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Analysis of combining ability in soybean cultivars

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ABSTRACT - Eight soybean cultivars (*Doko*, *Bossier*, *Ocepar-4*, *BR-15*, *FT-Cometa*, *Savana*, *Paraná* and *Cristalina*) were crossed in a diallel design. Plants of the F_1 generation and their parents were evaluated under short-day conditions for the determination of the general (GCA) and specific (SCA) combining ability. The estimated GCA and SCA values were significant for the evaluated traits except for the “total cycle”. Highest GCA effects for the traits “days to flowering”, “plant height”, “insertion height”, “number of branches” and “total cycle” were estimated for the cultivars *Doko*, *Cristalina* and *Savana*. The variability observed in the trait “days to flowering” can, for the most part, be explained by additive effects.

Key words: *Glycine max*, flowering, heterosis, diallel

INTRODUCTION

Knowledge on the mechanisms that control the main traits of agronomic interest of a species is fundamental for genetic improvement and can be acquired through methodologies of diallel crosses as the one developed by Griffing (1956). Values associated to the general combining ability (GCA) of each parent and to the specific combining ability (SCA) of each cross are estimated. Baker (1978) suggested the use of the diallel analysis in the sense of estimating the mean square of the GCA and SCA and emphasized the following interpretations: if the mean square of the SCA is not significant, the hypothesis prevails that the progeny performance can be predicted based on the GCA, where the best progeny can be obtained by a cross of two parents with the highest values. On the other hand, if the mean square of the SCA is significant, the interactions must be taken into account to determine the progeny performance.

Studies on the combining ability of autogamous species consider the ratio of the mean square values of GCA and SCA as indicators of the predominant type of gene action in the trait expression. According to Singh and Chaudhary (1985) it is appropriate to use the square components of the effects to indicate the type of corresponding gene action. The ratio $2\hat{\sigma}_g^2 / (2\hat{\sigma}_g^2 + \hat{\sigma}_s^2)$, proposed by Baker (1978), shows how much of the observed variance can be explained by the additive and non-additive effects. Values near the unit indicate the predominance of additive effects.

By method 2, proposed by Griffing (1956) the estimates of \hat{g}_i , \hat{s}_{ij} and \hat{s}_{ii} can be established. Cruz and Vencovsky (1989) demonstrated that in the additive-dominant models, estimator is \hat{s}_{ii} a measure of the genetic divergence of parent (i) in relation to the mean of the other parents considered in the diallel. If is negative, the heterosis (in relation to the parent mean)

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expressed in the hybrids of parent (i) will be, in the mean, positive. In other words, when \hat{s}_{ii} is negative, parent (i) contributes to a positive heterosis value. When \hat{s}_{ii} is positive, the opposite happens; when is zero or close to zero, the genetic divergence of parent (i) in relation to the other parents is small or zero, and the heterosis in the hybrids of parent (i) will be small or zero as well.

When the absolute value of \hat{g}_i is low (be it negative or positive), one can state that the mean of the parent to which it is related does not differ from the mean observed in the diallel for a particular trait. A high value however indicates that the parent is superior or inferior to the other parents involved in the diallel. A positive or negative signal, associated to a particular value, indicates the respective superiority or inferiority of one parent over the others (Cruz and Regazzi, 2001).

In autogamous plants, the heterosis manifested in the F_1 generation is reduced by 50% in each selfing generation since reduction occurs in the number of heterozygous plants in the same proportion (Ramalho et al. 2004). With the mean values of F_1 and the calculated heterosis, it is therefore possible to foresee/predict the population means in future generations through the following formula: $\bar{F}_n = \bar{F}_{n-1} - H/2^{n-1}$, where n = generation under study, \bar{F} = mean value and H = heterosis value. When the H value is positive, the mean observed in F_1 decreases with the selfing generations and increases when the H value is negative. To warrant the validity of the values established through the formula, the selfed populations may not be selected.

According to Cruz et al. (1987), the best hybrid combinations are those with the most favorable estimates for the SCA effects that have at least one parent with the most favorable GCA effect for the target trait. According to Cruz and Vencovsky (1989), the best hybrid is result of a cross between parent (a) selected based on GCA and parent (b), whose frequency of favorable alleles is superior to the mean population frequency and considerably divergent from parent (a). Crosses of two parents with high general ability do however not necessarily generate the best hybrid.

The methodology of analysis proposed by Griffing (1956) was used in soybean by Leffel and Weiss (1958), Singh et al. (1974), Kaw and Menon (1981), Toledo and Kihl (1982 b), Cruz et al. (1987), Gravina et al. (2003), among others. The GCA and SCA of cultivars were evaluated in relation to different traits, such as: "days

to flowering", "days to maturation", "number of nodes", "number of branches", "plant height" and "heritability of disease resistance".

The present study had the objectives of determining the general and specific combining ability of traits of agronomic interest in soybean and to provide base material for the soybean improvement program developed in Jaboticabal, state of São Paulo.

MATERIAL AND METHODS

The experiment was installed September 25, 1991, on an area of the Faculdade de Ciências Agrárias e Veterinárias - Unesp - Campus de Jaboticabal (21°15' 22") under a photoperiod of 12:10hs. The experimental design was of random blocks, where each plot consisted of five plants spaced 20cm within and 60 cm in-between rows. Due to the different number of seeds obtained from each cross, the treatments presented different numbers of replicates. Based on the soil analysis, a fertilization of 200 kg / ha of the formula 0-20-20 was applied, but no liming. The seeds were treated and stink bugs were controlled by spraying twice during the crop cycle.

For the diallel cross scheme, genotypes contrasting in the study traits Doko, Bossier, Ocepar-4, BR-15, FT-Cometa, Savana, Paraná, and Cristalina were used. The following traits were evaluated: Number of days to flowering - days between the emergence of the cotyledons and the opening of the first flower in any plant part (DF); Number of days to maturation - days between flowering and the moment when 95% of the pods presented the typical ripe pod coloring (DM); Number of nodes on the main stem (NN); Number of branches inserted in the main stem (NB); Insertion height of the first pods (IH); Plant height (PH) and Total cycle - days between emergence and maturation (TC).

The analysis of variance was performed with data means of the five plants in the plots for each trait under study and the diallel analysis according to Griffing (1956).

The effective number of replicates (r_e) was established as the harmonic mean [$1/r_e = 1/36 (1/r_1 + 1/r_2 + \dots + 1/r_{36})$] of the number of replicates of the parents and F_1 plants for each trait. This way, the analyses of unbalanced data of Martins Filho et al. (1992) and of balanced data of Griffing (1956) became more consistent. The square component of the effects of the general (A)

and specific (B) ability and the relation (C) between them was calculated according to Baker (1978):

A – Square component for general combining ability $\frac{1}{7} \sum_i \hat{g}_i^2$

B – Square component for specific combining ability $\frac{1}{28} \sum_i \sum_j \hat{s}_{ij}^2$

C – Relation between square components $2\hat{\sigma}_g^2 / (2\hat{\sigma}_g^2 + \hat{\sigma}_s^2)$

RESULTS AND DISCUSSION

The analysis of variance of data showed that the treatment effect was significant at 1% probability by the F test for the evaluated traits (Table 1). The observed mean values of the parents and the F₁ plants derived from crosses between them, to which the Tukey test was applied (5% probability), are presented in Table 2.

Even under short-day conditions, the cultivars Doko, Savana and Cristalina did not present early flowering, which left a period of over 50 days for plant growth. Cultivar Doko flowered approximately 70 days after plantlet emergence and the values of the F₁ plants were statistically below this mean. The second highest mean for the trait was observed in cultivar Savana (approximately 60 days). The values of the F₁ plants were below this mean, apart from the crosses with Doko and Cristalina.

The mean values observed for the trait “plant height” in the parents Paraná, Ocepar-4 and Bossier were not significantly different from the means of the respective F₁ plants. An exception was observed in the F₁ plants of the cross Paraná x FT-Cometa where the mean differed statistically from the parent with lowest

height. For “insertion height”, best results were observed in the cultivars Doko and Savana, which attained comparable mean values to mechanized harvesting. All F₁ means of plants of crosses involving cultivar Doko were statistically below the cultivar mean.

The cultivars Doko, Savana and Cristalina presented the highest mean values for the trait “number of branches”. The F₁ plant means of the crosses involving the three cultivars did not differ statistically from the best mean, observed in cultivar Doko.

The cultivars with the highest values for “number of nodes” were those with the highest values for the trait “plant height” (Savana, Doko and Cristalina) evidencing a direct relation between the traits. A high mean value was observed for the trait in cultivar FT-Cometa, but owing to the early flowering, the plants did not present high values for “plant height”. In relation to the trait “days to maturation”, the mean values observed in the F₁ plants did not differ statistically from the means of their respective parents, except for plants of the cross FT-Cometa and Cristalina. The lowest values of “total cycle” were observed in the F₁ plants derived from crosses of cultivar FT-Cometa with the cultivars Savana and Doko.

The degrees of freedom associated to the parents were then partitioned, resulting in values for the GCA and SCA effects (Tabela 3). The analysis of variance evidenced highly significant values for mean squares of the GCA and SCA effects for all traits, except for “total cycle”, in agreement with Leffel and Weiss (1958), Kaw and Menon (1981), Toledo and Kiihl (1982 b) and Cruz et al. (1987). The observed results can therefore be explained by the additive as much as the non-additive effects. For the trait “total cycle”, only the value of the

Table 1. Values of mean squares (preliminary analysis) of the traits evaluated in the experiment, coefficient of variation (CV) and effective mean number of replicates (r_e)

Evaluated trait	Sources of Variation				CV	r _e
	Parents		Error			
	df	MS	df	MS		
Days to flowering	35	496.34**	89	2.54	3.70	2.76
Days to maturation	35	213.90**	88	71.22	7.86	2.75
Plant height	35	734.83**	87	18.83	13.10	2.74
Insertion height	35	35.32**	83	1.43	15.48	2.66
Nodes on the main stem	35	49.95**	89	1.22	10.50	2.76
Number of branches	35	15.09**	86	0.97	17.26	2.73
Total cycle	35	887.80**	88	75.84	5.79	2.75

* * significant at 1% probability; df - Degree of freedom; MS – Mean square

Table 2. Mean values observed in the parents and F₁ plants derived from their crosses regarding the study traits

Parent Cross	DF	PH	IH	NB	NN	DM	TC
1	73.76	54.32	16.44	11.40	15.36	100.92	174.68
1 X 2	38.50* ns	17.34 * ns	5.08* ns	4.95* ns	6.01* ns	109.16 ns ns	147.66* ns
1 X 3	47.70* *	25.50 * ns	5.70 * ns	6.70* ns	9.10* ns	106.20 ns ns	153.90 ns ns
1 X 4	58.80* *	37.00* ns	11.30 ns	7.70* ns	12.20 ns ns	112.14 ns ns	170.94 ns ns
1 X 5	37.65* *	60.04 ns *	6.10* ns	6.90* *	17.61 ns *	113.65 ns ns	151.30 ns *
1 X 6	59.80* ns	48.60 ns ns	10.80* ns	7.40 ns ns	11.80 ns ns	103.60 ns ns	163.50 ns ns
1 X 7	44.60* *	22.20 * ns	8.40* ns	5.20* ns	8.00* ns	117.40 ns ns	162.00 ns ns
1 X 8	65.08* *	54.65 ns ns	12.83* ns	8.98 ns ns	16.11 ns ns	107.11 ns ns	172.19 ns ns
2	39.04	24.60	7.68	4.32	6.91	103.28	142.32
2 X 3	30.65* ns	18.30 ns ns	6.10 ns ns	3.70 ns ns	6.70 ns ns	105.80 ns ns	136.45 ns ns
2 X 4	35.65 ns *	19.34 ns ns	5.20 ns *	4.16 ns *	6.53 ns *	103.77 ns ns	139.42 ns ns
2 X 5	31.47 ns *	30.88 ns ns	5.38 ns ns	4.26 ns ns	10.72* ns	92.27 ns ns	123.61 ns ns
2 X 6	37.34 ns *	20.71 ns *	5.49 ns *	4.70 ns *	6.62 ns *	105.55 ns ns	141.65 ns *
2 X 7	32.56* ns	18.48 ns ns	5.44 ns ns	3.60 ns ns	6.60 ns ns	100.12 ns ns	134.04 ns ns
2 X 8	40.73 ns *	16.97 ns *	4.83 ns *	3.85 ns ns	6.00 ns *	103.53 ns ns	144.27 ns *
3	33.88	20.36	6.68	4.72	7.16	113.44	147.24
3 X 4	42.00 * ns	27.75 ns ns	6.25 ns ns	4.50 ns ns	6.75 ns ns	102.75 ns ns	144.75 ns ns
3 X 5	31.15 ns ns	26.73 ns ns	4.40 ns ns	3.30 ns ns	10.45 ns ns	106.15 ns ns	137.30 ns ns
3 X 6	44.43 * *	28.93 ns *	6.82 ns *	5.50 ns ns	8.62 ns *	95.57 ns ns	140.00 ns *
3 X 7	34.22 ns ns	18.12 ns ns	5.40 ns ns	4.28 ns ns	6.93 ns ns	103.82 ns ns	137.62 ns ns
3 X 8	43.30 * *	25.43 ns *	5.60 ns *	4.73 ns ns	9.00 ns *	114.55 ns ns	157.85 ns ns
4	49.36	31.56	10.45	7.47	10.35	116.23	165.59
4 X 5	34.63 * *	38.02 ns ns	5.74* ns	4.71* ns	13.68* ns	107.55 ns ns	142.18 ns ns
4 X 6	52.93 ns *	47.40 * ns	12.83 ns ns	9.38 ns ns	12.60 ns *	116.05 ns ns	168.98* ns
4 X 7	39.97 * ns	20.74 ns ns	5.20* ns	4.99* ns	7.36* ns	110.24 ns ns	150.33 ns ns
4 X 8	53.43 ns *	44.04 * ns	10.01 ns ns	8.84 ns ns	12.28 ns ns	121.19 ns ns	174.62* ns
5	29.40	34.56	6.90	2.91	12.00	94.09	123.49
5 X 6	37.33 * *	54.60 * ns	8.07 ns *	6.33* ns	15.87* ns	112.93 ns ns	150.27* ns
5 X 7	32.05 ns ns	37.96 ns *	5.64 ns ns	4.50 ns ns	11.83 ns *	98.73 ns ns	130.68 ns ns
5 X 8	36.88 * *	51.63 * ns	5.50 ns *	4.75 ns ns	17.13* ns	128.38* ns	165.25* ns
6	60.64	60.36	13.90	7.52	16.48	106.34	166.98
6 X 7	43.90 * *	30.20 * ns	7.40* ns	4.90 ns ns	10.00* ns	118.30 ns ns	162.27 ns ns
6 X 8	60.50 ns ns	57.93 ns ns	12.95 ns ns	7.90 ns ns	16.53 ns ns	116.93 ns ns	174.43 ns ns
7	35.98	19.24	5.99	3.94	7.39	101.82	137.80
7 X 8	44.78 * *	26.60 ns *	5.95 ns ns	5.93 ns ns	9.40 ns *	116.78 ns ns	161.55 ns ns
8	58.35	43.35	9.68	6.48	13.73	112.77	171.12

ns - non significant by the F test. * Significant at 5% probability by **Tukey's** test in relation to the 1st and 2nd parents, respectively. 1.Doko; 2. Bossier; 3. Ocepar-4; 4.BR-15; 5.FT-Cometa; 6.Savana; 7.Paraná; 8.Cristalina
DF- Days to flowering; PH - Plant height; IH - Insertion height; NB - Number of branches; NN - Nodes on the main stem; DM - Days to maturation; TC - Total cycle.

mean square of the GCA presented significance. The results can therefore be evaluated based only on the additive effects. Bonato and Vello (1999) concluded that the main component of genetic variation in the determination of the time to flowering is additive.

The GCA values are important for breeders who work with autogamous plants due to the additive

variance. The observed SCA values showed that there are crosses that present a different performance from what would be expected if only the additive effects were of influence. According to the value of the relation between the square components, proposed by Baker (1978), the additive effects explain between 45% and 93 % of the observed variability. It is therefore possible to

Table 3. Values of mean squares of the effects of the general (GCA) and specific combining ability (SCA), regarding the traits evaluated in the experiment and square components of the effects of the general (A) and specific combining ability (B) and the relation (C) between them, as proposed by Baker (1978)

FV	Target Trait																	
	PH			IH			NB			NN			DM			TC		
	df	MS	df	MS	df	MS	df	MS	df	MS	df	MS	df	MS	df	MS		
GCA	7	2167.15**	7	2797.87**	7	114.63**	7	63.60**	7	196.02**	7	467.80**	7	3873.42**				
SCA	28	78.63**	28	221.57**	28	15.79**	28	3.42**	28	13.43**	28	149.48**	28	130.58 ^{ns}				
Error	89	2.54	87	18.83	83	1.44	86	0.97	89	1.22	88	71.22	88	75.84				
Square Components																		
GCA	DF	78.43	PH	101.42	IH	4.26	NB	2.29	NN	7.06	DM	11.58	TC	138.09				
SCA	MS	27.57		73.99		5.39		0.90		4.42		28.46		19.91				
GCA/SCA		0.85		0.73		0.61		0.84		0.76		0.45		0.93				

** Significant at 1% probability by the F test.
 DF- Days to flowering; PH - Plant height; IH - Insertion height; NB - Number of branches; NN - Nodes on the main stem; DM - Days to maturation; TC - Total cycle SV - source of variation; MS - Mean square

predict the future generations for some traits, by the underlying mean F₁ population values.

The estimated GCA effects for the traits evaluated in the diallel are displayed in Table 4. The parents Doko, Cristalina and Savana presented, respectively, the highest GCA values in the sense of delaying flowering. In this case it is expected, even under short-day conditions, that the mean values of F₁ plants derived from crosses involving at least one of these cultivars would be higher than the mean value of the parent with earlier flowering.

In relation to the trait “plant height”, cultivars Savana and Doko attained the highest values for the GCA effects. Under the given experimental conditions, the mean height of F₁ plants was reduced in the crosses of the cultivars Bossier and Paraná. These considerations apply for the trait “insertion height” as well.

The cultivars Doko and Savana presented the highest positive GCA values for the traits “number of branches” and “number of nodes”. It is expected that the mean values of the F₁ plants derived from crosses involving at least one of these cultivars would be high, or that have more branches and nodes on the main stem. Cultivars Cristalina and BR-15 presented the highest positive GCA values in the sense of delaying plant maturation. The reduction of the total cycle can be associated to the reduction of this period, which would be of great importance.

The “total cycle”, evaluated from emergence until maturation, represents the periods emergence to flowering and flowering to maturation together. The parents Doko and Cristalina presented estimates for the GCA effects in the sense of increasing the total plant cycle. The number of days for the “total cycle” was 171 (Cristalina) and 175 (Doko). Parent Doko took longer to begin flowering, whereas the period flowering-maturation was abridged. Parent Cristalina began flowering earlier, but ripened later. The GCA effects estimated for Bossier and Ocepar-4 indicated a reduction of the total plant cycle. The values associated to parent FT-Cometa showed its contribution to early flowering and quicker pod maturation.

The values of the of effects in F₁ plants (Table 5) can be interpreted as deviations from the values observed in relation to what could be expected if only additive effects were of influence. When the estimate corresponds to the cross of a particular parent with

Table 4. Estimate of the effects of the general combining ability (\hat{g}_i) for the traits evaluated in the experiment involving eight parents in a diallel cross (method 2, Griffing model 1)

Parents	DF	PH	IH	NB	NN	DM	TC
Doko	11.539	8.779	2.728	2.275	2.053	-0.366	11.194
Bossier	-6.367	-10.923	-1.758	-1.315	-3.222	-3.734	-10.156
Ocepar-4	-4.975	-8.520	-1.306	-0.758	-2.142	0.507	-4.518
BR-15	2.301	-0.797	0.707	0.828	-0.267	4.478	6.804
FT-Cometa	-8.565	5.922	-1.778	-1.119	2.318	-3.635	-12.306
Savana	6.787	10.666	2.255	0.934	2.124	0.800	7.267
Paraná	-4.040	-7.440	-1.277	-0.897	-1.718	-1.918	-5.833
Cristalina	7.359	6.105	0.828	0.650	1.750	5.126	12.334
E.P. ($\hat{g}_i - \hat{g}_j$)	0.429	1.172	0.329	0.267	0.297	2.276	2.349

DF- Days to flowering; PH - Plant height; IH - Insertion height; NB - Number of branches; NN - Nodes on the main stem; DM - Days to maturation; TC - Total cycle.

itself, it is (Cruz and Vencovsky, 1989). For the trait “days to flowering”, the values are generally positive resulting in negative heterosis in the F_1 generation. When no selection is performed, the mean number of days to flowering would therefore increase down through the selfing generations, in comparison to the number observed in the F_1 population. The magnitude of the estimates indicates a greater divergence in the parents Bossier, Doko and Savana than in the overall mean, so that higher heterosis values are expected in the hybrids involving one of these parents.

Early flowering normally results in smaller plants and with lower yield. The presence of a long juvenile period can delay flowering (Miranda et al., 1986). In the present study crosses were observed in which a flowering period of around 36 days did not impair plant growth: FT-Cometa x Doko, FT-Cometa x Savana and FT-Cometa x Cristalina. The negative heterosis values in these crosses demonstrated that the means of the future generations will be considerably higher than those observed in the F_1 generation, when no selection is performed. The higher absolute values for the trait “plant height” were observed in the parents Bossier and FT-Cometa, indicating the greater divergence in relation to the overall diallel mean. The negative value

verified in FT-Cometa would generally result in a positive mean heterosis value in the F_1 plants of the crosses involving this parent.

The values for “insertion height” are generally positive, resulting in negative heterosis in the F_1 generation. In the absence of selection, the “insertion height” of the first pods would therefore increase over the selfing generations compared to the height observed in the F_1 population. The same considerations apply for the “number of branches” and “number of nodes”.

The cultivars Doko and FT-Cometa presented high negative values for the trait “days to maturation” which resulted in positive heterosis in the F_1 generation of their crosses. In the absence of selection, the mean number of “days to maturation” would therefore decrease over the selfing generations, compared to the number observed in the F_1 population. The magnitude of the estimates indicates a greater divergence in the parents Doko and FT-Cometa compared to the overall mean, so that higher heterosis values would be expected in the hybrids involving one of these parents.

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Análise da capacidade combinatória em cultivares de soja

RESUMO - Oito cultivares de soja (Doko, Bossier, Ocepar-4, BR-15, Savana, Paraná e Cristalina) foram cruzadas em esquema diallelo. Plantas da geração F_1 e seus genitores foram avaliadas sob condições de dias curtos para a determinação das capacidades geral (CGC) e específica (CEC) de combinação. Os valores estimados para CGC e CEC foram significativos

para todas as características avaliadas exceto para ciclo total. As cultivares Doko, Cristalina e Savana apresentaram os maiores valores para a estimativa dos efeitos de CGC para as características: dias para florescimento, altura de plantas, altura de inserção, número de galhos e ciclo total. A variabilidade observada em relação à característica dias para o florescimento pode ser explicada, em sua maior parte, por efeitos aditivos.

Palavras-chave: dialelo, florescimento, *Glycine max*, heterose.

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