

Genetic analysis of yield component traits in cowpea [*Vigna unguiculata* (L.) Walp.]

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Abstract: We investigated the genetic control of the three yield components in cowpea: number of grains per pod, pod length and grain size, in a biparental cross. Genetic parameters were estimated in generations of a cross between two contrasting genitors, using a randomized complete block design with three replications. Narrow-sense heritability estimates varied from 27% to 67%, suggesting that genetic gains can be achieved with selection. Pod length and grain size had the highest heritability values and genetic gains. The number of grains per pod is highly affected by the environment. Dominance was detected for all traits, mainly for pod length. However, additive gene effects accounted for more than 68% of the variation in all traits, which are controlled by at least 10 genes. It is possible to improve the evaluated traits via conventional breeding approaches, although large population sizes will be required in breeding stages.

Keywords: *Vigna unguiculata*, inheritance, genetic parameters, yield components, plant breeding

INTRODUCTION

Cowpea [*Vigna unguiculata* (L.) Walp.] is a legume species of great agronomic potential due to its wide adaptability to diverse environmental conditions, low production costs and high nutritional value (Boukar et al. 2019, Araújo et al. 2022, Raina et al. 2023). The crop has been cultivated in more than 100 countries, mainly between 40° N and 30° S latitudes, and it is expected to fulfill dietary requirements under the current changing climate (Gonçalves et al. 2016). In Brazil, cowpea is produced through traditional and corporate farming, creating a significant socioeconomic impact (Freire-Filho et al. 2017).


The high genetic diversity within cowpea species creates a great genetic potential to be exploited. The genetic breeding of this crop is the main way to increase its yield (Boukar et al. 2019, Raina et al. 2023). As yield is a complex trait, highly affected by environmental conditions, dissection in its yield component traits is an important strategy to address its improvement. Thus, evaluation of these traits is commonly performed to provide bases for selection procedures (Dias et al. 2016, Raina et al. 2023).

Although advances in cowpea breeding have contributed to expanding its cultivation in Brazil, there is a constant need to address market requirements. In addition to grain yield, important features of grains and pods are pursued by



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cowpea breeding programs, being improved according to specific preferences of consumers and producers (Rocha et al. 2017, Boukar et al. 2019). There is large variation in grain size for the commercial types (Araújo et al. 2023), and the market preference for a certain type has cultural influence. For pod length and number of grains per pod, cultivars with long pods and many grains are more suitable for manual harvesting. On the other hand, small pods with fewer grains are preferable for mechanized systems, as they reduce the possibility of pod breaking and losses during the harvesting process (Rocha et al. 2017).

Large variations of heritability estimates have been found in genetic studies for yield components in cowpea. Estimates varying from 6.6% to 87.6% have been reported for narrow-sense heritabilities for the number of grains per pod, pod length and grain size in studies using six generations (Lopes et al. 2003, Egbadzor et al. 2013, Pathak et al. 2017). Some studies have found four to eight genes controlling grain size (Lopes et al. 2003, Ayo-Vaughan et al. 2013, Egbadzor et al. 2013), while approximately six and five genes have been found for pod length and number of grains per pod, respectively (Ayo-Vaughan et al. 2013). Although there are some divergent findings, significances for additive, dominance and epistatic effects on these traits have been found (Lopes et al. 2003, Ayo-Vaughan et al. 2013, Egbadzor et al. 2013, Raut et al. 2017, Owusu et al. 2018, Edematie et al. 2021, Shinde et al. 2021). However, scarce studies of this nature have been performed with genotypes from Brazilian germplasm.

Due to their continuous phenotypic distribution, yield components are expected to follow a quantitative inheritance, where different gene interactions may occur. Therefore, estimating the most important gene effects controlling these traits will provide valuable information to support local breeders in deciding on the adequate breeding methodology to conduct their populations. In this context, the objective of this study was to investigate the genetic control of the number of grains per pod, pod length and grain size in populations of a cowpea cross, involving genotypes from a Brazilian germplasm.

MATERIAL AND METHODS

Genetic materials and field trial

The cowpea cross was performed with two elite lines from the Embrapa Meio-Norte Germplasm Collection: MNC05-828C-1-9-1 (P_1) and MNC04-792F-146 (P_2). The genotypes are contrasting for grain size, pod length and number of grains per pod. Generations F_1 ($P_1 \times P_2$), F_2 ($F_1 \times F_1$), BC_1 ($F_1 \times P_1$) and BC_2 ($F_1 \times P_2$) were obtained through controlled cross-fertilizations in a screen house in Teresina, Piauí, at Embrapa Meio-Norte (lat 5° 02' 21.36" S, long 42° 47' 22.44" W) between the years 2015 and 2018. The same generations were obtained for the reciprocal cross $P_2 \times P_1$, F_1 reciprocal ($P_2 \times P_1$), F_2 reciprocal (F_1 reciprocal $\times F_1$ reciprocal), BC_1 reciprocal (F_1 reciprocal $\times P_1$) and BC_2 reciprocal (F_1 reciprocal $\times P_2$). Each F_2 generation was obtained by self-fertilization of F_1 generation plants.

A field trial was performed at Embrapa Meio-Norte (lat 5° 05' 20" S, long 42° 48' 05" W, alt 72 m asl), from October 2018 to January 2019. All generations and the parents, totalizing 10 populations, were evaluated in a randomized complete block design with three replications. The seed samples of the generations were sown in rows with spacing of 0.80 m \times 0.25 m between the rows and between the holes, respectively. Plots differed in size among generations due to seed availability, keeping the same plot sizes among blocks. Plots consisted of three 2.5 m rows for parents, one 2.5 m row for F_1 generation and for backcross generations, and fifteen 2.5 m rows for F_2 population. All management practices were applied according to the crop requirements (Rocha et al. 2017). The type of soil in the experimental field is Ultisol with sandy loam texture. The total precipitation for the period of the experiment was 556.4 mm, with average minimum and maximum temperatures of 23.6 °C and 35.7 °C, respectively.

For data collection, the weight of one hundred grains, pod length and the number of grains per pod were evaluated in ten competitive plants in each row. Grain size is determined by the trait weight of one hundred grains. Pod length and the number of grains per pod were obtained as a mean of a sample of five pods randomly collected in each plant. For each parent plot, only the middle row was assessed, resulting in ten plants per block. The final number of plants evaluated for other generations was reduced due to losses during the trial, not compromising the sample representation to perform the genetic study.

Statistical analyses

The Scott-Knott clustering (≤ 0.05) was applied to group the means of the ten populations to evaluate their performances and the differences between F_1 and F_2 generations and their reciprocal generations, as evidence for maternal effect. The means clustering was plotted using the R[®] software, version 4.3.2 (R Core Team 2023), with the aid of the *ScottKnott* package (Jelihovschi et al. 2014). A density plot with the phenotypic distribution of the F_2 population for the traits was created using the *ggplot2* package (Wickham 2016).

The genetic study was performed based on the Generation Mean and Variance Analysis with the following six populations: P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 , according to Mather and Jinks (1974) and Cruz et al. (2012), using GENES software (Cruz 2013). The complete model was used for the estimation of genetic parameters, using the weighted least squares method. The parameters estimated were mean (m), the additive gene effect (a), the dominance gene effect (d), and the epistatic effects additive \times additive (aa), additive \times dominance (ad) and dominance \times dominance (dd).

The null hypothesis significance for each genetic parameter was evaluated by the t -test, while the contribution of each one to the total observed variation was analyzed by the non-orthogonal decomposition of the sum of squares applying the Gauss Elimination Method (Lopes et al. 2003, Cruz et al. 2012).

The Average Degree of Dominance (ADD) was estimated through the equation $ADD = \frac{2\bar{F}_1 - (\bar{P}_1 + \bar{P}_2)}{(\bar{P}_1 - \bar{P}_2)}$, using the F_1 generation mean (\bar{F}_1) and means of parents (\bar{P}_1 and \bar{P}_2). The minimum number of genes controlling each trait was estimated with the expression $n = \frac{R^2}{8\sigma_a^2}$, using the total phenotypic range in F_2 population (R) and the additive variance (σ_a^2) (Cruz et al. 2012).

Broad-sense heritability (h_b^2) was obtained through the formula $h_b^2 = \frac{\sigma_g^2}{\sigma_p^2} 100$, in which σ_g^2 is the total genotypic variance and σ_p^2 is the phenotypic variance, whose environmental variance was calculated by the expression $\sigma_e^2 = \frac{1}{4} (2\sigma_{F_1}^2 + \sigma_{P_1}^2 + \sigma_{P_2}^2)$. Narrow-sense heritability (h_n^2) was obtained with the expression $h_n^2 = \frac{\sigma_a^2}{\sigma_p^2} 100$, in which σ_a^2 is the additive variance, calculated with the equation $\sigma_a^2 = 2\sigma_{F_2}^2 - (\sigma_{BC_1}^2 + \sigma_{BC_2}^2)$, and σ_p^2 is the phenotypic variance. Expected gain (ΔG) in the F_3 generation, considering the selection of 20% of F_2 plants, was estimated by the model $\Delta G = h_n^2 \cdot sd$, in which h_n^2 is the narrow-sense heritability and sd is the selection differential, calculated by the difference between the original F_2 population mean and the selected population mean.

RESULTS AND DISCUSSION

The cross MNC05-828C-1-9-1 \times MNC04-792F-146 showed contrast between means of the parents for three traits (Figure 1), enabling the procedure for the genetic study with its populations. The phenotypic distribution of all traits in F_2 plants is typical of quantitative inheritance, presenting a normal curve and indicating the presence of individuals superior to the parents of higher performance (Figure 2). Such transgressive segregants facilitate the achievement of greater genetic gains in the breeding programs. Differences between F_1 and F_2 generations and their reciprocals were not found (Figure 1), suggesting that maternal gene effect is not evident for all traits. Owusu et al. (2020) also identified absence of maternal effect for pod length and seeds per pod, but presence for seed weight in cowpea populations. Therefore, selection can be started in F_2 population to take advantage of the wide genetic variability in this generation.

The weight of one hundred grains and the number of grains per pod showed means of the F_1 and F_2 generations between the parent values, pointing to the presence of additive gene action in the inheritance of these traits (Table 1). Presence of heterosis and dominance action is clearly observed for pod length, whose F_1 generation obtained a higher mean than F_2 and the parent with longer pods. Lachyan et al. (2016) also indicated the presence of dominance and transgression due to the superiority of the F_2 mean for pod length compared to the parents, while Edematie et al. (2021) noticed the dominance with the reduction of F_2 performance. For three traits, the difference between BC_1 and BC_2 means suggests a differential contribution of the parents to the progenies. Backcrosses with higher performance are the result of crossing F_1 with the superior parent, which must have contributed with more favorable alleles for this generation. This result demonstrates the importance of choosing appropriate genitors for hybridization in breeding programs. In addition, the backcross means are between the F_1 mean and the mean of the backcrossed parent (Table 1), which according to Ribeiro et al. (2014) reinforces the credibility of genetic parameter estimates in the genetic study.

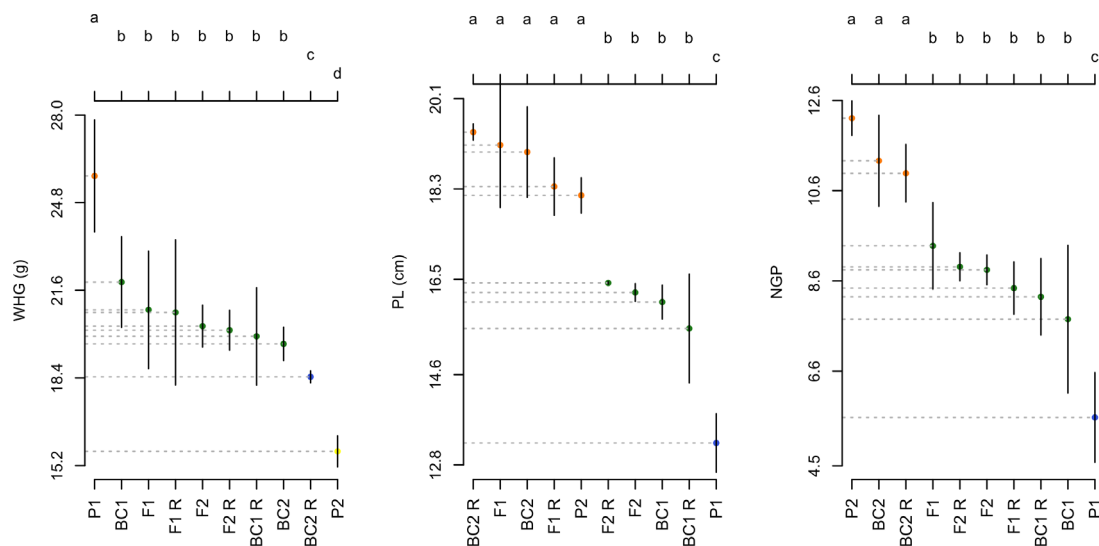


Figure 1. Means grouping of the weight of one hundred grains (WHG), pod length (PL) and number of grains per pod (NGP) evaluated in ten cowpea populations of the cross MNC05-828C-1-9-1 × MNC04-792F-146, with standard deviation for repetition means. Means followed by the same letter do not differ from each other by the Scott-Knott test ($P < 0.05$). F₁ R: F₁ reciprocal; F₂ R: F₂ reciprocal; BC₁ R: BC₁ reciprocal; BC₂ R: BC₂ reciprocal.

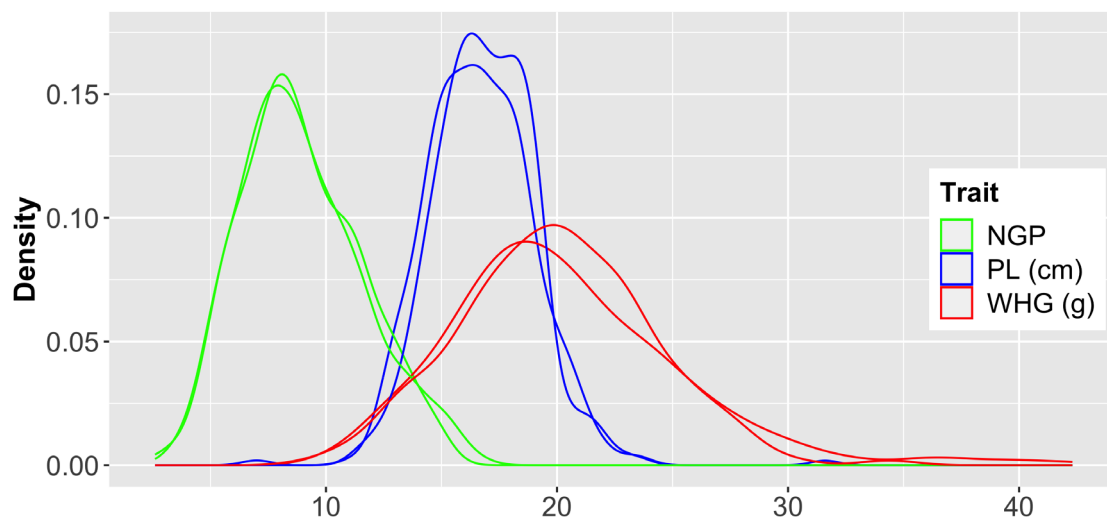


Figure 2. Frequency distribution in F₂ and F₂ reciprocal plants for the weight of one hundred grains (WHG), number of grains per pod (NGP) and pod length (PL) of the cowpea cross MNC05-828C-1-9-1 × MNC04-792F-146.

The three traits showed good variability, with Genotypic Coefficients of Variation (CVg) from 11.3 to 20.81% (Table 2). The Environment Coefficients of Variation (CVe) varied from 7.13 to 19.97%, representing high to intermediate experimental precisions. CVg/CVe ratios higher than the unit were found for the traits, indicating the possibility of selecting individuals with accuracy and efficiency (Vencovsky et al. 2012, Pathak et al. 2017), except for the number of grains per pod, which showed greater importance for the environment effect. According to Resende and Duarte (2007),

Table 1. Number of plants (N), mean (\bar{u}) and variance ($\hat{\sigma}^2$) for yield components evaluated in six populations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2) of the cross MNC05-828C-1-9-1 \times MNC04-792F-146

Populations	WHG (g)			PL (cm)		NGP	
	N	\bar{u}	$\hat{\sigma}^2$	\bar{u}	$\hat{\sigma}^2$	\bar{u}	$\hat{\sigma}^2$
P_1	30	25.77	7.62	13	1.38	5.73	2.27
P_2	30	15.72	3.59	18	1.31	12.20	4.64
F_1	14	20.87	9.61	19	1.54	9.37	3.28
F_2	326	20.29	26.17	16	5.06	8.88	6.40
BC_1	21	21.94	20.4	16	3.65	7.75	5.52
BC_2	21	19.64	19.88	19	3.05	11.25	5.50

WHG, weight of one hundred grains; PL, pod length; NGP, number of grains per pod.

the Relative Coefficient of Variation below 1 may represent a good scenario for selection depending on the number of replications in the trial. For a CVg/CVe ratio of 0.90 under 3 replications, a selection accuracy of 0.84 is achieved. Thus, good selection accuracy is expected even for the number of grains per pod.

These results corroborate the broad-sense heritability coefficients found in this study (Table 2). High magnitude is shown for the weight of one hundred grains and pod length (70.91% and 71.51%, respectively), showing that most of the phenotype is assigned to genetic causes and indicating the possibilities of genetic gains for the traits through selection. Furthermore, most of this heritability is due to additive variance, resulting in narrow-sense coefficients of 46.05% and 67.63% for both traits, respectively (Table 2). The superiority of this variance indicates facility in the identification of superior genotypes and favors the breeding of self-fertilizing crops (Dias et al. 2016, Melo et al. 2018).

For the number of grains per pod, the environmental variance was higher than that of genetic nature, resulting in a low proportion of broad- and narrow-sense heritabilities (47.29% and 27.57%, respectively) (Table 2). Thus, the phenotype has poor reliability for selecting superior genotypes, hindering the breeding process for this trait. On the other hand, more than half of the genetic variation has additive nature, showing the possibility of obtaining superior inbred genotypes from selection in populations derived from F_2 . Thus, depending on the environmental conditions, superior individuals can produce superior progenies for this trait. Large range of heritability coefficients has been found in genetic studies conducted with six generations in cowpea. For grain size, variations of 20.45-92.15% and 8.36-85.69% are found for broad- and narrow-sense heritability, respectively. For pod length, broad-sense heritabilities varying from 23.42 to 82.37% and narrow-sense heritabilities from 7.65 to 53.22% have been reported. For the number of grains per pod, variations of 38.68-91.04% have been reported for broad-sense heritability, while variations of 6.60-87.65% can be found for the narrow-sense heritability (Lopes et al. 2003, Alidu et al. 2013, Egbador et al. 2013, Pathak et al. 2017). Differences in the heritability coefficients of these traits demonstrate the specificity of this parameter for each population, which depends on the genetic background and the environment in which they are being evaluated. Therefore, it is important to perform genetic studies in populations from a breeding program in order to assess their potential for breeding.

The average degrees of dominance found in this study varied between low and high values (Table 2). The value for grain size was positive and almost null (0.025), which reflects a small presence of dominance in the trait expression,

Table 2. Estimates of variances and genetic parameters for yield components evaluated in six populations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2) of the cowpea cross MNC05-828C-1-9-1 \times MNC04-792F-146

Parameters	Estimates		
	WHG (g)	PL (cm)	NGP
Phenotypic variance	26.17	5.06	6.4
Environment variance	7.61	1.44	3.37
Genotypic variance	18.56	3.62	3.02
Environmental coefficient of variation (%)	13.32	7.13	19.97
Genotypic coefficient of variation (%)	20.81	11.3	18.9
Coefficient of variation ratio	1.56	1.58	0.94
Additive variance	12.05	3.42	1.76
Dominance variance	6.50	0.2	1.26
Broad-sense heritability (%)	70.91	71.51	47.29
Narrow-sense heritability (%)	46.05	67.63	27.57
Average degree of dominance	0.025	-1.42	-0.12
Number of genes	10.71	10.07	10.88
Expected gain with selection*	3.55	2.1	1.04
Predicted mean in F_3 after selection	23.84	18	9.92

WHG, weight of one hundred grains; PL, pod length; NGP, number of grains per pod.
* Expected gain with selection of 20% of plants in F_2 generation.

directed towards the expression of greater grain size. For the number of grains per pod, the average degree of dominance was low and negative (-0.12), revealing a low participation of dominant alleles in the inheritance, which occurs towards fewer seeds per pod. High magnitude of the average degree of dominance was obtained for pod length (-1.42), evidenced by the hybrid vigor presented by F₁ generation. The negative value of the estimate suggests that short pods were dominant over long pods. While additive effects are particularly interesting for breeders of autogamous species (Dias et al. 2016), dominance is a limiting factor to develop pure lines through early-generation selection. Therefore, selection in advanced generations is a good strategy to obtain a fixed population and avoid the interference of non-additive effects (Melo et al. 2018).

The estimated minimum number of genes was similar between traits: approximately 11 for grain size and for number of grains per pod, and 10 for pod length, featuring a polygenic trait control (Table 2). Lopes et al. (2003) found five genes controlling grain size in cowpea, while Ayo-Vaughan et al. (2013) reported four and Egbadzor et al. (2013) estimated eight genes. Ayo-Vaughan et al. (2013) also obtained estimates of 5.72 and 4.77 genes for pod length and number of grains per pod, respectively. Although the estimate of the number of genes is based on a series of assumptions, this information is useful as an indication of the trait polygenic or oligogenic nature and as a reference to the probability of obtaining a desired genotype in a segregating population (Cruz et al. 2012). The quantitative inheritance of the studied yield components suggests that large breeding populations will be required to find genotypes with a higher concentration of favorable alleles.

The additive variation of the populations allowed the estimation of expected gains with the selection of 20% of plants in F₂ generation. The gain for the weight of one hundred grains was 3.55 g, with predicted mean for the next

Table 3. T test of the null hypothesis significance for the genetic parameters based on the means of yield components evaluated in six populations (P₁, P₂, F₁, F₂, BC₁ and BC₂) of the cross MNC05-828C-1-9-1 × MNC04-792F-146

Effect ¹	WHG (g)			PL (cm)			NGP		
	Estimate	σ ²	t	Estimate	σ ²	t	Estimate	σ ²	t
m	18.04	9.05	6.23**	0.1262	1.55 ⁻⁴	10.15**	6.48	2.47	4.12**
a	5.02	0.093	16.43**	-0.023	0.2 ⁻⁵	-15.89**	-3.23	0.057	-13.46**
d	4.01	75.74	0.46	0.089	12.79 ⁻⁴	2.49*	6.70	20.92	1.46
aa	1.97	8.95	0.66	0.036	1.52 ⁻⁴	2.93**	2.48	2.41	1.59
ad	-5.45	8.04	-1.92	-0.011	1.37 ⁻⁴	-1.008	-0.53	2.33	-0.35
dd	-1.9	35.10	-0.32	-0.019	5.88 ⁻⁴	-0.79	-3.81	9.89	-1.21

¹m, mean of all possible homozygotes; a, measure of the additive genetic effect; d, measure of the dominance genetic effect; aa, additive × additive gene interaction effect; ad, additive × dominance gene interaction effect; dd, dominance × dominance gene interaction effect; σ², standard error variance. * and ** Significant at 5% and 1% of probability, respectively, by the t-test. WHG, weight of one hundred grains; PL, pod length; NGP, number of grains per pod.

Table 4. Analysis of variance by non-orthogonal decomposition of the sum of squares (SS) of parameters applying the Gauss Elimination Method, based on the means of yield components evaluated in six populations (P₁, P₂, F₁, F₂, BC₁ and BC₂) of the cross MNC05-828C-1-9-1 × MNC04-792F-146

Variation Source	WHG (g)		PL (cm)		NGP	
	SS	R ² (%)	SS	R ² (%)	SS	R ² (%)
m	38.9	12.41	103.061	27.68	17.00	8.31
a	270.19	86.17	252.71	67.88	18.36	88.61
d	0.21	0.07	6.24	1.68	2.14	1.05
aa	0.43	0.14	8.62	2.32	2.55	1.25
ad	3.69	1.18	1.01	0.27	0.12	0.06
dd	0.10	0.03	0.62	0.17	1.47	0.72
Total	313.55	100	372.3	100	204.66	100

m, mean of all possible homozygotes; a, measure of the additive genetic effect; d, measure of the dominance genetic effect; aa, measure of the genic interaction additive × additive; ad, measure of the genic interaction additive × dominance; dd, measure of the genic interaction dominance × dominance; S.S., Sum of squares; R², determination coefficient.

WHG, weight of one hundred grains; PL, pod length; NGP, number of grains per pod.

breeding cycle of 23.84 g (Table 2). In addition, it is possible to obtain 2.1 cm of pod length and one grain per pod in the next cycle. An average pod length of 18 cm and an average number of grains per pod of approximately 10 are expected for the next generation. The low heritability of the number of grains per pod promoted a reduced gain with selection.

The *t*-test showed significance ($P < 0.05$) of the mean and the additive components of the complete model for three traits, while the additive × additive interaction and the dominance effects were significant only for pod length (Table 3). According to Edematie et al. (2021), just like the additive component, the additive × additive component of epistasis is fixable, being easily exploited for the development of cowpea lines. However, the dominance effect hinders standard breeding approaches, as the trait tends to decrease its performance as generations are advanced.

The non-orthogonal decomposition of the sum of squares of the genetic parameters showed that the mean and the additive gene effects have a greater contribution in determining the evaluated yield components (Table 4). The additive genetic parameter explained more than 67.88% of the total observed variation. Consequently, the gene effects resulting from dominance and epistasis, detected for pod length, were less important for the trait expression. Owusu et al. (2018) and Shinde et al. (2021) also reported greater contribution of additive effects in the inheritance of pod length. Lopes et al. (2003) and Owusu et al. (2018) found the same result for grain size. On the other hand, Shinde et al. (2021) found greater importance of non-additive components for pod length, while Ayo-Vaughan et al. (2013) and Raut et al. (2013) found the same for these traits. Additionally, importance for additive, dominance and epistatic effects has been found for pod length and grain size (Egbadzor et al. 2013, Edematie et al. 2021) and for the number of grains per pod in cowpea (Edematie et al. 2021). For this latter situation, Egbadzor et al. (2013) suggested that selection should be performed from segregating populations to advanced generations. Contradicting results between reports could be attributed to differences in the genetic materials or in the statistical methodologies used among studies. Overall, the variability observed in the populations resulted mainly from additive gene effects, involving a cross derived from genotypes adapted to Brazilian conditions. Therefore, it is possible to develop superior lines for the traits through selection of plants derived from F_2 populations, since the additive variance is responsible for the fixation of favorable alleles with the inbreeding increase (Vencovsky et al. 2012, Edematie et al. 2021).

From this perspective, variability in the studied populations allows breeding for these yield components in both directions of selection, taking into account the market demand that the breeder intends to address. Grain size is a trait that will respond effectively to standard breeding methodologies due to its high heritability and contribution of additive gene effects. As pod length showed a high average degree of dominance and the number of grains per pod is highly affected by the environment, selection for these traits might face some strains, especially in early generations. Still, greater contribution of additive gene effects is found for all traits, accounting for more than 67.88% of the variation, which enables the use of standard breeding approaches to improve the yield components. However, the quantitative inheritance implies that large population sizes will be required to develop cowpea lines with favorable genes.

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REFERENCES

- Alidu MS, Atokple IDK and Akromah R (2013) Genetic analysis of vegetative-stage drought tolerance in cowpea. **Greener Journal of Agricultural Sciences** 3: 476-491.
- Araújo MS, Aragão WFL, Santos SPD, Freitas TKT, Saraiva VDC, Damasceno-Silva KJ, Dias LAS and Rocha MM (2022) Evaluation of adaptability and stability for iron, zinc and protein content in cowpea genotypes using GGE biplot approach. **Heliyon** 8: e11832.
- Araújo MS, Chaves SFS, Damasceno-Silva KJ, Dias LAS and Rocha MM (2023) Modeling covariance structures for genetic and non-genetic effects in cowpea multi-environment trials. **Agronomy Journal** 11: 1248-1256.
- Ayo-Vaughan MA, Ariyo OJ and Alake CO (2013) Combining ability and genetic components for pod and seed traits in cowpea lines. **Italian Journal of Agronomy** 8: 73-78.
- Boukar O, Belko N, Chamarthi S, Togola A, Batiemo J, Owusu E, Haruna M, Diallo S, Umar ML, Olufajo O and Fatokun C (2019) Cowpea (*Vigna unguiculata*): Genetics, genomics and breeding. **Plant Breeding** 138: 415-424.
- Cruz CD (2013) GENES: software para análise de dados em estatística experimental e em genética quantitativa. **Acta Scientiarum** 35: 271-276.

- Cruz CD, Regazzi AJ and Carneiro PCS (2012) **Modelos biométricos aplicados ao melhoramento genético**. Editora UFV, Viçosa, 514p.
- Dias FTC, Bertini CHCM and Freire Filho FR (2016) Genetic effects and potential parents in cowpea. **Crop Breeding and Applied Biotechnology** **16**: 315-320.
- Edematie VE, Fatokun C, Boukar O, Adetimirin VO and Kumar L (2021) Inheritance of pod length and other yield components in two cowpea and yard-long bean crosses. **Agronomy** **11**: 682.
- Egbadzor KF, Dadoza M, Danquah EY, Yeboah M, Offei SK and Ofori K (2013) Genetic control of seed size in cowpea (*Vigna unguiculata* (L.) Walp.). **International Journal of Agriculture Sciences** **5**: 367-371.
- Freire-Filho FR, Ribeiro VQ, Rodrigues JELF and Vieira PFMJ (2017) A cultura: aspectos socioeconômicos. In Dovale JC, Bertini C and Borém A (eds) **Feijão-caupi: do plantio à colheita**. Editora UFV, Viçosa, p. 9-34.
- Gonçalves A, Goufo P, Barros A, Domínguez-Perles R, Trindade H, Rosa EAS, Ferreira L and Rodrigues M (2016) Cowpea (*Vigna unguiculata* L. Walp.), a renewed multipurpose crop for a more sustainable agri-food system: nutritional advantages and constraints. **Journal of the Science of Food and Agriculture** **96**: 2941-2951.
- Jelihovschi EG, Faria JC and Allaman IB (2014) ScottKnott: A package for performing the Scott-Knott clustering algorithm in R. **Trends in Applied and Computational Mathematics** **15**: 3-17.
- Lachyan TS, Desai SS and Dalvi VV (2016) Inheritance study of qualitative and quantitative characters in cowpea varieties (*Vigna unguiculata* (L.) Walp.). **Electronic Journal of Plant Breeding** **7**: 708-713.
- Lopes ACA, Gomes RLF and Freire Filho FR (2003) Genetic control of cowpea seed sizes. **Scientia Agricola** **60**: 315-318.
- Mather RK and Jinks JL (1974) **Biometrical genetics: the study of continuous variation**. Cornell University Press, New York, 382p.
- Melo RCD, Trevisani N, Corrêa SC, Guidolin AF and Coimbra JLM (2018) Inheritance of root distribution in common bean and selection strategy. **Crop Breeding and Applied Biotechnology** **18**: 373-381.
- Owusu EY, Amegbor IK, Darkwa K, Oteng-Frimpong R and Sie EK (2018) Gene action and combining ability studies for grain yield and its related traits in cowpea (*Vigna unguiculata*). **Cogent Food & Agriculture** **4**: 1519973.
- Owusu EY, Mohammed H, Manigben KA, Adjebeng-Danquah J, Kusi F, Karikari B and Sie EK (2020) Diallel analysis and heritability of grain yield, yield components, and maturity traits in cowpea (*Vigna unguiculata* (L.) Walp.). **The Scientific World Journal** **2020**: 1-9.
- Pathak AR, Naik MR and Joshi HK (2017) Heterosis, inbreeding depression and heritability for yield and yield components in cowpea. **Electronic Journal of Plant Breeding** **8**: 72-77.
- R Core Team (2023) **R: A language and environment for statistical computing**. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>
- Raina A, Laskar RA, Wani MR and Khan S (2023) Improvement of yield in cowpea varieties using different breeding approaches. In Raina A, Wani MR, Laskar RA, Tomlekova N and Khan S (eds) **Advanced crop improvement**. Springer, Cham, p. 145-172.
- Raut DM, Tamnar AB, Burungale SV and Badhe PL (2017) Half diallel analysis in cowpea [*Vigna unguiculata* (L.) Walp.]. **International Journal of Current Microbiology and Applied Sciences** **6**: 1807-1819.
- Ribeiro HLC, Boiteux LS and Santos CAF (2014) Genetic parameters of earliness and plant architecture traits suitable for mechanical harvesting of cowpea (*Vigna unguiculata*). **Australian Journal of Crop Science** **8**: 1232-1238.
- Resende MDV and Duarte JB (2007) Precisão e controle de qualidade em experimentos de avaliação de cultivares. **Pesquisa Agropecuária Tropical** **37**: 182-194.
- Rocha MM, Damasceno-Silva KJ and Menezes-Júnior JAN (2017) Cultivares. In Dovale JC, Bertini, C and Borém A (eds) **Feijão-caupi: do plantio à colheita**. Editora UFV, Viçosa, p. 111-142.
- Shinde RJ, Toprope VN, Sargar PR, Dharkne VR and Chavan SS (2021) Generation mean analysis studies in cowpea (*Vigna unguiculata* L. Walp.). **International Journal of Theoretical & Applied Sciences** **14**: 22-25.
- Vencovsky R, Ramalho MAP and Toledo FHRB (2012) Contribution and perspectives of quantitative genetics to plant breeding in Brazil. **Crop Breeding and Applied Biotechnology** **12**: 7-14.
- Wickham H (2016) **Ggplot2: Elegant graphics for data analysis**. Springer, New York, 260p.