

## Genetic control of traits related to maturity in cowpea

Samíria Pinheiro dos Santos<sup>1</sup>, Kaesel Jackson Damasceno-Silva<sup>2</sup>, Walter Frazão Lelis de Aragão<sup>1</sup>, Maurício dos Santos Araújo<sup>1</sup> and Maurisrael de Moura Rocha<sup>2\*</sup>

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**Abstract:** *The aim of this study was to investigate genetic control of the traits number of days to flowering (NDF) and number of days to maturity (NDM) in a cowpea cross. Genetic parameters were estimated in segregating and non-segregating generations of a cross between two contrasting cowpea genotypes (MNC05-828C-1-9-1 × MNC04-792F-146). No evidence for maternal effect was found for either trait. Broad and narrow sense heritability estimates were above 50%, allowing genetic gains from selection of plants in the F<sub>2</sub> generation. High significance of additive gene effects and low contribution of dominance and epistatic effects were detected for both traits. The estimated number of genes controlling the traits was around 4 for NDF and 5 for NDM. The results suggest that early-maturing cowpea self-fertilized cultivars can be developed through standard breeding approaches, meeting the demands of modern agricultural systems for more crop seasons per year and mechanized harvesting.*

**Keywords:** *a*, genetic parameters, genetic inheritance, days to flowering, maturation cycle.


### INTRODUCTION

Cowpea (*Vigna unguiculata* (L.) Walp.) is a legume of great socioeconomic importance, cultivated in more than 100 countries, mainly in tropical and subtropical zones of the world. Due to the high protein, carbohydrate, fiber, vitamin, and mineral content of its grain, it has become a relevant source of nutrition for poorer populations (Singh 2014, Carvalho et al. 2017). In Brazil, it is grown mainly in the North and Northeast regions; however, it has expanded to the Central-West and Southeast regions among mid-sized and corporate growers (Freire Filho et al. 2017). Brazilian cowpea production reached 733 thousand tons and a yield of 504 kg ha<sup>-1</sup> in 2018/19, occupying 1.455.4 ha of planted area (CONAB 2019).

The incorporation of high technological management in cowpea growing has been a trend in recent decades. In addition to higher grain yield and grain quality, characteristics related to plant architecture have been improved to obtain erect and more compact plants with shorter maturity cycles grown at higher densities to enable mechanized harvesting (Freire Filho et al. 2017). Thus, early and uniform maturity are characteristics desired for development of cowpea cultivars.

**\*Corresponding author:**

E-mail: [maurisrael.rocha@embrapa.br](mailto:maurisrael.rocha@embrapa.br)

 ORCID: 0000-0001-5817-2794

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<sup>1</sup> Universidade Federal do Piauí, Departamento de Fitotecnia, Campus Universitário Ministro Petrônio Portella, 64.049-550, Teresina, PI, Brazil

<sup>2</sup> Embrapa Meio-Norte, Avenida Duque de Caxias, 64.008-780, Teresina, PI, Brazil

Early maturity is an important adaptation in agroecological zones with short growing seasons to avoid stress conditions and provide crop benefits. A shorter cycle can avoid terminal drought and stabilize production in regions with long drought periods; it can also be used to avoid the incidence of pests or diseases and unfavorable temperatures during flowering and podding stages. A shorter cycle is useful for crop rotation, and it allows up to three crop seasons per year, providing additional seed for the main crop season (Singh 2014, Rocha et al. 2017, Owusu et al. 2018a).

As early-maturing cowpea cultivars tend to have lower yield per plant (Owusu et al. 2018a), high population density is required to achieve high grain yield. However, simultaneous selection has allowed cowpea breeding programs to release high-yielding early cultivars (Rocha et al. 2017). Greater information concerning the genetic basis for early maturity is a valuable tool to develop such cultivars.

Some studies have been conducted to understand inheritance of the number of days to flowering and number of days to maturity traits in cowpea. Owusu et al. (2018a) reported absence of maternal effect in both traits. With respect to gene action, additive, dominance, and epistasis effects have been reported by Rashwan (2010) and Patel et al. (2013) for the number of days to flowering trait in cowpea. Significance for additive and epistatic components and absence of dominance have been indicated by other studies (Ishiyaku et al. 2005, Adeyanju and Ishiyaku 2007); yet the importance of only non-additive effects has also been found for this trait (Owusu et al. 2018b).

Fewer studies have investigated inheritance of the days to maturity trait. Greater involvement of additive gene action and a low contribution of the additive  $\times$  dominant interaction were indicated by Ribeiro et al. (2014), Raut et al. (2017), and Owusu et al. (2018b). In terms of number of genes involved, Ishiyaku et al. (2005) reported seven genes controlling days to flowering, and Ribeiro et al. (2014) found around three genes for the days to grain maturity trait.

A wide range of heritability has been reported in genetic studies conducted with segregating cowpea populations. For number of days to flowering, variations of 37.46% to 89.7% can be found for broad sense heritability, while narrow sense heritability has ranged from 4.26% to 90.87% (Ishiyaku et al. 2005, Adeyanju and Ishiyaku 2007, Pathak et al. 2017, Owusu et al. 2018a). For number of days to maturity, genetic studies have shown broad sense heritability from 34.52% to 95.83% and variations from 4.79% to 93.73% for narrow sense heritability (Ribeiro et al. 2014, Pathak et al. 2017, Owusu et al. 2018a).

In the literature, information is insufficient and results are divergent for the type of gene action and the number of genes involved in inheritance of traits related to maturity. Additional information in this respect would be a valuable tool for breeding cultivars with a short and consistent maturity cycle. The continuous phenotypic distribution observed for number of days to flowering and to maturity in cowpea suggests quantitative inheritance. As each gene may contribute differently to the phenotype of a quantitative trait, it is possible that more than one allelic or gene interaction occurs in genetic control of a trait. It is important to identify the most significant gene effects for these traits to determine an appropriate breeding strategy.

From this perspective, the objective of this study was to investigate genetic control of the number of days to flowering and number of days to maturity in segregating and non-segregating generations of a cowpea cross to determine the possibility of developing early maturing cowpea lines from these populations.

## **MATERIAL AND METHODS**

The two cowpea genotypes used as parents in the crosses were MNC05-828C-1-9-1 ( $P_1$ ) and MNC04-792F-146 ( $P_2$ ), from the Embrapa Meio-Norte germplasm collection. The lines are contrasting for number of days to flowering, around 37 and 44 days, respectively, and for number of days to maturity, around 54 and 61 days, respectively. Crosses were performed in a shade house in Teresina, Piauí, Brazil, at Embrapa Meio-Norte (lat 5° 02' 21.36" S, long 42° 47' 22.44" W, alt 72 m asl) from 2015 to 2018, obtaining the generations  $F_1$  ( $P_1 \times P_2$ ),  $F_2$  ( $F_1 \times F_1$ ),  $BC_1$  ( $F_1 \times P_1$ ), and  $BC_2$  ( $F_1 \times P_2$ ) and the same generations for the reciprocal crosses:  $F_1$  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 through self-fertilization of plants of each  $F_1$  generation.

All populations, along with the parents, were evaluated in a field experiment at Embrapa Meio-Norte, from October 2018 to January 2019. A randomized block design was applied, with three replications and ten treatments. Each block

consisted of 42 rows of 2.5 m, containing plots of the ten populations:  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_1$  reciprocal,  $F_2$ ,  $F_2$  reciprocal,  $BC_1$ ,  $BC_1$  reciprocal,  $BC_2$ , and  $BC_2$  reciprocal. Due to differences in the availability of the seed obtained for each generation, plots differed in size, which consisted of three 2.5 m rows for each parent ( $P_1$  and  $P_2$ ), one 2.5 m row for each  $F_1$  ( $F_1$  and  $F_1$  reciprocal) and for each backcross generation ( $BC_1$ ,  $BC_1$  reciprocal,  $BC_2$ , and  $BC_2$  reciprocal), and fifteen 2.5 m rows for each  $F_2$  population ( $F_2$  and  $F_2$  reciprocal), with plants spaced at 0.80 m × 0.25 m.

The number of days from sowing to the beginning of flowering and the number of days to maturity were evaluated in 10 competitive plants in each row. The final number of plants evaluated was reduced due to losses during the experiment and, in the case of maturity, due to a large amount of rainfall after plant germination. However, the number of plants and final data well represented the variability of all the populations evaluated and was sufficient to proceed with the genetic control study.

The means of the populations were clustered by the Scott-Knott test at 5% probability to evaluate differences among the performance of generations and to evaluate differences between the  $F_1$  and  $F_2$  generations and their reciprocal generations as evidence for maternal effect.

The study of trait inheritance was performed based on the means and variances of the 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 estimation of the genetic parameters through the weighted least squares method since the means of the six populations were not obtained with the same precision. The effect of mean (m), the additive gene effect (a), the dominance gene effect (d), and the effects of additive × additive (aa), additive × dominance (ad) and dominance × dominance (dd) epistasis were estimated. The null hypothesis significance for each of these parameters was evaluated by the *t*-test.

The contribution of each genetic parameter to the total observed variation was analyzed by the non-orthogonal decomposition of the sum of squares for the parameters associated with the model into sums of squares attributed to each individual parameter, applying the Gauss elimination method (Lopes et al. 2003, Cruz et al. 2012).

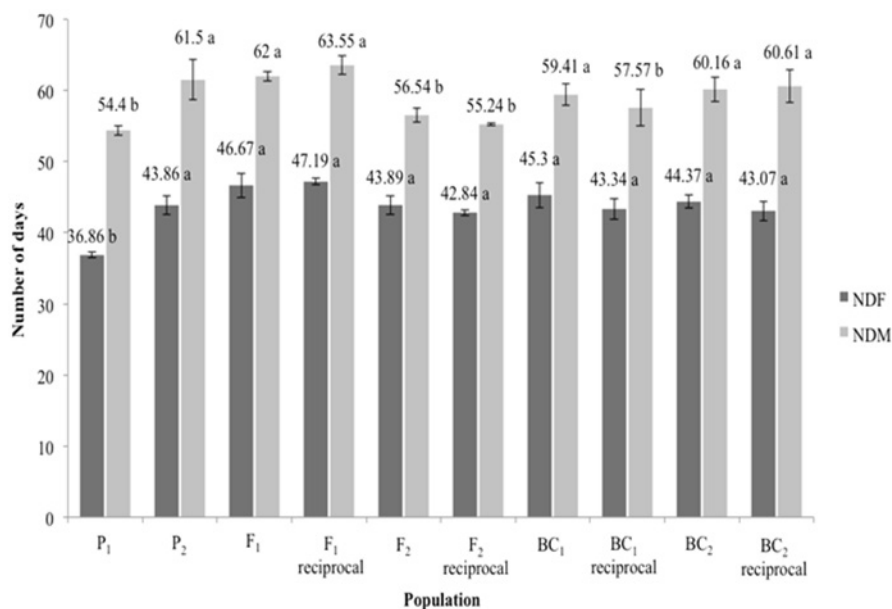
The average degree of dominance (ADD) was estimated according to the equation  $ADD = [2\bar{F}_1 - (\bar{P}_1 + \bar{P}_2)] / (\bar{P}_1 + \bar{P}_2)$ , where  $\bar{F}_1$  is the  $F_1$  generation mean,  $\bar{P}_1$  is the parent 1 mean, and  $\bar{P}_2$  is the parent 2 mean. The number of genes controlling each trait was estimated by the formula  $n = [R^2 (1 + k^2 \times 0.50)] / 8\sigma_g^2$ , where  $R^2$  is the total phenotypic range in the [ $F_1(1 + k^2 \times 0.50)$ ]/ $8\sigma_g^2$  population,  $\sigma_g^2$  is the  $F_2$  genotypic variance, and  $k$  is the degree of dominance based on variances ( $k = \sqrt{2\sigma_d^2 / \sigma_a^2}$ , where  $\sigma_d^2$  is the dominance variance and  $\sigma_a^2$  is the additive variance) (Cruz et al. 2012).

Broad sense heritability ( $h_b^2$ ) was estimated by the equation  $h_b^2 = (\sigma_g^2 / \sigma_p^2) 100$ , where  $\sigma_g^2$  is the total genotypic variance and  $\sigma_p^2$  is the phenotypic variance, whose environmental variance was calculated by the expression  $\sigma_e^2 = \frac{1}{4} (2\sigma_{F_2}^2 + \sigma_{P_1}^2 + \sigma_{P_2}^2)$ . Narrow sense heritability ( $h_n^2$ ) was obtained by the formula  $h_n^2 = (\sigma_a^2 / \sigma_p^2) 100$ , where  $\sigma_a^2$  is the additive variance, calculated by the equation  $\sigma_a^2 = 2\sigma_{F_2}^2 - (\sigma_{BC_1}^2 + \sigma_{BC_2}^2)$ , and  $\sigma_p^2$  is the phenotypic variance. Expected gain ( $\Delta G$ ) in the  $F_3$  generation from the selection of 20% of  $F_2$  plants was estimated by the model  $\Delta = h_n^2 \cdot sd$ , where  $h_n^2$  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. The genotypic coefficient of variation ( $CV_g$ ) and environmental coefficient of variation ( $CV_e$ ) were calculated according to the estimators:  $CV_g = (\sqrt{\sigma_g^2} / X) 100$  and  $CV_e = (\sqrt{\sigma_e^2} / X) 100$ , where  $\sigma_g^2$  is the genotypic variance,  $\sigma_e^2$  is the environmental variance, and  $X$  is the mean for the trait. The coefficient of variation ratio ( $CV_r$ ) was obtained by  $CV_r = CV_g / CV_e$ .

## RESULTS AND DISCUSSION

The number of days to flowering showed differences between parents ( $P < 0.05$ ), allowing more accurate study of genetic control of this trait. The MNC05-828C-1-9-1 parent was earlier than the other parent line, while the cross populations were generally late to flower, and their means were not significantly different (Figure 1).

The number of days to maturity was also contrasting between parents. The parent MNC05-828C-1-9-1,  $F_2$  generations, and one of the backcrosses had mean values for early maturity and are populations with potential for development of early maturity cowpea lines. Earliness of crop maturity is one of the objectives of the cowpea breeding program, due to high demand for this trait and its importance to producers. Early maturity enables crop rotation and more crop seasons



**Figure 1.** Means grouping of the traits number of days to flowering (NDF) and number of days to maturity (NDM) in ten populations of the cross MNC05-828C-1-9-1 (P<sub>1</sub>) × MNC04-792F-146 (P<sub>2</sub>). Means followed by the same letter do not differ from each other by the Scott-Knott test ( $P < 0.05$ ).

per year, and it is extremely valuable to avoid some stress conditions when growing cowpea (Singh 2014, Rocha et al. 2017, Owusu et al. 2018a).

The F<sub>1</sub> and F<sub>2</sub> generations did not differ from their reciprocals ( $P < 0.05$ ) (Figure 1), suggesting that cytoplasmic gene effects are not evident for either trait. Absence of maternal effect was corroborated by Owusu et al. (2018a) in their study of days to flowering and days to pod maturity. These results indicate that selection for early maturity should occur in the F<sub>2</sub> generation, which provides access to maximum genetic variability.

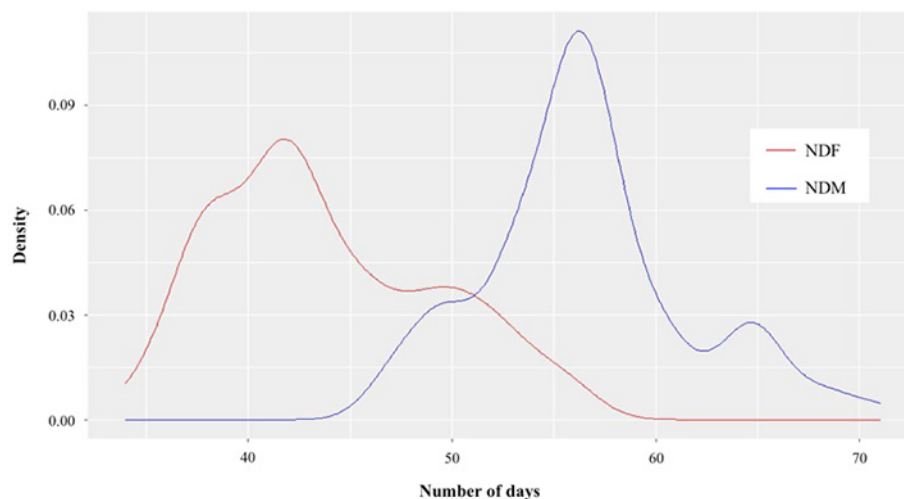
The F<sub>1</sub> generation means for both traits were higher than the means of the MNC04-792F-146 parent, with a reduction in the means at F<sub>2</sub> (Table 1). An asymmetric distribution of the F<sub>2</sub> population is also observed for both traits (Figure 2). This response shows a heterotic effect and dominance gene action in the inheritance of these traits (Ramalho et al. 2012a).

Relative variability was found for both traits, with genotypic coefficients of variation of 9.93% for number of days to flowering and 7.32% for number of days to maturity (Table 2). Lower estimates were found for the environmental coefficients of variation, showing high experimental accuracy. Coefficient of variation ratios higher than one and heritability values higher than 63% show that the phenotype is mostly attributable to genetic causes, indicating accuracy and efficiency in selection of early maturity individuals (Vencovsky et al. 2012, Pathak et al. 2017).

**Table 1.** Mean and variance estimates for number of days to flowering (NDF) and number of days to maturity (NDM) in six populations of the cross MNC05-828C-1-9-1 × MNC04-792F-146

Population	NDF (day)				NDM (day)			
	N <sup>1</sup>	$\bar{u}$	$\hat{\sigma}^2$	V( $\bar{u}$ )	N	$\bar{u}$	$\hat{\sigma}^2$	V( $\bar{u}$ )
P <sub>1</sub> (MNC05-828C-1-9-1)	30	36.8	2.6	0.086	25	54.4	5.62	0.22
P <sub>2</sub> (MNC04-792F-146)	30	43.8	13.1	0.438	22	61.5	21.01	0.95
F <sub>1</sub>	21	46.6	13.3	0.635	4	62	1.33	0.33
F <sub>2</sub>	321	43.8	29.2	0.091	90	56.5	26.02	0.28
BC <sub>1</sub> (F <sub>1</sub> × MNC05-828C-1-9-1)	23	45.3	29.4	1.28	12	59.4	22.44	1.87
BC <sub>2</sub> (F <sub>1</sub> × MNC04-792F-146)	24	44.3	14.4	0.60	18	60.1	15.55	0.86

<sup>1</sup> Number of plants (N), mean ( $\bar{u}$ ), variance ( $\hat{\sigma}^2$ ), and mean variance (V( $\bar{u}$ )).



**Figure 2.** Frequency distribution of  $F_2$  plants for number of days to flowering (NDF) and for number of days to maturity (NDM) of the cross MNC05-828C-1-9-1  $\times$  MNC04-792F-146.

**Table 2.** Estimates of variances and genetic parameters for the number of days to flowering (NDF) and number of days to maturity (NDM) traits 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

Parameter	Estimates	
	NDF (day)	NDM (day)
Phenotypic variance	29.29	26.02
Environmental variance	10.61	7.32
Genotypic variance	18.68	18.69
Environmental coefficient of variation	7.48	4.58
Genotypic coefficient of variation	9.93	7.32
Coefficient of variation ratio	1.32	1.59
Additive variance	14.68	14.04
Dominance variance	4.001	4.65
Broad sense heritability (%)	63.77	71.85
Narrow sense heritability (%)	50.11	53.97
Average degree of dominance	-1.88	-1.10
Number of genes	4.12	5.12
Expected gain from selection of 20% of plants in $F_2$ generation.	-3.31	-6.35
Predicted mean in $F_3$ after selection	40.49	52.95

The proportions of genotypic variance due to additive and dominance variances were equivalent for the two traits. Additive variance was higher, resulting in high proportions of total heritability. Narrow sense heritability was 50.11% for number of days to flowering and 53.97% for number of days to maturity. Accordingly, just over half of the phenotype is controlled by genetic inheritance of an additive nature. High additive variance is favorable to fixation of alleles in the gene loci that control these traits on the individual level (genotype) in the population during the selection process and ensures genetic gains; it is the variance most desired in breeding programs (Cruz et al. 2012, Ramalho et al. 2012b).

These heritable phenotypic proportions are within the limits found in the literature for segregating populations of cowpea crosses. Pathak et al. (2017) obtained broad sense heritability ranging from 37.46% to 86.43% for number of days to flowering and from 34.52% to 95.83% for days to maturity. In the narrow sense, they found heritability with variations from 4.26% to 82.34% for days to flowering and 4.79% to 93.73% for days to maturity. Ishiyaku et al. (2005) reported a narrow sense heritability of 86% for days to flowering, while Adeyanju and Ishiyaku (2007) found a value of

90.87% under screen house conditions. Owusu et al. (2018a) reported a narrow sense heritability value of 82.2% for number of days to flowering and 73.6% for number of days to maturity, while Ribeiro et al. (2014) obtained 69.73% in broad sense heritability and 69.28% in narrow sense heritability coefficients for number of days to maturity.

Although additive variance was more important, the average degree of dominance detected total dominance or overdominance in expression of both traits (Table 2). This confirms the conclusions reached for superiority of the  $F_1$  generation means and the asymmetric phenotypic distribution of the  $F_2$  generations. Although hybrid vigor is not commercially exploited in cowpea, highly heterozygous individuals have high potential for diversity and for production of desirable transgressive segregants in later generations for selection (Pethe et al. 2017).

Negative dominance deviations indicate dominance for fewer days to flowering and maturation, which can delay the development of early cowpea lines, a major focus of current breeding programs, as there is a risk of selecting heterozygous plants, with early phenotypes, which will segregate in the following generations also for days to flowering and for late maturation. Therefore, selection should work toward greater concentration of dominant alleles. The dominance effect in reducing days to flowering was also reported by Owusu et al. (2018a, b) in segregating populations from different cowpea crosses.

The number of genes controlling the traits was low: 4 for number of days to flowering and 5 for number of days to maturity (Table 2). Ishiyaku et al. (2005) found 7 genes controlling days to flowering, while Ribeiro et al. (2014) found an average of 3 genes for number of days to grain maturity. Although these values differ from those obtained in the present study, these studies confirm the oligogenic nature of these traits.

A small number of genes controlling the traits also explains the asymmetry of the  $F_2$  phenotypic distribution (Figure 2). Asymmetry is accentuated when few genes are involved; as the number of genes increases, asymmetry decreases, and  $F_2$  tends toward a normal curve. However, the existence of few genes controlling the traits is an advantage for cowpea breeders, since the probability of finding individuals with extreme phenotypes within the segregating population increases (Ramalho et al. 2012b). Consequently, large segregating populations will not be required during breeding stages, facilitating selection to obtain early maturing cowpea genotypes.

The expected gain from selection of 20% of the  $F_2$  plants was greater for number of days to maturity, which may be explained by the lower influence of the environment on control of this trait. Nevertheless, the gains were satisfactory for both traits, with a reduction of approximately 3 and 6 days, and a predicted  $F_3$  population mean of approximately 40 days for flowering and 53 days for maturation. The transgressive segregation observed in the distribution of  $F_2$  phenotypic classes (Figure 2) in relation to the mean of the early parent (Table 1) allows the selection of individuals with shorter maturity cycles. Earlier maturity is therefore expected in the population in the cycle after selection.

The study of means and variances from the complete model demonstrated the significance of the mean, additive, dominance, and epistatic interaction effects by the *t*-test ( $P < 0.05$ ) (Table 3). The additive  $\times$  dominant interaction was significant for number of days to flowering and the additive  $\times$  additive interaction for number of days to maturity, confirming the presence of more than one gene controlling these traits.

**Table 3.** *t*-test of the significance of the null hypothesis for the genetic parameters based on means of number of days to flowering (NDF) and number of days to maturity (NDM) 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

Effect <sup>1</sup>	NDF (day)			NDM (day)		
	Estimate	Variance	t-test	Estimate	Variance	t-test
m	36.24	9.12	12**	44.82	15.86	11.25**
a	-3.5	0.13	-9.65**	-3.77	0.29	-6.95**
d	19.54	75.45	2.24*	29.69	119.95	2.71**
aa	4.11	8.99	1.37	12.98	15.56	3.29**
ad	8.85	8.05	3.12**	6.05	12.12	1.73
dd	-8.83	34.65	-1.5	-12.52	50.89	-1.75

<sup>1</sup>m, mean of all possible homozygotes; a, measure of the additive genetic effect; d, measure of the dominance genetic effect; aa, additive  $\times$  additive gene interaction effect; ad, additive  $\times$  dominance gene interaction effect; dd, dominance  $\times$  dominance gene interaction effect.

\* and \*\* Significant at 5% and 1% of probability, respectively, by the *t*-test.

**Table 4.** Analysis of variance by non-orthogonal decomposition of the sum of squares of parameters applying the Gauss Elimination Method, based on the means of number of days to flowering (NDF) and number of days to maturity (NDM) 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

Source of variation <sup>1</sup>	NDF (day)		NDM (day)	
	Sum of squares	R <sup>2</sup> (%) <sup>2</sup>	Sum of squares	R <sup>2</sup> (%)
m	144.0	56.2	126.68	63.57
a	93.29	36.41	48.31	24.24
d	5.06	1.97	7.35	3.7
aa	1.88	0.74	10.83	5.43
ad	9.73	3.8	3.02	1.51
dd	2.25	0.88	3.08	1.55
Total	256.24	100	199.28	100

<sup>1</sup> m, mean of all possible homozygotes; a, measure of the additive genetic effect; d, measure of the dominance genetic effect; aa, additive  $\times$  additive gene interaction effect; ad, additive  $\times$  dominance gene interaction effect; dd, dominance  $\times$  dominance gene interaction effect.

<sup>2</sup> R<sup>2</sup>: coefficient of determination.

Although decomposition of the sum of squares by the Gauss elimination method is not orthogonal (Table 4), the coefficient of determination ( $R^2$ ) is used to estimate the importance of a particular genetic effect on the variability observed for the trait under study (Cruz et al. 2012).  $R^2$  values indicate the mean as the most important effect, followed by the additive effect and the epistatic effect (additive  $\times$  dominant for number of days to flowering and additive  $\times$  additive for number of days to maturation); the dominance effect has a lower contribution.

A greater influence of additive gene action for expression of the traits suggests that dominance and epistasis will not have significant adverse effects on achieving gains from selection, since the fixation of favorable alleles in generations with greater inbreeding is expected. Consequently, it is possible to develop cowpea lines with a better combination of favorable alleles for early flowering and maturity from the  $F_2$  generation plants of this cross.

These results agree with those reported by Rashwan (2010) and Patel et al. (2013). The authors reported significance for additive, dominance, and epistatic effects for number of days to flowering, where the types of gene interactions varied among different cowpea crosses. Owusu et al. (2018b) found more importance for non-additive effects in controlling this trait in cowpea. In contrast, Ishiyaku et al. (2005) obtained significance only for the mean, the additive effect, and the additive  $\times$  dominant interaction effect. Significance for all types of genetic effects, except for dominance, was found by Adeyanju and Ishiyaku (2007) for days to flowering. Other studies reported a greater contribution of the additive component, followed by a low contribution of the additive  $\times$  dominant interaction in controlling the number of days to maturity in cowpea (Ribeiro et al. 2014, Raut et al. 2017, Owusu et al. 2018b).

Divergence of results among studies may be related to differences in genetic materials or in the types of sampling or statistical methodologies used, which intensifies the need to conduct genetic studies in breeding populations. However, it is important to notice that the contribution of the additive component in control of the traits evaluated is common in findings in the literature. Self-fertilization will therefore be favorable for the development of early cowpea lines obtained from selection of plants in the segregating populations of this cross.

The use of breeding approaches that perform selection in more inbred generations is more favorable for dissipating dominance effects, such as those based on plant competition during generation advances (Vencovsky et al. 2012, Borém and Miranda 2013). However, early maturing plants may not necessarily be competitive and might be lost during bulk conduction of generations or progenies. Thus, the use of methodologies that exploit genetic variability and make consecutive selections, such as pedigree selection, can eliminate late maturing plants in early generations, and such methodologies are an appropriate alternative for breeding aiming at early maturity in this population. Further evaluations is required to provide a basis for simultaneous trait selection in the study population, in order to combine a short maturity cycle and high grain yield.

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## REFERENCES

- Adeyanju AO and Ishiyaku MF (2007) Genetic study of earliness in cowpea (*Vigna unguiculata* (L.) Walp.) under screen house condition. **International Journal of Plant Breeding and Genetics** 1: 34-37.
- Borém AE and Miranda GV (2013) **Melhoramento de plantas**. UFV, Viçosa, 523p.
- Carvalho M, Lino-Neto T, Rosa E and Carnide V (2017) Cowpea: a legume crop for a challenging environment. **Journal of the Science of Food and Agriculture** 97: 4273-4284.
- CONAB - Companhia Nacional de Abastecimento (2019) Acompanhamento da safra brasileira de grãos, sexto levantamento, safra 2018/19. Available at: <<https://www.conab.gov.br/info-agro/safras/graos/boletim-da-safra-de-graos>>. Accessed on July 11, 2019.
- Cruz CD (2013) GENES: software para análise de dados em estatística experimental e em genética quantitativa. **Acta Scientiarum. Agronomy** 35: 271-276.
- Cruz CD, Regazzi AJ and Carneiro PCS (2012) **Modelos biométricos aplicados ao melhoramento genético**. UFV, Viçosa, 514p.
- 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.
- Ishiyaku MF, Singh BB and Craufurd PQ (2005) Inheritance of time to flowering in cowpea (*Vigna unguiculata* (L.) Walp.). **Euphytica** 142: 291-300.
- 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.
- Owusu EY, Akromah R, Denwar NN, Adjebeng-Danquah J, Kusi F and Haruna M (2018a) Inheritance of early maturity in some cowpea (*Vigna unguiculata* (L.) Walp.) genotypes under rain fed conditions in Northern Ghana. **Advances in Agriculture** 2018: 1-10.
- Owusu EY, Amegbor IK, Darkwa K, Oteng-Frimpong R and Sie EK (2018b) Gene action and combining ability studies for grain yield and its related traits in cowpea (*Vigna unguiculata*). **Cogent Food & Agriculture** 4: 1519973.
- Patel H, Patel JB, Sharma SC and Acharya S (2013) Genetics of seed yield and its components in cowpea [*Vigna unguiculata* (L.) Walp.]. **Trends in Biosciences** 6: 631-636.
- 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.
- Petthe UB, Dodiya NS, Bhavé SG, Dadheech A and Meghwal DR (2017) Heterosis for yield and yield related traits in cowpea (*Vigna unguiculata* L. Walp.). **Journal of Pharmacognosy and Phytochemistry** 6: 1247-1249.
- Ramalho MAP, Abreu AFB, Santos JB and Nunes JAR (2012a) **Aplicações da genética quantitativa no melhoramento de plantas autógamas**. UFLA, Lavras, 522p.
- Ramalho MAP, Santos JB, Pinto CABP, Souza EA, Gonçalves FMA and Souza JC (2012b) **Genética na agropecuária**. UFLA, Lavras, 472p.
- Rashwan AMA (2010) Estimation of some genetic parameters using six populations of two cowpea hybrids. **Asian Journal of Crop Science** 2: 261-267.
- 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.
- 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.
- Singh BB (2014) **Cowpea: The food legume of the 21st century**. Crop Science Society of America, Madison, 192p.
- 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.