# Diallel and generation analysis in F<sub>2</sub> soybean populations

S.B. Ferreira<sup>1,\*</sup>, B.H. Gomes<sup>1</sup>, O.T. Hamawaki<sup>2</sup>, P.A.S. Dias<sup>3</sup>, C.D.L. Hamawaki<sup>2</sup>, R.L. Hamawaki<sup>2</sup> and A.P.O. Nogueira<sup>1</sup>

<sup>1</sup>Universidade Federal de Uberlândia, Instituto de Biotecnologia, CEP 38405-320, Uberlândia, MG, Brasil
<sup>2</sup>Universidade Federal de Uberlândia, Instituto de Ciências Agrárias, CEP 38410-337, Uberlândia, MG, Brasil
<sup>3</sup>Instituto Federal Goiano, Campus Urutaí, Núcleo de Agronomia, CEP 75790-000, Urutaí, GO, Brasil
\*Correspondence: ferreirasb@ hotmail.com

Received: June 14th, 2024; Accepted: September 9th, 2024; Published: Noember 19th, 2024

Abstract. The present study aimed to obtain estimates of the general (GCA) and specific (SCA) combining abilities of three soybean parents by means of the half table balanced diallel and to estimate genetic parameters of agronomic traits in  $F_2$  populations. The experiment was organized in complete randomized blocks with ten replications. The plants obtained from the combinations between the parents UFU 510, UFUS 7415 and MG/BR 46 Conquista were individually evaluated for thirteen agronomic traits. The results indicated that the parent UFUS 7415 had the highest and most positive GCA values for the production components. The best cross was UFU 510 × UFUS 7415, with the highest number of total pods and grain production. The three combinations showed a high coefficient of heritability for the number of productive nodes. At the crossing UFU 510 × UFUS 7415, greater selection gains and higher averages were observed for the number of pods with one, two and three grains and the number of total pods.

Key words: diallel, estimation of genetic parameters, segregating populations.

## INTRODUCTION

The genetic breeding of plants is essential for maintaining the global food supply and must evolve to offer products that meet population growth and cultivars capable of overcoming the effects of climate change. The world consumption of oilseeds is expected to continue, not only due to the expectation of population growth, but mainly due to the increase in the consumption of animal protein (Nadathur et al., 2024). In the Brazilian agricultural scenario, soybean crop (*Glycine max* (L.) Merrill) stands out as one of the main commodities. In this sense, investments in soybean breeding programs are indispensable for the search for more productive and adapted to climate change genotypes.

For the success of the genetic breeding of soybean, to be informed about the genetic parameters and to know the combinatorial ability of the available genotypes, makes it possible to develop segregating populations for selective processes. The analysis of

genetic parameters in soybean for agronomic traits is important to direct crosses and maximize the genetic variability of segregating populations. These and other questions can be answered from crosses that follow some genetic design (Bornhofen, 2019), such as half table balanced diallel cross.

With the diallel analysis it is possible to obtain information about the behavior of the involved parents and the hybrid combinations that result in superior segregating populations by means of estimates of the general (GCA) and specific (SCA) combining abilities (Teodoro et al., 2019). Evaluation of the combining ability of self-pollinating species often use the relation between GCA and SCA to indicate the predominant type of gene action in trait expression. GCA primarily reflects additive gene effects and additive  $\times$  additive interactions, whereas SCA is associated with dominance effects, epistatic deviations, and genotype  $\times$  environment interactions (Rialch & Sharma, 2019).

For soybeans, diallel analysis has proven effective in exploring genetic variability and identifying the best parents for crosses. Bagateli et al. (2020) used a partial diallel to estimate GCA and SCA for eight soybean genotypes, focusing on traits related to production, plant architecture and maturity, which enabled them to select the optimal genotypes combinations. Similarly, Soares et al. (2023) obtained valuable genetic information on ten soybean parents and their F1 hybrids through diallel analysis, allowing them to evaluate the dissimilarity between parents and crosses. Also, Chagas et al. (2023) estimated the combining ability of soybean cultivars in the  $F_2$  generation, for agronomic, nutritional and industrial traits with the goal of identifying superior segregating parents and populations.

In soybean crop there is a limitation regarding the use of  $F_1$  generation plants for diallel analysis due to the low availability of seeds (Friedrichs et al., 2016) and the predominance of dominance deviations. An alternative is the evaluation of the diallel in  $F_2$  populations. In advanced generations, the dominance deviation is reduced and there is a possibility that the effect of SCA is not meaningful (Pimentel et al., 2014).

Given the above, the objectives of the study were to obtain the GCA and SCA estimates of three soybean parents through the half table balanced diallel, determine genetic parameters of important agronomic traits and estimate the gain selection in  $F_2$  populations, in order to identify the genotypes and the combinations considered promising for the development of superior lines.

#### **MATERIALS AND METHODS**

The experiment was carried out in the 2017/2018 season, in an experimental area located at São Lourenço Farm (18° 31' 20.6" S and 46° 04' 49.5" W), in the municipality of Varjão de Minas, Minas Gerais, Brazil. The seeds of the F<sub>2</sub> generation were obtained from the crosses UFU 510 × UFUS 7415, UFU 510 × MG/BR 46 Conquista and UFUS 7415 × MG/BR 46 Conquista. The parents show resistance to the nematode of the galls *Meloidogyne incognita* and *Meloidogyne javanica* (MG/BR 46 Conquista), high yield potential, early cycle and tolerance to Asian soybean rust (UFUS 7415) and tolerance to white mold (UFU 510).

The area was prepared in the conventional tillage system with plowing and two harrows, followed by furrowing. Sowing fertilization was carried out with the formula NPK 02-28-18, at a dose of 400 kg ha<sup>-1</sup>. Prior to sowing, the seeds were treated with fungicide (Carbendazim and Tiram) and inoculated with *Bradyrhizobium japonicum*,

SEMIA 5079 and SEMIA 5080 strains. Each  $F_2$  generation was sown in pits, with a spacing of 0.50 m between rows and 0.25 m between plants. A randomized complete block design with ten replications was adopted. During the conduct of the experiment, the management of pests and diseases were carried out through applications of insecticides and fungicides, based on technical recommendations and the need of the crop (Embrapa, 2013). To assist in biological nitrogen fixation, 30 days after emergence, cobalt and molybdenum were applied via foliar at a dosage of 100 mL ha<sup>-1</sup>.

The plants were evaluated individually to obtain information about the following agronomic traits: Plant height at flowering (PHF) and maturity (PHM): measured in cm, from the soil surface to the end of the main stem when the plants were in the reproductive stage R1 and R8; Number of nodes on the main stem at flowering (NNF) and maturity (NNM): determined by counting the number of nodes on the main stem, when the plants were in the reproductive stage R1 and R8; Number of productive nodes (NPN): number of nodes with pods at maturity; Number of days for flowering (NDF) and for maturity (NDM): defined as the number of days from emergence to flowering, when approximately 50% of the plants in the useful plot had at least one open flower (R1) and when 95% of the pods in the useful area of the plot were mature (R8); Insertion height of the first pod (IHP): distance, in cm, measured from the soil surface to the first pod; Number of pods with one grain (NP1), with two grains (NP2) and with three grains (NP3): after harvesting, the number of pods with one, two and three grains was counted; Total number of pods per plant (TNP): obtained by the sum of number of pods with one, two and three grains; Grain production per plant (GP): after harvesting, the plants were traced manually, and their grains had their mass determined on an analytical balance, with four decimal places.

The data for each trait was submitted to analysis of variance and the significance level was analyzed using the F-test, at 5% probability. After obtaining the mean of the crossings for the evaluated traits, a half table balanced diallel analysis was carried out according to Griffing's (1956) method 2 and adapted by Geraldi & Miranda Filho (1988).

The effect of the treatments (averages of the three  $F_2$  populations and the three parents) was estimated using the mathematical model:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + \overline{\varepsilon_{ij}}$$
(1)

where  $Y_{ij}$ : average value of the hybrid  $(i \neq j)$  or parent combination (i = j);  $\mu$ : general mean of the diallel;  $g_i$  and  $g_j$ : effects of the general combining ability of the i-th and the j-th parent, respectively;  $s_{ij}$ : effect of specific combining ability for crosses between parents of order i and j;  $\varepsilon_i$ : mean experimental error.

From the phenotypic values of individuals from the generations of parents and  $F_2$ , the genetic parameters described below were estimated (Cruz et al., 2012):

Genotypic variance in F<sub>2</sub>:

$$\hat{\sigma}_{G(F2)}^2 = \hat{\sigma}_{F(F2)}^2 - \hat{\sigma}_{e(F2)}^2$$
(2)

where  $\hat{\sigma}_{G(F2)}^2$ : genetic variance of the F<sub>2</sub> population;  $\hat{\sigma}_{F(F2)}^2$ : phenotypic variance of the F<sub>2</sub> population;  $\hat{\sigma}_{e(F2)}^2$ : environmental variance of the F<sub>2</sub> population.

Environmental variance in F<sub>2</sub>:

$$\hat{\sigma}_{e(F2)}^2 = \frac{1}{2} \left[ \hat{\sigma}_{(P1)}^2 + \hat{\sigma}_{(P2)}^2 \right]$$
(3)

where  $\hat{\sigma}_{e(F2)}^2$ : environmental variance;  $\hat{\sigma}_{(P1)}^2$ : phenotypic variance of the parent 1;  $\hat{\sigma}_{(P2)}^2$ : phenotypic variance of the parent 2. Phenotypic variance in F<sub>2</sub>:

$$\hat{\sigma}_{F(F2)}^2 = \hat{\sigma}_{G(F2)}^2 - \hat{\sigma}_{e(F2)}^2 \tag{4}$$

where  $\hat{\sigma}_{F(F2)}^2$ : genetic variance of the F<sub>2</sub> population;  $\hat{\sigma}_{G(F2)}^2$ : phenotypic variance of the F<sub>2</sub> population;  $\hat{\sigma}_{e(F2)}^2$ : environmental variance of the F<sub>2</sub> population.

Heritability in the broad sense:

$$h_a^2 = \frac{\hat{\sigma}_{G(F2)}^2}{\hat{\sigma}_{F(F2)}^2} \cdot 100$$
 (5)

where  $h_a^2$ : heritability in the broad sense;  $\hat{\sigma}_{G(F2)}^2$ : genetic variance of the F<sub>2</sub> population;  $\hat{\sigma}_{F(F2)}^2$ : phenotypic variance of the F<sub>2</sub> population.

Prediction of gains by selection:

$$\Delta G\% = \frac{\Delta G}{X_0} \tag{6}$$

where  $\Delta G$ : selection gain; obtained by  $DS \ge h^2$ ; DS: selection differential, given by  $DS = \overline{X_s} - \overline{X_0}$ : average of selected;  $\overline{X_0}$ : observed average of the F<sub>2</sub> population;  $h^2$ : heritability.

Number of genes involved in the trait expression:

$$\eta = \frac{R^2 - (1 + 0.5K^2)}{8\,\hat{\sigma}_G^2} \tag{7}$$

where n: number of genes; R: amplitude between the means of the parents or  $R = \overline{P_1} + \overline{P_2}$ ;  $\hat{\sigma}_G^2$ : genetic variance.

The means were compared by the Tukey test at the 5% probability level. All analyzes were performed using the Computational Program in Genetics and Statistics - GENES (Cruz, 2016).

#### **RESULTS AND DISCUSSION**

Significant effects were found for the general (GCA) and specific (SCA) combining abilities for the agronomic traits number of days to maturity (NDM), plant height at flowering (PHF), plant height at maturity (PHM), number of pods with one and two grains (NP1 e NP2), total number of pods per plant (TNP) and grain production per plant (GP) (Table 1). The significance of the parameters for GCA indicates that there is variability in the additive gene effects and the significance for SCA indicates the predominance of dominance deviations. In breeding programs, the information about GCA and SCA are essential to identify parents that result in promising combinations (Gayosso-Barragán et al., 2019; Kibalnik et al., 2021).

The coefficients of variation (CV) were good, ranging from 0.74% (NDM) to 40.66% (NP1) (Table 1). Higher CV estimates were observed for production components (NP1 and NP3), which is common and occurs because these traits are quantitative, controlled by many genes and highly influenced by the environment (Leite et al., 2015).

The effects of SCA are more important than those of GCA, since the mean square associated with SCA was significant for most of the traits analyzed, which reinforces the greater contribution of non-additive gene action in the control of these traits (Table 1). Bagateli et al. (2020) informs that positive SCA estimates indicate the presence of numerous heterozygous loci leading to greater potential genetic variability, besides being associated with elevated mean values.

EV	DE	Medium square									
ΓV	Dr	NDF	NDM	PHF	PHM	NNF	NNM	NPN			
Genotypes	5	1.48 <sup>ns</sup>	3.66**	280.36**	187.59*	2.90*	24.05 ns	8.56 <sup>ns</sup>			
GCA	2	0.05 <sup>ns</sup>	2.05*	628.78**	184.13 <sup>ns</sup>	3.23 <sup>ns</sup>	12.35 <sup>ns</sup>	1.21 <sup>ns</sup>			
SCA	3	2.44 <sup>ns</sup>	4.74**	48.09 <sup>ns</sup>	189.90*	2.68 <sup>ns</sup>	31.85 <sup>ns</sup>	13.46 <sup>ns</sup>			
Residue	45	0.91	0.58	52.61	62.01	1.01	16.52	6.12			
Overall Average		44.85	103.61	53.54	67.39	12.49	15.97	14.17			
CV (%)		2.13	0.74	13.54	11.68	8.05	25.44	17.46			
EV	DE	Medium square									
ΓV	Dr	HIP	NP1	NP2	NP3	TN	Р	GP			
Genotypes	5	2.36 <sup>ns</sup>	260.92*	* 475.06*	* 493.43	<sup>ns</sup> 2,6	79.72*	473.84**			
GCA	2	$1.70^{\mathrm{ns}}$	31.89 <sup>ns</sup>	184.38 <sup>ns</sup>	410.23	<sup>ns</sup> 1,2	20.51 <sup>ns</sup>	225.30 <sup>ns</sup>			
SCA	3	2.81 ns	413.61**	* 668.85*	* 548.90	<sup>ns</sup> 3,6	52.54*	639.54**			
Residue	45	1.12	67.26	103.46	308.90	866	5.70	100.82			
Overall Average		10.11	20.16	52.01	60.49	132	2.67	49.97			
CV (%)		10.46	40.66	19.55	29.05	22.	18	20.09			

**Table 1.** Summary of the analysis of variance of the partial diallel involving three parents and their hybrid combinations

\*\*, \*: significant at the level of 1% and 5% probability, respectively, by the F and <sup>ns</sup> test, not significant by the F test. DF: Degrees of freedom; CV: coefficient of variation; NDF: number of days for flowering; NDM: number of days to maturity; PHF: plant height at flowering; PHM: plant height at maturity; NNF: number of nodes on the main stem in flowering; NNM: number of nodes on the main stem at maturity; NPN: number of productive nodes; HIP: height of insertion of the first pod; NP1, NP2 e NP3: number of pods with one, two and three grains; TNP: total number of pods per plant; GP: grain production per plant.

Colombo et al. (2018), when analyzing the GCA and SCA of soybean genotypes for agronomic attributes, also identified the predominance of SCA. In contrast, Soares et al. (2023) found highest GCA estimates, which indicates a predominance of additive gene effects in controlling the traits. The differing results can be attributed to the specific population under study, as estimates of genetic parameters are inherently tied to the target population (Soares et al., 2023). Additionally, the complexity of quantitative trait inheritance and the influence of genotype-environment interactions may account for the observed discrepancies (Goksoy et al., 2019).

Estimates of the effects of the GCA of each genotype for the evaluated traits are shown in Table 2. Positive or negative values for GCA indicate that the parent is higher or lower, respectively, than the average of the other parents (Cruz et al., 2012). For production components (NP1, NP2, NP3, TNP and GP), the UFUS 7415 genotype showed the highest and most positive values of the GCA estimates (0.74, 1.67, 3.26, 5.69 and 2.20, respectively). In the crossings in which this parent participates, there will be a contribution to the increase of production components, a desired trait in soybean breeding programs. Rocha et al. (2019) also found positive GCA values for total number of pods and for grain production per plant in segregating soybean populations.

Genotynes	GCA												
Genotypes	NDF	NDM	PHF	PHM	NNF	NNM	NPN	HIP	NP1	NP2	NP3	TNP	GP
UFU 510	0.03	0.21	-3.95	-2.10	0.01	0.26	0.06	-0.20	0.10	-2.00	-1.20	-3.19	-2.03
UFUS 7415	-0.03	-0.03	1.04	0.43	-0.25	-0.57	-0.17	0.15	0.74	1.67	3.26	5.69	2.20
MG/BR 46	-0.00	-0.18	2.90	1.66	0.24	0.30	0.11	0.04	-0.84	0.41	-2.06	-2.49	-0.17
Conquista													
Constrance	SCA	SCA											
Genotypes	NDF	NDM	PHF	PHM	NNF	NNM	NPN	HIP	NP1	NP2	NP3	TNP	GP
1x1	0.10	0.25	1.43	-4.01	0.43	-1.43	-0.94	0.18	-2.79	-1.87	-6.73	-11.40	-6.64
1x2	-0.63	-0.64	-2.52	4.24	-0.20	0.42	0.68	-0.59	8.76	6.57	8.89	24.23	7.50
1x3	0.42	0.13	-0.33	3.78	-0.67	2.44	1.20	0.21	-3.18	-2.81	4.58	-1.41	5.78
$2 \times 2$	0.31	0.65	1.90	-0.72	0.10	0.16	-0.56	0.49	-5.13	-7.69	-3.85	-16.68	-5.31
$2 \times 3$	0.01	-0.65	-1.27	-2.78	-0.00	-0.76	0.45	-0.39	1.49	8.81	-1.18	9.13	3.13
$3 \times 3$	-0.21	0.25	0.80	-0.49	0.33	-0.84	-0.83	0.08	0.84	-3.00	-1.70	-3.85	-4.45

**Table 2.** Estimates of the effects of the general (GCA) and specific (SCA) combining abilities of agronomic traits evaluated in a partial diallel with three parents

NDF: number of days for flowering; NDM: number of days to maturity; PHF: plant height at flowering; PHM: plant height at maturity NNF: number of nodes on the main stem in flowering; NNM: number of nodes on the main stem at maturity; NPN: number of productive nodes; HIP: height of insertion of the first pod; NP1, NP2 e NP3: number of pods with one, two and three grains; TNP: total number of pods per plant; GP: grain production per plant; 1: UFU 510; 2: UFUS 7415; 3: BR/MG 46 Conquista.

The height of the plant at flowering and maturity is an important trait, as it influences lodging, another trait that limits the yield potential of the crop (Hwang & Geon, 2019). For PHF and PHM, the parent UFU 510 presented negative values of the GCA estimates (-3.95 and -2.10, respectively), which contributes to the reduction of the average in the analyzed traits, since soybean plants with heights less than 100 cm are ideal (Table 2). Mishra (2019), in order to evaluate six soybean genotypes by means of the general and specific combining abilities in  $F_1$  and  $F_2$  generations, obtained significant and negative (-2.49) value of GCA for plant height in one of the analyzed genotypes.

For the height of insertion of the first pod, the values observed were -0.20, 0.15 and 0.04 for the parents UFU 510, UFUS 7415 and MG/BR 46 Conquista, respectively (Table 2). IHP is an important trait to be analyzed, as the traditional cultivation of soybean depends on mechanized harvesting and cultivars with low values for this trait can be damaged during the harvesting process. In addition, the height of insertion of the first pod is a trait that positively correlates with yield (Jiang et al., 2018).

For the variables NNF, NNM and NPN, the MG/BR 46 Conquista genotype showed the highest positive values, which indicates that it is a promising parent for the manufacture of more productive plants (Table 2). Leite et al. (2016) observed a positive and significant genotypic correlation between the traits grain yield and number of nodes per plant, indicating that the selection of plants with a higher number of nodes would result in more productive plants. It is noteworthy that one of the main objectives of soybean breeding programs is to seek cultivars with higher and earlier values of yield.

The flowering and maturation period are important agronomic traits and it is crucial to select early maturing varieties that minimally affect seed yield and weight (Copley et al., 2018). In this perspective, the parents UFUS 7415 and MG/BR 46 Conquista presented negative estimates for NDF and NDM, which indicates the contribution of these genotypes to reduce the cycle. When considering the effects of GCA, it was observed that the traits analyzed obtained wide variation in the estimates. The parents

showed independent behaviors, which contributes to increase or decrease the average of the analyzed variables.

The SCA demonstrates the behavior of hybrids based on the general combining ability of their parents and is related to nonadditive gene effects (Cruz et al., 2012). Estimates of the effects of SCA to determine the best hybrid combinations are shown in Table 2. The cross UFU 510 × UFUS 7415 presented negative SCA estimates for the traits NDF (-0.63), NDM (-0.64), IHP (-0.59) and high magnitude and positive estimates for the production components NP1 (8.76), NP2 (6.57), NP3 (8.89), TNP (24.23) and GP (7.50). The means described in Table 3 for the traits mentioned were satisfactory and within the recommended for soybean. The good performance of the F<sub>2</sub> generation, which obtained values higher than its parents for the production componentes, stands out.

Table 2 shows that the combination UFU  $510 \times BR/MG$  46 Conquista demonstrated the best positive SCA estimates for the variables NNM (2.44) and NPN (1.20). The averages (Table 3) ranged from 15.07 to 19.00 for the number of nodes on the main stem at maturity and 13.35 to 15.55 for PN. The segregating population obtained higher estimates for the traits analyzed.

	Populati	on A		Populati	ion B		Population C UFUS 7415 (P <sub>2</sub> ) x MG/BR 46 Conquista (P <sub>3</sub> )			
Traits	UFU 51	$0(P_1)x$		UFU 51	$0(P_1)x$					
	UFUS 7	415 (P <sub>2</sub> )		MG/BR	46 Conqu	uista (P <sub>3</sub> )				
	<b>P</b> <sub>1</sub>	P <sub>2</sub>	$F_2$	<b>P</b> <sub>1</sub>	P <sub>3</sub>	F <sub>2</sub>	P <sub>2</sub>	P <sub>3</sub>	F <sub>2</sub>	
NDF	45.02	45.10	44.22	45.02	44.62	45.30	45.10	44.62	44.82	
NDM	104.30	104.20	103.15	104.30	103.50	103.78	104.20	103.50	102.80	
PHF	47.06	57.53	48.10	47.06	60.15	52.16	57.53	60.15	55.67	
PHM	59.17	67.53	69.97	59.17	70.21	70.73	67.53	70.21	67.09	
NNF	12.95	12.07	12.04	12.95	13.32	12.08	12.07	13.32	12.34	
NNM	15.07	15.00	16.09	15.07	15.75	19.00	15.00	15.75	14.91	
NPN	13.35	13.25	14.74	13.35	13.57	15.55	13.25	13.57	14.13	
HIP	9.89	10.92	9.54	9.89	10.30	10.18	10.92	10.30	10.13	
NP1	17.57	16.52	29.78	17.57	19.32	16.24	16.52	19.32	21.74	
NP2	45.95	47.67	58.17	45.95	49.85	47.52	47.67	49.85	63.51	
NP3	51.35	63.17	71.45	51.35	54.65	61.81	63.17	54.65	62.41	
TNP	114.87	127.37	159.40	114.87	123.82	125.57	127.37	123.82	147.66	
GP	39.26	49.06	57.64	39.26	45.17	53.55	49.06	45.17	55.03	

Table 3. Averages of agronomic traits of three soybean parents and F2 populations

NDF: number of days for flowering; NDM: number of days to maturity; PHF: plant height at flowering; PHM: plant height at maturity NNF: number of nodes on the main stem in flowering; NNM: number of nodes on the main stem at maturity; NPN: number of productive nodes; HIP: height of insertion of the first pod; NP1, NP2 e NP3: number of pods with one, two and three grains; TNP: total number of pods per plant; GP: grain production per plant; F<sub>2</sub>: F<sub>1</sub> self-fertilization.

For PHF (-1.27) and PHM (-2.78), negative effects of SCA were observed on the cross UFUS 7415 × BR/MG 46 Conquista (Table 2). These observations, added to the fact that the parents have the best averages (Table 4) for the analyzed variables, allows us to affirm that this crossing brings together desirable traits, because very low plants (less than 60 cm) compromise yield and very high plants (over 100 cm) are more susceptible to lodging (Sediyama et al., 2015). Bagateli et al. (2020), in order to estimate the general and specific combining abilities of eight soybean genotypes, found negative

SCA values and averages within the recommended for soybean culture in seven of the fifteen analyzed combinations.

For the agronomic attributes of economic interest, the cross UFU  $510 \times$  UFUS 7415 presents itself as the most favorable, since it has the best means and estimates of SCA (Tables 2 and 3) and is composed of the best ranked parent from the GCA for the components of production (Table 2). Hybrid combinations involving at least one parent with favorable GCA estimates are of greater interest to breeders, as they are more important than SCA, since the objective is not to obtain hybrids, but is indicative of heterosis caused by the effects of the combination (Rocha et al., 2019).

The estimates of the variance components for quantitative traits generate information about the genetic structure of a segregating population, favoring the selection of superior genotypes. The phenotypic variance ranged from 4.47 (NDF) to 7540.82 (TNP) in the combination UFU 510 × UFUS 7415; from 2.79 (NDF) to 2748.34 (TNP) for the combination UFU 510 × BR/MG 46 Conquista; and from 2.27 (NDF) to 2753.86 (TNP) for the combination UFUS 7415 × BR/MG 46 Conquista (Table 4).

0000000		1 110 11011									
	Populatio	on A		Populatio	on B		Population C				
Traits	UFU 510	$(\mathbf{P}_1) \mathbf{x}$		UFU 51(	$(P_1) x$		UFUS 7415 (P <sub>2</sub> ) x MG/BR 46 Conquista (P <sub>3</sub> )				
	UFUS 74	15 (P <sub>2</sub> )		MG/BR	46 Conquis	sta (P <sub>3</sub> )					
	$\widehat{\sigma}_{f}^{2}$	$\hat{\sigma}_e^2$	$\hat{\sigma}_{g}^{2}$	$\hat{\sigma}_{f}^{2}$	$\hat{\sigma}_e^2$	$\widehat{\sigma}_{g}^{2}$	$\widehat{\sigma}_{f}^{2}$	$\widehat{\sigma}_{e}^{2}$	$\hat{\sigma}_{g}^{2}$		
NDF	4.47	1.67	2.80	2.79	1.38	1.40	2.27	1.49	0.77		
NDM	5.13	2.47	2.66	4.75	2.33	2.42	4.24	0.95	3.28		
PHF	112.20	94.89	17.31	136.45	148.49	-	149.21	153.65	-		
PHM	437.57	78.10	359.47	194.10	176.15	17.97	118.31	164.45	-		
NNF	2.80	2.57	0.23	3.58	4.13	-	3.45	2.96	0.49		
NNM	12.51	3.16	9.34	930.72	4.64	926.08	7.94	2.96	4.97		
NPN	30.13	2.70	27.43	94.42	3.60	90.82	69.51	2.68	66.83		
HIP	8.97	1.94	7.02	3.60	0.95	2.64	8.00	1.64	6.35		
NP1	2,864.96	93.53	2771.42	76.40	79.26	-	111.85	85.31	26.53		
NP2	684.64	396.26	288.38	497.64	353.11	144.53	584.39	449.33	135.06		
NP3	1,343.07	962.29	380.78	1,052.21	613.38	438.82	872.99	858.42	14.57		
TNP	7,540.82	2,359.35	5,181.47	2,748.34	1,500.61	1,247.73	2,753.86	2,470.63	283.23		
GP	530.27	220.89	309.38	484.42	128.38	356.04	675.62	231.83	443.78		

**Table 4.** Estimates of variances of agronomic traits for three combinations of soybean cultivars obtained from  $F_2$  and their parents

 $\hat{\sigma}_f^2$ : phenotypic variance;  $\hat{\sigma}_e^2$ : environmental variance;  $\hat{\sigma}_g^2$ : genotypic variance; NDF: number of days for flowering; NDM: number of days to maturity; PHF: plant height at flowering; PHM: plant height at maturity NNF: number of nodes on the main stem in flowering; NNM: number of nodes on the main stem at maturity; NPN: number of productive nodes; HIP: height of insertion of the first pod; NP1, NP2 e NP3: number of pods with one, two and three grains; TNP: total number of pods per plant; GP: grain production per plant; -: negative estimates.

In population A (UFU 510 × UFUS 7415), the genotypic variance was greater than the environmental variance for the agronomic traits NDF, NDM, PHM, NNM, NPN, IHP, NP1, TNP and GP; in population B (UFU 510 × BR/MG 46 Conquista) for NDF, NDM, NNM, NPN, IHP and GP; and in population C (UFUS 7415 × BR/MG 46 Conquista), for the traits NDM, NNM, NPN, IHP e GP (Table 4). The highest estimates observed in the three populations for genotypic variance ranged from 283.23 to 5181.47 for TNP (Table 4), which indicates potential for the selection of that trait. The results of the present study are similar to those found by Santos et al. (2019), who observed genetic variance superior to the environmental variance for the total number of pods per plant when evaluating the genetic and agronomic parameters in soybean  $F_2$  progenies from twenty two-parent crosses.

In breeding programs, it is essential to know the genetic variation of a given trait and the effects on the phenotype, since the variance from the environment makes it difficult to recognize superior genotypes (Hamawaki et al., 2012). Heritability is one of the most useful genetic parameters for breeding, as it enables inferences about selection gains (Silva et al., 2021). When heritability is high, it means that the phenotypic variation is mainly due to the additive (inheritable) effects of the genes (Falconer & Mackay, 1996). Heritability estimates in the broad sense of high magnitude can be observed in the three populations analyzed for the NPN. The values were between 91.03% to 96.18% (Table 5). The results observed for the NPN were higher than those found by Teixeira et al. (2017) and Vianna et al. (2019), with heritability estimates for the NPN trait of 73.57% and 48.54%, respectively.

**Table 5.** Estimates of genetic parameters of agronomic traits in generations  $P_1$ ,  $P_2$  and  $F_2$  for three combinations of soybean cultivars

		•											
Population A					Population B				Population C				
	UFU .	UFU 510 (P <sub>1</sub> ) x				510 (I	<b>P</b> <sub>1</sub> ) <b>x</b>		UI	FUS 74	15 (P <sub>2</sub> )	х	
Traits	UFUS 7415 (P <sub>2</sub> )				MG/BR 46 Conquista (P <sub>3</sub> )				MG/BR 46 Conquista (P <sub>3</sub> )				
	$h_a^2$	η	GS (%)	Average*	$h_a^2$	η	GS (%)	Average*	$h_a^2$	η	GS (%)	Average*	
NDF	62.60	6.42	-3.42	42.70	50.35	8.87	-2.11	44.34	33.94	13.13	-1.16	44.29	
NDM	51.90	9.18	-1.40	101.70	50.86	13.21	-1.22	102.50	77.51	5.47	-1.77	100.97	
PHF	15.43	20.35	4.16	50.11	-	-	-2.17	51.02	-	9.32	-0.70	55.28	
PHM	82.15	3.54	28.67	90.03	9.25	40.17	2.35	72.40	-	-	-7.93	61.77	
NNF	8.32	34.23	1.43	12.21	-	-	-2.87	11.73	14.17	65.25	2.18	12.60	
NNM	74.71	2.62	20.34	19.37	99.50	12.97	63.47	31.05	62.62	11.08	14.49	17.07	
NPN	91.03	10.93	33.97	19.74	96.18	5.10	51.41	23.55	96.14	7.42	48.64	21.00	
HIP	78.33	4.00	30.54	12.45	73.39	4.72	16.87	11.89	79.39	8.66	24.20	12.58	
NP1	96.73	4.58	137.14	70.62	-	-	-2.89	15.77	23.72	13.73	15.99	25.21	
NP2	42.12	9.11	25.04	72.73	29.04	7.32	18.94	56.52	23.11	11.81	11.67	70.92	
NP3	28.35	9.48	19.37	85.29	41.70	6.23	30.19	80.47	1.66	177.89	1.08	63.08	
TNP	68.71	5.53	49.71	238.63	45.39	4.76	26.01	158.23	10.28	31.22	4.84	154.82	
GP	58.34	6.56	31.46	75.78	73.49	4.42	42.74	76.44	65.68	3.68	41.57	77.91	

 $h_a^2$ : Heritability in the broad sense;  $\eta$ : number of genes; GS: prediction of gains by selection; NDF: number of days for flowering; NDM: number of days to maturity; PHF: plant height at flowering; PHM: plant height at maturity NNF: number of nodes on the main stem in flowering; NNM: number of nodes on the main stem at maturity; NPN: number of productive nodes; HIP: height of insertion of the first pod; NP1, NP2 e NP3: number of pods with one, two and three grains; TNP: total number of pods per plant; GP: grain production per plant; -: negative estimates; \*Average predicted for the 1st cycle after selection.

When analyzing population A, it is also observed estimates of heritability higher than 70% for the traits PHM, NNM, IHP and NP1; in population B for the traits NNM and IHP; and in population C for NDM and IHP (Table 4). Values above 70% for

heritability indicate that simple selection methods can generate considerable gains, since the environment has no significant influence on the analyzed variable (Santos et al., 2018).

Another important genetic parameter to be analyzed is the number of genes. The estimation of this parameter shows us whether the trait under study is controlled by many or few genes. According to Stacke et al. (2020) the inheritance can be classified as monogenic (one gene), oligogenic (a few genes), or polygenic (many genes). The combinations UFU 510 × UFUS 7415, UFU 510 × BR/MG 46 Conquista and UFUS 7415 ×BR/MG 46 showed the highest number of genes, respectively, for NNF (34.23), PHM (40.17) and NP3 (177.89) (Table 5) and are considered as polygenic traits. Silva et al. (2021) also found polygenic inheritance for traits related to production and plant cycle. Important agronomic traits are considered polygenics and have low heritability with their expression significantly influenced by environment conditions (Baldissera et al., 2014, Silva et al., 2021).

Based on the analysis of genetic parameters for the three crosses, the possibility of selecting superior genotypes in the  $F_2$  generation was verified. Thus, the selection gain obtained and the average for the first cycle after selection were estimated (Table 5). The greatest genetic gains were obtained for the traits NP1 (137.14%), NNM (63.47%) and NPN (48.64%) in populations A, B and C, respectively (Table 5). In this work, greater positive selection gains were observed in the combination UFU 510 × UFUS 7415, with a higher predicted average, when compared to other crosses, for the production components NP1 (70.62), NP2 (72.73), NP3 (85.29) and TNP (238.63).

For the NDM trait, the estimates for selection gain were negative, corroborating with the results found by Amaral et al. (2020) and diverging from those found by Leite et al. (2018) who studied agronomic traits in soybeans and obtained positive values for the mentioned trait. For PHM and IHP, the selection gain was 28.67 and 30.54 for the combination UFU 510 × UFUS 7415; 2.35 and 16.87 for the combination UFU 510 × BR/MG 46 Conquista; and -7.93 and 24.20 for UFUS 7415 × BR/MG 46 Conquista (Table 5). The average predicted for PHM was between 61.77 cm and 90.03 cm and for HIFP between 11.89 cm and 12.58 cm. Thus, it was observed that the three segregating populations met the criteria considered ideal for culture.

The average predicted for GP ranged from 75.78 g to 77.91 g when analyzing the three combinations (Table 5). In addition, positive values for GP were observed in all segregating populations that ranged between 31.46% and 42.74%, which indicates the possibility of gains with the selection. Bizari et al. (2017), Teixeira et al. (2017) and Silva et al. (2021) also observed gains for grain production in segregating soybean population. Hamawaki et al. (2012) explains that selection gains are directly associated with the differences between the means of the selected group and the original population and also linked to increased heterogeneity.

### CONCLUSIONS

The parent UFUS 7415 presents the highest and most positive values of the GCA estimates for the production components. The cross UFU 510  $\times$  UFUS 7415 presents the highest number of total pods and grain production. The combinations

UFU 510 × UFUS 7415, UFU 510 × MG/BR 46 Conquista and UFUS 7415 × MG/BR 46 Conquista show a high heritability coefficient for the number of productive nodes. In the population of the crossing UFU 510 × UFUS 7415, greater selection gains and higher averages are observed for the production components NP1, NP2, NP3 and TNP.

ACKNOWLEDGMENTS. The authors thank CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), Fapemig, the Soybean Breeding Program (PMG) and to Instituto Federal Goiano, Campus Urutaí, for the structural and financial support.

#### REFERENCES

- Amaral, L.O., Bruzi, A.T., Resende, P.M. & Silva, K.B. 2019. Pure line selection in a heterogeneous soybean cultivar. Crop Breeding and Applied Biotechnology 19, 277–284.
- Bagateli, J.R., Bahry, C.A., Silva, R.N.O., Carvalho, I.R., Conte, G.G., Villela, F.A., Gadotti, G.I. & Meneghello, G.E. 2020. Estimates of heterosis and combining ability of soybean diallel crossings. *Plant Omics*, 7–14.
- Baldissera, J.N.C., Valentini, G., Coan, M.M.D., Guidolin, A.F. & Coimbra, A.J.L.M. 2014. Genetics factors related with the inheritance in autogamous plant populations. *Revista de Ciências Agroveterinárias* 13, 181–189 (in Portuguese).
- Bizari, E.H., Val, B.H.P., Pereira, E.M., Mauro, A.O.D., Unêda-Trevisoli, S.H., Bizari, E.H., Val, B.H.P., Pereira, E.M., Mauro, A.O.D., Unêda-Trevisoli, S.H. 2017. Selection indices for agronomic traits in segregating populations of soybean. *Revista Ciência Agronômica* 48, 110–117.
- Bornhofen, E. 2019. *Genetic analysis reveals opportunities and obstacles of tolerance to the Asian soybean rust fungus*. Doutorado em Genética e Melhoramento de Plantas, Universidade de São Paulo, Piracicaba, 126 pp. (in Portuguese).
- Chagas, P.H.M., Teodoro, L.P.R., Santana, D.C., Teixeira Filho, M.C.M., Coradi, P.C., Torres, F.E., Bhering, L.L. & Teodoro, P.E. 2023. Understanding the combining ability of nutritional, agronomic and industrial traits in soybean F2 progenies. *Scientific Reports* 13, e17909.
- Colombo, G.A., Carvalho, E.V., Daronch, D.J. & Peluzio, J.M. 2018. Diallel analysis of the combining ability of soybean genotypes under low latitude Brazilian cerrado conditions. *Revista de Ciências Agrárias Amazonian Journal of Agricultural and Environmental Sciences* **61**, 1–9 (in Portuguese).
- Copley, T.R., Duceppe, M.O. & O'Donoughue, L.S. 2018. Identification of novel loci associated with maturity and yield traits in early maturity soybean plant introduction lines. *BMC Genomics* **19**, 167.
- Cruz, C.D. 2016. Genes Software extended and integrated with the R, Matlab and Selegen. *Acta Scientiarum Agronomy* **38**, 547–552.
- Cruz, C.D., Regazzi, A. & Carneiro, P. 2012. Biometric models applied to genetic breeding. *Viçosa: Editora UFV* **1**, 514. (in Portuguese).
- Embrapa Brazilian Agricultural Research Company. 2013. Soybean production technology Central Region of Brazil 2014. Londrina, 226 pp. (in Portuguese).
- Falconer, D.S. & Mackay, T.F.C. 1996. *Introduction to quantitative genetics*. 4<sup>th</sup> ed. New York: Longman, 464 pp.
- Friedrichs, M.R., Burton, J.W. & Brownie, C. 2016. Heterosis and Genetic Variance in Soybean Recombinant Inbred Line Populations. *Crop Science* **56**, 2072–2079.
- Gayosso-Barragán, O., López-Benítez, A., Rodríguez-Herrera, S.A., Ek-Maas, J.N., Hidalgo-Ramos, D.M. & Alcala-Rico, J.S.G.J. 2019. Studies on combining ability in tomato (Solanum lycopersicum L.). Agronomy Research 17, 77–85.

- Geraldi, I.O. & Miranda Filho, J.B. 1988. Adapted models for the analysis of combining ability of varieties in partial diallel crosses. *Revista Brasileira de Genética* **11**, 419–430.
- Goksoy, A.T., Sıncık, M., Erdogmus, M., Ergin, M., Aytac, S., Gumuscu, G., Gunduz, O., Keles, R., Bayram, G. & Senyıgıt, E. 2019. The parametric and non-parametric stability analyses for interpreting genotype by environment interaction of some soybean genotypes. *Turkish Journal of Field Crops* 24, 28–38.
- Griffing, B. 1956. Concept of General and Specific Combining Ability in Relation to Diallel Crossing Systems. *Australian Journal of Biological Sciences* **9**, 463–493.
- Hamawaki, O.T., de Sousa, L.B., Romanato, F.N., Nogueira, A.P.O., Santos Júnior, C.D. & Polizel, A.C. 2012. Genetic parameters and variability in soybean genotypes. *Comunicata Scientiae* 3, 76–83.
- Hwang, S. & Lee, T.G. 2019. Integration of lodging resistance QTL in soybean. *Scientific Reports* 9, 6540.
- Jiang, H., Li, Y., Qin, H., Li, Y., Qi, H., Li, C., Wang, N., Li, R., Zhao, Y., Huang, S., Yu, J., Wang, X., Zhu, R., Liu, C., Hu, Z., Wi, Z., Xin, D., Wu, X. & Chen, Q. 2018. Identification of major QTLs associated with first pod height and candidate gene mining in soybean. *Frontiers in Plant Science* 9, 1280.
- Kibalnik, O., Kukoleva, S., Semin, D., Efremova, I. & Starchak, V. 2021. Evaluation of the combining ability of CMS lines in crosses with samples of grain sorghum and Sudan Grass. *Agronomy Research* 19, 1781–1790.
- Leite, W.S., Pavan, B.E., Filho, C.H.A.M., Neto, F.A., Oliveira, C.B. & Feitosa, F.S. 2016. Genetic parameters estimation, correlations and selection indexes for six agronomic traits in soybean lines F8. *Comunicata Scientiae* 7, 302–310 (in Portuguese).
- Leite, W.S., Unêda-Trevisoli, S.H., Silva, F.M., Silva, A.J. & Mauro, A.O.D. 2018. Identification of superior genotypes and soybean traits by multivariate analysis and selection index. *Revista Ciência Agronômica* 49, 491–500.
- Leite, W.D.S., Pavan, B.E., Matos Filho, C.H.A., Feitosa, F.S. & de Oliveira, C.B. 2015. Estimates of genetic parameters and correlations between morphological traits in soybean genotypes. *Nativa* 3, 241–245 (in Portuguese).
- Mishra, A.K. 2019. Estimation of Gene Action Through Combination Ability in Soybean. *Soybean Research* 17, 22–29.
- Nadathur, S., Wanasundara, J.P.D. & Scanlin, L. 2024. Feeding the globe nutritious food in 2050: obligations and ethical choices. *Sustainable Protein Sources* **2**, 649–668.
- Pimentel, A.J.B., Souza, M.A., Carneiro, P.C.S., Rocha, J.R.A.S.C., Machado, J.C. & Ribeiro, G. 2014. Partial diallel analysis in advanced generations for selection of wheat segregating populations. *Pesquisa Agropecuária Brasileira* 48, 1555–1561 (in Portuguese).
- Rialch, I. & Sharma, J.D. 2019. Combining ability studies for yield and related traits in soybean (*Glycine max*). *Indian Journal of Agricultural Sciences* **89**, 1334–1339.
- Rocha, M.R., Hamawaki, O.T., Nogueira, A.P.O., Machado Junior, C.S., Hamawaki, C.D.L. & Hamawaki, R.L. 2019. Combinatorial analysis of agronomic characters in soybean. *Ciência e Agrotecnologia* 43, 1–7.
- Santos, E.R., Spehar, C.R., Pereira, P.R., Capone, A. & Barros, H.B. 2019. Genetic parameters and agronomic evaluation progenies F<sub>2</sub> soy the federal district, Brazil. *Revista Brasileira de Ciências Agrárias (Agrária)* 14, 1–8.
- Santos, E.R., Spehar, C.R., Capone, A. & Pereira, P.R. 2018. Estimation of genetic variation parameters in F2 soybean progenies and parents with presence and absence of lipoxygenases. *Nucleus* 15, 61–70 (in Portuguese).
- Sediyama, T., Silva, F. & Borém, A. 2015. *Soybean: from planting to harvest*. Viçosa: UFV, 333 pp. (in Portuguese).

- Silva, C.O., Hamawaki, O.T., Nogueira, A.P.O., Almeida, M.R.C., Castro, D.G., Marques, F.S., Hamawaki, R.L., Hamawaki, C.D.L, Cardoso, G.M. & Diniz, V.H.R. 2021. Genetic parameters and selection indexes in F2 and F2:3 soybean populations. *Agronomy Journal* 113, 2991–3004.
- Soares, S.L., Simon, G.A., Alvares, R.C. & Silva, F.H.L. 2023. Combining performance and estimated genetic diversity among soybean parents and F1 populations. *Revista Ceres* **70**, 81–90.
- Stacke, R.F., Godoy, D.N., Pretto, V.E., Führ, F.M., Gubiani, P.S., Hettwer, B.L., Garlet, C.G., Somavilla, J.C., Muraro, D.S. & Bernardi, O. 2020. Field-evolved resistance to chitin synthesis inhibitor insecticides by soybean looper, *Chrysodeixis includens* (Lepidoptera: Noctuidae), in Brazil. *Chemosphere* 259, e127499.
- Teixeira, F.G., Hamawaki, O.T., Nogueira, A.P.O., Hamawaki, R.L., Jorge, G.L., Hamawaki, C.L., Machado, B.Q.V. & Santana, A.J.O. 2017. Genetic parameters and selection of soybean lines based on selection indexes. *Genetics and Molecular Research* 16, 1–17.
- Teodoro, L.P.R., Bhering, L.L., Gomes, B.E.L., Campos, C.N.S., Baio, F.H.R., Gava, R., Júnior, C.A.S. & Teodoro, P.E. 2019. Understanding the combining ability for physiological traits in soybean. *PLOS ONE* 14, e0226523.
- Vianna, M.S., Nogueira, A.P.O., Hamawaki, O.T., Sousa, L.B., Gomes, G.F., Glasenapp, J.S., Hamawaki, R.L. & Silva, C.O. 2019. Selection of lineages, genetic parameters, and correlations between soybean characters. *Bioscience Journal* 35, 1300–1314.