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Original Article

Heritability of yield and fruit characteristics in *Solanum quitoense* Lam.

Hereditariedade da produtividade e das características dos frutos em *Solanum quitoense* Lam.

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Abstract

The lulo (*Solanum quitoense* Lam.) is a fruit tree of great importance for southern Colombia, given its demand and its potential as an exotic fruit in the international market. However, there is no information on variation and heritability, fundamental aspects for evaluating selection. The objective of this research was to estimate the heritability of yield, fruit weight (FW), total soluble solids (TSS) and maturity index (MI) in half-sib families (HSF) of lulo from the first cycle of recurrent selection. Strict sense heritability (h_e^2) across four locations in the 50 HSF were low for yield, MI and for FW, while for TSS it was high. The 50 FMH showed a high h_e^2 in yield in Arboleda, Cartago, Tangua and La Unión. TSS was high in all four locations. For FW it was moderate in Cartago, Tangua, La Unión and Arboleda. In MI it was high in Tangua and La Unión and low in Arboleda and Cartago. The h_e^2 in 10 HSF selected across four locations presented values higher than 50 HSF, with a high value for yield in Arboleda, moderate in Cartago and Tangua and low in La Unión; In FW it was high in Arboleda, Tangua and La Unión, and moderate in Cartago. The results indicate the existence of adequate genetic variance to be able to select and achieve high genetic gain in the traits evaluated in HSF of lulo.

Keywords: yield, fruit weight, genetic progress, additive variance.

Resumo

O lulo (*Solanum quitoense* Lam.) é uma árvore frutífera de grande importância para o sul da Colômbia, devido à sua demanda e ao seu potencial como fruta exótica no mercado internacional; no entanto, não há informações sobre componentes de variância e herdabilidade, aspectos fundamentais para avaliar o progresso da seleção. O objetivo deste estudo foi estimar a herdabilidade da produção, o peso do fruto (PF), os sólidos solúveis totais (SST) e o índice de maturidade (IM) em famílias de meios-irmãos (FMI) de lulo do primeiro ciclo de seleção recorrente. A herdabilidade estrita em quatro locais em 50 FMI foi baixa para produção, IM e PF, enquanto para SST, foi alta. O 50 FMI apresentou alta produção em Arboleda, Cartago, Tangua e La Unión. O SST foi alto em todos os quatro locais. Para PF, foi moderado em Cartago, Tangua, La Unión e Arboleda. Em relação à IM, foi alta em Tangua e La Unión, e baixa em Arboleda e Cartago. As 10 FMI selecionadas nas quatro localidades apresentaram valores acima de 50 FMI, com valor alto para produção em Arboleda, moderado em Cartago e Tangua, e baixo em La Unión; em relação ao PF, foi alto em Arboleda, Tangua e La Unión, e moderado em Cartago. Os resultados indicam a existência de uma variância genética adequada para poder selecionar e obter um alto ganho genético nas características avaliadas na FMI do lulo.

Palavras-chave: produtividade, peso do fruto, progresso genético, variância aditiva.

1. Introduction

Research and genetic improvement of *Solanum quitoense* is still in progress, especially in basic aspects of selection, such as the study of genetic parameters related to variance components and heritability in economically as well as agronomically important characters such as yield, fruit weight, and total soluble solids.

In lulo, one suggestion is to find a plant archetype to guide the selection of genetic materials. In addition to genetically known traits, attributes related to the absence of thorns, erect growth habit, and a high fruit set. It is important for selection to know the inheritance and heritability of the traits of interest for their inclusion in any species improvement program (Morillo Coronado et al., 2019). Heritability was originally defined by Lush as the proportion of phenotypic variance among individuals in a population due to heritable genetic effects (Villanueva Verduzco et al., 2020).

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In plant breeding, heritability estimates have been identified in reference populations: these include family mean heritability or the proportion of phenotypic variance between family means that are due to family genetic effects, and broad sense heritability or the proportion of phenotypic variation that is due to all genetic effects (Villanueva Verduzco et al., 2020). Narrow heritability is defined as the proportion of phenotypic variance between individuals in a population that is due to additive genetic effects. Similarly, broad heritability is defined as the proportion of phenotypic variance that is attributable to all genetic factors that affect phenotype expression. This type of heritability includes the sum of additive, dominance, and epistatic effects. Using the variation among half-sib families, information about heritability can be obtained in the strict sense (Sohail et al., 2018).

In many cases, an important part of the variance can be attributed to genetic factors with the environment being less important. In other cases, the environment may have a greater impact on the phenotypic variance of a population. Heritability has also been the proportion of the phenotypic variance of a progeny that is inherited. If the genetic variance of a progeny is large relative to the environmental variance, then heritability will be high; otherwise heritability will be low. Selection is most effective when the ratio of genetic variance to environmental variance is high (Vieira et al., 2019).

The relative magnitude of the additive, dominance, and epistasis components of genetic variance indicates whether the base population has sufficient genetic variability and which is the most appropriate breeding method to apply. If the additive variance exceeds the dominance variance, it is preferable to improve the crop by selection or, in contrast, to improve by hybridization. The additive variance is that which is inherited from parents to their offspring only by gene transmission and which determines the response to selection. The existence of additive variance is desirable in recurrent selection programs that aim to accumulate favorable genes to improve desirable traits in a population per se (Villanueva-Verduzco et al., 2020).

In *Solanum quitoense*, heritability studies have not been reported; however, knowing the magnitude of this parameter allows laying the genetic basis for the genetic improvement of the species (Terfa and Gurmu, 2020). Various researchers have reported estimates of genetic parameters for agronomic traits in different agricultural species, and this has allowed obtaining changes of great importance in economic traits and in the development of cultivars according to the needs of the farmer and final consumer. Estimation of genetic variability in any population is fundamental to knowing the response to selection, as well as genetic progress (Terfa and Gurmu, 2020). In other members of the Solanaceae related to lulo such as, for example, Capsicum, the broad sense of heritability in freshly picked fruit quality is moderate to low, thus limiting the improvement of this trait (Nahak et al., 2018). In another study of *Capsicum annuum* L., heritability is highest for fruit weight, followed by the number of fruits per plant, the number of fruits per plant affected by borer, and the maximum genetic advance for the number of plants per plot affected by leaf roll, followed by fruit weight and fruit borer per plant (Nahak et al., 2018).

Lanzl et al. (2023) state that selection of HSF can occur between and within families. The selection between families is based on the means of the HSFs that are compared with the population mean or the mean of all HSFs. The genetic variance between HSF $\left(\sigma_g^2\right)$ corresponds to the covariance between half-sib families $\left(\widehat{\mathrm{CovMH}}\right)$ and can be used to estimate the additive genetic variance $\left(\sigma_A^2\right)$, thus ($\sigma_g^2 = \widehat{CovMH} = 1/4\hat{\sigma}_A^2$). If it is assumed that the inbreeding coefficient (F) is equal to zero and there is an absence of epistasis, then: $\left(h_e^2\right)$ $\hat{\sigma}_A^2 = 4\sigma_g^2$. Now, heritability in the strict sense (h_e^2), corresponds to $h_e^2 = {\hat{\sigma}_A^2}\big/{\sigma_F^2}$, where the phenotype is the mean of a genotype in a environments and ***r*** replicates per trial. The phenotype has a variance denoted as σ_F^2 (Holland et al., 2010; Nyquist and Baker, 2008) and is equal to: $\sigma_F^2 = \hat{\sigma}_g^2 + \frac{\hat{\sigma}_{ge}^2}{e} + \frac{\hat{\sigma}_e^2}{re}$. In this case, $\hat{\sigma}_{ge}^2$ is the variance of the genotype x environment interaction, $\hat{\sigma}_e^2$ is the variance of the residual error for a balanced series of e environments arranged under a randomized complete block design with ***r*** replicates.

Most importantly, heritability in the broad (H^2) or strict sense (h_e^2), can be used to predict response to selection, given by $R = h_e^2 \times SD$ (or $\ddot{u}\ ^2 \times$), where SD is the selection differential, which is the deviation of the mean phenotypic value of selected individuals as an expression of the parents from the population mean, and this is perhaps the main use for the plant breeder. Both the development of new cultivars and the recommendation of newly released varieties require that a selection be made from a larger pool of candidate genotypes, so that an estimation of genotypic values are at the heart of any breeding effort (Lanzl et al., 2023).

On the basis of the above, the hypothesis proposed in this work was that there is sufficient genetic variability in the reference population to carry out selection processes and obtain genetic gains that contribute to genetic improvement. Therefore, the objective was to estimate the heritability in the strict sense in 50 half-sib families (50 HSF) of lulo (*Solanum quitoense*) and in 10 HSF selected from the 50 HSF in characters related to yield and fruit quality.

2. Materials and Methods

2.1. Location

The 50 HSF were evaluated in four localities in the municipalities of San Pedro de Cartago located at 1°33'03"N, 77°07'08"W and 1,750 masl, Tangua at 1°05'42"N, 77°23'39"W and 2,000 masl, Arboleda at 5°35'00"N, 75°09'00"O and 2,100 masl and La Unión at 1°36'18"N, 77°08'01"W and 1,726 masl, all located in the high Andean region of the department of Nariño. Based on this evaluation, ten half-sib families were selected and evaluated in the following localities: Arboleda at

01°30'45"N, 77°08'42.0"W at 2,100 masl, with an average temperature of 19 °C; San Pedro de Cartago at coordinates 01°32'24.8"N, 77°08'07.7"W, altitude of 2,396 masl and an average temperature of 18 °C; Tangua at 01°3'44.74"N, 77°25'12.26"W, 2,420 masl and an average temperature of 16 °C; and La Unión at 01°29'3.7"N, 77°13'47.3"W, 1,405 masl with an average temperature of 19 °C.

2.2. Experimental design

Each trial was established under the randomized complete block design with the 50 HSF as treatments. The 50 HSF (50HSF) trial was done with three replicates, while the selections (10HSF) trial were done with four replicates. In 50HSF, the experimental plot consisted of four plants with 2.5 m between them. The spacing between rows (plots) was 3 m. The area of the experimental plot was 30 m^2 and the area of the useful plot was 22.5 m^2, which corresponded to three central plants on which the evaluations were carried out. The 10HSF experimental plot was formed with a furrow of six plants sown at planting distances of 2.5 m x 3 m, with an area of 45 m^2 and a useful plot of 30 m^2, corresponding to the four central plants. In the 10HSF trial, the control treatment was the Castilla cultivar.

2.3. Variables evaluated

The variables related to yield potential were fruit weight (FW) in grams and yield in t ha^{-1}. Those related to fruit quality were taken based on the average of 12 mature fruits from the useful plot. Titratable acidity (TA) was recorded using the potentiometric titration method, total soluble solids (TSS) obtained by the refractometric method and corrected for TA using the equation TSSc =0.194×TA+TSS, where TSSc = corrected TSS, and finally, the maturity index (MI), calculated by the ratio between TSSc and TA.

2.4. Statistical analysis

The information obtained in each trial was subjected to an analysis of combined variance (ANOVA) with SAS® 9.4 software under a mixed model that is described below (Equation 1):

$$X_{ijk} = \mu + L_k + R(L)_{j(k)} + G_i + \left(L \times G\right)_{ki} + \varepsilon_{ijk} \qquad (1)$$

where X_{ijk} = response variable in t he ith genotuype, L_k = random effect of the kth location (k=1,2,3,4), $R(L)_{j(k)}$= random effect of the jth replicate within the kth location (j_{50FMH} = 1, 2, 3; j_{10FMH} = 1, 2, 3, 4), G_i= random effect of the ith genotype in the 50HSF (i_{50HSF} = 1,2,…,50) and fixed effect at the 10HSF (i_{10FMH} = 1,2,..,10), $(L \times G)_{ki}$ = interaction effect of the kth location by the ith genotype, ε_{ijk} = experimental error associated with the ith genotype, kth location, jth replicate within the kth location.

Based on the model described above, the structure of the analysis of variance (ANOVA) to obtain the expectation of mean squares (EMS) and determine the genetic, phenotypic and environmental variance components is presented in Table 1.

The estimation of the genotypical variance components and the genotype-by-environmental interaction component was calculated based on Cruz (2012) and corresponds to (Equations 2 and 3):

$$\sigma_g^2 = \frac{MS3 - MS4}{er} \qquad (2)$$

$$\hat{\sigma}_{ge}^2 = \frac{MS4 - MS5}{r} x \frac{g-1}{g} \qquad (3)$$

Phenotypic variance was estimated as a function of the mean square of the HSF (MS3) (Equation 4):

$$\hat{\sigma}_F^2 = \hat{\sigma}_g^2 + \frac{\hat{\sigma}_{ge}^2}{e} + \frac{\hat{\sigma}_e^2}{re} \qquad (4)$$

where σ_F^2 = estimated phenotypic variance.

Then, the estimated narrow-sense heritability ($\hat{h}_e^2$) considering the additive variance (σ_A^2) was obtained by the following Equation 5:

$$\hat{h}_e^2 = \frac{\sigma_A^2}{\hat{\sigma}_g^2 + \frac{\hat{\sigma}_{ge}^2}{e} + \frac{\hat{\sigma}_e^2}{re}} \qquad (5)$$

Table 1. ANOVA under the mixed model and the expectation of mean squares (EMS) to obtain the variance components.

Source	***DF***	***MS***	***EMS***	***Fc***
Environments (*e*)	*e-1*	MS2	$\sigma^2 + g\sigma_r^2 + gr\sigma_e^2$	CM2/CM4
Blocks (*r*)/e	*e(r-1)*	MS1	$\sigma^2 + g\sigma_r^2$	
HSF (*g*)	*g-1*	MS3	$\sigma^2 + rl\sigma_{ge}^2 + ar\sigma_g^2$	CM3/CM4
HSF x e (*ge*)	*(e-1)(g-1)*	MS4	$\sigma^2 + rl\sigma_{ge}^2$	CM4/CM5
Error	*e(g-1)(r-1)*	MS5	σ^2	

e = environments; l = g/(g-1); g = genotypes (HSF); HSF = half-sib families; DF = degrees of freedom; MS = mean squares; Fc = Fisher's coefficient calculated.

where σ_A^2 = additive variance which is equal to four times the genotypic variance ($\hat{\sigma}_g^2$) or variance between the HSF, estimated as: $\sigma_A^2 = 4\hat{\sigma}_g^2$ given that $\hat{\sigma}_g^2 = 1/4\sigma_A^2$.

Since σ_A^2 is overestimated and the expected genetic progress could be larger than the observed progress and since the denominator is not multiplies by four, the correct estimate of heritability would be $h_e^2 = 1/4\hat{h}_e^2$. In those variables where the HSF x e (*ge*) interaction was significant, variance and heritability components were estimated in the strict sense (Hallauer et al., 2010).

The genetic progress obtained among HSF, was calculated as follows: $\Delta G = k\left(\frac{1}{4}\right)\sqrt{\sigma_F^2}\,h_e^2$. Genetic gain (GS) as a function of the selected fraction, was obtained by: $GS = kSDh_e^2$, where k is the selection differential at 20% selection intensity, equivalent to 1.139 (Allard, 1967; Hallauer et al., 2010), SD is the difference between the mean of the selected fraction and the mean of the reference population: $SD = \bar{x}_S - \bar{x}_O$, where: $\bar{x}_O$ = mean of X in the original population (50 HSF) and y $\bar{x}_S$ = mean of X in the selected fraction and h_e^2 is the heritability in the narrow sense.

The genetic (CV_g), phenotypic (CV_f) and environmental (CV_e) coefficients of variation were calculated according to Pistorale et al. (2008), as follows (Equation 6):

$$CV_g = \frac{\sqrt{\sigma_g^2}}{\bar{X}_o} \times 100;\ CV_F = \frac{\sqrt{\sigma_F^2}}{\bar{X}_o} \times 100; CV_e = \frac{\sqrt{\sigma_e^2}}{\bar{X}_o} \times 100 \quad (6)$$

3. Results

The combined ANOVA (Table 2) showed significance for all the traits evaluated in the 50 HSF of lulo and in the interaction of the HSF with the environment (***ge***). In the 10HSF trial, both FW, TSS, and MI indicated significant values among HSF. Only in yield and FW were significant values obtained in the ***ge*** interaction. In yield, there were no significant differences between HSF, so there is a high degree of influence of the environmental component and a low genetic component in the expression of the phenotype. In the other variables where there were significant differences between HSF, the variation can be explained by the genetic component.

The maximum genetic increase (G) was obtained by FW (0.72 g), followed by TSS (0.06 °Brix), yield (0.01 t ha^{-1}) and MI (0.01) (Table 3), establishing that 50 HSF tend to increase these traits, therefore, the selected population will allow progression by 0.24% yield, 1% for FW, 0.61% for TSS, and 0.25% for MI. Hence, an increase (ΔG(%)) for each selection cycle within the 50 HSH population is predicted to be 0.09 t ha^{-1} for yield, 3.60 g for FW, 0.39°Brix for TSS and 0.05 units in MI. On the other hand, for FW, higher $\boldsymbol{h_e^2}$ was observed along with high ΔG.

The $\boldsymbol{h_e^2}$ for the FW obtained a minimum value in Arboleda with 18%. In Tangua it was 37%, in Cartago 38% and in La Unión 40% (Table 4).

The h_e^2 value for yield was 41.24% and a ΔG of 0.11 t ha^{-1} and a genetic advance of 1.27%, for FW of 88.09% and a ΔG of 1.84 g and a genetic advance of 1.85%, for TSS of

Table 2. Mean squares of the combined ANOVA for yield, fruit weight (FW), total soluble solids (TSS) and maturity index (MI) evaluated in 50 HSF and 10 HSF from a first cycle of recurrent selection in the natural Andean region of the department of Nariño.

Source (50 HSF)	**DF**	**Yield**	**FW**	**TSS**	**MI**
Environment (e)	3	577.92*	15455.74*	111.20*	6.20*
Blocks (r)/e	8	2.14*	307.86	0.52*	0.08
HSF (*g*)	49	11.81*	458.52*	2.39*	0.24*
HSF x *e* (*ge*)	141	11.33*	274.12*	1.34*	0.20*
Error	321	0.52	208.15	0.24	0.09
CV (%)		12.83	19.90	4.97	10.48
R^2		0.96	0.62	0.89	0.67
Mean		5.60	72.51	9.83	2.90
Source (10 HSF)	**DF**	**Yield**	**FW**	**TSS**	**MI**
Environment (*e*)	3	388.43*	635.01*	9.76*	0.69*
Blocks (*r*)/*e*	12	38.82*	127.78*	1.71*	0.45*
HSF (*g*)	10	15.65	863.11*	2.03*	0.98*
HSF x *e* (*ge*)	30	9.38*	106.22*	0.46	0.13
Error	120	4.93	66.92	0.47	0.10
CV (%)		24.71	8.25	7.32	10.48
R^2		0.78	0.66	0.59	0.64
Mean		8.98	99.20	9.40	2.99

*significant effects ($\alpha = 0.05$); CV = coefficient of variation; R^2 = coefficient of determination; HSF = half-sib families; DF = degrees of freedom.

Table 3. Variance components and heritability in the strict sense and realized in yield, fruit weight (FW), total soluble solids (TSS) and fruit maturity index (MI) of 50 HSF of lulo evaluated through four environments of the natural Andean region of the department of Nariño.

Parameter	***Yield***	***FW***	**TSS**	***MI***
σ_g^2	0.04	15.37	0.09	0.00
σ_A^2	0.16	61.47	0.35	0.01
σ_{ge}^2	2.65	16.16	0.27	0.03
σ_F^2	0.75	36.75	0.17	0.02
σ_e^2	0.52	208.15	0.24	0.09
$\boldsymbol{h_e^2}$	5.37	41.81	50.04	18.97
CV$_g$	3.57	5.41	3.01	1.99
CV$_A$	7.14	10.81	6.02	3.98
CV$_F$	15.42	8.36	4.25	4.57
CV$_e$	12.83	19.90	4.97	10.48
Mo	5.60	72.51	9.83	2.90
Ms	7.14	80.07	10.52	3.13
SD	1.54	7.56	0.69	0.23
ΔG	0.01	0.72	0.06	0.01
ΔG(%)	0.24	1.00	0.61	0.25
GG	0.09	3.60	0.39	0.05

σ = variance; σ_e^2 = environmental variance; σ_g^2 = genetic variance; σ_A^2 = additive variance; σ_{ge}^2 = interaction variance HSF x environment; h_e^2 = heritability in the narrow sense; CV$_g$ = coefficient of genetic variation; CV$_A$ = additive coefficient of variation; CV$_F$ = phenotypic coefficient of variation; CV$_e$ = coefficient of environmental variation; Mo = mean of the 50 HSF; Ms = mean of the selected fraction; SD = selection differential; Δ = increment; ΔG = genetic increment; ΔG(%) = (ΔG/Mo)*100; GG = genetic gain.

77.30% and a ΔG of 0.08 °Brix and a genetic advance of 0.83% and for MI of 87% and a ΔG of 0.06 and a genetic advance of 2.05% (Table 5). Such estimates are higher than those for the 50 HSF (Table 3).

Due to the significant ***ge*** interaction for yield and FW in the 10 HSF (Table 2), Table 6 presents the variance components and heritabilities in the strict sense for these two variables in the municipalities of Arboleda, Cartago, Tangua and La Unión. As was the case for the 50 HSF, the additive variance of the yield was greater in each of the localities than across them, except in La Unión where there was a decrease. A similar behavior was observed for FW, whose additive variance was greater in three of the four localities than in the four localities. Cartago was the environment with an additive variance lower than that obtained across localities. The influence of environments on the expression of h_e^2 was notorious (Table 6). In general, for both yield and FW, some express a higher value than between localities. In the yield, Arboleda showed the highest value of h_e^2 (80.45%), followed by Tangua (44.33%). These heritabilities were higher than those expressed by this variable in the four localities (Table 4), while Cartago (35.40%) and La Unión (11.13%) showed lower values.

As for the FW, the h_e^2 of the 10 HSF were higher than those of the 50 HSF and very similar to that obtained across the four locations in the 10 HSF, except for Cartago, which obtained the lowest value with 43.15%. Arboleda, Tangua and La Unión obtained h_e^2 values between 79% and 84%, considered high. In Arboleda, the selection of 10 HSF allowed obtaining a greater increase in yield (ΔG = 0.61), with 5.26% more genetic advance than the 50 HSF. For the FW trait, the increase was greater at the locations of Arboleda (ΔG = 2.65) and Tangua (ΔG = 2.25), with a genetic advance of 2.55% and 2.25% more than the 50 HSF, respectively (Table 6). The CV$_A$s were high in Tangua and La Unión and were higher than those of the 50 HSF; in contrast, in Arboleda and Cartago, they were low and lower than those of the 50 HSF (Tables 4 and 6). This confirms the need to stratify environments to obtain improvements in the progress of selection and heritability values.

4. Discussion

According to the criteria proposed by Hollifield et al. (2024), the heritability in the strict sense (he^2) for the 50 HSF shows low values for yield (5.37%), moderate values for fruit weight (FW) (41.81%), total soluble solids (TSS) (50%), and maturity index (MI) (19%). These results corroborate the findings of the combined ANOVA (Table 2), which showed differences between the HSF. Low heritability values indicate slow progress in selection when conducted across the four environments considered. Moderate heritability suggests higher probabilities of improving the traits evaluated in the 50 HSF of lulo due to additive gene

Table 4. Variance components and heritability in the strict sense in yield, fruit weight (FW), total soluble solids (TSS) and fruit maturity index (MI) of 50 HSF of lulo evaluated in four localities of the department of Nariño.

Par	***Arboleda***				***Cartago***			
	Yield	***FW***	***TSS***	***MI***	***Yield***	***FW***	***TSS***	***MI***
σ_e^2	0.46	190.61	0.17	0.12	0.77	284.70	0.32	0.09
σ_g^2	1.75	13.50	0.07	0.004	9.90	55.96	0.22	0.01
σ_A^2	7.01	53.99	0.29	0.02	39.61	223.86	0.88	0.05
σ_F^2	2.21	204.11	0.24	0.13	10.68	340.67	0.54	0.10
$h_e^2\,(\%)$	***92.00***	***18.00***	***57.00***	***10.00***	***98.00***	***38.00***	***68.00***	***29.00***
CV_g	20.48	6.21	2.96	2.22	45.27	9.62	5.14	3.80
CV_A	40.99	12.41	6.02	4.96	90.56	19.23	10.27	8.50
CV_F	23.01	24.14	5.47	12.65	47.02	23.72	8.05	12.02
CV_e	10.50	23.33	4.61	12.15	12.63	21.69	6.20	11.41
Mo	6.46	59.19	8.95	2.85	6.95	77.80	9.13	2.63
Ms	8.50	74.15	9.49	3.21	12.08	93.55	9.78	2.93
SD	2.04	14.96	0.54	0.36	5.13	15.75	0.65	0.30
ΔG	0.39	0.73	0.08	0.01	0.91	2.00	0.14	0.03
ΔG(%)	6.03	1.24	0.89	0.36	13.12	2.57	1.56	0.99
GG	2.14	3.07	0.35	0.04	5.73	6.82	0.50	0.10

Par	***Tangua***				***La Unión***			
	Yield	***FW***	***TSS***	***MI***	***Yield***	***FW***	***TSS***	***MI***
σ_e^2	0.48	114.67	0.17	0.06	0.30	256.05	0.30	0.10
σ_g^2	1.93	22.41	0.49	0.04	0.36	56.06	3.82	0.08
σ_A^2	7.73	89.64	1.95	0.25	1.42	224.23	15.28	0.31
σ_F^2	2.41	137.08	0.66	0.13	0.66	312.10	4.12	0.18
$h_e^2\,(\%)$	***93.00***	***37.00***	***90.00***	***76.00***	***78.0***	***40.00***	***97.00***	***69.00***
CV_g	22.23	5.68	6.62	6.58	27.27	11.12	18.25	9.09
CV_A	44.48	11.36	13.20	16.45	54.17	22.24	36.50	17.90
CV_F	24.84	14.04	7.68	11.86	36.93	26.23	18.95	13.64
CV_e	11.09	12.84	3.90	8.06	24.90	23.76	5.11	10.17
Mo	6.25	83.38	10.58	3.04	2.20	67.34	10.71	3.11
Ms	8.28	93.63	11.78	3.54	3.34	85.7	12.38	3.57
SD	2.03	10.25	1.20	0.50	1.14	18.36	1.67	0.46
ΔG	0.41	1.23	0.21	0.08	0.18	2.01	0.56	0.08
ΔG(%)	6.58	1.48	1.97	2.57	8.20	2.99	5.23	2.68
GG	2.15	4.32	1.23	0.43	1.01	8.36	1.85	0.36

Par = parameter; = variance; σ_e^2 = environmental variance; σ_g^2 = genetic variance; σ_A^2 = additive variance; σ_F^2 = phenotypic variance; h_e^2 = heritability in the narrow sense (Nyquist and Baker, 2008); CV_g = coefficient of genetic variance; CV_A = additive coefficient of variation; CV_F = coefficient of genetic variance; CV_e = coefficient of environmental variance; Mo = mean of the 50 HSF; Ms = mean of the selected fraction; SD = selection differential; Δ = increment; ΔG = genetic increment; ΔG(%) = (ΔG/Mo)*100; GG = genetic gain.

action, making selection effective for the improvement of these traits (Lourenço et al., 2020).

Although these heritabilities are considered moderate, the moderately high coefficients of additive variation (CVA) ranging from 11.36 to 22.24 indicate good genetic influence, with the possibility of identifying and selecting superior genotypes and inheriting favorable genes from their descendants (Silva-Díaz et al., 2018) for FW and its incidence in yield, given that these two traits are positively correlated. This suggests that advances in selection can be

Table 5. Variance components and heritability in the strict sense in yield, fruit weight (FW), total soluble solids (TSS) and fruit maturity index (MI) of 10 HSF of lulo evaluated through four environments of the natural Andean region of the department of Nariño.

Parameter	***Yield***	***FW***	***TSS***	***MI***
σ_g^2	0.39	47.31	0.10	0.05
σ_A^2	1.57	189.22	0.39	0.21
σ_{ge}^2	1.00	8.84	0.00	0.01
σ_F^2	0.95	53.70	0.13	0.06
σ_e^2	4.93	66.92	0.47	0.10
$\mathbf{h_e^2}$	**41.24**	**88.09**	**77.30**	**87.00**
CV_g	6.97	6.93	3.33	7.71
CV_A	13.94	13.87	6.66	15.42
CV_F	10.85	7.39	3.84	8.19
CV_e	24.73	8.25	7.29	10.58
Mean	8.98	99.20	9.40	2.99
ΔG	0.11	1.84	0.08	0.06
ΔG(%)	1.27	1.85	0.83	2.05

σ = variance;σ_g^2 = genetic variance; σ_A^2 = additive variance; σ_{ge}^2 = interaction variance HSF x environment; = phenotypic variance; σ_e = environmental variance; h_e^2 = heritability in the narrow sense; CV_g = genetic coefficient of variance; CV_A = additive coefficient of variance; CV_F = phenotypic coefficient of variance; CV_e = environmental coefficient of variance; Δ = increment; ΔG = genetic increment; ΔG(%) = (ΔG/Media)*100.

Table 6. Variance components and heritability in the strict sense in yield and fruit weight (FW) of 10 HSF of lulo evaluated in Arboleda, Cartago, Tangua and La Unión, department of Nariño.

Par	***Arboleda***		***Cartago***		***Tangua***		***La Unión***	
	Yield	***FW***	***Yield***	***FW***	***Yield***	***FW***	***Yield***	***FW***
σ_e^2	3.45	71.45	6.49	82.51	7.62	39.83	2.15	73.91
σ_g^2	3.55	67.02	0.89	15.65	1.52	49.85	0.07	95.82
σ_A^2	14.19	268.09	3.56	62.61	6.07	199.40	0.27	383.27
σ_F^2	7.00	138.48	7.38	98.16	9.14	89.68	2.22	169.72
h_e^2	***80.45***	***78.96***	***35.40***	***43.15***	***44.33***	***83.35***	***11.13***	***83.83***
CV_g	16.36	7.89	10.64	4.02	11.52	7.06	5.46	10.35
CV_A	32.70	15.78	21.27	8.04	23.03	14.12	10.71	20.69
CV_F	22.97	11.34	30.63	10.07	28.25	9.47	30.72	13.77
CV_e	16.12	8.15	28.72	9.23	25.80	6.31	30.23	9.09
Media	11.52	103.77	8.87	98.36	10.7	100.03	4.85	94.62
ΔG	0.61	2.65	0.27	1.22	0.38	2.25	0.05	3.11
ΔG(%)	5.26	2.55	3.09	1.24	3.57	2.25	0.97	3.29

Par = parameter; = variance; σ_e^2 = environmental variance; σ_g^2 = genetic variance; σ_A^2 = additive variance; σ_F^2 = phenotypic variance; h_e^2 = heritability in the narrow sense (Nyquist and Baker, 2008); CV_g = genetic coefficient of variance; CV_A = coefficient of additive variance; CV_F = coefficient of phenotypic variance; CV_e = coefficient of environmental variance; Δ = increment; ΔG = genetic increment; ΔG(%) = (ΔG/mean)*100.

obtained from the recombination of these 10 HSF, given that the heritability estimates were based on a balanced design that improved their precision compared to the 50 HSF trial, where some plots were lost, affecting the precision of the evaluated parameters. Consequently, the CVAs were also higher, an aspect that increases the potential for increasing genetic gains (Vamsi et al., 2022) in the selection of these traits.

It is necessary to consider that the values of additive variances (σA^2) are significant when compared with estimates from other populations. This is not applicable to lulo due to the lack of available studies for such comparisons; using values from a single population can lead to erroneous conclusions, so it is preferable to compare the coefficients of additive genetic variability (AGV) of the studied traits. Low additive genetic variability is given by low AGV, which limits the selection of half-sib or full-sib families aimed at exploiting additive variance components (Brito et al., 2020).

Since the genotype by environment (GE) interaction was significant for all variables in the 50 HSF trial and only for yield and FW in the 10 HSF trial (Table 2), the variance and heritability components are discussed and analyzed within each location. For yield, he^2 values were high, above 70%, indicating a high genetic component in the expression of this variable (Sohail et al., 2018). The CVAs were moderately low for Arboleda and Tangua and high for Cartago and La Unión (Table 4). These results indicate that the environment plays a fundamental role in the heritability of yield; therefore, it would be advisable to stratify the environments for the selection of lulo genotypes by yield.

As observed for yield and FW, the he^2 estimates for TSS and MI increased in each of the four locations compared to the estimates across them, but the values for TSS were high compared to those for MI. This corroborates what was previously described for yield and FW in the sense of stratifying environments to take advantage of the magnitude of he^2 and achieve high rates of genetic gain (Table 4).

Regarding the MI of the 50 FMH, he^2 was high in La Unión (69%) and Tangua (76%) and moderate in Cartago (29%). The CVAs are relatively low in all locations despite the high he^2 values, except for Arboleda where both parameters are low. This coincides with (Kaur and Kumar, 2024) who indicates that some characters exhibiting high heritabilities in the strict sense do not necessarily imply high levels of additive genetic variation; and characters with low heritabilities tend to have high levels of additive genetic variation, characteristic of species with low levels of artificial selection. La Unión obtained the highest CVA and is the location where MI selection could be more efficient since it also showed a high he^2 value (69%) (Table 4).

The he^2 values for yield, FW, TSS, and MI increased at each of the locations compared to the values across the four locations due to higher ΔG, ΔG (%), and GG values. High ΔG indicates additive gene action with values under non-additive gene action. Therefore, heritability values are reliable if accompanied by high ΔG and GG (Lourenço et al., 2020).

Regarding the genetic variance components established in the 10 HSF across locations, we found that the first cycle of recurrent selection allowed maintaining and, in some cases, expressing higher levels of additive variance and he^2 than those found in the 50 HSF, demonstrating the advantages of recurrent selection concerning maintaining genetic variability cycle to cycle (Brito et al., 2020).

The CVAs were high within and across the four locations except La Unión for yield, where it was low (Tables 5 and 6). A strategy to exploit variance and make progress in selection was to stratify environments. In locations and traits where high CVAs are manifested, it is easier to obtain selection progress. It is important to note that in most of the locations, the CVA increased compared to those observed in the 50 HSF, confirming that recurrent selection of half-sib families can contribute to the manifestation of additive variance since it is possible to have better environmental control and a greater possibility of stronger exploitation of the additive variance, along with improving the experimental technique (Brito et al., 2020). In fact, in the 10 HSF trial, there was no loss of experimental plots, reducing the MS value of HSF x e compared to the 50 HSF trial (Table 2).

Based on the results described above, the tendency of heritability estimates to be higher when calculated in a particular environment than across environments can be detected. This may be a function of HSF x e variance effects that differ from one variable to another, although they are more determinant in yield, where the effects of GE interaction outweighed genetic effects in the two trials. Wessel-Beaver and Scott (2019) found similar results *in Lycopersicon esculentum* Mill.

It is necessary to consider that the ideal selection site must meet two requirements (Chifarelli et al., 2022). First, the genetic differences found at that site must also be expressed in the target environment, and second, the response to selection obtained at the selection site must be maintained to some extent in the target environment. The suitability of selection sites that differ in environmental conditions is assessed by heritability. Since the interactions of HSF x environment are important at the evaluated locations, there is a need for increased evaluations in years and environments to identify genotypes with region-specific adaptation.

Adaptation to an environment is best achieved by selection in that environment. Selection in a high-yielding environment does not identify genotypes suitable for low-yielding environments. Selection in low-yielding environments appears to be more efficient (Chifarelli et al., 2022), hence establishing heritability within an environment is valid for advancing selection for the conditions of that environment.

Based on these results, it can be determined that it is necessary to adjust the experimental technique, increase the number of years, environments, and the number of genotypes evaluated to improve he^2 estimates (Lourenço et al., 2020).

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References

ALLARD, R.W., 1967. *Principios de la mejora genética de las plantas*. Barcelona: Omega, 498 p.

BRITO, O.G., JÚNIOR, V.C.D.A., AZEVEDO, A.M., SILVA, N.O., FERNANDES, J.S.C. and ALVES, K.A., 2020. Genetic parameters, selection gains and genotypic correlations in kale half-siblings progenies. *Emirates Journal of Food and Agriculture*, vol. 32, no. 8, pp. 591-599. http://doi.org/10.9755/ejfa.2020.v32.i8.2136.

CHIFARELLI, V., SENILLIANI, M.G., LONGHI-SANTOS, T., MOGLIA, J.G. and GIMÉNEZ, A.M., 2022. *Gonopterodendron sarmientoi* Lorentz ex Griseb (palo santo): evaluation of growth for timber purposes. *Madera y Bosques*, vol. 28, no. 1, e2812401. http://doi.org/10.21829/myb.2022.2812401.

CRUZ, C., 2012. *Princípios de genética quantitativa*. Viçosa: Universidad Feederal de Viçosa, vol. 1, 349 p.

HALLAUER, A.R., CARENA, M.J. and MIRANDA FILHO, J., 2010. *Handbook of plant breeding.* New York: Springer.

HOLLAND, J.B., NYQUIST, W.E. and CERVANTES-MARTÍNEZ, C.T. (2010). Estimating and interpreting heritability for plant breeding: an update. In: J. JANICK, ed. *Plant breeding reviews*. Hoboken: John Wiley & Sons, vol. 22. http://doi.org/10.1002/9780470650202.ch2.

HOLLIFIELD, M.K., LOURENCO, D. and MISZTAL, I., 2024. Estimation of heritability with genomic information by method R. *Journal of Animal Breeding and Genetics*. In press. http://doi.org/10.1111/jbg.12863. PMid:38523564.

KAUR, S. and KUMAR, A., 2024. A comprehensive study of wheat genotypes for combining ability and heritability in drought tolerance. *Plant Science Today*, vol. 47, no. 2, pp. 10-13. http://doi.org/10.14719/pst.3487.

LANZL, T., MELCHINGER, A.E. and SCHÖN, C.C., 2023. Influence of the mating design on the additive genetic variance in plant breeding populations. *Theoretical and Applied Genetics*, vol. 136, no. 11, pp. 236. http://doi.org/10.1007/s00122-023-04447-2. PMid:37906322.

LOURENÇO, V.M., OGUTU, J.O. and PIEPHO, H.P., 2020. Robust estimation of heritability and predictive accuracy in plant breeding: evaluation using simulation and empirical data. *BMC Genomics*, vol. 21, no. 1, pp. 43. http://doi.org/10.1186/s12864-019-6429-z PMid:31937245.

MORILLO CORONADO, A.C., RODRÍGUEZ FAGUA, A.D.P. and MORILLO CORONADO, Y., 2019. Caracterización morfológica de lulo (*Solanum quitoense* Lam.) en el municipio de Pachavita, Boyacá. *Acta Biologica Colombiana*, vol. 24, no. 2, pp. 291-298. http://doi.org/10.15446/abc.v24n2.75832.

NAHAK, S.C., NANDI, A., SAHU, G.S., TRIPATHY, P., DASH, S.K. and PATNAIK, A., 2018. Studies on variability, heritability and genetic advance for yield and yield contributing characters in chilli (*Capsicum annuum* L.). *Journal of Pharmacognosy and Phytochemistry*, vol. 7, no. 1, pp. 2506-2510.

NYQUIST, W.E. and BAKER, R.J., 2008. Estimation of heritability and prediction of selection response in plant populations. *Critical Reviews in Plant Sciences*, vol. 10, no. 3, pp. 235-322. http://doi.org/10.1080/07352689109382313.

PISTORALE, S.M., ABBOTT, L.A. and ANDRÉS, A., 2008. Diversidad genética y heredabilidad en sentido amplio en agropiro alargado, Thinopyrum ponticum. *Ciencia e Investigación Agraria*, vol. 35, no. 3, pp. 259-264. http://doi.org/10.4067/S0718-16202008000300003.

SILVA-DÍAZ, R., GARCÍA-MENDOZA, P., FALEIRO-SILVA, D. and SOUZA, C.L., 2018. Determinación de componentes de la varianza y parámetros genéticos en una población segregante de maíz tropical. *Bioagro-*, vol. 30, no. 1, pp. 67-77.

SOHAIL, A., RAHMAN, H., HUSSAIN, Q., HADI, F., ULLAH, U. and KHAN, W., 2018. Genetic variability, heritability and correlation studies in half-sib recurrent families of CIMMYT Maize population CZP-132011. *Journal of Agricultural and Biological Science*, vol. 13, pp. 106-112.

TERFA, G.N. and GURMU, G.N., 2020. Genetic variability, heritability and genetic advance in linseed (*Linum usitatissimum* L) genotypes for seed yield and other agronomic traits. *Oil Crop Science*, vol. 5, no. 3, pp. 156-160. http://doi.org/10.1016/j.ocsci.2020.08.002.

VAMSI, D.M., MEENA, H., SANDHYA SREE, G. and PAYASI, S., 2022. Assessment of genetic variability, heritability and genetic advance in sunflower (*Helianthus annuus* L.) genotypes for seed yield and other agronomic traits. *Environment and Ecology*, vol. 40, no. 2, pp. 451-457.

VIEIRA, S.D., ARAUJO, A.L.R., SOUZA, D.C., RESENDE, L.V., LEITE, M.E. and RESENDE, J.T.V., 2019. Heritability and combining ability studies in strawberry population. *Journal of Agricultural Science*, vol. 11, no. 4, pp. 457. http://doi.org/10.5539/jas.v11n4p457.

VILLANUEVA-VERDUZCO, C., AYALA-ESTEBAN, J.A., VILLANUEVA-SÁNCHEZ, E., SAHAGEN-CASTELLANOS, J., SÁNCHEZ CABRERA, I., CHANING MERRICK, L. and IRIZAR GARZA, M.B.G., 2020. Changes of genetic variances and heritability by effect of selection in a Mexican local variety of Squash. *Journal of Applied Biotechnology & Bioengineering*, vol. 7, no. 5, pp. 225-230. http://doi.org/10.15406/jabb.2020.07.00237.

WESSEL-BEAVER, L. and SCOTT, J.W., 2019. Genetic variability of fruit set, fruit weight, and yield in a tomato population grown in two high-temperature environments. *Journal of the American Society for Horticultural Science*, vol. 117, no. 5, pp. 867-870. http://doi.org/10.21273/JASHS.117.5.867.