

Multi-trait evaluation and index-based selection of advanced F₁₀ quinoa (*Chenopodium quinoa* Willd.) lines under Peruvian highland conditions

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ABSTRACT

Quinoa (*Chenopodium quinoa* Willd.) is an Andean grain crop valued for its high nutritional quality and broad environmental adaptability. Increasing climatic variability in the Peruvian highlands threatens quinoa productivity, highlighting the need for cultivars that combine high yield potential with early maturity. This study evaluated nine advanced F₁₀ lines, five parental varieties, and two commercial control cultivars during the 2019-2020 growing season at Potojani Farm, Puno, Peru. A randomized complete block design with four replicates was used, and linear mixed-effects models were fitted to obtain best linear unbiased estimates (BLUEs) and predictors (BLUPs). Broad-sense heritability was estimated using the Cullis method. Significant genotypic differences were detected for yield, phenological, and architectural traits ($P < 0.05$). Thousand-kernel weight and days to physiological maturity exhibited high heritability ($H^2 = 0.98$ and 0.88 , respectively), whereas seed yield per plant showed moderate heritability ($H^2 = 0.68$). Correlation and principal component analyses revealed partial independence between phenological and architectural traits and yield-related traits, indicating that productivity can be improved without extending the duration of vegetative growth. A weight-free Elston selection index integrating seed yield, maturity, plant height, stem diameter, and thousand-kernel weight identified Salcedo INIA × Pandela Rosada 171 as the superior multi-trait genotype, followed by SAL × Negra Collana 30 and SAL × COL 37. These findings confirm the presence of exploitable genetic variability and demonstrate measurable genetic progress toward the development of genotypes with balanced yield performance and phenological adaptation under highland conditions.

Key words: Broad-sense heritability, Elston selection index, multi-trait selection, quinoa breeding, highland.

INTRODUCTION

Climate change threatens agricultural productivity through increasing temperature variability, altered precipitation patterns, and a greater frequency of extreme weather events (Xiong et al., 2022). Under these conditions, current cropping systems often struggle to maintain stable yields (Rahman et al., 2025), increasing the need for resilient cultivars capable of sustaining productivity in stress-prone environments (Heikonen et al., 2025). High yield potential, early maturity, and adaptive plasticity are therefore critical traits for maintaining food security under climatic uncertainty.

Quinoa (*Chenopodium quinoa* Willd.), domesticated in the Andean region more than 7000 yr ago, has gained global recognition as a climate-resilient crop (Martínez et al., 2015). Its tolerance to drought, salinity, and frost, combined with its exceptional nutritional value, has facilitated its expansion beyond its center of origin (López-

Marqués et al., 2020). Despite its resilience, modern cultivars remain only partially improved relative to traditional germplasm, and important traits such as yield potential, earliness, uniformity, and seed quality require further improvement through structured breeding programs (Vleugels et al., 2024).

Peru is highly vulnerable to climate-related agricultural risks (Useche et al., 2021). In the Puno region, high-altitude conditions, heterogeneous soils, and interannual climatic variability significantly influence quinoa performance (Ponce, 2020). Delayed maturity and yield instability remain major production constraints, highlighting the need for genotypes that combine early maturity with high and stable productivity under local edaphoclimatic conditions.

Plant breeding plays a key role in addressing these challenges through the identification and development of superior genotypes adapted to specific environments (Xiong et al., 2022). The ideotype concept, which defines optimal combinations of traits for productivity and adaptation, provides a practical framework for crop improvement under stress conditions (Debnath et al., 2024). Effective implementation of this approach requires accurate phenotypic characterization and reliable estimates of genetic variability and heritability (Carbajal-Friedrich and Burgess, 2024). The substantial diversity present within Andean quinoa germplasm offers considerable potential for the development of elite, locally adapted lines.

Therefore, the objectives of this study were to: (i) Evaluate agronomic performance, quantify genetic variability, and estimate broad-sense heritability in nine advanced quinoa lines; (ii) characterize relationships among agronomic traits across advanced lines, parental varieties, and commercial control cultivars; and (iii) apply a multi-trait Elston selection index to identify elite lines combining high yield, early maturity, and favorable agronomic performance for climate-resilient breeding in Puno, Peru.

MATERIALS AND METHODS

Experimental site and soil characteristics

The field experiment was conducted during the 2019-2020 growing season at the Potojani Experimental Farm (Agrarian Region of Puno) (15°56'23" S, 69°52'46.8" W; 3850 m a.s.l.), located in the Chucuito District, Puno Province, Peru. Prior to the establishment of the experiment, the site had been cultivated with oat (*Avena sativa* L.) during the 2018-2019 growing season.

Soil samples were collected from the 0-30 cm depth prior to sowing using a zigzag sampling pattern and analyzed at the Soil, Water, and Fertilization Laboratory of the National Institute of Agrarian Innovation (INIA), Puno, Peru. The soil was classified as a silty loam, containing 47.44% silt and 41.4% sand, with a neutral pH (6.34) and low electrical conductivity (0.421 dS m⁻¹). Organic matter content was 1.63%. Available P was low (7.08 mg kg⁻¹), whereas exchangeable K was moderate (103.6 mg kg⁻¹). The exchange complex was dominated by Ca (60-75 cmol⁺ kg⁻¹) and Mg (15-20 cmol⁺ kg⁻¹).

Meteorological conditions

Meteorological data from October 2019 to June 2020 were obtained from the Rincón Cruz de Ácora meteorological station (SENAMHI) and were used to characterize the environmental conditions during the 2019-2020 growing season. The mean maximum temperature reached 18.2 °C in November 2019, whereas minimum temperatures decreased to 0.33 and -1.5 °C in May and June 2020, respectively, during the late stages of crop development. Precipitation was concentrated in December and January, with totals of 6.53 and 7.04 mm, respectively, while rainfall was minimal from April to June. Relative humidity increased from 72% in October to 87% in February. A discontinuity in the meteorological time series occurred between March and April 2020 due to restrictions associated with the COVID-19 lockdown (Figure 1).

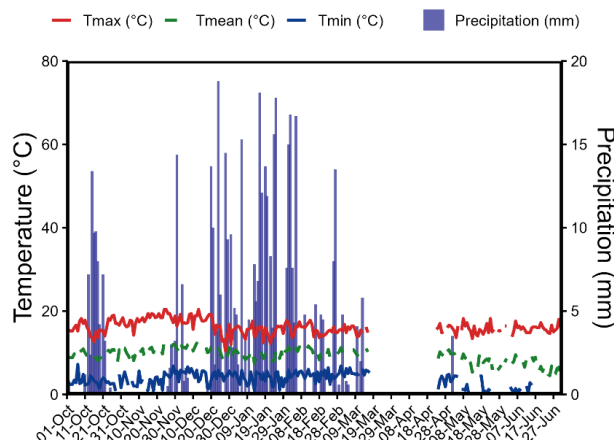


Figure 1. Daily temperature and precipitation during the 2019-2020 growing season at Potojani, Puno, Peru.

Plant material

Controlled hybridizations were performed in 2012 under greenhouse conditions at the Universidad Nacional del Altiplano (Puno, Peru) following standard emasculation and pollination procedures (Emrani et al., 2020). The resulting progenies were advanced through bulk selfing to the F_5 generation to increase homozygosity. Selection based on grain yield was conducted at the F_6 generation, followed by advanced selection and registration trials from F_7 to F_9 . The present study evaluated the F_{10} generation as the continuation of this breeding and selection strategy.

The genetic material consisted of five parental varieties, two commercial control cultivars, and nine advanced F_{10} lines, for a total of 16 genotypes (Table 1). The parental varieties, Salcedo INIA (SAL), Huariponcho (HUA), Kcancolla (KCA), Negra Collana (COL), and Pandela Rosada (PAN), were obtained from the Germplasm Bank of the Universidad Nacional del Altiplano and were selected for their contrasting agronomic characteristics. The commercial cultivars Altiplano (ATP) and Choclito (CHO) were included as control varieties (Tapia et al., 2000; Mujica et al., 2001). The nine F_{10} lines were derived from the following simple crosses: HUA $\times$ KCA 53, HUA $\times$ KCA 194, HUA $\times$ KCA 174, SAL $\times$ PAN 171, SAL $\times$ PAN 165, SAL $\times$ PAN 58, SAL $\times$ COL 30, SAL $\times$ COL 37, and SAL $\times$ COL 46. Seed used in the experiment was harvested during the previous F_9 growing season (2018-2019).

Table 1. The F_{10} quinoa lines obtained through selfing, along with their parental varieties and commercial controls varieties evaluated in the 2019-2020 agricultural season.

Lines	Parents	Controls
Huariponcho $\times$ Kcancolla 53	Negra Collana	Altiplano
Huariponcho $\times$ Kcancolla 194	Salcedo INIA	Choclito
Huariponcho $\times$ Kcancolla 174	Kcancolla	
Salcedo INIA $\times$ Pandela Rosada 171	Pandela Rosada	
Salcedo INIA $\times$ Pandela Rosada 165	Huariponcho	
Salcedo INIA $\times$ Pandela Rosada 58		
Salcedo INIA $\times$ Negra Collana 30		
Salcedo INIA $\times$ Negra Collana 37		
Salcedo INIA $\times$ Negra Collana 46		

Experimental design

The experiment was established using a randomized complete block design (RCBD) with 16 treatments, consisting of nine F₁₀ lines, five parental varieties, and two commercial control varieties, arranged in four replicates, resulting in a total of 64 experimental units. Treatments were randomly assigned within each block to minimize the effects of environmental variation. Each experimental unit consisted of five furrows, 10 m in length and spaced 0.6 m apart, corresponding to a gross plot area of 30 m² and a net plot area of 25 m². This plot size ensured adequate plant density for the accurate evaluation of agronomic traits while minimizing border effects.

The statistical model for the RCBD was expressed as:

$$Y_{ij} = \mu + T_i + B_j + \varepsilon_{ij}$$

where Y_{ij} denotes the observed response (yield) of the i^{th} treatment in the j^{th} block; μ represents the overall mean; T_i is the fixed effect of the i^{th} treatment (lines), and B_j is the random effect of the j^{th} block (replicate). The residual error term ε_{ij} represents unexplained variation and was assumed to be independently and normally distributed. Random block effects were assumed to follow a normal distribution with mean zero and variance σ_B^2 .

Agronomic management

The experiment was managed according to standard agronomic practices commonly used in the Puno highlands. Land preparation was carried out using conventional tillage. Sowing was performed on 5 November 2019 using a continuous-row method, with 30 g seed per plot sown at a depth of 2 cm. Fertilization was applied at a rate of 80-40-00 (N-P-K) using urea and diammonium phosphate, divided into two equal applications at the first weeding and hilling stages. Weed control was performed manually. Thinning was conducted 40 d after sowing to maintain a plant spacing of 15 cm, and hilling was carried out 75 d after sowing. Harvesting was performed at physiological maturity for each genotype. Twenty plants were sampled from the central rows of each plot to minimize border effects. Panicles were manually threshed, grains were cleaned by wind separation, and seed weight was determined using an analytical balance.

Evaluation of agronomic traits

Agronomic traits were evaluated according to the standardized quinoa descriptors developed by Bioversity International et al. (2013). Ten plants were randomly selected from the central rows of each plot to minimize border effects. The evaluated traits included days to onset of flowering (d), days to flowering (d), days to physiological maturity (d), plant height (cm), grain yield per plant (g), thousand-kernel weight (g), main stem diameter (mm), panicle length (cm), panicle width (cm), grain width (mm), harvest index (%), biomass per plant (g), and grain yield of 10 plants (g). These measurements were used to evaluate the agronomic performance and adaptation of the F₁₀ lines under highland growing conditions.

Broad-sense heritability

Agronomic traits were analyzed using linear mixed-effects models fitted according to the randomized complete block design. For the estimation of variance components, both genotypes and blocks were treated as random effects, allowing the estimation of genetic and residual variance components and the prediction of best linear unbiased predictors (BLUPs). Broad-sense heritability (H^2) was estimated following the method of Cullis et al. (2006).

Genotypes were considered random effects for variance component estimation and prediction of genotypic values because the objective was to quantify genetic variability and obtain BLUPs for heritability estimation. To evaluate the performance of the specific quinoa genotypes included in this study, the model was subsequently refitted with genotypes treated as fixed effects and blocks as random effects. This approach enabled the estimation of adjusted genotype means (BLUEs), their associated standard errors, and pairwise comparisons among genotypes. Heritability was calculated as:

$$H^2 = 1 - \frac{\overline{V}_{\Delta}^{BLUP}}{2\sigma_g^2}$$

where σ_g^2 is the genotypic variance, and $\overline{V}_{\Delta}^{BLUP}$ represents the average variance of the difference between two genotypic BLUPs.

In addition, plot-based repeatability (w) was estimated to assess the consistency of genotype performance within the experimental environment and was calculated as:

$$w = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_e^2}{R}}$$

where σ_e^2 denotes the residual error variance, and R is the number of replicates.

Multi-trait selection via Elston index

Multi-trait ranking of the nine F_{10} lines was conducted using the weight-free Elston selection index (Elston, 1963), which penalizes suboptimal performance in any component trait and favors balanced agronomic profiles. The index was calculated from best linear unbiased estimates (BLUEs) obtained from the mixed-model analysis. Traits included grain yield per plant, days to physiological maturity, plant height, main stem diameter, and thousand-kernel weight, representing productivity, earliness, and structural adaptation. Days to physiological maturity were reverse-scaled to assign higher values to earlier-maturing genotypes. The Elston index:

$$I = \prod_{k=1}^p (x_{ik} - L_k),$$

where x_{ik} represents the BLUE of the k^{th} trait for the i^{th} genotype, L_k is the minimum acceptable threshold for trait k , and p is the total number of traits included in the index. Genotypes with values below the threshold for any trait receive reduced or negative index values, effectively penalizing unbalanced performance.

Statistical analysis

All analyses and graphical outputs were performed in R version 4.4.3 (R Core Team, 2025). Variance components, broad-sense heritability, best linear unbiased estimates (BLUEs), and predictors (BLUPs) were obtained using linear mixed-effects models fitted with the lme4 package (Bates et al., 2015). Principal component analysis (PCA) was conducted to examine multivariate trait structure, and Pearson correlation coefficients were calculated to assess pairwise trait associations. Mean comparisons among genotypes were performed using Tukey-adjusted tests based on BLUEs, with significant groupings summarized by compact letter displays. Multi-trait ranking was implemented using the Elston (1963) index. All results were derived from model-adjusted BLUE means.

RESULTS

Agronomic performance, genetic variability, and heritability of key traits in nine quinoa lines

Nine F_{10} quinoa lines were evaluated under field conditions in Puno to quantify phenotypic variation and estimate the genetic contribution to key agronomic traits. Linear mixed-effects models were fitted with genotype treated as a fixed effect and block as a random effect, and best linear unbiased estimates (BLUEs) were used for genotype comparisons. Significant genotypic differences were detected for all evaluated traits ($P < 0.05$) (Table 2). Seed yield per plant ranged from 28.5 to 42.4 g, with the highest values observed in SAL $\times$ PAN 171 (42.4 g) and SAL $\times$ COL 46 (40.1 g), followed by HUA $\times$ KCA 194 (33.3 g). Lower yields were recorded for SAL $\times$ COL 37 and SAL $\times$ PAN 165. Phenological traits also varied among the evaluated lines. The earliest flowering was observed in HUA $\times$ KCA 194 (90.5 d), followed by SAL $\times$ PAN 171 (95.3 d). Physiological maturity occurred earliest in HUA $\times$ KCA 174 and HUA $\times$ KCA 194 (163 d), whereas SAL $\times$ PAN 171 and SAL $\times$ COL 46 matured later (175-180 d). Thousand-kernel weight reached a maximum value of 5.4 g, with SAL $\times$ COL 30, SAL $\times$ COL 46, and SAL $\times$ COL 37 exhibiting the highest values (Figure 2). Plant height ranged from 85.7 cm in SAL $\times$ COL 46 to 107.9 cm in HUA $\times$ KCA 174, whereas stem diameter showed relatively limited variation, reaching a maximum of 14.0 mm in SAL $\times$ COL 46 and SAL $\times$ PAN 165. Broad-sense heritability varied among traits (Table 3). Thousand-kernel weight exhibited the highest heritability estimate ($H^2 = 0.98$), followed by physiological maturity ($H^2 = 0.88$), mean seed diameter ($H^2 = 0.81$), and flowering time ($H^2 = 0.80$). Seed yield per plant showed moderate heritability ($H^2 = 0.68$), whereas plant height exhibited the lowest estimate ($H^2 = 0.58$).

Table 2. Best linear unbiased estimates (BLUEs $\pm$ SE) of agronomic traits for nine F₁₀ quinoa lines derived from linear mixed-effects models. Values are best linear unbiased estimates. Different superscript letters within the same column indicate significant differences among F₁₀ lines according to Tukey's multiple comparison test at $P < 0.05$. HUA: Huariponcho; KCA: Kcancolla; SAL: Salcedo INIA; COL: Negra Collana; PAN: Pandela Rosada.

Cultivars	Plant height	Flowering time	Maturity time	Seed yield	Stem diameter	Thousand-kernel
	cm	d	d	g	mm	g
HUAxKCA_174	107.9 $\pm$ 4.5 ^b	98.5 $\pm$ 1.7 ^{ab}	163.3 $\pm$ 1.9 ^a	30.6 $\pm$ 2.7 ^{ab}	11.3 $\pm$ 0.8 ^{abc}	3.4 $\pm$ 0.1 ^{ab}
SALxCOL_37	99.4 $\pm$ 4.5 ^{ab}	102 $\pm$ 1.7 ^b	172.7 $\pm$ 1.9 ^{bc}	29.2 $\pm$ 2.7 ^{ab}	13.8 $\pm$ 0.8 ^c	4.8 $\pm$ 0.1 ^c
HUAxKCA_53	98.6 $\pm$ 4.5 ^{ab}	99.3 $\pm$ 1.7 ^b	168.7 $\pm$ 1.9 ^{ab}	32.6 $\pm$ 2.7 ^{ab}	9.9 $\pm$ 0.8 ^{ab}	3.5 $\pm$ 0.1 ^{ab}
SALxPAN_58	97 $\pm$ 4.5 ^{ab}	97.5 $\pm$ 1.7 ^{ab}	173.5 $\pm$ 1.9 ^{bc}	32.3 $\pm$ 2.7 ^{ab}	13 $\pm$ 0.8 ^{abc}	3.7 $\pm$ 0.1 ^b
SALxPAN_171	95.9 $\pm$ 4.4 ^{ab}	95.3 $\pm$ 1.7 ^{ab}	175.1 $\pm$ 1.9 ^{bc}	42.4 $\pm$ 2.9 ^b	13.6 $\pm$ 0.8 ^{bc}	3.6 $\pm$ 0.1 ^{ab}
SALxPAN_165	93.2 $\pm$ 4.5 ^{ab}	103.2 $\pm$ 1.7 ^b	173.2 $\pm$ 1.9 ^{bc}	28.5 $\pm$ 2.7 ^a	14 $\pm$ 0.8 ^c	3.9 $\pm$ 0.1 ^b
HUAxKCA_194	92.2 $\pm$ 4.5 ^{ab}	90.5 $\pm$ 1.7 ^a	163.3 $\pm$ 1.9 ^a	33.3 $\pm$ 2.7 ^{ab}	9.5 $\pm$ 0.8 ^a	3.1 $\pm$ 0.1 ^a
SALxCOL_30	87.5 $\pm$ 4.5 ^{ab}	97.3 $\pm$ 1.7 ^{ab}	171.5 $\pm$ 1.9 ^{abc}	32.9 $\pm$ 2.7 ^{ab}	13.3 $\pm$ 0.8 ^{abc}	5.4 $\pm$ 0.1 ^d
SALxCOL_46	85.7 $\pm$ 4.7 ^a	99 $\pm$ 1.8 ^b	180 $\pm$ 1.9 ^c	40.1 $\pm$ 2.8 ^{ab}	14 $\pm$ 0.8 ^c	5 $\pm$ 0.1 ^{cd}

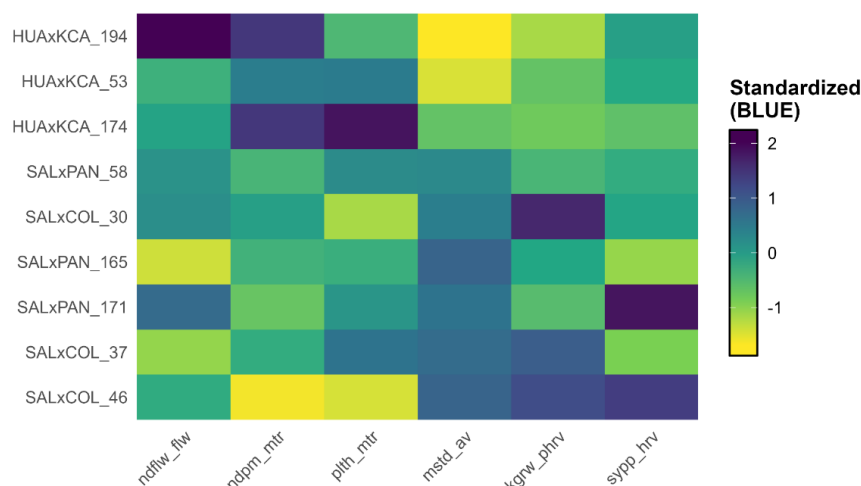


Figure 2. Heatmap of standardized best linear unbiased estimates (BLUEs) for agronomic traits across nine F₁₀ quinoa lines: Number of days to flowering (ndflw), number of days to physiological maturity (ndpm), plant height (plth), main stem diameter (mstd), thousand-kernel weight (kgrw), seed yield per plant (sypp). HUA: Huariponcho; KCA: Kcancolla; SAL: Salcedo INIA; PAN: Pandela Rosada; COL: Negra Collana. Measurements were recorded at flowering (flw), physiological maturity (mtr), harvest (hrv), post-harvest (phrv), whereas av denotes the average value.

Table 3. Descriptive statistics, variance components, and Cullis broad-sense heritability estimates for agronomic traits across F₁₀ quinoa lines. V.g: Genotypic variance; V.e: residual variance; H²: broad-sense heritability estimated according to Cullis et al. (2006).

Traits	Mean	Standard deviation	V.g	V.e	H ²
Plant height, cm	95.26	6.65	25.79	74.03	0.58
Maturity time, d	171.25	5.41	25.92	12.37	0.88
Seed yield per plant, g	33.53	4.71	15.14	22.33	0.68
1000-grain weight, g	4.03	0.81	0.6	0.04	0.98
Main stem diameter, mm	12.49	1.77	2.56	2.36	0.81
Flowering time, d	98.05	3.72	11.14	10.88	0.8

Relationships among agronomic traits across quinoa genotypes

Pearson correlation analysis revealed structured associations among phenological, architectural, and yield traits (Figure 3). Strong positive correlations were observed between days to onset of flowering and days to flowering ($r = 0.95$, $p < 0.001$), and between days to flowering and days to physiological maturity ($r = 0.81$, $p < 0.001$). Days to physiological maturity was moderately correlated with plant height ($r = 0.56$, $p < 0.05$) and main stem diameter ($r = 0.50$, $p < 0.05$). Panicle width was positively associated with plant height ($r = 0.52$, $p < 0.05$) and physiological maturity ($r = 0.76$, $p < 0.001$), while grain width correlated with stem diameter ($r = 0.64$, $p < 0.01$). Yield-related traits exhibited strong internal associations. Biomass per plant correlated with 10-plant yield ($r = 0.94$, $p < 0.001$) and seed yield per plant ($r = 0.92$, $p < 0.001$). Seed yield per plant was positively associated with biomass ($r = 0.92$, $p < 0.001$), harvest index ($r = 0.70$, $p < 0.01$), and 10-plant yield ($r = 0.99$, $p < 0.001$).

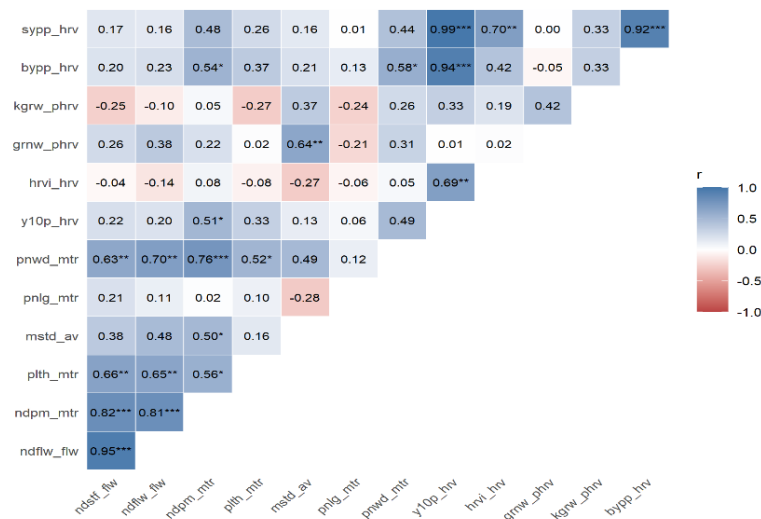


Figure 3. Pearson correlation matrix of phenological, architectural, and yield traits based on best linear unbiased estimates across 16 quinoa genotypes. Significance levels are indicated. ndflw: Number of days to flowering; ndpm: number of days to physiological maturity; plth: plant height; mstd: main stem diameter; pnlg: panicle length; pnwd: panicle width; y10p: yield of 10 plants; hrvi: harvest index; grnw: grain width; kgrw: thousand-kernel weight; bypp: biomass yield per plant; and sypp: seed yield per plant. Measurements were recorded at flowering (flw), physiological maturity (mtr), harvest (hrv), and post-harvest (phrv), whereas av denotes the average value.

Principal component analysis (PCA) summarized the multivariate relationships among the 16 evaluated genotypes. The first two principal components accounted for 62.20% of the total phenotypic variation, with PC1 and PC2 explaining 39.91% and 22.29%, respectively (Figure 4). Principal component 1 (PC1) was primarily associated with phenological and architectural traits, including plant height, stem diameter, grain width, flowering time, and physiological maturity, indicating that these variables contributed substantially to the variation explained by this component. Principal component 2 (PC2) was mainly associated with biomass, seed yield, 10-plant yield, and harvest index, reflecting the strong contribution of these traits to the variation captured by the second component (Figure 4a). In the genotype projection (Figure 4b), SAL × COL 46, SAL × PAN 171, SAL × COL 30, and SAL × PAN 58 were located in the positive region of both PC1 and PC2, whereas PAN_parent, HUA_parent, KCA_parent, and COL_parent were positioned in the opposite region. SAL_parent, ATP_control, CHO_control, SAL × COL 37, and SAL × PAN 165 occupied intermediate positions. In contrast, PAN_parent was clearly separated from the remaining genotypes, primarily along the PC1 axis.

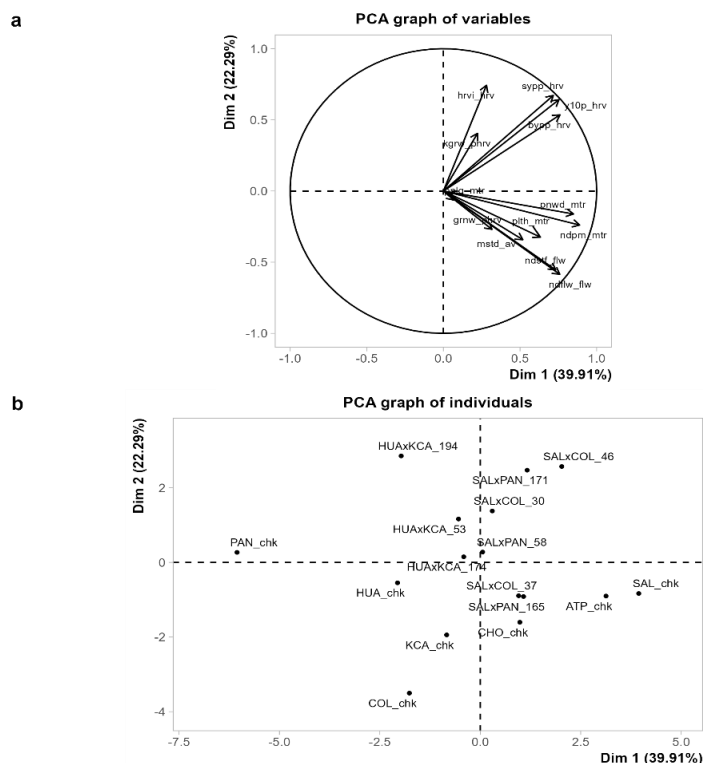


Figure 4. Principal component analysis of agronomic traits and genotypes: Trait loadings (a), genotype projection (b). Percentages indicate variance explained by each principal component. ndstf: Number of days to start flowering; ndflw: number of days to flowering; ndpm: number of days to physiological maturity; plth: plant height; mstd: main stem diameter; pnlg: panicle length; pnwd: panicle width; y10p: yield of 10 plants; hrvi: harvest index; grnw: grain width; kgrw: thousand-kernel weight; bypp: biomass yield per plant; and sypp: seed yield per plant. Measurements were recorded at flowering (flw), physiological maturity (mtr), harvest (hrv), post-harvest (phrv), whereas av denotes the average value. Genotypes, HUA: Huariponcho; KCA: Kcancolla; SAL: Salcedo INIA; PAN: Pandela Rosada; COL: Negra Collana; ATP: Altiplano; CHO: Choclito.

Multi-trait selection and ranking of quinoa lines using the Elston index

The Elston multi-trait index was used to integrate seed yield per plant, plant height, days to physiological maturity (reverse-scaled), thousand-kernel weight, and main stem diameter into a composite measure of agronomic performance based on standardized best linear unbiased estimates (BLUEs). When all genotypes (nine F_{10} lines, five parental varieties, and two control cultivars) were included in the analysis, substantial variation in index values was observed (Figure 5a). SAL $\times$ COL 37 achieved the highest index value (35.14), followed by SAL $\times$ PAN 171 (23.99) and SAL $\times$ COL 30 (21.25). Intermediate values were recorded for SAL $\times$ COL 46, SAL $\times$ PAN 165, and SAL $\times$ PAN 58, whereas several parental varieties and one control cultivar ranked lower. The COL_parent, CHO_control, PAN_parent, and SAL_parent received index values of zero due to suboptimal performance in at least one component trait.

When the analysis was restricted to the nine F_{10} lines (Figure 5b), SAL $\times$ PAN 171 ranked first (5.77), followed by SAL $\times$ COL 30 (2.38), SAL $\times$ PAN 58 (2.37), and SAL $\times$ COL 37 (2.07). HUA $\times$ KCA 174 and HUA $\times$ KCA 53 exhibited lower index values, whereas SAL $\times$ PAN 165, HUA $\times$ KCA 194, and SAL $\times$ COL 46 received values of zero. Overall, the Elston index effectively differentiated the advanced lines based on their combined performance across multiple agronomic traits.

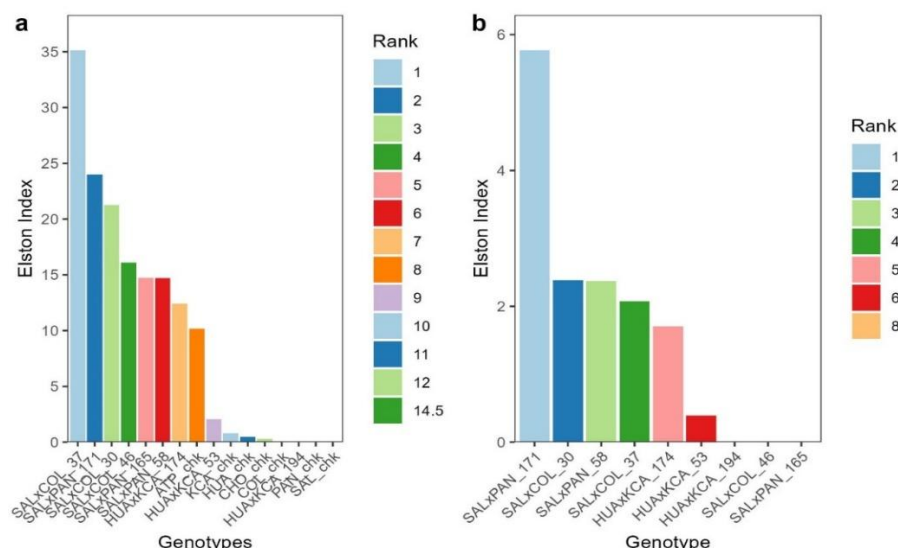


Figure 5. Multi-trait ranking of quinoa lines, parents, and control varieties, based on the Elston selection index derived from BLUEs. a) Elston index selection for the 9 lines, 5 parental varieties, and 2 commercial control varieties. b) Elston index for only the 9 lines. Genotypes, HUA: Huariponcho; KCA: Kcancolla; SAL: Salcedo INIA; PAN: Pandela Rosada; COL: Negra Collana; ATP: Altiplano; CHO: Choclito.

DISCUSSION

Agronomic traits and heritability behavior

Quinoa breeding in highland environments requires the simultaneous consideration of phenology, plant architecture, and yield because of environmental variability and complex trait interactions (Feng et al., 2025). Consequently, identifying genotypes that combine high yield potential with appropriate phenological adaptation, particularly reduced time to maturity without compromising yield, is a key objective of breeding programs targeting environments characterized by erratic rainfall and terminal stress (Kopeć, 2024).

Seed yield per plant exhibited substantial variation, with Salcedo INIA (SAL) × Pandela Rosada (PAN) 171 and SAL × Negra Collana (COL) 46 outperforming the other evaluated lines, suggesting the presence of favorable allelic combinations under the conditions of this study. However, seed yield showed moderate broad-sense heritability ($H^2 = 0.68$), consistent with its quantitative inheritance and sensitivity to environmental influences (Xu et al., 2026). Higher heritability estimates reported in other studies ($H^2 = 0.88$; De Santis et al., 2016) may reflect differences in environmental stability and population structure.

In contrast, thousand-kernel weight exhibited very high heritability ($H^2 = 0.98$), indicating that genetic factors accounted for a large proportion of the observed phenotypic variation under the evaluated conditions. This finding is consistent with the high repeatability of seed size traits reported by Bertero et al. (2004). The high heritability and repeatability associated with this trait support its use as a reliable selection criterion in quinoa breeding programs (López-Marqués et al., 2020). Phenological traits, including days to flowering ($H^2 = 0.80$) and physiological maturity ($H^2 = 0.88$), also exhibited high heritability, confirming the strong genetic regulation of developmental timing. Early-maturing lines such as Huariponcho (HUA) × Kcancolla (KCA) 194 and HUA × KCA 174 are particularly relevant for high-altitude production systems affected by frost and terminal drought (Manjarres-Hernández et al., 2021). Similar associations between later maturity and increased plant height have been reported by Emrani et al. (2024). In contrast, architectural traits exhibited lower heritability estimates ($H^2 = 0.58$ - 0.68), indicating a greater influence of environmental factors. Comparable heritability estimates for plant height were reported by Valverde-Ramos et al. (2022). Furthermore, adaptive shifts in biomass allocation toward stem thickening at high altitudes (Zurita-Silva et al., 2014), together with the sensitivity of stem diameter to management practices and plant density (Lozano-Isla et al., 2023), further support the environmental responsiveness of these traits.

Trait associations and multivariate structure of agronomic performance

Understanding the relationships among agronomic traits is essential for designing efficient selection strategies in quinoa, particularly given the physiological trade-offs among phenology, plant architecture, biomass production, and grain yield (Curti et al., 2018). Strong positive correlations among days to onset of flowering, days to flowering, and days to physiological maturity confirm phenological synchrony among the evaluated genotypes (Manjarres-Hernández et al., 2021), consistent with the facultative short-day behavior of quinoa and the genetic regulation of reproductive timing (Emrani et al., 2024).

The positive association among maturity, plant height, and stem diameter indicates that late-maturing genotypes tended to exhibit greater vegetative development. An extended growth period may allow prolonged C assimilation (Yang and Liang, 2025); however, increased plant size does not necessarily result in higher grain yield, reflecting a phenotypic trade-off between vegetative growth and reproductive performance (Curti et al., 2018). Furthermore, the association among plant height, panicle width, and total biomass suggests that panicle expansion is more closely related to overall plant vigor than to panicle length alone (Habib et al., 2024).

Plant height exhibited a weak and nonsignificant correlation with seed yield per plant ($r = 0.26$), indicating that taller plants do not necessarily achieve higher yields (Gómez et al., 2022). Excessive vegetative growth may reduce yield efficiency through increased lodging risk and greater respiratory demand (Akram et al., 2023), supporting the desirability of genotypes with moderate plant height and a high harvest index. Grain width was positively associated with stem diameter, suggesting that structural robustness may facilitate grain development (Zurita-Silva et al., 2014). However, its weak association with total yield indicates a degree of independence between seed size and seed number (Böndel and Schmid, 2021).

Principal component analysis further supported the differentiation among genotypes observed in the multivariate dataset. Similar relationships among agronomic traits and patterns of genotype differentiation have been reported in quinoa evaluated under contrasting environmental conditions, where grain yield was closely associated with biomass production and plant architectural traits (Czékus et al., 2025). The first principal component was primarily associated with flowering time, physiological maturity, plant height, stem diameter, and panicle-related traits, whereas the second principal component was mainly associated with biomass, seed yield, 10-plant yield, and harvest index. SAL × COL 46, SAL × PAN 171, SAL × COL 30, and SAL × PAN 58 were located in the positive region of the PCA space and were associated with favorable values for yield-related traits. In contrast, several parental and control varieties occupied distinct regions of the PCA space, reflecting differences in their phenological and agronomic characteristics. Similar multivariate differentiation among quinoa genotypes has been reported in breeding populations evaluated for agronomic performance (Zurita-Silva et al., 2014; Böndel and Schmid, 2021). SAL × COL 37 and SAL × PAN 165 occupied intermediate positions, suggesting balanced combinations of agronomic traits, whereas the distinct position of PAN_parent further highlighted the phenotypic differentiation observed among the evaluated genotypes.

Selection of elite lines based on multi-trait evaluation

The Elston weight-free selection index enabled the integration of seed yield per plant, plant height, days to physiological maturity (reverse-scaled), thousand-kernel weight, and main stem diameter into a composite measure of agronomic performance. Because the index penalizes genotypes that perform below the population mean for any component trait, it tends to favor genotypes with balanced performance across multiple traits rather than those exhibiting exceptional performance for a single characteristic (Elston, 1963).

When all 16 genotypes were evaluated jointly, most advanced lines outperformed the parental and control varieties, forming a distinct group of superior genotypes. This pattern indicates measurable genetic progress relative to the parental and commercial control varieties included in the trial as reference germplasm and highlights the limitations of selection based exclusively on yield (Debnath et al., 2024). The SAL × COL 37 achieved the highest index value (35.14), followed by SAL × PAN 171 (23.99) and SAL × COL 30 (21.25). Although SAL × COL 37 did not exhibit the highest absolute seed yield, it ranked first because of its balanced performance for plant height (99 cm), thousand-kernel weight (4.8 g), and stem diameter (13.8 mm), illustrating a fundamental principle of index-based breeding: Balanced trait expression may outweigh extreme performance in a single trait (Lozano-Isla et al., 2023). The strong performance of SAL-derived lines is consistent with previous reports describing the high yield potential and adaptive value associated with the SAL genetic background (Reguera et al., 2018). In contrast, several parental and control genotypes received index values of zero, reflecting penalization resulting from suboptimal performance in at least one component trait (Elston, 1963).

When the analysis was restricted to the nine F_{10} lines, the ranking changed, with SAL $\times$ PAN 171 emerging as the highest-ranked genotype (5.77), followed by SAL $\times$ COL 30, SAL $\times$ PAN 58, and SAL $\times$ COL 37. This shift is statistically expected because the exclusion of parental and control genotypes alters the population mean used in the index calculation (Elston, 1963). Under direct comparison among advanced lines, SAL $\times$ PAN 171 demonstrated the most consistent multi-trait superiority, combining the highest seed yield (42.4 g) with moderate plant height, adequate stem diameter, and an appropriate maturity duration. This performance profile suggests efficient assimilate partitioning during grain filling rather than excessive allocation to vegetative growth (Emrani et al., 2024). Overall, these findings support the use of multi-trait selection as a more reliable framework for identifying agronomically balanced quinoa genotypes adapted to high-altitude environments.

CONCLUSIONS

The evaluation of advanced F_{10} quinoa lines, parental varieties, and commercial control cultivars under highland conditions in Puno revealed significant genetic differentiation for key agronomic traits, confirming the presence of exploitable genetic variability for the simultaneous improvement of yield and phenological adaptation. Moderate to high broad-sense heritability estimates for seed yield, thousand-kernel weight, and physiological maturity indicate substantial genetic control of these traits. Among the evaluated genotypes, Salcedo INIA (SAL) $\times$ Pandela Rosada (PAN) 171 exhibited the most favorable multi-trait performance, combining high seed yield with intermediate plant height, appropriate maturity, and adequate stem diameter. The SAL $\times$ Negra Collana (COL) 30 and SAL $\times$ COL 37 also displayed balanced agronomic profiles. The superior performance of these lines relative to the parental and control varieties reflects measurable genetic progress achieved through selection. Multivariate analysis revealed partial independence between phenological and architectural traits and yield-related components, indicating that reproductive efficiency can be improved without extending the duration of vegetative growth. Furthermore, the multi-trait selection index proved effective in identifying superior genotypes based on balanced trait expression under high-altitude conditions.

Author contribution

Conceptualization: M.R.-U. Methodology: M.R.-U., R.L.-P., A.M. Software: M.R.-U. Validation: A.M. Formal analysis: M.R.-U., R.L.-P., A.U. Investigation: M.R.-U., R.L.-P. Resources: A.M. Data curation: M.R.-U. Writing-original draft: M.R.-U. Writing-review & editing: M.R.-U. Visualization: M.R.-U. Supervision: A.M. Project administration: A.U., A.M. Funding acquisition: M.R.-U., A.U. All co-authors reviewed the final version and approved the manuscript before submission.

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