GENETICAL AND ENVIRONMENTAL ANALYSES OF YIELD IN SIX BIPARENTAL SOYBEAN CROSSES[1]

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ABSTRACT - The yearly genetic progress obtained by breeding for increased soybean yield has been considered acceptable worldwide. It is common sense, however, that this progress can be improved further if refined breeding techniques, developed from the knowledge of the genetic mechanisms controlling soybean yield, are used. In this paper, data from four cultivars and/or lines and their derived sets of F2, F3, F7, F8, F9 and F10 generations assayed in 17 environments were analyzed to allow an insight of the genetic control of soybean yield under different environmental conditions. The general picture was of a complex polygene system controlling yield in soybeans. Additive genetic effects predominated although dominance was often found to be significant. Complications such as epistasis, linkage and macro and micro genotype x environment (G x E) interactions were also commonly detected. The overall heritability was 0.29. The relative magnitude of the additive effects and the complicating factors allowed the inference that the latter are not a serious problem to the breeder. The low heritability values and the considerable magnitude of G x E interactions for yield, however, indicated that careful evaluation through experiments designed to allow for the presence of these effects is necessary for successful selection.

Index terms: *Glycine max,* genetic control, selection, polygenes, genotype environment interaction, breeding methods.

ANÁLISE GENÉTICA E AMBIENTAL DA PRODUTIVIDADE DA SOJA EM SEIS CRUZAMENTOS BIPARENTAIS

RESUMO - O progresso genético obtido para produtividade em soja é mundialmente considerado razoável. Entretanto, acredita-se que esse progresso possa ser significativamente aumentado se forem usadas técnicas refinadas de melhoramento, desenvolvidas a partir do melhor conhecimento do controle genético e do ambiente sobre a produtividade. Foram analisados, neste trabalho, os dados referentes a quatro linhagens ou cultivares e as populações descendentes F2, F3, F7, F8, F9 e F10, obtidos em ensaios realizados em 17 ambientes, para permitir uma avaliação dos efeitos genéticos controladores da produtividade na soja. Os efeitos genéticos aditivos predominaram, e foram detectados níveis significativos de dominância, em várias oportunidades. Também foram freqüentemente detectados efeitos genéticos, como: epistasia, ligação gênica e interações entre genótipo e ambiente. A herdabilidade no sentido restrito foi de 0,29. As análises mostraram que, em geral, o controle genético da produtividade da soja é realizado por poligenes com efeitos aditivos. A magnitude dos fatores complicadores comparativamente à dos efeitos aditivos permite prever que eles não representarão problema num programa de melhoramento. Entretanto, a baixa herdabilidade do carácter e os consideráveis níveis de interação entre genótipo e ambiente exigem que a avaliação da produtividade seja criteriosamente realizada para haver progresso genético por seleção.

Termos para indexação: *Glicyne max,* controle genético, seleção, poligenes, interação genótipo-ambiente, métodos de melhoramento.

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INTRODUCTION

High seed yield is the primary goal of most soybean breeding programs worldwide. In Brazil, the annual gains for the early and semi-early maturity groups grown in Paraná State were 1.8% and 1.3% for the period 1981/82 to 1985/86 and 0.9% and 0.4% for the period 1985/86 to 1989/90, respectively (Toledo et al, 1990; Alliprandini et al, 1993). These gains were significant when compounded over the years, but were highly variable within each five year period considered. Although positive in the majority of the years, the genetic progress was nil or even negative in a few others. It was concluded that the understanding of the genetic control of yield and its interactions with the environment would help to enhance the chances of taking the correct selection decisions and prevent the gain fluctuations.

G x E interactions are highly relevant in soybean yield expression as already reported by Alliprandini et al. (1994, 1998) and Triller & Toledo (1996). Some reports on the genetical control of soybean yield are available in the literature (Brim & Cockerham 1961; Hanson et al., 1967; Brim, 1973). They emphasized the predominance of the additive effects, and detected the presence of dominance and additive x additive non-allelic interaction. Oliveira (1994) used several genetical designs to analyze the genetic control of yield of a soybean cross in three environments. Additive effects were ubiquitous but several complications such as epistasis, linkage and genotype x environment (G x E) interactions were also detected.

Most of the breeding strategies for developing productive and adapted soybean cultivars described in the literature (Cooper, 1990; Fehr, 1987; Hartwig, 1973; Schillinger, 1985) were developed to take advantage of the additive gene action. A few recommend the use of quantitative genetics theory to fully explore the crosses potential to obtain the target results (St. Martin, 1985; Toledo, 1989).

The objective of this work was to study the genetic control and the environment effect on soybean yield using models fitted to yield data of six crosses between highly productive and adapted lines or cultivars grown in 17 environments.

MATERIAL AND METHODS

Four parents, BR-13, FT-2, OCEPAR 8 and BR85-29009, selected for their day length response and high yield, were crossed in all possible ways, including reciprocals, to generate the F2, F3, F5, F7, F8, F9 and F10 generations. These materials were field grown in Londrina, PR, Brazil (23°, 23' SL) with sowings carried out on 26th September 1988, 14th October 1988, 18th November 1988, 17th October 1991, 28th November 1991, 13th December 1991, 15th October 1992, 9th November 1992, 2nd December 1992, 27th September 1993, 20th October 1993, 17th November 1993, 17th December 1993, 20th September 1994, 20th October 1994, 17th November 1994 and 14th December 1994 totaling 17 environments. These different sowing dates in each year were chosen to represent specific day length (photoperiod) situations and to evaluate the response of the soybean genotypes to these photoperiods. The generations included the parents and their derived F2 and F3 (families) populations in all years, plus the sets of randomly derived inbred lines (RILs) F7 in 1991/92, F8 in 1992/93, F9 in 1993/94 and F10 in 1994/95 growing seasons.

The experiment was formed by single-plant hill plots arranged in a completely randomized design in each environment. The plots were spaced 20 cm and 1.5 m within and between rows, respectively. Two border rows of bulked remnant seeds were sown between rows and around the experiment, resulting in a final between rows distance of 50 cm and an average plant density of 250,000 plants/ha. Supplementary irrigation was used to warrant experimental conditions suitable for normal plant development. A total of 73,300 hill plots were evaluated for grain yield.

Parental genotypes were common in all the environments and their data were used to perform the joint variance analysis according to the statistical model:

$y_{ijkl} = \mu + Y_i + S_j + YS_{ij} + G_k + GY_{ik} + GS_{jk} + GYS_{ijk} + E_{l(ijk)}$

where:

y_{ijkl} is the grain yield of the l^{th} plant of the k^{th} genotype evaluated in the j^{th} sowing of the i^{th} year;

μ is the general mean;

Y_i is the year effect ($i = 1$ to 5);

S_j is the sowing date ($j = 1$ to 3 in the first three years and $j = 1$ to 4 in the last two years); YS_{ij} is the year by sowing date interaction;

G_k is the genotype effect ($k = 1$ to 4);

GY_{ik} is the genotype by year interaction;

GS_{jk} is the genotype by sowing date interaction;

GYS_{ijk} is the triple interaction among the main factors; and $E_{l(ijk)}$ is the error related to the l^{th} plant or plot of the k^{th} genotype evaluated in the j^{th} sowing date of the i^{th} year.

This analysis was planned to provide an insight of the relative importance of sowing dates and years among the environmental sources affecting soybean grain yield.

Individual plant scores were taken and means and variances (pooled over reciprocals) were calculated for each parent and derived generations in each environmental combination (years and sowing dates). The models fitted to these data in each environment provided estimates of mean and variance genetic parameters and environmental components (Cavalii, 1952; Hayman, 1960; Mather & Jinks, 1982). F2 based, narrow sense heritabilities, were also calculated.

RESULTS AND DISCUSSION

The joint analysis of variance (Table 1) showed that except for the non-significance and 5% significance of sowing date and years effects, respectively, all other sources of variation were highly significant ($P<0.01$). The relative magnitudes of the mean squares suggest that differences among parental genotypes were the main cause of variation. The inbred line BR85-29009 was the highest yielding parent (34.66 g/plant, data not presented in tables) that significantly ($P<0.01$) differed from the cultivars OCEPAR 8 and FT-2 (28.17 and 26.58 g/plant, respectively). 'OCEPAR 8' and 'FT-2' differed significantly ($P<0.01$) from cultivar BR-13 (17.49 g/plant). As in previous reports (Alliprandini et al., 1994), the main environmental effects such as date of sowing and year were less important than the interaction effects. Therefore, the combinations of year and date of sowing characterized different environments, which became the factor affecting the germplasm performance.

TABLE 1. Joint analysis of variance for soybean grain yield using four parent mean data collected in 17 environments, including five years and four sowing dates.

Source of variation	df	Mean square	F value
Year (Y)	4	596.27	4.12*
Sowing date (S)	3	232.43	1.60^{ns}
Y x S	12	116.23	9.53**
Genotypes (G)	3	818.99	20.05**
G x Y	12	40.84	3.35**
G x S	9	75.03	6.15**
G x Y x S	27	12.20	4.62**
Residual	2811	2.64	-

^{ns}, * and ** Non-significant and significant at 5% and 1% level of probability, respectively; C.V.=12.73%; mean = 27.44 g/plant.

Genotypes interacted more with sowing dates than with years as expected, because of the high photoperiod sensitivity of the soybean genotypes. It was also evident that yield levels in the four sowing dates followed the expected pattern – October > November > December > September (Carraro et al., 1984) – in spite of the non-significance of the main effect. Decrease in early sowings probably occurred because the plants were early induced to flowering and stopped growing before reaching adequate plant high for full yield expression. The parents were also sensitive to late sowing (December), when the plant development and grain yield are more affected by diverse environmental stresses. These stresses include a decrease in the number of daylight hours, which affect the vegetative and reproductive phases of the soybean plant, and may include excessive rainfall. The September, October, November and December sowings yields were 23.33, 30.79, 26.30 and 24.57 g/plant, respectively.

The estimated genetic components of means and variances were jointly analyzed to provide complementary information (Mather & Jinks, 1982). The genetic models fitted to the grain yield means and variances of the generations of each of the six crosses, sowing dates and years are shown in Table 2. Most of the mean models included additive [d], dominance [h] and epistatic effects {[i] and [l]} while, in the variance models, additive genetic and environmental effects predominated, although dominance, linkage between gene displaying additive effects and genotype x micro-environmental interaction were also detected. Table 3 presents the observed frequency of the different significant genetic and environment effects within years, sowing dates and crosses, allowing the visualization of the relative importance of them. The overall picture is one of complex control of yield in all crosses.

The predominance of additive genetic effects was evident from the mean and variance models (presence of [d], D, D plus linkage, that is D1 and/or D2 parameters) shown in Table 2. The [d] component is

TABLE 2. **Genetic parameters adjusted to soybean grain yield (g/plant) means and variances of the six crosses in three sowing dates in the 1988/89, 1991/92 and 1992/93 growing seasons and four sowing dates in the 1993/94 and 1994/95 growing seasons.**

Genetic parameters, goodness of fit χ^2 test and degrees of freedom	BR85 -29009 x FT-2	BR85 -29009 x BR-13	BR85 -29009 x OC-8	FT-2 x BR-13	FT-2 x OC-8	BR-13 x OC-8
			(i) 26th September 1988			
m	31.77±1.27	28.71±1.21	37.35±1.46	26.77±0.64	38.60±0.84	22.50±2.10
[d]	5.63±1.48	9.85±1.34	-	3.72±1.03	5.65±1.30	9.42±1.18
[h]	11.34±3.96	18.28±3.82	13.53±5.02	-	-	17.44±5.91
[i]	-	-	-	-4.23±1.22	-6.57±1.55	5.75±2.41
χ^2	1.58^{ns}	0.01^{ns}	1.14^{ns}	3.38^{ns}	0.09^{ns}	--[1]
df	1	1	2	1	1	
D	59.34	70.30±30.51	416.65±91.38	-	160.00±37.53	152.87±35.62
D1[2]	-	-	-	39.99±19.97	-	-
D2	-	-	-	330.44±76.46	-	-
E	-	-	169.83±28.99	56.44±9.24	77.36±12.64	73.44±12.17
E1[3]	167.77±32.29	188.75±32.18	-	-	-	-
E2	76.80±19.78	40.74±11.35	-	-	-	-
χ^2	5.65^{ns}	6.05^{ns}	5.19^{ns}	2.98^{ns}	4.72^{ns}	4.68^{ns}
df	2	2	3	2	3	3
			(ii) 14th October 1988			
m	50.33±1.79	46.31±1.25	60.68±2.68	39.84±1.04	54.16±2.48	60.68±2.68
[d]	-	17.79±2.17	-	10.61±2.01	-	-
[h]	41.69±11.21	-	-72.93±25.70	-	58.64±24.66	-93.95±25.63
[l]	-	-	187.32±49.45	-	-114.08±46.85	127.08±48.45
χ^2	3.78^{ns}	3.36^{ns}	1.50^{ns}	0.18^{ns}	3.19^{ns}	1.50^{ns}
df	2	2	1	2	1	1
D	297.92±105.44	391.89±112.56	519.71±153.36	209.84±76.71	322.59±126.59	777.29±141.16
E	318.63±46.39	-	381.30±59.06	-	430.84±58.47	-
E1	-	390.33±88.02	-	106.89±32.76	-	277.98±72.21
E2	-	105.32±32.72	-	352.29±68.55	-	109.24±34.02
χ^2	7.24^{ns}	1.89^{ns}	1.41^{ns}	7.17[4]	3.94^{ns}	0.82^{ns}
df	3	2	3	2	3	2
			(iii) 18th November 1988			
m	36.45±0.93	32.35±1.14	35.33±1.17	29.13±1.18	40.87±0.99	33.21±1.22
[d]	4.79±1.25	2.38±1.27	-	-	4.19±1.31	-
[h]	-	16.20±3.70	10.41±4.01	15.32±3.65	-	12.72±3.85
[i]	-5.73±1.56	-	-	-	-10.72±1.64	-
χ^2	0.04^{ns}	2.49^{ns}	0.67^{ns}	5.65^{ns}	1.74^{ns}	3.05^{ns}
df	1	1	2	2	1	2
D	-	106.76±36.22	244.17±54.49	103.35±37.93	-	151.37±48.32
D1	-	-	-	-	124.38±45.24	-
D2	-	-	-	-	522.29±145.14	-
E	176.85±15.08	108.08±15.36	105.35±17.43	115.88±16.22	104.90±18.59	137.24±19.59
χ^2	9.88[3]	4.56^{ns}	5.06^{ns}	4.85^{ns}	2.44^{ns}	5.19^{ns}
df	4	3	3	3	2	3

cont.

TABLE 2. Continuation.

Genetic parameters, goodness of fit χ^2 test and degrees of freedom	BR85 -29009 x FT-2	BR85 -29009 x BR-13	BR85 -29009 x OC-8	FT-2 x BR-13	FT-2 x OC-8	BR-13 x OC-8
(iv) 17th October 1991						
m	35.23±0.57	32.85±1.13	45.44±2.33	24.51±0.99	42.24±1.74	32.44±1.54
[d]	6.56±1.53	12.90±1.38	2.88±1.75	6.34±0.84	3.68±1.36	10.11±1.20
[h]	-	-23.02±2.97	-153.31±17.41	-32.19±8.73	-67.85±15.57	-72.02±13.22
[i]	-4.64±1.63	-8.60±1.78	-11.17±2.92	-6.83±1.30	-14.53±2.21	-11.16±1.96
[l]	-	-	285.81±30.20	55.45±15.85	113.78±28.31	119.17±23.91
χ^2	3.18^{ns}	1.40^{ns}	--[1]	--[1]	--[1]	--[1]
df	2	1				
D	87.64±19.44	-	-	115.33±15.22	342.14±46.75	-
D2	-	-	558.53±298.44	-	-	519.61±79.28
H1[3]	-	-	-	-	-	1012.86±149.99
H6	-	-	-	-	-	11931.36±3658.26
CP[3]	-	-	361.18±67.28	-	-	-
E	-	-	313.59±43.64	-	-	-
E1	304.07±31.25	-	-	123.72±13.12	404.89±44.37	25.06±5.33
E2	101.38±20.22	-	-	26.57±5.56	119.26±24.07	208.68±36.78
χ^2	7.41^{ns}	--[6]	2.82^{ns4}	7.17^{ns}	8.88^{ns}	3.37^{ns}
df	4		2	4	4	2
(v) 28th November 1991						
m	31.93±0.77	30.16±0.76	27.85±0.76	25.54±0.56	33.93±1.12	25.59±0.49
[d]	2.85±1.23	4.42±1.12	5.71±1.02	-	2.28±1.00	0.71±0.85
[h]	7.04±2.62	-6.17±2.37	-47.55±7.50	16.26±2.16	-35.59±10.54	-
[i]	-3.05±1.46	-2.86±1.36	-	-	-10.19±1.50	-3.42±0.99
[l]	-	-	99.60±14.52	-	60.09±19.54	-
χ^2	5.03^{4}	0.004^{ns}	2.75^{ns}	7.20^{ns}	--[1]	4.59^{ns}
df	1	1	1	3		2
D	73.08±17.01	75.39±13.72	-	38.39±11.22	-	-
D1	-	-	99.57±21.10	-	190.36±27.55	182.02±22.68
D6	-	-	-	-	4508.99±1458.60	3017.42±1011.33
H	-	-	-	319.39±75.02	-	-
E	149.29±9.82	-	-	103.33±8.49	-	95.55±7.19
E1	-	171.63±20.40	157.25±18.30	-	208.63±23.12	-
E2	-	84.29±15.64	57.77±11.46	-	67.15±13.46	-
χ^2	8.27^{ns}	2.46^{ns}	3.81^{ns5}	5.21^{ns}	4.65^{ns}	6.17^{ns}
df	5	4	2	4	3	4
(vi) 13th December 1991						
m	36.45±0.71	35.65±0.48	33.41±0.99	33.33±0.63	36.61±1.00	29.58±0.74
[d]	-	1.87±1.12	3.35±1.13	2.95±1.13	4.26±1.15	-
[h]	-10.41±7.33	-	-54.59±8.44	7.44±2.28	-29.44±9.74	-17.82±7.89
[i]	-	-4.26±1.22	-3.50±1.50	-	-5.78±1.52	-
[l]	27.94±14.02	-	116.84±15.52	-	53.97±17.99	42.31±15.21
χ^2	6.09^{ns}	6.10^{ns}	--[1]	4.25^{ns}	--[1]	6.11^{ns}
df	2	2		2		2
D	26.90±9.61	87.08±14.75	-	40.84±12.96	105.91±16.71	-
D1	-	-	-	-	-	66.98±17.54
D2	-	-	-	-	-	93.43±35.22
D6	-	-	-	-	-	3197.23±1076.63
H	-	-	-	213.87±82.59	-	-
CP	-	-	71.77±11.50			
E	131.66±8.07	120.35±8.15	123.67±7.05	131.68±10.67	128.95±8.75	100.33±8.57
χ^2	6.95^{ns}	1.56^{ns}	0.83^{ns5}	3.81^{ns}	6.67^{ns}	7.72^{ns}
df	5	5	3	4	5	3

cont.

TABLE 2. Continuation.

Genetic parameters, goodness of fit χ^2 test and degrees of freedom	BR85 -29009 x FT-2	BR85 -29009 x BR-13	BR85 -29009 x OC-8	FT-2 x BR-13	FT-2 x OC-8	BR-13 x OC-8
			(vii) 15th October 1992			
m	26.86±0.44	24.02±0.62	28.19±0.83	20.49±0.35	25.81±0.54	21.27±0.59
[d]	-	7.41±0.80	2.74±1.04	7.45±0.56	2.42±0.90	4.67±0.79
[h]	6.41±1.89	-24.05±6.82	-38.02±9.50	-21.45±4.53	-18.64±7.75	-30.99±6.24
[i]	-	-3.68±1.01	-3.18±1.33	-	-	-3.66±0.99
[l]	-	46.68±13.66	98.65±20.55	45.82±9.63	50.60±16.32	62.54±12.76
χ^2	6.00^{ns}	--[1]	--[1]	0.19^{ns}	1.41^{ns}	--[1]
df	3			1	1	
D	30.89±6.51	-	-	-	64.18±10.67	-
D1	-	74.26±12.21	160.00±31.47	24.59±5.44	-	94.83±12.91
D7	-	3244.98±1066.69	6103.55±1893.16	2112.36±628.12	-	1964.23±818.18
H1	-	-	374.30±161.12	-	-	-
E	73.35±4.65	-	91.91±8.72	-	82.90±5.52	-
E1	-	95.51±10.48	-	51.98±6.32	-	73.75±8.60
E2	-	13.27±3.10	-	13.26±3.05	-	12.75±2.97
χ^2	3.33^{ns}	5.50^{ns}	5.53^{ns}	3.79^{ns}	4.85^{ns}	7.52^{ns}
df	5	3	3	3	5	3
			(viii) 9th November 1992			
m	26.66±0.50	23.26±0.42	25.15±0.46	20.72±0.37	24.19±0.52	21.08±0.49
[d]	2.18±0.85	5.70±0.83	4.07±0.78	3.48±0.73	1.65±0.70	1.81±0.69
[h]	-7.72±6.73	6.59±2.01	5.49±2.19	-14.38±5.22	7.33±2.12	5.45±1.97
[l]	37.96±14.35	-	-	38.70±11.15	-2.41±0.87	-2.76±0.84
χ^2	3.98^{ns}	4.95^{ns}	4.47^{ns}	1.40^{ns}	2.18^{ns}	0.41^{ns}
df	1	2	2	1	1	1
D	-	31.77±6.76	-	9.71±3.23	-	-
D1	-	-	62.34±12.55	-	-	-
D2	57.85±14.35	-	-	-	56.89±15.43	84.90±15.59
D7	-	-	-	-	5348.79±1129.42	-
H1	107.26±51.84	-	-	-	286.92±56.19	138.20±44.95
H2	-	-	-	-	272.88±93.18	-
E	76.70±5.30	-	-	49.73±3.12	35.13±5.82	56.10±3.77
E1	-	143.85±51.45	137.48±12.99	-	-	-
E2	-	56.60±4.26	35.46±8.11	-	-	-
χ^2	8.52^{ns}	6.03^{ns}	9.67^{ns}	7.52^{ns}	0.68^{ns}	7.47^{ns}
df	4	4	4	5	2	4
			(ix) 2nd December 1992			
m	21.09±0.47	18.25±0.26	17.93±0.31	15.04±0.20	16.60±0.35	14.05±0.28
[d]	0.57±0.65	3.89±0.56	1.98±0.61	3.47±0.56	1.36±0.63	2.13±0.53
[h]	-14.48±5.54	-	5.08±1.46	-	5.36±1.46	-8.03±3.87
[i]	-2.63±0.80	-3.11±0.62	-	-	-	-
[l]	41.97±11.61	-	-	-	-	23.58±8.36
χ^2	--[1]	1.04^{ns}	3.46^{ns}	7.75^{ns}	0.02^{ns}	3.28^{ns}
df		2	2	3	2	1
D	-	19.07±3.38	20.90±3.99	-	-	10.79±2.31
D1	48.98±7.70	-	-	-	36.20±6.12	-
H	-	-	49.42±25.14	-	-	-
E	37.61±2.36	29.23±1.93	26.41±2.02	-	34.04±2.12	24.59±1.60
E1	-	-	-	30.87±3.85	-	-
E2	-	-	-	16.19±3.37	-	-
χ^2	6.73^{ns}	8.43^{ns}	4.55^{ns}	8.52^{ns}	3.68^{ns}	8.92^{ns}
df	5	5	4	5	5	5

cont.

TABLE 2. Continuation.

Genetic parameters, goodness of fit χ^2 test and degrees of freedom	BR85 -29009 x FT-2	BR85 -29009 x BR-13	BR85 -29009 x OC-8	FT-2 x BR-13	FT-2 x OC-8	BR-13 x OC-8
			(x) 27th September 1993			
m	29.74±0.44	28.08±0.90	33.57±0.73	19.17±0.38	28.62±0.50	24.23±0.84
[d]	4.33±0.99	11.17±0.90	6.89±1.00	6.61±0.71	2.38±0.86	4.28±0.73
[h]	-	-37.41±8.76	-	-3.10±1.48	-	-23.92±8.92
[i]	-	-4.26±1.27	-5.47±1.24	-	-5.03±1.00	-7.30±1.12
[l]	-	52.92±17.10	-	-	-	36.90±17.22
χ^2	4.09^{ns}	--[1]	5.38^{ns}	1.34^{ns}	3.17^{ns}	--[1]
df	3		2	2	2	
D	55.33±10.81	133.78±18.22	174.82±32.51	35.65±5.63	82.94±13.84	-
D1	-	-	-	-	-	80.75±19.14
D2	-	-	-	-	-	217.72±38.22
H	-	-	765.15±179.85	-	-	-
E	116.00±7.14	-	-	-	-	-
E1	-	108.71±16.48	126.71±25.38	51.05±7.71	87.42±15.34	71.98±12.54
E2	-	29.83±6.31	71.19±14.45	25.54±5.15	84.33±14.81	31.49±6.59
E3	-	125.08±10.46	224.36±18.67	41.42±3.46	130.97±11.05	115.45±9.62
χ^2	4.84^{ns}	7.99^{ns}	2.10^{ns}	8.40[4]	3.75^{ns}	0.03^{ns}
df	5	3	2	3	3	2
			(xi) 20th October 1993			
m	42.54±0.69	39.11±1.01	51.35±1.27	26.76±0.49	43.09±0.71	38.48±1.06
[d]	7.69±1.35	16.35±1.30	4.26±1.62	9.43±0.99	3.13±1.42	12.09±1.30
[h]	6.07±3.07	-12.21±3.70	-35.38±15.71	-	-	-48.35±12.85
[i]	-	-6.49±1.64	-6.63±2.06	-	-5.76±1.59	-10.11±1.68
[l]	-	-	90.69±32.67	-	-	71.98±26.35
χ^2	4.41^{ns}	0.74^{ns}	--[1]	6.11^{ns}	0.84^{ns}	--[1]
df	2	1		3	2	
D	71.11±15.71	216.41±31.09	355.18±47.92	133.46±19.14	144.15±27.07	76.86±18.52
H	-	-	-	-	408.55±169.62	501.02±185.17
E	192.54±11.74	-	262.60±17.30	-	183.50±13.31	-
E1	-	224.77±33.11	-	129.29±20.49	-	256.18±48.49
E2	-	68.54±13.81	-	68.78±13.34	-	71.09±14.57
E3	-	206.36±17.24	-	113.55±9.63	-	181.77±15.59
χ^2	6.54^{ns}	1.96^{ns}	3.26^{ns}	10.10[4]	5.27^{ns}	0.07^{ns}
df	5	3	5	3	4	2
			(xii) 17th November 1993			
m	40.03±0.59	34.00±0.55	39.83±0.74	26.30±0.54	32.81±0.59	30.60±0.83
[d]	9.79±1.14	14.61±1.24	7.98±1.21	4.84±1.15	-	6.72±1.21
[h]	-	-	8.93±3.88	-	-	-7.35±3.29
[i]	-3.53±1.28	-	-	-4.43±1.26	-4.47±1.25	-6.85±1.47
χ^2	2.98^{ns}	5.90^{ns}	2.32^{ns}	0.19^{ns}	3.56^{ns}	0.47^{ns}
df	2	3	2	2	3	1
D	95.90±17.02	126.44±19.92	171.86±30.45	79.18±14.20	71.12±15.05	133.19±21.56
H	-	-	641.04±191.65	-	-	-
E	159.41±9.92	151.94±9.68	177.89±12.76	133.63±8.36	176.45±10.77	170.05±10.84
χ^2	4.65^{ns}	1.41^{ns}	6.75^{ns}	3.89^{ns}	7.59^{ns}	3.41^{ns}
df	5	5	4	5	5	5

cont.

TABLE 2. Continuation.

Genetic parameters, goodness of fit χ^2 test and degrees of freedom	BR85 -29009 x FT-2	BR85 -29009 x BR-13	BR85 -29009 x OC-8	FT-2 x BR-13	FT-2 x OC-8	BR-13 x OC-8
			(xiii) 17th December 1993			
m	35.48±0.74	34.05±0.56	30.09±0.62	22.01±0.50	25.40±0.53	23.59±0.51
[d]	7.62±0.99	11.31±0.95	9.50±1.08	3.86±0.92	-	-
[h]	6.63±3.16	-	8.73±2.89	10.36±2.49	-	-
[i]	-3.86±1.23	-6.12±1.10	-	-	-2.99±1.18	-5.70±1.11
χ^2	0.08^{ns}	1.55^{ns}	1.83^{ns}	5.58^{ns}	4.97^{ns}	3.40^{ns}
df	1	2	2	2	3	3
D	48.96±12.98	97.95±16.05	75.40±15.03	39.09±9.24	40.74±11.30	39.16±10.29
H	251.84±109.80	-	-	234.50±77.53	-	-
E	145.34±10.61	125.97±8.16	152.31±9.84	91.32±6.69	135.93±9.06	121.22±8.08
χ^2	8.60^{ns}	8.50^{ns}	7.30^{ns}	4.39^{ns}	10.48^{ns}	8.10^{ns}
df	4	5	5	4	5	5
			(xiv) 20th September 1994			
m	21.55±0.38	21.56±0.65	27.62±0.58	13.96±0.35	20.21±0.38	18.43±0.41
[d]	6.66±0.84	8.33±0.76	-	1.67±0.52	7.50±0.81	9.29±0.61
[h]	-	-14.13±2.12	6.27±2.84	-3.97±1.33	-	-
[i]	-2.54±0.92	-4.22±1.00	-	-3.28±0.63	-	-
χ^2	2.82^{ns}	1.44^{ns}	3.97^{ns}	0.06^{ns}	6.42^{ns}	3.68^{ns}
df	2	1	3	1	3	3
D	42.46±7.32	-	-	23.53±3.58	51.00±8.93	95.21±12.84
E1	94.47±10.04	-	-	36.93±4.05	35.95±7.30	14.85±2.98
E2	35.78±7.11	-	-	14.95±2.85	121.57±11.78	124.77±9.86
χ^2	2.44^{ns}	--[6]	--[6]	5.01^{ns}	2.64^{ns}	1.97^{ns}
df	4			4	4	4
			(xv) 20th October 1994			
m	35.08±0.55	33.16±1.11	46.90±1.00	23.12±0.67	34.70±0.84	31.33±0.96
[d]	5.36±1.22	11.61±1.11	-	6.26±0.74	5.02±1.12	11.27±1.00
[h]	-	-65.12±10.36	-	-19.22±7.84	6.02±3.10	-10.41±3.41
[i]	-4.60±1.34	-8.94±1.57	-11.46±1.70	-4.26±1.00	-4.56±1.40	-7.45±1.39
[l]	-	103.68±20.55	-	33.20±16.22	-	-
χ^2	4.48^{ns}	--[1]	3.87^{ns}	--[1]	2.54^{ns}	2.23^{ns}
df	2		3		1	1
D	80.38±14.31	-	438.83±67.41	111.49±13.39	130.50±20.40	262.07±29.58
E	-	-	-	-	152.62±9.68	-
E1	181.88±13.03	-	206.86±28.75	77.52±5.74	-	29.46±5.96
E2	83.82±15.25	-	384.75±32.29	30.56±5.98	-	179.18±13.10
H	-	-	751.38±316.57	-	-	-
χ^2	5.25^{ns}	--[6]	5.16^{ns}	3.16^{ns}	7.11^{ns}	2.60^{ns}
df	4		3	4	5	4

cont.

TABLE 2. Continuation.

Genetic parameters, goodness of fit χ^2 test and degrees of freedom	BR85 -29009 x FT-2	BR85 -29009 x BR-13	BR85 -29009 x OC-8	FT-2 x BR-13	FT-2 x OC-8	BR-13 x OC-8
			(xvi) 17th November 1994			
m	34.81±0.70	31.24±0.50	34.15±0.54	28.47±0.54	34.55±0.55	29.50±0.53
[d]	-	2.53±0.91	-	2.26±0.97	-	3.04±0.93
[h]	8.63±2.82	-	-	15.62±2.74	-	14.40±2.38
[i]	-5.27±1.21	-3.79±1.04	-3.80±1.09	-	-4.61±1.14	-
[l]	-	-	-	-	-	-
χ^2	0.48^{ns}	0.96^{ns}	6.04^{ns}	6.58^{ns}	1.66^{ns}	4.91^{ns}
df	2	2	3	2	3	2
D	60.83±12.15	73.15±12.65	115.27±16.61	46.68±11.25	100.39±16.01	67.63±12.13
H		-	-	299.87±97.05	-	-
E	133.18±8.18	113.24±7.11	106.23±6.82	121.55±8.62	121.02±7.75	115.61±7.19
χ^2	9.90^{ns}	9.35^{ns}	10.29^{ns}	5.73^{ns}	5.66^{ns}	10.87^{ns}
df	5	5	5	4	5	5
			(xvii) 14th December 1994			
m	21.44±0.41	17.90±0.45	19.14±0.52	17.80±0.28	20.88±0.53	17.11±0.32
[d]	2.64±0.76	2.65±0.58	1.33±0.61	5.00±0.63	3.58±0.76	1.32±0.53
[h]	6.56±1.82	-15.44±5.18	-13.12±6.19	-	-19.72±6.41	-
[i]	-	-2.55±0.73	-2.47±0.80	-	-1.97±0.93	-3.08±0.62
[l]	-	30.24±10.75	39.52±13.04	-	44.32±13.71	-
χ^2	4.71^{ns}	--[1]	--[1]	6.37^{ns}	--[1]	0.49^{ns}
df	2			3		2
D	32.16±6.21	31.44±5.06	40.86±6.94	20.46±4.53	33.69±6.67	33.65±5.84
H			116.40±43.69	-	96.41±45.02	100.14±35.18
E	65.37±4.03	40.80±2.56	-	-	-	34.56±2.43
E1	-	-	40.22±7.99	73.30±9.35	77.51±5.93	-
E2	-	-	30.63±6.12	23.15±4.58	29.90±6.00	-
E3	-	-	69.20±5.79	44.89±3.75	-	-
χ^2	5.90^{ns}	8.06^{ns}	1.46^{ns}	1.47^{ns}	3.47^{ns}	4.39^{ns}
df	5	5	2	3	3	4

^{ns} No-significance of the goodness of fit χ^2 test.

[1] Perfect fit, no degree of freedom left for testing the model goodness of fit.

[2] D1, D2 ... Dn and/or H1, H2 ... Hn and/or CP indicate additive and dominance effects in the presence of linkage and their cross products, respectively.

[3] E1 and E2 indicate environmental effects in the presence of genotype x micro-environment interaction.

[4] Best model found.

[5] According to Oliveira (1994).

[6] No model could be fitted.

frequently made small by dispersion of genes among the parents, but was detected in approximately 80% of the models, being least frequent in 1988/89 with a frequency of 56%. The D, D1 or D2 effects were present in, approximately, 93% of the models indicating that the additive effects are ubiquitous in the analyzed materials. The relative frequency of the [i] epistatic effect showed a marked variation among years, with frequencies of only 28% of the models in 1988/89 and 1992/93, reaching more than 70% in 1991/92 and 1994/95. A similar picture is observed for the [i] presence among crosses, with the frequency varying from 29% in the cross FT-2 x BR-13 to 71% in BR85-29009 x BR-13 and FT-2 x OCEPAR 8.

TABLE 3. Proportion of significant estimates for the genetic parameters obtained from the mean and variance models for grain yield in the years and sowing dates for each biparental cross, in Londrina, PR.

Year	Mean and variance genetic parameters[1]											Total
	[d]	[h]	h+ h-	[i]	[i]+ [i]-	[l]	[l]+ [l]-	D[2]	H	Linkage	G x E	
1988/89	0,56	0,67	0,56 0,11	0,28	0,06 0,22	0,17	0,11 0,06	0,83	0,00	0,11	0,28	18
1991/92	0,83	0,83	0,17 0,67	0,72	0,00 0,72	0,56	0,56 0,00	0,56	0,11	0,33	0,39	18
1992/93	0,94	0,89	0,39 0,50	0,28	0,00 0,28	0,61	0,50 0,11	0,39	0,06	0,56	0,33	18
1993/94	0,88	0,50	0,21 0,29	0,67	0,00 0,67	0,17	0,17 0,00	0,96	0,25	0,04	0,33	24
1994/95	0,79	0,58	0,25 0,33	0,71	0,00 0,71	0,21	0,21 0,00	0,88	0,21	0,00	0,46	24
Sowing date[3]												
Early	0,89	0,56	0,28 0,28	0,56	0,06 0,50	0,11	0,11 0,00	0,78	0,06	0,11	0,61	18
Normal	0,76	0,70	0,31 0,39	0,54	0,00 0,54	0,37	0,31 0,06	0,74	0,09	0,20	0,35	54
Late	0,83	0,70	0,30 0,40	0,57	0,00 0,57	0,37	0,37 0,00	0,73	0,27	0,20	0,23	30
Cross												
BR85 x FT-2	0,76	0,65	0,47 0,18	0,53	0,00 0,53	0,18	0,18 0,00	0,82	0,06	0,12	0,24	17
BR85 x BR-13	1,00	0,65	0,18 0,47	0,71	0,00 0,71	0,24	0,24 0,00	0,76	0,00	0,06	0,41	17
BR85 x OCEPAR 8	0,65	0,82	0,41 0,41	0,47	0,00 0,47	0,41	0,41 0,00	0,65	0,29	0,24	0,29	17
FT-2 x BR-13	0,88	0,65	0,29 0,35	0,29	0,00 0,29	0,24	0,24 0,00	0,82	0,24	0,12	0,53	17
FT-2 x OCEPAR 8	0,76	0,53	0,24 0,29	0,71	0,00 0,71	0,41	0,29 0,12	0,76	0,12	0,24	0,29	17
BR-13 x OCEPAR 8	0,76	0,76	0,24 0,53	0,59	0,06 0,53	0,47	0,41 0,06	0,65	0,12	0,35	0,41	17

[1] Mean genetic parameters: additive [d], dominant [h], additive by additive interaction [i] and dominant by dominant interaction [l]; and genetic variance parameters: additive (D), dominance (H), additive and/or dominance linkage affected parameters (presence of D1, D2 ... Dn and/or H1, H2 ... Hn, respectively), and genotype by micro-environment interaction (G x E, presence of E1 and/or E2).

[2] The total occurrence of additive or dominance variance effect is the result of the sum of the frequencies of D, D1, D2 ... Dn and H, H1, H2 ... Hn, respectively.

[3] The early sowing date includes evaluations of 26th September 1988, 27th September 1993, 20th September 1994; the normal includes 14th October 1988 and 18th November 1988, 17th October 1991, 15th October 1992 and 9th November 1992, 20th October 1993 and 17th November 1993, and 20th October 1994 and 17th November 1994 sowing dates; and the late sowing dates includes 28th November 1991 and 13th December 1991, 2nd December 1992, 17th December 1993, and 14th December 1994.

This latter case is expected since the magnitude of the [i] estimate is greatly affected by gene dispersion among the parents. On the other hand, [i] was uniformly frequent among sowing dates, with an average of 56% of the cases. The sign of [i] was predominantly negative, indicating that the mean yield of the F_∞ lines derived from each cross will be smaller than the mean of their two parents. This is an indication that a large number of inbred lines should be derived from each cross to increase the chances of high yielding individuals appearing.

Dominance is not affected by gene dispersion and was better detected by the mean than by the variance analyses (higher frequency of [h] in relation to H). This is expected due to the higher sensitivity (smaller errors of estimates) of the mean comparatively to the variance analyses. Directional dominance was detected on an average of 69% of the occasions (Table 2). The sign of [h] in each cross alone is not sufficient to inform about the presence or absence of bi-directional dominance, but it is acceptable to suppose that bi-directional dominance existed in the crosses considering the whole set of results. The presence of bi-directional dominance would indicate that dominance probably played a secondary role in the soybean evolution. The presence [l] in opposite sign to [h] indicates duplicate gene epistasis, but since it happened on all the occasions when they occurred together, it may simply indicate that the statistical procedure used to estimate them is influenced by the strong correlation among both estimates (Oliveira, 1994). This correlation may be biasing the estimate and hiding the true sign of [h]. In fact, on 17 out of 20 occasions that [h] was detected without [l} in the models, it was positive. The algebraic sum of [h] and [l] may provide an indication of the true direction of the effect. In any case, it is well known that dominance has little or no influence on the soybean selection process. The rather rare presence of a significant dominance or dominance with linked genes component in the variance models (19 cases in a total of 104 models), comparatively to its frequent detection by the mean analyses (69 cases in 104 models), is probably due to the smaller coefficients attached to this component comparatively to the additive genetic and environmental components, that results in a smaller precision in the estimation of dominance variance (Mather & Jinks, 1982). Other complicating factors, such as epistasis and linkage, although less ubiquitous were an important source of variability in several of the crosses.

The environmental influence on [d] was detected through its different frequency and magnitude within crosses under diverse environments. Similarly, the magnitude of [h] varied within crosses in different years or sowings reflecting the environmental influence on the effect (Table 2). The environmental effect on the genetic modeling was evident not only from the mentioned differences in the magnitudes of the parameters [d] and [h], but also by inclusion or exclusion of other effects as the environments changed. A joint analysis of the data to include modeling genotype, year, sowing and their interactions effects following the methods described by Eberhart & Russell (1966) and Bucio-Alanis et al (1969), will be treated later.

The magnitude of [h] was frequently greater than [d]. It has already been mentioned that the presence of [l] in the model tended to change the signal of [h] and also to increase its magnitude, and that the magnitude of [d] is strongly affected by gene dispersion between the parents. This picture turns difficult to interpret correctly the genetic meaning of the [h] / [d] ratio, since it is not the traditional dominance ratio. On the other hand, considering that in the current data set this ratio was frequently greater than two (Table 2), it may be an indication that heterosis remains present in soybean. The main practical use of this ratio, however, is to serve as an indicator of the presence of exploitable genetic variability among the cross descendents. The constant presence of D, D_1 or D_2 coupled with the high frequency of [d] in the models, showed that additive effect was the predominant genetic effect controlling grain yield trait in this material. The cross BR85-29009 x OCEPAR 8 showed the highest proportion of significant [h] and H among the models (Table 3). The detection of heterosis was not correlated with the presence of a high proportion of epistasis or linkage or genotype by micro-environment interaction effects. This is in contrast to the work of Jinks (1981, 1983), that reported heterotic crosses as displaying those effects more often than non-heterotic ones. Comprehensive discussions on the influence of the genetic effects on heterosis are also available from Paterniani (1973) and Sprague (1983).

Yield is, in general, a low heritability trait. The overall mean for the narrow sense heritability of soybean yield, in the seventeen environments of this work varied from 0.19 for the cross BR85-29009 x FT-2 to 0.33 for the cross

BR-13 x OCEPAR 8 (Table 4). The highest narrow sense heritability was observed for the cross BR-13 x OCEPAR 8 at the 14th October 1988 sowing. The mean heritabilities for each sowing date are shown on the right hand side of Table 4. The overall mean heritability was 0.29 (ranging from 0.16 to 0.40), compared to an average of 0.33 for the early sowing heritabilities (ranging from 0.30 to 0.38) and to 0.23 for the late sowing heritabilities (ranging from 0.16 to 0.28). The environmental effects on the heritability values are evident and, although some degree of repeatability existed when similar sowing dates were compared, the environmental influence was still large.

The earlier reports on the genetical control of soybean yield (Brim & Cockerham, 1961; Fehr, 1987) refer to USA germplasm grown in environments very different from those of this work. However, their results also emphasized the predominance of the additive effects, detected the presence of the additive x additive non-allelic interaction in the control of soybean yield, and found low heritability values. More recently, Oliveira (1994) used several genetical designs, including the powerful triple-test cross (Kearsey & Jinks, 1968), to analyze the genetic control of yield of the soybean cross BR85-29009 x OCEPAR 8, in three different sowing dates. His results were similar to those reported here: ubiquity of additive effects and the presence of dominance, epistatic, linkage effects and G x E interaction (Table 2).

TABLE 4. Narrow sense heritability estimates for soybean grain yield obtained from 17 different environments (years and sowing dates) for each of the biparental crosses.

Sowing date[1]	BR85 -29009 x FT-2	BR85 -29009 x BR-13	BR85 -29009 x OC-8	FT-2 x BR-13	FT-2 x OC-8	BR-13 x OC-8	Mean
26th Sep 1988 (E)	0.20	0.23	0.55	0.26	0.51	0.51	0.38
14th Oct 1988 (N)	0.32	0.44	0.41	0.31	0.27	0.67	0.40
18th Nov 1988 (N)	--	0.33	0.54	0.31	0.37	0.36	0.38
1988 mean	0.26	0.34	0.50	0.29	0.38	0.51	-
17th Oct 1991 (N)	0.18	--	--	0.43	0.39	--	0.34
28th Nov 1991 (L)	0.20	0.23	0.32	0.09	0.41	0.49	0.29
13th Dec 1991 (L)	0.09	0.27	--	0.10	0.29	0.25	0.20
1991 mean	0.16	0.25	0.32	0.21	0.36	0.37	-
15th Oct 1992 (N)	0.17	0.41	0.30	0.27	0.28	0.52	0.33
9th Nov 1992 (N)	--	0.14	0.26	0.09	--	--	0.16
2nd Dec 1992 (L)	0.39	0.25	0.21	--	0.35	0.18	0.28
1992 mean	0.28	0.26	0.26	0.18	0.31	0.35	-
27th Sep 1993 (E)	0.19	0.43	0.21	0.31	0.29	0.36	0.30
20th Oct 1993 (N)	0.16	0.39	0.40	0.39	0.20	0.12	0.28
17th Nov 1993 (N)	0.23	0.29	0.20	0.23	0.17	0.28	0.23
17th Dec 1993 (L)	0.11	0.28	0.20	0.12	0.13	0.14	0.16
1993 mean	0.17	0.35	0.25	0.26	0.20	0.22	-
20th Sep 1994 (E)	0.25	--	--	0.31	0.24	0.41	0.30
20th Oct 1994 (N)	0.23	--	0.31	0.51	0.30	0.56	0.38
17th Dec 1994 (N)	0.19	0.24	0.35	0.11	0.29	0.23	0.23
14th Dec 1994 (L)	0.20	0.28	0.21	0.18	0.18	0.22	0.21
1994 mean	0.22	0.26	0.29	0.28	0.25	0.35	-
Overall mean	0.19	0.30	0.32	0.25	0.28	0.33	0.29

[1] Sowing dates were classified as early (E), normal (N) and late sowings (L).

The genotype by micro-environment interaction G x E (Table 3) was detected in 36% of the fitted models. It was more frequent in early sowings and in the crosses including the parental BR-13. The parental variances, important to estimate the environmental (E) parameter, decreased in the early sowings as happened for the mean yield. The magnitude of this reduction obviously depended on the genotype. The parental BR-13, that is a traditional cultivar in photoperiod response, prematurely stopped its growth in early sowings. Unequal reduction of variance among the parents, proportionally greater for BR-13, could explain the higher proportion of G x E effect in the early sowing date.

The general picture portrayed by these results is that any selection procedure adopted should take into account the predominance of additive effects and allow for the influence of the environment.

A study on the cross potential to produce superior inbred lines, using the method proposed by Jinks & Pooni (1976) and Toledo (1987), was carried out by Triller & Toledo (1996) using part of this data set. The F3 based predictions were performed to evaluate each biparental cross potential on the diverse sowing dates within each year. The predicted values for the breeding potential to produce superior inbred lines were compared with the proportion of superior inbred lines evaluated for each cross on the four sowing dates of 1993/94 and 1994/95. According to the authors, at least two environments should be considered to overcome environmental interference on the predictions, which were then reliable even in the presence of the complicating factors found in the genetic models.

CONCLUSIONS

1. Soybean yield is controlled by polygenes with predominantly additive effects, and, therefore, selection methods designed for exploiting additive variability should be used.

2. The low narrow sense heritability and the frequent presence of significant G x E interaction require that the selection in a breeding program allow for their presence.

3. The genetic complications such as epistasis, linkage and micro-G x E effects have relatively small size comparatively to the additive effects and are not likely to pose a serious threat to efficient selection.

4. The successful prediction of the cross breeding potential to generate superior inbred lines using part of the data of this work, corroborates the idea of the importance of the additive genetic effects.

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