trunk quality (1-3 scale), Fruit production (0-4 scale), Fruit quality (0-3 scale), Foliage quality (1-3
scale).

Heritability and tree selection

Understanding the genetic improvement potential of *Neltuma pallida* in the regions of Piura and Tumbes requires quantifying the proportion of phenotypic variation attributable to genetic versus environmental effects. In this study, phenotypic characterization of 631 individuals belonging to two populations, one in Tumbes (n = 274) and one in Piura (n = 357), enabled the estimation of genetic variance (Vg), error variance (Ve), total phenotypic variance (Vp), and broad-sense heritability (H²) for seven morphological and functional traits across five localities in Tumbes and eight in Piura. The values of H² varied considerably among traits and populations, allowing the identification of those with greater genetic control and, therefore, higher potential for selection and breeding programs.

In the Tumbes population, the trait with the highest heritability was fruit production (fruit_production) with H² = 0.92, indicating a stable, genetically controlled phenotypic characteristic. This was followed by tree form (tree_form, H² = 0.71) and diameter at breast height (dbh, H² = 0.78), both showing favorable variance component ratios for genetic expression (Vg:Vp:Ve = 1:1.4:3.2 and 1:1.3:2.3, respectively). Total tree height (total_height) also displayed moderate heritability (H² = 0.78), with genetic variance exceeding error variance. In contrast, branch height (branch_height) exhibited the lowest H² (0.28) in this population.

In the Piura population, a similar pattern was observed, though with generally higher heritability values. Fruit production again exhibited high heritability (H² = 0.95). Likewise, total height (H² = 0.78), stem diameter (dbh, H² = 0.67), and tree form (H² = 0.68) showed consistently strong genetic expression in key structural traits. Additionally, crown diameter (H² = 0.75), trunk quality (trunk_quality, H² = 0.72), and branch height (H² = 0.73) also presented high values, suggesting favorable prospects for their use in selection programs.

Table 5: Morphological and phenotypic characterization of *Neltuma pallida* populations across 13 localities in the departments of Piura and Tumbes, Peru. Variance components and broad-sense heritability (H²) were estimated following the approach of <u>Cullis et al., (2006)</u>. Variance components include: genetic variance (Vg), phenotypic variance (Vp), and error variance (Ve). The "Ratio" represents the variance ratio relative to Vg for each component (Vg/Vg : Vp/Vg : Ve/Vg), serving as an indicator of the relative contribution of genetic versus environmental effects. The analysis was based on 631 individuals.

Population	Trait	Localities	mean	std	min	max	V.g	V.e	V.p	Heritability	Ratio
Tumbes	DBH	5	20.82	5.83	15.6	28.34	28.64	65.91	36.88	0.78	1:1.3:2.3
	Crown diameter	5	7.84	1.28	6.05	9.59	1.27	9.38	2.45	0.52	1:1.9:7.4
	Branch height	5	2.13	0.56	1.32	2.7	0.28	0.87	0.38	0.72	1:1.4:3.2
	Total height	5	7.59	1.66	4.68	8.79	2.53	4.93	3.14	0.8	1:1.2:1.9
	Tree form	5	2.16	0.3	1.77	2.55	0.08	0.26	0.11	0.71	1:1.4:3.2
	Trunk quality	5	1.9	0.34	1.38	2.33	0.1	0.44	0.16	0.65	1:1.5:4.4
	Fruit production	5	1.18	0.26	1	1.57	0.06	0.05	0.07	0.92	1:1.1:0.7
Piura	DBH	8	38.48	8.75	23.6	50.07	67.44	269.9	101.18	0.67	1:1.5:4
	Crown diameter	8	12.05	2.49	6.69	14.43	6	16.29	8.03	0.75	1:1.3:2.7
	Branch height	8	2.72	0.77	1.59	3.89	0.53	2.07	0.79	0.67	1:1.5:3.9
	Total height	8	11.01	1.64	9.77	14.44	2.62	5.81	3.34	0.78	1:1.3:2.2
	Tree form	8	1.92	0.45	1.32	2.5	0.18	0.68	0.27	0.68	1:1.5:3.7
	Trunk quality	8	2.11	0.43	1.58	2.64	0.17	0.53	0.24	0.72	1:1.4:3
	Fruit production	8	2.56	1.31	1	4.58	1.7	0.06	1.71	1	1:1:0

A multivariate analysis was conducted, excluding variables with low contributions to explained variance. After preliminary evaluation, branching and branch height were removed due to their minimal influence on the multivariate structure of the dataset.

Principal component analysis (PCA) was then applied to explore phenotypic variability among individuals. The first two principal components explained 71.00% of the total system variance, with Dim 1 accounting for 54.30% and Dim 2 for 16.70%. In Dim 1, the variables contributing most to variance were crown diameter (15.75%), fruit production (15.02%), fruit quality (14.89%), and total height (14.29%). Dim 2 was mainly influenced by tree form (40.75%) and trunk quality (24.58%) ([Figure 5](#)).

The variable biplot showed clear groupings according to their contribution and orientation within the factorial space ([Figure 5a](#)). Three main associations were identified: (i) tree form and trunk quality aligned with Dim 2; (ii) DBH, total height, and crown diameter strongly correlated with Dim 1; and (iii) fruit production, fruit quality, and foliage quality, also associated with Dim 1 but positioned toward the positive quadrant of the axis ([Figure 5a](#)).

At the individual level, trees from Monte Azul, Samán Chico, and Fundo Valdez clustered in the region associated with higher values of DBH, total height, and crown diameter ([Figure 5b](#)). Monte Azul and Samán Chico were further distinguished by high fruit production, very sweet fruit quality, and excellent foliage quality, characterized by leaf coverage over the entirety of branches. In contrast, trees from Rica Playa, ISA REP, and SENASA occupied the opposite quadrant, associated with lower values of tree form and trunk quality ([Figure 5b](#)).
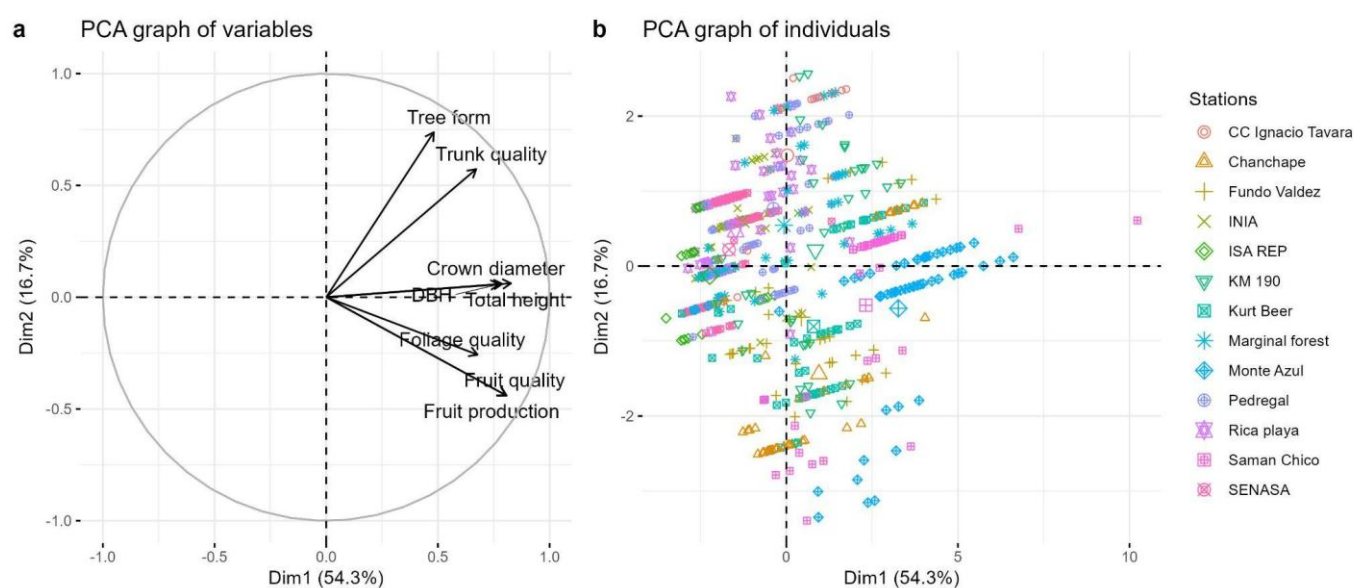

Figure 5: Principal component analysis (PCA) of morphological and phenotypic traits in *Neltuma pallida* populations from Piura and Tumbes. (a) Projection of morphological and phenotypic variables onto the first two principal components, which explain the largest proportion of system variance. (b) Distribution of individuals grouped by locality in the multivariate space defined by the principal components, based on morphological and phenotypic characteristics. The analysis was conducted on 631 individuals (n = 631).

Outstanding trees were identified belonging to the locality of Monte Azul, La Matanza, Morropón – Piura. These individuals were distinguished by their high vigor, well-formed boles, strong fruiting capacity, and dense foliage cover. They met all favorable qualitative and quantitative selection criteria and displayed outstanding morpho-phenotypic expression compared with the rest of the population. Their superior attributes included abundant fruit production, vigorous biomass development, and close correspondence with favorable habitat conditions and conservation status.

Quantitatively, the superior trees exhibited the highest values for the evaluated traits. Mean DBH reached 59.52 cm. Branching height ranged from 4.20 m to 6.20 m, substantially exceeding the population mean, which rarely surpassed 3 m. Total height averaged 16.05 m, considered optimal for fully developed individuals. Crown diameter averaged 15.83 m, reflecting a globose architecture with abundant biomass.

Qualitatively, all superior trees exhibited single stems with no bifurcations. Tree form was classified as dominant single-stemmed, while trunk quality was rated as "good," meaning free of or with only minimal defects. All superior trees produced abundant fruits, distributed across 50–100% of branches, with fruits consistently rated as sweet to very sweet. Foliage quality was also outstanding, with leaf cover extending over at least two-thirds to the entirety of branches.

DISCUSSION

The present study analyzed the morphological and phenotypic diversity of *Neltuma pallida* across 13 localities characterized by distinct edaphoclimatic conditions, where differences were found in soil fertility, climate, and topography. Our results reveal that the phenotypic traits of individuals from various localities in the departments of Piura and Tumbes exhibit a high degree of polymorphism, indicating genetic variability among the studied populations. In this context, heritability coefficients of the traits were estimated to identify those under greater genetic control and with higher potential for response to selection. As a result, individuals with superior phenotypes were identified as potential candidates for inclusion in a germplasm bank, aiming at their utilization in future breeding programs focused on the restoration and conservation of this species.

Edaphoclimatic conditions

The edaphoclimatic analysis revealed marked differences in soil, climatic, and physiographic variables among the study sites (Figure 2), consistent with evidence that such factors influence vegetation distribution and development [44,45]. Soil variables exerted the strongest influence on the morpho-phenotypic expression of N. pallida. Monte Azul and Chanchape showed higher concentrations of N, P, K, and organic matter (OM), associated with more vigorous individuals, larger structural dimensions, and superior phenotypes in fruit production and foliage quality. By contrast, Rica Playa e ISA REP exhibited higher $CaCO_3$ levels and alkaline pH, associated with unfavorable morpho-phenotypic traits. These patterns may be explained by phosphorus availability - often limiting in nutrient-poor soils [46] - as well as by organic matter, which improves both soil fertility and structure [47], and pH, which affects nutrient availability and microbial activity [48,49].

This evidence supports the hypothesis that the reduced vigor observed in ISA REP and Rica Playa may be linked to salinity stress resulting from high $CaCO_3$ content and elevated soil pH [50]. Similar responses were reported by Meglioli [51], in *Neltuma flexuosa* and *N. chilensis*, where reductions in height and aboveground biomass under saline stress were observed, although tolerant individuals were also detected, suggesting a role for genetic variability. Samán Chico provides further evidence of this pattern, as despite high $CaCO_3$ and electrical conductivity (EC), it contained well-developed individuals, suggesting potential genetic tolerance to salinity [52,53].

Climatic variables such as precipitation (pp), Tmin, and Tmean were slightly higher in Rica Playa, Pedregal, and Marginal forest, with lower relative humidity (RH), while Monte Azul and Chanchape presented intermediate values

(Figure 2). Physiographic variables (e.g., distance to water bodies [DW], slope, and elevation [SLI]) showed no consistent influence on phenotypic traits. Although Pedregal, KM 190, and Fundo Valdez were closer to water bodies, and CC Ignacio Távara, KM 190, and Monte Azul were at higher elevations, these differences did not correlate with phenotypic variation. This aligns with Sadia [54], who emphasized that edaphic factors such as pH, OM, P, and K availability are key determinants of plant distribution, but their effects must be understood in interaction with biotic and abiotic variables. Similarly, Barboza [8] identified climatic variables (mean temperature of the wettest quarter, maximum temperature of the warmest month, elevation, and annual precipitation) as critical for *N. pallida* suitability, but in our study the relative climatic homogeneity reduced their influence. These findings are consistent with Baselly-Villanueva and Rufasto-Peralta [55,56], who observed that at local scales, edaphic variables are often more determinant than climatic or physiographic ones. Overall, the interaction between soil, environment, and genetic background must be considered in conservation, restoration, and breeding strategies for *N. pallida.*

Morphological diversity in algarrobo populations

The morpho-phenotypic characterization revealed high polymorphism within and among populations in Piura and Tumbes (Table 4), suggesting considerable genetic diversity. The Shannon–Weaver diversity index (H′) showed high values, reflecting broad variability among traits [57,58]. Fruit production displayed the greatest diversity, whereas branching presented moderate diversity. Among dendrometric traits, analysis of variance indicated significant heterogeneity (Figure 3), suggesting structural differences among populations. Similar findings were reported by Bessega [59] in *N. flexuosa*, where differences in height and basal diameter were partly genetically based but modulated by local environmental conditions. Likewise, Vega [60] argued that *N. alba* exhibits strong adaptive capacity to environmental heterogeneity, favoring local adaptation processes.

Our results are also consistent with Esparza-Orozco [61], who identified significant phenotypic differences among *Neltuma* populations associated with geographic origin. These findings suggest that phenology and morphology in this genus are strongly influenced by ecological factors. Vidaković [62] further emphasized that interactions between environment and geography can explain observed phenotypic variation, reflecting potential processes of isolation by environment and by distance. In our study, Monte Azul, Chanchape, and Samán Chico (Piura) were distinguished by superior morphological and phenotypic performance, while Rica Playa, ISA REP, and SENASA (Tumbes) were associated with lower performance. This pattern supports the hypothesis of simultaneous environmental and geographic isolation shaping genetic and phenotypic structuring in *N. pallida* populations. According to Wang [63], high phenotypic variation often reflects high genetic diversity; thus, phenotypic evaluation represents a direct and effective approach for estimating diversity in forest germplasm resources.

Genetic influence and identification of superior trees

The genetic influence observed in *N. pallida* aligns with patterns reported in other forest species from contrasting environments, where high heritability coefficients predict genetic gains in selection programs. In this study, fruit production exhibited high heritability ($H^2 \approx 0.92$–1.00), confirming strong genetic control and limited environmental influence, ensuring high response to selection. Moderate-to-high heritability values for structural traits such as DBH, total height, and crown diameter also suggest that vegetative growth traits are suitable targets for breeding programs. These findings are consistent with recent studies in *Pinus pinaster* and *Juglans mandshurica*, where size-related traits displayed higher heritability than form-related traits, highlighting their value in early breeding cycles [64,65]. Prioritizing traits with high heritability and temporal stability, such as bole straightness or branch insertion angle, optimizes selection accuracy while minimizing environmental and genotype × environment (G×E) effects, which is crucial in heterogeneous ecosystems such as dry forests.

In the present study, individuals with superior phenotypes belonging to the Monte Azul locality were identified, exhibiting outstanding characteristics in growth and pod production, thus representing the most promising material for inclusion in a germplasm bank. Nevertheless, considering the results obtained from populations such as Rica Playa and ISA REP, where lower mean values were recorded for morphological and phenotypic variables, it is important to emphasize that even in these less favorable environments, individuals with exceptional performance can be identified [66]. These specimens could be considered complementary candidates for selection, as their adaptation to more restrictive environmental conditions suggests the presence of genetic traits associated with tolerance and resilience to environmental stress [67]. The incorporation of individuals from marginal populations could strengthen the genetic base of breeding programs, contributing useful variability for ecological restoration in dry forest ecosystems.

Identification of superior trees was based on individual assessment, allowing the selection of outstanding trees in terms of fruit production, vegetative vigor, and crown architecture across 13 localities in Piura and Tumbes. Approximately 90% of individuals with superior traits were concentrated in these regions, consistent with Castro [14]. While phenotypic selection was used here, comparisons with neighboring trees can further reduce microsite and age-related biases, increasing accuracy of genetic estimates [68]. Multivariate analyses confirmed that individuals from Monte Azul, Chanchape, and Samán Chico clustered in dimensions associated with higher productivity and biomass. Consolidating these candidates requires validation through progeny tests and clonal banks, as well as the integration of modern tools such as high-throughput phenotyping and genomic selection, which have proven effective in accelerating breeding cycles and mitigating G×E effects in forest programs [14,69]. The selected individuals provide a robust foundation for establishing seed orchards and germplasm banks, contributing to the productive and sustainable restoration of Peruvian dry forests.

Limitations and perspectives

Despite progress in identifying superior *N. pallida* individuals, questions remain regarding whether the highlighted traits reflect true genetic potential or are mainly influenced by local edaphoclimatic conditions. Soil fertility heterogeneity, salinity levels, and nutrient availability likely conditioned phenotypic expression, raising the risk of overestimating individuals favored by environmental plasticity rather than genetic superiority. Future studies should complement morpho-phenotypic selection with molecular marker analyses and progeny testing to more precisely disentangle environmental effects. Integrating these approaches will strengthen breeding programs and ensure that selected individuals not only express desirable traits under specific site conditions but also maintain adaptive advantages - such as abiotic stress tolerance and growth potential - across diverse ecological scenarios.

CONCLUSIONS

The morpho-phenotypic characterization of *Neltuma pallida* in the regions of Piura and Tumbes revealed substantial intra- and inter-population variability, reflected in the high degree of polymorphism observed. Edaphoclimatic differences among localities influenced the expression of evaluated traits, while heritability estimates enabled the identification of characters with greater potential response to selection. These findings led to the identification of superior individuals classified as superior trees, providing a foundation for the establishment of germplasm banks and the development of genetic improvement programs aimed at the conservation and ecological restoration of this species within tropical dry forest ecosystems.

STATEMENTS

Author Contributions

Conceptualization, W.N.; methodology, S.C.-N., J.R.B.-V., E.J.S.H., S.Y.C.V., and W.N.; formal analysis, S.C.-N. and F.L.-I.; investigation, W.N. and N.T.T.; data curation, S.C.-N. and F.L.-I.; writing—original draft preparation, S.C.-N., J.R.B.-V., E.J.S.H., S.Y.C.V., N.T.T., and F.L.-I.; writing—review and editing, F.L.-I.; visualization, S.C.-N. and F.L.-I.; software, S.C.-N. and F.L.-I.; resources, M.R.R.; project administration, M.R.R.; funding acquisition, M.R.R. All authors have read and agreed to the published version of the manuscript.

Funding

Data Availability Statement

The original contributions presented in this study are included in the article and its supplementary material. Reproducible datasets and data analysis scripts are provided in Supplementary File 1 and are publicly accessible via the GitHub repository at: https://github.com/Sebass96/INIA_algarrobo.git

Acknowledgments

Conflict of Interest

The authors declare no conflict of interest.

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