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Heterosis in Soybeans for Seed Yield Components and Associated Traits

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ABSTRACT

The objective of this research was to quantify heterosis of agronomic traits and evaluate direct and indirect correlations among seed yield and other traits. A diallel involving six parents was grown in two localities. Seed yield (PG), one-hundred seed weight (PCS), number of pods per plant (NV), weight of aerial part of the plant (PPA), harvest index (IC) and number of seeds per pod (NGV) were evaluated. Positive values of heterosis were detected for all traits. Estimates of heterosis components were significative for most traits, showing effects of aditivity and dominance. The specific heterosis was more important than the variety heterosis, mainly in the locality Anhembi. MTBR-95-123800 presented the best potential per se and as parent in crosses, but it was excelled by some of the hybrids in the two localities. Number of pods per plant demonstrated to be suitable for indirect selection for PG.

Key words: Breeding, indirect selection, correlations among traits, path analysis, *Glycine max*

INTRODUCTION

The soybean breeding programs have developed homozygous lines, which represent the totality of cultivars available in the market. Recently, some works have been accomplished with the objective of verifying the occurrence of heterosis in soybeans, motivated mainly by the success of F_1 hybrids in other crops. Among the various advantages of the use of hybrids, one is the possibility to obtain more vigorous and productive plants, larger homeostasis, easiness of accumulating complementary dominant alleles in an heterozygotic genotype. On the other hand, the heterosis can difficult the selection in segregant generations because it is due to non additive variation.

The heterosis or hybrid vigor can be defined as the superiority of individuals of the F_1 generation in relation to their parents (Fehr, 1987). This phenomenon has been explored during the last 70 years. Heterosis can be considered as one of the most important contributions of the genetics to agriculture, with great reflexes in agricultural seed yield. Specifically in soybeans, for the commercial hybrids to turn reality, two requirements are pointed as fundamentals: presence of heterosis for seed yield, and an economical method for production of hybrid seed in wide scale (Paschal and Wilcox, 1975). For a trait with high number of genes and with dominance effect it is easier to obtain a hybrid than a line with superior genotypes

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(Burton, 1987). The most accepted hypotheses to explain heterosis involve dominance and the overdominance, besides epistatic effects.

The values of heterosis in soybean are very variable for the different agronomic traits, especially for seed yield, and some works have pointed out positive heterosis for this trait. Nelson and Bernard (1984) evaluated 27 hybrids and found five superiors for seed yield, with values between 13 and 19% in relation to the superior parent. Positive values of 26.1% on average, for a group of hybrids, with values until 68% superior in relation to the best parent were reported by Chaudary and Singh (1974). Some researches have demonstrated positive heterosis for seed yield and, also, established associations with its components (Campos, 1979). In a general way, positive heterosis has been observed for number of pods per plant and number of seeds per plant (Kunta et. al., 1985; Raut et. al., 1985). Negative or insignificant heterosis was reported for seed weight and number of seeds per pod (Chaudary and Singh, 1974; Paschal and Wilcox, 1975; Nelson and Bernard, 1984; Gadag and Upadhyaya, 1995). In soybean, heterosis values for weight of the aerial part of the plant were similar to the ones reported for seed yield. For harvest index, the hybrids presented intermediate values in relation to the parents or very low values of heterosis (Paschal and Wilcox, 1975; Campos, 1979; Nelson and Bernard, 1984).

The traits of agronomic importance can be correlated to each other in different magnitudes (Cruz and Regazzi, 1994). This implicates that selection for a trait can bring reflexes in others, with interest or not to the plant breeding. The knowledge of the direct and indirect correlations, especially with seed yield, allows the breeder to use this additional information to discard or to promote the genotypes of interest. High direct correlations can make possible the practice of indirect selection in early generations or during the vegetative cycle and can be useful in the achievement of genetic gains.

The objective of this work was to evaluate heterosis for components of the seed yield through diallel experiments involving six parents and the F_1 generation of the 15 crosses among them. Besides, the direct and indirect effects of the associations among these traits were studied.

MATERIAL AND METHODS

The six parents include three lines with the acronym USP [USP1-11 (3), USP2-16 (4), USP5-19 (6)], developed by the Section of Genetics Applied to Autogamous Species of the Department of Genetics of ESALQ/USP, and the genotypes Hartwig (1), Conquista (2) and MTBR-95-123800 (5). Except for Hartwig and MTBR-95-123800 the parents have bean adapted to the conditions of the State of São Paulo, Brazil, and all of them present genes of interest for breeding programs. The lines USPs and Hartwig present genes for multiple resistance to different races of soybean cyst nematode - NCS (*Heterodora glycines*); MTBR-95-123800 and Conquista possess genes for photoperiod tolerance, high seed yield and resistance to the soybean stem canker (CHS; caused by the fungus *Diaphorthe phaseolorum* f. sp. *meridionalis*).

The experiments were developed at two localities: ESALQ and Anhembi Experimental Station, both located in State of São Paulo, Brazil, with 22°42'30 " of South latitude, 47°39'00 " of West longitude and 543m of altitude. The area in ESALQ's headquarters has a high fertile soil (kandiudalfic eutrudox, "terra roxa estruturada eutrófica"), with clay texture, and hilly relief. In the Anhembi Experimental Station, located about 60 km from the ESALQ's headquarters, the soil (typic udifluvent, a soil type commonly found in Brazilian savannas or "cerrados") is dystrophic alluvial, with acidity neutralized by lime application, and flat relief.

The F_1 seeds were obtained during the 1997/98 agricultural year in tropical greenhouse, in a complete 6 x 6 diallel, without reciprocals. In the 1998/99 agricultural year, the 21 treatments, six parents and the 15 F_1 hybrids among them, were evaluated in the field. The experiments were carried out in a complete randomized design. Each plot was represented by a single hill with one individual plant, spaced 0.80m x 0.80m. According to the seed availability, 12 to 30 plants per treatment in each locality were used. The F_1 seeds were germinated in controlled environmental conditions, transplanted to plastic cups (200 ml volume), containing soil as substratum and transplanted to the field on November 10, 1998. This procedure was accomplished for all the treatments with the objective of avoiding any loss of hybrid seed.

The data were collected in individual plants and the following traits were evaluated: seed yield(PG), in g/plant; one-hundred seed weight (PCS), in g; number of pods per plant (NV), counted manually; weight of the aerial part of the plant (PPA), after harvesting; harvest index (IC), obtained dividing seed yield by weight of the aerial part of the plant; and number of seeds per pod (NGV), obtained from the following expression: NGV = (100 x PG)÷(PCS x NV). The exploratory analysis of the data was made in SAS LAB of the SAS program (SAS INSTITUTE INC, 1996). The transformation of data using the logarithm of base 10 was used for the traits NV, PPA, PCS and PG, but for the trait IC an multiplication index of 2.8 was used, in order to correct deviations in relation to normality of the data distribution and homogeneity of the variances.

The individual analysis of variance for each locality and the combined analysis were developed considering the fixed effects of treatments (parents and crosses) and localities. The diallel analysis followed the methodology proposed by Gardner and Eberhart (1966), whose complete model is: $\bar{Y}_{ij} = m + (v_i+v_j) / 2 + \theta (\bar{h} + h_i + h_j + s_{ij}) + \bar{\varepsilon}_{ij}$, where $\bar{Y}_{ij}$ is the observed mean of a parent or hybrid; $\bar{\varepsilon}_{ij}$ is the experimental error; m corresponds to the effect of the general mean of the trait; v_i and v_j are the effects of the varieties (parents i and j); $\bar{h}$ is the mean heterosis of all the hybrids; h_i and h_j are effects of heterosis of the varieties i and j, measured by the deviations among the heterosis that occurs in the hybrids involving each variety and the medium heterosis; and, s_{ij} is the effect of specific heterosis of the hybrid ij. The variable θ assumes the value zero for the parents and the value one for the hybrids. The sums of squares and the parameters of the model were calculated matricially, weighted by the number of observations of each treatment. The general combining ability (g_i) was calculated by the formula $g_i = (1/2)v_i + h_i$ (Cruz, 1997). The comparison of means of the parents was made through Tukey test at 5% probability and the means of the crosses were compared by the procedure of Scott-Knott (1974) at 5% probability.

A study of phenotypic, genotypic and environmental correlations among the evaluated traits was carried out. In order to verify the direct and indirect effects of each one of the components of the seed yield, the path coefficient was utilized (Cruz and Regazzi, 1994). The SAS (SAS INSTITUTE INC, 1996) and GENES (Cruz, 1997) statistical packages were used.

RESULTS AND DISCUSSION

In the individual analysis of variance (Table 1), the mean squares of the genotypes effect were significant for all the traits. The effect of localities was equally significant, except for NV. In the combined analysis, besides the genotypes effect, there was significant effect of genotype x locality interaction for all the traits. The differential performance of the genotypes in the two localities evidenced the need to consider each locality individually to the achievement and interpretation of the estimates of parameters related to the group of parents and crosses.

Study of means

The parental means formed different groups for all the traits (Tukey test at 5% probability, Table 2). For NV, the means oscillated between 210.14 and 759.90 pods/plant. The means of NGV varied from 1.325 to 1.912 seeds/pod, and the parent Conquista presented the lowest mean in ESALQ and the highest in Anhembi, showing strong effect of genotype x locality interaction for this trait. For PCS, the means varied from 14.25 to 20.07g, and Conquista, USP1-11 and USP5-19 parents presented the highest seed size. For PPA, the means oscillated from 133.14 to 487.56g, with the parent MTBR-95-123800 standing out. The means of IC varied from 0.27 to 0.45, with prominence for the parent USP2-16 in both localities.

For PG there was wide variation among the parents, with means oscillating from 48.45 to 89.20 g/plant (Table 2), and the parent MTBR-95-123800 was superior to the others in both localities. The great differences of means among the parents reflected the existence of genetic variability for the different traits. The largest means were observed at Anhembi, demonstrating that this environment was more favorable than ESALQ. None of the evaluated traits maintained the same ranking of the parents among the two localities, evidencing again the effect of genotype x locality interaction.

Table 1 - Mean squares and significance of analysis of variance by local and combined for the traits for the traits number of pods per plant (NV), number of seeds per pod (NGV), one-hundred seed weight (PCS), weight of aerial part of the plant (PPA), harvest index (IC) and seed yield (PG). ESALQ and Anhembi, 1998/99.

S.V.	NV	NGV	PCS	PPA	IC	PG
ESALQ						
Genotypes	0.105114 **	0.234598 **	0.013262 **	0.108624 **	0.005543 **	0.127967 **
Error	0.008674	0.109622	0.001256	0.008343	0.000703	0.019369
C.V.	3.56	18.99	2.91	3.71	35.73	6.84
ANHEMBI						
Genotypes	0.093521 **	0.140193 **	0.012402 **	0.106233 **	0.002294 **	0.143772 **
Error	0.010167	0.065831	0.001247	0.012950	0.000604	0.014911
C.V.	3.81	14.53	2.86	4.55	26.56	5.73
COMBINED						
Localities (L)	0.028327 ^{ns}	0.695294 **	0.045281 **	0.086386 **	0.021067 **	0.556088 **
Genotypes (G)	0.176517 **	0.231104 **	0.023150 **	0.187178 **	0.006025 **	0.233880 **
L x G	0.017281 *	0.148844 *	0.002234 *	0.024778 **	0.001457 **	0.039540 *
Error	0.009337	0.085408	0.001253	0.010361	0.000659	0.017317
C.V.	3.67	19.95	2.88	4.11	31.16	6.33

** and * significative at 1 and 5% probability by F test.

Table 2 - Parent means for the traits number of pods per plant (NV), number of seeds per pod (NGV), one-hundred seed weight (PCS), weight of aerial part of the plant (PPA), harvest index (IC) and seed yield (PG). ESALQ and Anhembi, 1998/99.

	NV		NGV		PCS		PPA		IC		PG	
ESALQ												
1:Hartwig	210.14	c	1.4328	ab	15.81	bc	133.14	c	0.3241	b	48.45	cd
2:Conquista	375.60	b	1.3251	b	19.61	a	314.80	b	0.2727	b	86.25	bc
3:USP1-11	356.50	b	1.9070	a	17.43	ab	293.67	b	0.4125	a	123.03	ab
4:USP2-16	439.78	b	1.9117	a	14.73	bc	280.67	b	0.4353	a	114.73	abc
5:MTBR-95-123800	720.38	a	1.4250	ab	14.25	bc	480.38	a	0.2803	b	134.69	ab
6:USP5-19	319.00	b	1.6880	ab	17.08	b	241.60	b	0.3412	b	81.23	bc
ANHEMBI												
1:Hartwig	258.29	c	1.4511	a	16.73	bcd	167.14	cd	0.3529	b	57.80	d
2:Conquista	396.33	b	1.8252	a	20.07	ab	329.67	bc	0.4312	a	142.96	abc
3:USP1-11	389.00	bc	1.8094	a	18.26	ab	320.40	bc	0.3993	ab	115.98	bc
4:USP2-16	392.86	b	1.6843	a	15.73	cde	230.00	bcd	0.4552	a	100.90	bc
5:MTBR-95-123800	759.90	a	1.6301	a	14.80	de	487.56	a	0.3621	b	189.20	a
6:USP5-19	317.43	bc	1.5269	a	18.45	ab	237.14	bcd	0.3698	b	87.34	c

In each column, the differences between means followed by a same letter were not significant (Tukey's test, P=0.05).

It is observed from the Table 2 that the parent MTBR-95-123800 presented superior values for NV, PPA and PG in relation to the other parents in the two environments. However, an opposite performance was observed for the parent Hartwig that presented the lowest means for these traits, probably, because this genotype was not adapted to Brazilian conditions, being included in the breeding program as donor of genes for multiple resistance to races of soybean cyst nematode. Although a larger number of groups for the traits PPA and PG was formed in the two environments, little variation was observed for the trait IC. This probably occurred because IC was a proportion between PG and PPA, and there were biological limitations regulating its variation, once the seed yield depended on the ability of the plant to produce photoassimilates (Ritchie, 1985).

The comparison of means by Scott-Knott test among F_1 hybrids (Table 3) allowed the formation of groups without overlapping, and this fact facilitated the understanding and visualization of the superior genotypes. For NV, two groups were formed in Anhembi and three groups in ESALQ, and the crosses Conquista x USP2-16 (2 x 4), Conquista x USP5-19 (2 x 6) and MTBR-95-123800 x USP5-19 (5 x 6) were in the superior group in the two localities. For the trait NGV, there was no formation of different groups. The trait PCS presented wide variation, with prominence for the crosses Conquista x USP5-19 (2 x 6) and USP-11 x USP 5-19 (3 x 6) that presented superior means at both localities.

At Table 3 showed that for the trait PPA, two different groups were formed at both localities, with prominence for the crosses Conquista x USP2-16 (2 x 4), USP1-11 x MTBR-95-123800 (3 x 5). For IC there was no formation of different groups in Anhembi, while at ESALQ only the crosses Conquista x USP1-11 (2 x 3) and Conquista x MTBR-95-123800 (2 x 5) were the group with the smallest means. For the trait PG, only two groups were formed and a large number of hybrids was included in the most productive group. The cross Hartwig x Conquista (1 x 2) presented strong positive interaction with the locality Anhembi, reaching a PG of 132.10g/plant.

Heterosis

The heterosis of hybrids in relation to the mean of the superior parent (HGS) and to parental mean (HMG) are presented in Table 3. For the trait NV, most of the hybrids presented means similar or superior to the best parent and positive values of heterosis in relation to parental mean, in both the localities. For NGV, most of the hybrids had means similar to the superior parent in Anhembi, while in ESALQ 47% of the hybrids had means inferior to the best parent.

However, in both localities there were not crosses with negative heterosis in relation to parental mean. For PCS, values of negative heterosis prevailed in relation to the superior parent (53% of the cases in ESALQ and 73% in Anhembi); however, in relation to the parental mean, most of the hybrids were similar or superior in seed size.

For PPA, in both localities, the great majority of the hybrids did not differ significantly in comparison to the superior parent. For this trait, 47% and 53% of the hybrids respectively in ESALQ and Anhembi, presented positive and significant heterosis in relation to the parental mean. The heterosis for PPA presented higher values in Anhembi in relation to ESALQ, indicating that the locality Anhembi acted in a positive way, allowing a better expression of the potential of the hybrids with regards to the development of the plant. The traits IC and PG presented similar results to each other, with the predominance of hybrids with mean equal or superior to the best parent and absence of hybrids with negative heterosis in relation to the parental mean. The most favorable performance was showed for PG that presented the most expressive values of heterosis among the studied traits (Table 3). Because the existence of genotype x location interaction, the relative ranking of the crosses differed between the two localities, as indicated by the means (Table 3) and by the low value (r=0.182) of the Spearman correlation among the ranks of HGS for PG.

In a general way for all traits, there was a tendency of occurring more crosses superior than inferior to the parental mean. This was probably due to the presence of dominance for genes that acted in the sense of increasing the traits. From the point of view of plant breeding, great interest exists in genotypes that overcome the superior parent. However, for this, it is necessary to exist complementarity between the parents, in other words, both should possess dominant genes to the increase of the trait in different loci controlling seed yield and other important characters for the adaptation of the plants to the local environment, mainly disease resistance, photoperiod tolerance (long juvenile period), and an appropriate type of growth habit.

Seed yield is a very complex quantitative trait, whose control involves a series of genes, because practically all traits have some influence, at big or small scale, on the seed yield. However, heterosis occurred practically for all traits in different magnitudes. Probably, positive and highest heterosis observed for PG was explained by the sum of favorable values of heterosis for the different traits correlated with seed yield.

Diallel analysis

The mean squares of the diallel analysis of variance, (model 4 of Gardner and Eberhart, Table 4) were significant for almost all the effects, in the evaluated traits in both localities. At ESALQ, there were exceptions for mean heterosis, variety heterosis and specific heterosis for the trait NGV; mean heterosis for PCS and variety heterosis for PG. At Anhembi, the effect of variety heterosis for NV, NGV, PPA and IC, and the effect of mean heterosis for PCS were not significant.

Table 3 - Means of the F_1 hybrids in relation to superior parent (HGS) and to parental mean (HMG) for the traits number of pods per plant (NV), number of seeds per pod (NGV), one-hundred seed weight (PCS), weight of aerial part of the plant (PPA), harvest index (IC) and seed yield (PG). ESALQ and Anhembi, 1998/99.

	NV			NGV			PCS			PPA			IC			PG		
F_1	Media	HGS	HMG	Media	HGS	HMG	Media	HGS	HMG	Media	HGS	HMG	Media	HGS	HMG	Media	HGS	HMG
ESALQ																		
1X2	353.50 c	-5.88	20.70*	1.7086 a	19.25*	23.91*	17.55 a	-10.46*	-0.87	249.13 a	-20.86*	11.23*	0.4164 a	28.48*	39.54*	98.50 b	14.20	46.25*
1X3	412.20 b	15.62	45.49*	1.9265 a	1.02	15.37	14.87 c	-14.70*	-10.55*	261.60 a	-10.92	22.58*	0.4314 a	4.57	17.12	137.58 a	11.83	60.46*
1X4	508.43 a	15.61	56.46*	1.6790 a	-12.17*	0.41	14.54 c	-8.01	-4.74	294.00 a	4.75	42.09*	0.4198 a	-3.56	10.56	124.73 a	8.72	52.88*
1X5	315.50 c	-56.20*	-32.19*	1.6254 a	14.06	13.75	17.13 b	8.33	13.94*	212.50 a	-55.76*	-30.73*	0.4074 a	25.68*	34.79*	85.97 b	-36.17*	-6.12
1X6	396.00 b	24.14	49.68*	1.9300 a	14.34	23.69*	15.32 c	-10.34*	-6.87	262.25 a	8.55	39.96*	0.4262 a	24.92*	28.12*	109.46 b	34.75*	68.81*
2X3	426.63 b	13.58	16.55	1.5733 a	-17.50*	-2.65	18.82 a	-3.98	1.67	353.33 b	12.24	16.14	0.3124 b	-24.27*	-8.82	110.64 b	-10.06	5.74
2X4	616.38 a	40.16*	51.19*	1.6799 a	-12.12*	3.80	16.32 b	-16.78*	-4.94	433.50 b	37.71*	45.60*	0.3896 a	-10.52	10.03	168.12 a	46.54*	67.30*
2X5	520.29 a	-27.78*	-5.06	1.2477 a	-12.45*	-9.27	18.02 a	-8.08*	6.46*	374.29 b	-22.08	-5.86	0.2838 b	1.24	2.63	141.32 a	4.92	27.93*
2X6	470.33 a	25.22*	35.43*	1.9462 a	15.29	29.18*	18.04 a	-8.00*	-1.67	364.67 b	15.84	31.08*	0.4390 a	28.69*	43.03*	147.98 a	71.57*	76.71*
3X4	482.44 a	9.70	21.17*	1.8529 a	-3.08	-2.96	16.98 b	-2.57	5.62	336.44 b	14.57	17.16	0.4515 a	3.71	6.50	142.56 a	15.88*	19.92
3X5	554.83 a	-22.98	3.05	1.8148 a	-4.83	8.93	16.69 b	-4.25*	5.35*	415.67 b	-13.47	7.40	0.3596 a	-12.83	3.81	153.32 a	13.83	18.98
3X6	361.67 c	1.45	7.08	1.7220 a	-9.70*	-4.20	18.19 a	4.37	5.41	261.00 a	-11.12	-2.48	0.4332 a	5.02	14.96	116.09 b	-5.64	13.67
4X5	440.33 b	-38.87*	-24.09*	1.6749 a	-12.39*	0.39	15.54 c	5.53	7.26*	281.33 a	-41.43*	-26.07*	0.4355 a	0.03	21.70*	131.03 a	-2.71	5.07
4X6	409.40 b	-6.91	7.91*	1.7472 a	-8.60*	-2.92	15.15 c	-11.29*	-4.72	265.60 a	- 5.37	1.71	0.4231 a	-2.82	8.97	106.64 b	-7.05	8.84
5X6	623.40 a	-13.46	19.96	1.6470 a	-2.43	5.81	16.53 b	-3.20	5.54	386.00 b	-19.65	6.93*	0.4322 a	26.69*	39.09*	189.92 a	41.00*	75.91*
ANHEMBI																		
1X2	540.60 a	36.40*	65.16*	1.8827 a	3.15	14.93*	18.28 b	-8.91*	-0.66	400.80 a	21.58	61.35*	0.4456 a	3.33	13.65*	232.98 a	62.98*	132.10*
1X3	541.25 a	39.14*	67.24*	2.2159 a	22.47*	35.92*	15.93 c	-12.74*	-8.93*	391.00 a	22.03	60.40*	0.4893 a	22.53*	30.09*	176.11 a	51.85*	102.68*
1X4	408.00 b	3.85	25.32*	1.9124 a	13.55*	21.99*	15.65 c	-6.47*	-3.60	259.00 b	12.61	30.43*	0.4508 a	-0.97	11.56*	121.66 b	20.58*	53.32*
1X5	357.13 b	-53.00*	-9.85*	1.7489 a	7.29	13.52	16.25 c	-2.87	3.10	231.50 b	-52.52*	-29.28	0.4268 a	17.88*	19.39*	105.63 b	-44.17*	-14.47
1X6	326.40 b	2.83	13.39*	1.7597 a	15.25*	18.18	16.77 c	-9.11*	-4.67	215.20 b	-9.25	6.46	0.4236 a	14.55*	17.22*	95.50 b	9.34	31.59*
2X3	457.33 b	15.39	16.47*	1.8127 a	-0.68	-0.25	18.70 b	-6.81*	-2.42	363.00 a	10.11	11.68	0.4053 a	-6.01	-2.39	153.02 a	7.04	18.19
2X4	514.40 a	30.94*	30.36*	2.0498 a	12.31	16.82	17.89 b	-10.82*	-0.03	397.20 a	20.49	41.94*	0.4663 a	2.44	5.21*	166.74 a	16.64	36.76*
2X5	458.20 b	-39.70*	-0.74*	1.7627 a	-3.42	2.03	17.96 b	-10.49*	3.04	360.80 a	26.00*	-11.70	0.4017 a	-6.84	1.28	164.01 a	-13.31	-1.25
2X6	499.83 a	26.11	40.06*	1.8183 a	-0.38	8.49*	20.82 a	3.76	8.11*	436.67 a	32.46*	54.08*	0.4457 a	3.35	11.28*	191.33 a	33.84*	66.16*
3X4	439.33 b	11.83	12.38*	1.6878 a	-6.72	-3.38	16.79 c	-8.04*	-1.21	288.00 b	-10.11	4.65	0.4358 a	-4.26	2.00	134.07 b	15.60	23.63
3X5	655.67 a	-13.72 *	14.14*	1.7499 a	-3.29	1.75	16.98 c	-7.00*	2.74	458.67 a	-5.93	13.54	0.4219 a	5.67	10.84*	182.79 a	-3.39	19.79*
3X6	366.00 b	-5.91	3.62	2.0896 a	15.48*	25.26*	21.90 a	19.95*	19.32*	379.00 a	18.29	35.95*	0.4518 a	13.15*	17.49*	155.97 a	34.48*	53.43*
4X5	506.20 a	-33.39*	-2.18*	1.8967 a	12.61*	14.45*	16.16 c	2.67	5.82*	333.20 a	-31.66*	-7.13	0.4661 a	2.40	14.06*	174.99 a	-7.51	20.64
4X6	572.88 a	45.82*	61.31*	1.7560 a	4.26	9.37*	17.51 b	-5.12*	2.43	430.25 a	81.43*	84.20*	0.4165 a	-8.50*	0.97	175.77 a	74.20*	86.75*
5X6	624.17 a	-17.86*	15.87*	1.7618 a	8.08	11.61*	16.99 c	-7.93*	2.19	429.00 a	-12.01	18.39*	0.4341 a	17.40*	18.64*	186.44 a	-1.46	34.84*

In each column, the differences between means followed by a same letter were not significant (Scott-Knott's test, P=0.05).
* significative at 5% probability by t test.

The model 4 was used for all the traits, because these presented significant specific heterosis, except the trait NGV (ESALQ) for which the model 1 was used. The significance of the varieties effect (Table 4) indicated that these did not constitute a homogeneous group (Vencovsky, 1970). Table 5 showed, by considering the best genotypes at the two localities that the parent MTBR-95-123800 (5) exceeded in relation to the variety effect (v_i) for the traits NV, PPA and PG, while the line USP2-16 (4) showed high and positive values of v_i for IC. For the trait NGV, the parents USP2-16 (ESALQ), Conquista (Anhembi), and USP1-11 (in the two localities) presented the most favorable estimates. The parent Conquista (2) presented the most expressive values of v_i for PCS. The highest values of general combining ability (g_i) for PG were presented by the parents Conquista (2) and MTBR-95-123800 (5). However, the order of the parents was not the same for g_i and for v_i, probably, because the influence of significative h_i on g_i estimates, that is, the variety effect was essentially due to the additive gene action, while the g_i contained dominance effects. Low estimates of g_i, positive or negative, indicated that the values expressed by the parents, obtained through the hybrids, did not differ from general mean of the crosses in the diallel (Oliveira Júnior et al., 1999). More expressive values of g_i constituted an indication of genes with effects predominantly additive. The parents with higher estimates were suitable to the constitution of new segregant populations, and their use could facilitate the selection of superior genotypes and to provide genetic gains in intrapopulation breeding programs. The g_i could be considered as a good criterion for the formation of the base population in programs of recurrent selection (Cruz and Vencovsky, 1989). The arguments favorable to the use of this criterion were the association of g_i with the additive variance and the performance *per se* of the involved genotypes (Vencovsky, 1970). It could be worth to point out that among the best hybrids obtained in diallels, generally one of the parents involved in the cross had a superior value of g_i.

Table 4 - Mean squares of the analysis of variance of the diallel model for the traits number of pods per plant (NV), number of seeds per pod (NGV), one-hundred seed weight (PCS), weight of aerial part of the plant (PPA), harvest index (IC) and seed yield (PG). ESALQ and Anhembi, 1998/99.

S.V.	DF	NV	NGV	PCS	PPA	IC	PG
ESALQ							
Treatments	20	0.002017 **	0.00802812 **	0.00018820 **	0.002225 **	0.00008990 **	0.00240935 **
Varieties	5	0.004352 **	0.01463466 **	0.00053514 **	0.006149 **	0.00013924 **	0.00423394 **
Heterosis	15	0.001239 **	0.00582594	0.00007255 **	0.000918 **	0.00007345 **	0.00180116 **
Mean heterosis	1	0.003951 **	0.01345940	0.00001690	0.001980 **	0.00044170 **	0.01102370 **
Variety heterosis	5	0.000867 **	0.00442862	0.00008578 **	0.000754 **	0.00004686 **	0.00057978
Specific heterosis	9	0.001144 **	0.00575406	0.00007138 **	0.000890 **	0.00004730 **	0.00145498 **
Error		0.000193	0.00375933	0.00001962	0.000170	0.00001435	0.000395
ANHEMBI							
Treatments	20	0.002111 **	0.007315 **	0.00028527 **	0.002524 **	0.000071 **	0.003037 **
Varieties	5	0.003352 **	0.005630 *	0.00084438 **	0.004539 **	0.000050 *	0.003977 **
Heterosis	15	0.001697 **	0.007876 **	0.00009890 **	0.001852 **	0.000078 **	0.002724 **
Mean heterosis	1	0.004984 **	0.045108 **	0.00008620	0.008357 **	0.000510 **	0.018710 **
Variety heterosis	5	0.000681	0.003773	0.00008134 **	0.000875	0.000042	0.001088 **
Specific heterosis	9	0.001896 **	0.006019 *	0.00011007 **	0.001672 **	0.000050 *	0.001857 **
Error		0.000336	0.002531	0.00002545	0.000428	0.000020	0.000304

** and * significative at 1 and 5% probability by F test.

The significance of the effect of heterosis justified the separation into its components (mean heterosis - $\bar{h}$, variety heterosis - h_i and specific heterosis - s_{ij}) (Table 4). The significance of $\bar{h}$ for most of the traits indicated the presence of dominance and differences in gene frequency among varieties, at least for part of the loci with dominance; this fact also showed that the parents were divergent in these loci. The significance of h_i depended on the value of the mean gene frequency and on the dispersion of these frequencies around the mean (Gardner and Eberhart, 1966). The most expressive values of h_i for the traits NV and PPA were obtained by the parents Conquista (2), USP2-16 (4) and USP5-19 (6), but the order differed among localities. The same happened with Hartwig (1) and USP5-19 (6) for NGV and IC. For PG, the highest estimates of h_i were obtained by the parents USP5-19 (6) and Conquista (2), in this order in both localities. According to Table 5, the smallest h_i values for the traits NV, PPA and PG were presented by the parent MTBR-95-123800 (5), whose very high means indicated that it possessed high concentration of favorable genes. Although this parent presented high general combining ability and was involved in some of the most productive crosses, the performance of these hybrids could be attributed mainly to the additive effects, as indicated by the high value of v_i. This line was developed at the Central-West region of Brazil in area with latitudes near 15°, but it showed great potential for using in the central part of São Paulo State.

The non-significance of the mean heterosis and the significant variety and specific heterosis, as occurred for PCS in the two localities (Table 4) indicated the occurrence of non directional dominance (positive in some loci and negative for others), or the existence of non directional epistatic effects (Vencovsky, 1970).

Table 5 - Estimates of the effects of variety (v_i), variety heterosis (h_i) and general combining ability (g_i) for the traits number of pods per plant (NV), number of seeds per pod (NGV), one-hundred seed weight (PCS), weight of aerial part of the plant (PPA), harvest index (IC) and seed yield (PG). ESALQ and Anhembi, 1998/99.

Traits		Hartwig	Conquista	USP1-11	USP2-16	MTBR-95-123800	USP5-19
ESALQ							
NV	v_i	-193.4231	-27.9660	-47.0660	36.2119	316.8091	-84.5660
	h_i	18.8416	36.4856	8.6982	21.8623	-119.0936	33.2059
	g_i	-77.8700	22.5026	-14.8348	39.9682	39.3109	-9.0771
NGV	v_i	-0.1821	-0.2898	0.2921	0.2968	-0.1899	0.0731
	h_i	0.1605	0.0359	-0.0716	-0.1379	-0.0505	0.0636
	g_i	0.0694	-0.1090	0.0744	0.0105	-0.1455	0.1002
PCS	v_i	-0.6732	3.1218	0.9441	-1.7582	-2.2321	0.5977
	h_i	-0.6191	-0.1798	0.1069	-0.2949	1.2861	-0.2992
	g_i	-0.9557	1.3811	0.5790	-1.1740	0.1700	-0.0004
PPA	v_i	-157.5657	24.0915	2.9582	-10.0419	189.6665	-49.1086
	h_i	2.7095	35.7399	9.5899	11.7983	-73.3289	13.4914
	g_i	-76.0734	47.7856	11.0690	6.7773	21.5043	-11.0629
IC	v_i	-0.0203	-0.0717	0.0682	0.0910	-0.0641	-0.0032
	h_i	0.0303	-0.0090	-0.0421	-0.0207	0.0066	0.0349
	g_i	0.0202	-0.0448	-0.0081	0.0248	-0.0255	0.0333
PG	v_i	-49.6135	-11.8114	24.9641	16.6647	36.6277	-16.8314
	h_i	0.2107	8.8930	-11.0900	-3.7163	-6.5790	12.2817
	g_i	-24.5960	2.9873	1.3920	4.6160	11.7348	3.8660
ANHEMBI							
NV	v_i	-160.6817	-22.6342	-29.9675	-26.1104	340.9326	-101.5389
	h_i	18.0694	23.2935	24.2643	17.6420	-125.7419	42.4729
	g_i	-62.2715	11.9764	9.2806	4.5868	44.7244	-8.2966
NGV	v_i	-0.2034	0.1707	0.1549	0.0298	-0.0244	-0.1276
	h_i	0.1562	-0.0792	-0.0139	-0.0146	-0.0832	0.0347
	g_i	0.0545	0.0061	0.0636	0.0003	-0.0954	-0.0291
PCS	v_i	-0.6070	2.7253	0.9197	-1.6059	-2.5430	1.1111
	h_i	-1.0239	0.0017	0.0683	-0.2463	0.3075	0.8927
	g_i	-1.3274	1.3644	0.5282	-1.0492	-0.9640	1.4482
PPA	v_i	-128.1751	34.3487	25.0820	-65.3180	192.2376	-58.1751
	h_i	-9.3111	24.6687	9.6021	11.7979	-90.6007	53.8431
	g_i	-73.3986	41.8431	22.1431	-20.8611	5.5181	24.7556
IC	v_i	-0.0422	0.0361	0.0042	0.0601	-0.0330	-0.0253
	h_i	0.0316	-0.0254	0.0005	-0.0196	0.0057	0.0071
	g_i	0.0106	-0.0073	0.0026	0.0104	-0.0108	-0.0055
PG	v_i	-57.8919	27.2589	0.2839	-14.7973	73.5012	-28.3548
	h_i	10.5001	11.9739	-1.0685	-0.7122	-34.7042	14.0109
	g_i	-18.4458	25.6033	-0.9266	-8.1109	2.0464	-0.1665

The significance of mean heterosis, followed for the non-significance of the variety heterosis, as occurred for the traits PG in ESALQ, and for NV, NGV, PPA and IC in Anhembi indicated that there was not sufficient variability among the heterotic answers of the crosses in study. This occurred when the varieties did not differed of the mean gene frequency and they presented the same dispersion of gene frequencies (Vencovsky and Barriga, 1992).

For specific heterosis (Table 6), the highest values of NV and PG were of cross MTBR-95-123800 x USP5-19 (5 x 6) in ESALQ and Anhembi. Still for PG, the hybrid Hartwig x Conquista (1 x 2, Anhembi), Hartwig x USP1-11 (1 x 3, ESALQ and Anhembi) and Conquista x USP2-16 (2 x 4, ESALQ) presented superior values of s_{ij}. For the trait PCS, the outstanding crosses were Hartwig x Conquista (1 x 2), Hartwig x MTBR-95-123800 (1 x 5) and USP1-11 x USP5-19 (3 x 6). In a general way, there was inconsistency in the s_{ij} estimates between localities, again reflecting the effect of genotype x locality interaction on the performance of parents and hybrids. Significance of the specific heterosis depends on the value of the mean gene frequencies of the varieties involved in the cross and on the complementation of gene frequencies among varieties, but in case of non significance the reciprocal can not be considered true (Gardner and Eberhart, 1966; Vencovsky, 1970).

The genic complementation between parents is due to the genetic divergence that can be measured by several methods, including the coefficient of parentage estimated from the parental pedigrees. The genetic divergence involves minor genes controlling quantitative traits like seed yield as the major genes responding for important adaptative traits.

Table 6 - Estimates of specific heterosis (s_{ij}) for the traits number of pods per plant (NV), number of seeds per pod (NGV), one-hundred seed weight (PCS), weight of aerial part of the plant (PPA), harvest index (IC) and seed yield (PG). ESALQ and Anhembi, 1998/99.

Estimates	NV	NGV	PCS	PPA	IC	PG
ESALQ						
s_{12}	-50.554	0.030	0.483	-39.341	0.03691	-10.815
s_{13}	45.483	0.064	-1.403	9.851	0.01519	29.857
s_{14}	86.909	-0.119	0.028	46.542	-0.02927	13.788
s_{15}	-105.363	-0.017	1.266	-49.685	0.00859	-32.095
s_{16}	23.525	0.042	-0.375	32.633	-0.03142	-0.735
s_{23}	-40.465	-0.110	0.219	-22.275	-0.03882	-24.658
s_{24}	94.482	0.060	-0.536	62.183	0.00554	29.593
s_{25}	-0.950	-0.216	-0.176	-11.758	-0.05002	-4.326
s_{26}	-2.514	0.237	0.010	11.190	0.04639	10.205
s_{34}	-2.111	0.050	0.928	1.844	0.03071	5.629
s_{35}	70.935	0.168	-0.708	66.340	-0.01094	9.268
s_{36}	-73.843	-0.171	0.964	-55.760	0.00386	-20.095
s_{45}	-98.368	0.092	-0.102	-63.702	0.03211	-16.241
s_{46}	-80.913	-0.082	-0.319	-46.868	-0.03909	-32.769
s_{56}	133.744	-0.026	-0.281	58.805	0.02026	43.393
ANHEMBI						
s_{12}	106.403	-0.038	0.603	74.137	0.00356	64.690
s_{13}	109.749	0.238	-0.906	84.037	0.03736	34.350
s_{14}	-18.808	-0.003	0.388	-4.959	-0.00897	-12.916
s_{15}	-109.820	-0.071	0.906	-58.838	-0.01174	-39.100
s_{16}	-87.524	-0.126	-0.990	-94.376	-0.02020	-47.024
s_{23}	-48.416	-0.117	-0.833	-59.205	-0.02874	-32.792
s_{24}	13.345	0.183	-0.060	17.999	0.02442	-11.882
s_{25}	-82.993	-0.008	-0.078	-44.780	-0.01897	-24.777
s_{26}	11.661	-0.019	0.368	11.849	0.01973	4.761
s_{34}	-59.026	-0.236	-0.326	-71.501	-0.01597	-18.028
s_{35}	117.170	-0.079	-0.222	72.787	-0.00864	20.538
s_{36}	-119.476	0.195	2.287	-26.118	0.01598	-4.068
s_{45}	-27.603	0.132	0.529	-9.676	0.02769	19.917
s_{46}	92.093	-0.076	-0.531	68.137	-0.02717	22.908
s_{56}	103.247	0.026	-1.135	40.507	0.01166	23.423

The pedigree analysis revealed, for example, the conspicuous presence of the ancestor Forrest among the parents; the ancestors Forrest and PI 437.654, were sources of genes for resistance to soybean cyst nematode; the parents Conquista and MTBR-95-123800 had genes for photoperiod tolerance that were originated from the ancestors PI 240.664 and IAC-71-1113; the parent USP 1-11 presented genes for indeterminate growth habit inherited from ancestor IAC-Foscarin-31. The different combinations of these major genes among the crosses probably were more determining of the hybrid performance than the arrangements of minor genes controlling seed yield and other quantitative traits.

In autogamous species, as soybeans, the knowledge of the heterosis, which is of great importance to obtain hybrids, can also be useful in obtaining the pure lines, if there is significant contribution of the additive x additive epistatic interaction (Pimentel, 1991). Besides, the knowledge of its magnitude can help the breeder in the choice of the selection method and in the identification of the predominant gene effect in the evaluated crosses. The expressive levels of heterosis found for seed yield may justify the choice of recurrent selection method, and the future use of commercial hybrids in soybeans.

Correlations among traits and path coefficients

According to Table 7, the most expressive genotypic correlations were found among the following pairs of traits: NV and PPA, NV and PG, PPA and PG, NGV and IC. High positive correlations of NV with PG have been observed by other authors (Santos et al.. 1995). At Anhembi, the correlation between NGV and PG presented intermediate value (0.56), although at ESALQ it was lower (0.20). Negative estimates of correlation among these traits have been reported; the variation of estimates could probably be due to the different groups of genotypes used.

In traits of difficult evaluation which presented high correlation with a trait of easy evaluation and high heritability, selection could be practiced through the correlated trait, being especially useful in early generations (Moro et al., 1992).

Table 7 - Phenotypic (r_F), genotypic (r_G) and environmental correlations (r_E) among the traits number of pods per plant (NV), number of seeds per pod (NGV), one-hundred seed weight (PCS), weight of aerial part of the plant (PPA), harvest index (IC) and seed yield (PG). ESALQ and Anhembi, 1998/99. ESALQ (above diagonal) e Anhembi (below diagonal), 1998/99.

		NV	NGV	PCS	PPA	IC	PG
NV	r_F		-0.03	-0.26	0.93	-0.03	0.81
	r_G		0.02	-0.29	0.95	-0.04	0.88
	r_E		-0.24	0.07	0.80	0.11	0.32
NGV	r_F	0.29		-0.26	-0.09	0.62	0.22
	r_G	0.49		-0.31	-0.13	0.66	0.20
	r_E	-0.20		-0.23	0.05	0.67	0.32
PCS	r_F	-0.25	0.14		0.02	-0.38	-0.07
	r_G	-0.29	0.24		0.01	-0.43	-0.08
	r_E	0.11	-0.13		0.12	0.04	0.02
PPA	r_F	0.88	0.43	0.09		-0.18	0.79
	r_G	0.89	0.56	0.06		-0.21	0.84
	r_E	0.83	0.17	0.33		0.05	0.40
IC	r_F	0.02	0.75	-0.14	0.08		0.33
	r_G	-0.03	0.99	-0.13	0.08		0.33
	r_E	0.24	0.37	-0.17	0.09		0.36
PG	r_F	0.76	0.45	0.12	0.79	0.18	
	r_G	0.79	0.56	0.12	0.81	0.17	
	r_E	0.59	0.28	0.10	0.65	0.24	

However, the simple correlations could be associated with other traits that influenced the resulted values, and could lead to an erroneous interpretation. To avoid this problem, the genotypic correlations were decomposed in direct and indirect effects of the evaluated traits in relation to the seed yield (Table 8). Among the traits that presented high correlation with seed yield, the most outstanding estimate of indirect effect involved the traits PPA and PG in ESALQ. These traits presented correlation of 0.84 (Table 7), and in its majority (0.568, Table 8) which was due to the indirect effects of PPA through NV. Similarity at Anhembi, the correlation of 0.81 (Table 7) between PPA and PG was largely due to the indirect effects of NV. These results demonstrated that among the evaluated seed yield components, the trait that had potential for indirect selection for seed yield was the number of pods per plant.

Table 8 - Direct (diagonal) and indirect (lines) effects of the traits number of pods per plant (NV), number of seeds per pod (NGV), one-hundred seed weight (PCS), weight of aerial part of the plant (PPA), harvest index (IC) on seed yield (PG). ESALQ and Anhembi, 1998/99.

Traits	NV	NGV	PCS	PPA	IC
ESALQ					
NV	**0.600**	-0.0005	-0.080	0.324	-0.023
NGV	0.012	**-0.022**	-0.084	-0.045	0.338
PCS	-0.176	0.007	**0.273**	0.003	-0.220
PPA	0.568	0.003	0.002	**0.342**	-0.107
IC	-0.027	-0.015	-0.118	-0.072	**0.508**
ANHEMBI					
NV	**0.490**	0.186	-0.041	0.145	0.005
NGV	0.241	**0.379**	0.034	0.092	-0.184
PCS	-0.144	0.093	**0.139**	0.009	0.025
PPA	0.436	0.214	0.008	**0.163**	-0.014
IC	-0.014	0.377	-0.019	0.013	**-0.185**

Actually, NV presented high correlation values with PG and was less influenced by indirect effects. Therefore, NV could be used as a criterion of indirect selection to obtain correlated response in seed yield. However, the number of pods per plant is a difficult trait to quantify and some alternative method has to be adopted in the breeding programs in order to allow the visual selection at the field for this trait. A possibility could be the attribution of a scale of visual scores for NV to aid in the selection of more productive genotypes.

CONCLUSIONS

Positive values of heterosis were found for the all the evaluated traits and the most expressive values were obtained for seed yield. The effects of varieties and of heterosis were significant for most of the traits in both the localities, showing that additive and dominance gene effects participated in the genetic control of these traits. The specific heterosis was more important than the variety heterosis, mainly in Anhembi locality. The genotype MTBR-95-123800 presented great potential of use per se and in crosses for high seed yield. Several crosses showed high potential for the future use as F1 hybrid, but the best cross differed between localities. The trait number of pods per plant demonstrated to have potential for the indirect selection of more productive genotypes.

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RESUMO

O efeito da heterose tem sido pouco estudado em soja, especialmente em germoplasma adaptado às condições do Brasil. O objetivo deste estudo foi quantificar a heterose de caracteres agronômicos e avaliar as correlações diretas e indiretas em relação à produtividade. Um dialelo envolvendo seis genitores foi conduzido em dois locais. Foram avaliados produtividade de grãos (PG), peso de cem sementes (PCS), número de vagens por planta (NV), peso da parte aérea (PPA), índice de colheita (IC) e número de grãos por vagem (NGV). Valores positivos de heterose foram detectados para todos os caracteres, especialmente PG. As estimativas dos componentes da heterose foram significativas para a maioria dos caracteres avaliados, evidenciando efeitos gênicos de aditividade e de dominância. A heterose específica foi mais importante que a heterose de variedade, principalmente no local Anhembi. MTBR-95-123800 (5) apresentou grande potencial de uso *per se* e em cruzamentos, sendo superado por alguns cruzamentos, nos dois locais. O caráter número de vagens por planta demonstrou ter potencial para a seleção indireta de genótipos mais produtivos.

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