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Research Article

Genetic control of soybean (*Glycine max*) yield in the absence and presence of the Asian rust fungus (*Phakopsora pachyrhizi*)

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Abstract

Soybean is one of the most important crops in Brazil and continuously generates demands for production technologies, such as cultivars resistant to diseases. In recent years, the Asian rust fungus (*Phakopsora pachyrhizi* Syd. & P. Syd 1914) has caused severe yield losses and the development of resistant cultivars is the best means of control. Understanding the genetic control and estimating parameters associated with soybean (*Glycine max*) resistance to *P. pachyrhizi* will provide essential information for cultivar selection. We investigated quantitative genetic control of *P. pachyrhizi* and estimated parameters associated to soybean yield in the absence and presence of this phytopathogen. Six cultivars and their 15 diallel derived F_2 and F_3 generations were assessed in experiments carried out in the absence and presence of *P. pachyrhizi*. The results indicated that soybean yield in the presence and absence of *P. pachyrhizi* is controlled by polygenes expressing predominantly additive effects that can be selected to develop new cultivars resistant or tolerant to *P. pachyrhizi*. These cultivars may prove to be a useful and more durable alternative than cultivars carrying major resistance genes.

Key words: genetic components, genetic potential, yield prediction.

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Introduction

Soybean (*Glycine max* (L.) Merrill) is the most important crop in Brazilian agriculture, with a current cultivated area of 20.6 million hectares and an average yield of 2,809 kg ha^{-1} equivalent to an annual production of approximately 58 million tons (CONAB, 2007). Brazil contributes 20% of the world soybean production ranking second in soybean production (CONAB, 2006). However, average yield could be greater than 3,200 kg ha^{-1} if the effect of diseases was reduced (Almeida, 2001). Asian soybean rust (ASR) caused by the fungus *Phakopsora pachyrhizi* Syd. & P. Syd 1914) is the most aggressive soybean disease and can result in losses of 10% to 90% of the crop (Hartman *et al.*, 1999).

A recent doctoral thesis on the mapping of rust resistance genes and quantitative trait loci (QTL) involved in soybean resistance to septoriosis caused by phytopathogenic fungi of the genera *Septoria* pointed out that economic and effective control of *P. pachyrhizi* can be obtained using resistant or tolerant soybean cultivars (Brogin, RL. Mapeamento de genes de resistência à ferrugem e de QTLs envolvidos na resistência à septoriose em soja, Ph. D. thesis, Escola Superior de Agricultura Luiz de Queiroz, São Paulo University, Piracicaba-SP, Brazil 2005).

In addition to the classical *Rpp1, Rpp2, Rpp3* and *Rpp4* resistance genes several major resistance genes have been identified in new plant introductions or cultivars (Bromfield and Hartwig, 1980; Hartwig, 1986; Hartman *et al.* 2004; Pierozzi *et al.* (submitted to Genet Mol Biol)). However, resistance to *P. pachyrhizi* expressed by single genes does not promise to be durable since the *Rpp1* and *Rpp3* genes proved not effective in soybean in the second year (2002) after *P. pachyrhizi* was first detected in Brazil. Although staking individual resistance genes could perhaps prove effective for somewhat longer periods of time, the search for horizontal quantitative resistance must be performed to ensure long lasting resistance or tolerance. Some soybean cultivars have shown more tolerance to *P. pachyrhizi* than others, which could be due to the presence of quantitative resistance genes in the plants. The development of resistant or tolerant cultivars in a breeding program can be greatly helped by a knowledge of the various types

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of gene action in the segregating populations. Plant breeding efficiency depends on a good knowledge of the genetic variability and type of predominant gene action in the control of the trait (Ramalho and Vencovsky, 1978).

Assessing the yield of soybean parent plants and their biparental cross derived F_2 and F_3 generations in the presence and absence of *P. pachyrhizi* is, therefore, likely to provide important clues on the possibilities open to breeders interested in developing soybean cultivars which are not only high-yielding but also resistant or tolerant to *P. pachyrhizi*. Ribeiro *et al.* (2007) assessed the severity of *P. pachyrhizi* attack on leaves of soybean cultivars FT-2, EMBRAPA 48, BRS 154, BRS 184, BRS 214, BRS 231 and reported that genes for resistance or tolerance to *P. pachyrhizi* displayed predominantly additive effects and are dispersed among soybean genotypes. If similar results can be obtained for yielding controlling genes, strategies for efficient cultivar development can be efficiently drawn. We investigated the same cultivars as Ribeiro *et al.* (2007) to assess the Genetic control of soybean yield in the presence and absence of *Phakopsora pachyrhizi*.

Material and Methods

We investigated six commercial cultivars (FT-2, Embrapa-48, BRS 154, BRS 184, BRS 214 and BRS 231) in biparental diallel crosses which produced 15 sets each of F_2, reciprocal F_2 (RF_2), F3 and reciprocal F_3 (RF_3) generations. The six parental cultivars had expressed different levels of resistance and/or tolerance to *P. pachyrhizi* in several greenhouse tests conducted at the Brazilian Agricultural Research Corporation (Empresa Brasileira de Pesquisa Agropecuária - Embrapa) National Center for Soybean Research (Embrapa Soybean, Londrina, Paraná State, Brazil.) and are high-yielding and well-adapted to the growing conditions in the Brazilian state of Paraná. The FT-2 cultivar carries a single gene for *P. pachyrhizi* resistance, probably *Rpp1* or *Rpp3*, which express resistance to the *P. pachyrhizi* strain isolated from southern Brazil but not to the strain isolated in the Brazilian state of Mato Grosso (the "MT" strain). All cultivars show similar growth cycle, which, in genetic studies, is important in minimizing the effects of time on *P. pachyrhizi* infection.

During the 2004/05 cropping season at the Embrapa Soybean experimental farm (23°11' S; 51°10' W) in Paraná we carried out two completely randomized experiments involving 11,400 (2 X 5,700) single-plant hill-plots, with one plant being equal to one hill-plot. Single plant hill-plots were used to allow growing the large number of plants (replications) in a restricted experimental area to reduce soil heterogeneity and to avoid having two experimental errors (between plots and between plants within plots) in the experiments, which would only add complexity to the genetic parameter estimation process. In each experiment, each parent was represented by 50 plants, each F_2 and RF_2 by 80 plants and each F_3 and RF_3 by 20 families of five plants each. In experiment I we sprayed the plants at the V_2 plant growth stage with the fungicide Impact (0.6 L ha^{-1} equivalent to 75 g ha^{-1} of Flutriafol a.i.) and at the R_3 and R_6 plant growth stages with the fungicide Folicur (0.5 L ha^{-1} equivalent to 100 g ha^{-1} of Tebuconazole a.i.) to preclude development of *P. pachyrhizi.* In experiment II, we used no fungicide but instead inoculated the plants twice (once at plant development stage V3 and once at stage V5) with *P. pachyrhizi* strain MT using a suspension containing about 1×10^4 spores mL^{-1}. The spores were produced on *P. pachyrhizi* infected leaves of the soybean cultivar BRS Bacuri in a contained green-house environment. Cultivar BRS Bacuri was chosen because it is resistant to the southern Brazil strain and susceptible to the MT strain of *P. pachyrhizi*, which are the two prevalent strains in Brazil, therefore ensuring predominance of the MT strain in our inoculum. The *P. pachyrhizi* strain MT original spores were collected in the State of Mato Grosso by Dr. Tadashi Yorinori in 2002 and kept in the Embrapa Soybean plant pathology collection under freeze-dried stored conditions. Both experiments received all recommended agricultural practices to ensure normal soybean plant development, including irrigation. The experiments were monitored three times a week to ensure prompt response to any abnormality that could cause the collected data to be unreliable. Details of other experiment characteristics and on the inoculation procedures are given in Ribeiro *et al.* (2007).

Individual single-plant plots were harvested at the R7 stage and plants taken to a shed for drying to 13% moisture prior to threshing and weighing of the soybeans to calculate grain-yield.

For both experiments, genetic models (Mather and Jinks, 1982) were fitted to the yield means and variances of the generations to estimate genetic parameters, narrow sense heritabilities based on F_3 family means and predict the genetic potential of each biparental cross for generating high-yielding inbred lines (Jinks and Pooni, 1976; Toledo, 1987).

Results

Table 1 shows the degrees of freedom, means and variances of the parents and their derived F_2 and F_3 generations in both experiments after pooling over reciprocals since no significant ($p = 0.05$) reciprocal effects were detected for yield in any generation. Significant yield differences were detected for each cultivar between experiments and also between cultivars within experiments. The largest yield reductions (in parentheses) between the two experiments were for BRS 214 (-86.04%), FT-2 (-83.59%), Embrapa 48 (-82.20%), BRS 154 (-75.07%) and BRS 184 (-75.02%). Cultivar BRS 231, which has been reported to carry quantitative genes for resistance or tolerance to *P. pachyrhizi* (Ribeiro *et al.*, 2007), showed a smaller yield reduction of -67.83% be-

Table 1 - Degrees of freedom (df), means and variances of the six parent soybean cultivars and their derived biparental cross F_2 and F_3 generations in experiments I and II. Data refer to grams per plant.

Parents	Experiment I			Experiment II		
	df	Means[1]	Variances	df	Means[1]	Variances
FT-2	49	24.13 c	79.83	49	3.96 c	6.26
Embrapa 48	49	26.91 bc	66.90	48	4.79 c	6.79
BRS 154	49	22.74 c	78.67	49	5.67 bc	13.76
BRS 184	48	30.31 ab	99.02	48	7.57 ab	18.00
BRS 214	49	35.25 a	168.87	49	4.92 c	10.95
BRS 231	49	27.45 bc	73.73	45	8.83 a	24.85
[1]Means followed by the same letters did not differ significantly by the Tukey test at p = 0.05.						
Crosses						
FT-2 x Emb 48	df	Means	Variances	df	Means	Variances
F_2	157	26.26	85.30	156	5.52	7.37
F_3	194	27.37	107.88	197	5.49	10.22
__F_3 between families	39		235.79	39		12.13
__F_3 within families	155		74.65	158		9.74
FT-2 x BRS 154	df	Means	Variances	df	Means	Variances
F_2	159	29.85	138.46	158	5.97	13.18
F_3	196	27.68	120.84	197	5.88	13.99
__F_3 between families	39		190.06	39		24.45
__F_3 within families	157		103.13	158		11.33
FT-2 x BRS 184	df	Means	Variances	df	Means	Variances
F2	154	32.35	110.97	155	7.48	14.82
F3	197	30.26	147.12	197	6.48	15.76
__F_3 between families	39		326.85	39		30.04
__F_3 within families	158		101.50	158		12.14
FT-2 x BRS 214	df	Means	Variances	df	Means	Variances
F_2	159	34.20	166.97	157	6.06	17.55
F_3	196	32.12	163.11	197	6.25	11.69
__F_3 between families	39		245.34	39		10.93
__F_3 within families	157		142.07	158		11.88
FT-2 x BRS 231	df	Means	Variances	df	Means	Variances
F_2	154	28.02	122.31	153	8.00	29.28
F_3	194	25.80	143.59	191	6.29	18.52
__F_3 between families	39		241.94	39		25.92
__F_3 within families	155		117.90	152		16.55
Emb 48 x BRS 154	df	Means	Variances	df	Means	Variances
F_2	155	27.72	150.54	157	5.76	16.01
F_3	198	25.63	106.73	195	6.12	21.23
__F_3 between families	39		179.01	39		35.38
__F_3 within families	159		88.52	156		17.58
Emb 48 x BRS 184	df	Means	Variances	df	Means	Variances
F_2	156	32.94	106.38	158	6.73	14.10
F_3	197	30.15	92.23	194	6.60	13.77
__F_3 between families	39		103.28	39		17.54
__F_3 within families	158		89.43	155		12.79
Emb 48 x BRS 214	df	Means	Variances	df	Means	Variances
F_2	158	29.92	147.38	155	5.19	12.42
F_3	194	29.26	152.88	194	5.80	14.68
__F_3 between families	39		293.14	39		20.93
__F_3 within families	155		116.44	155		13.05
Emb 48 x BRS 231	df	Means	Variances	df	Means	Variances
F_2	155	32.58	142.39	153	8.20	31.66
F_3	199	25.02	97.45	195	4.68	6.10
__F_3 between families	39		120.65	39		7.06
__F_3 within families	160		91.65	156		5.85

Table 1 (cont.)

Crosses						
BRS 154 x BRS 184	df	Means	Variances	df	Means	Variances
F_2	156	34.17	158.40	156	8.35	28.64
F_3	194	30.39	161.01	197	8.15	32.61
__F_3 between families	39		222.68	39		61.14
__F_3 within families	155		144.99	158		25.37
BRS 154 x BRS 214	df	Means	Variances	df	Means	Variances
F_2	156	34.78	168.74	159	6.75	15.60
F_3	196	30.94	180.42	196	6.38	19.90
__F_3 between families	39		209.89	39		35.16
__F_3 within families	157		172.88	157		15.99
BRS 154 x BRS 231	df	Means	Variances	df	Means	Variances
F_2	157	30.12	134.53	158	8.09	27.45
F_3	199	25.38	88.22	196	5.58	14.26
__F_3 between families	39		114.93	39		18.76
__F_3 within families	160		81.55	157		13.11
BRS 184 x BRS 214	df	Means	Variances	df	Means	Variances
F_2	158	39.92	172.02	159	7.56	23.27
F_3	197	35.48	148.59	199		19.31
__F_3 between families	39		205.37	39		24.00
__F_3 within families	158		134.18	160		18.13
BRS 184 x BRS 231	df	Means	Variances	df	Means	Variances
F_2	157	35.62	172.59	154	8.80	43.8
F_3	195	28.02	173.63	187	7.95	41.34
__F_3 between families	39		295.51	39		59.67
__F_3 within families	156		142.21	148		36.16
BRS 214 x BRS 231	df	Means	Variances	df	Means	Variances
F_2	158	31.83	151.67	153	6.32	22.88
F_3	196	28.50	139.52	188	5.79	14.05
__F_3 between families	39		177.82	39		21.72
__F_3 within families	157		129.67	149		11.95

tween experiments and was top yielding in experiment II. The BRS 184 cultivar also showed some degree of tolerance to *P. pachyrhizi* as its yield did not significantly differ from that of BRS 231 in either experiment.

The mean and variance genetic parameters estimated for yield are shown in Table 2 for experiment I and Table 3 for experiment II.

In experiment I, out of the 15 crosses investigated additive ([d]) gene effects were significant in 11 crosses and dominant ([h]) effects in 13 crosses. Dominance was predominantly positive towards increased yield. The estimated variance parameters indicated a prevalence of additive (D) effects in nine out of the 15 crosses with the presence of repulsion linkage between genes expressing additive effects in the Embrapa 48 x BRS 154 cross (D1 > D2, data not shown). No significant dominant (H) variance was observed and significant genotype x micro-environment interaction (E1 ≠ E2) was detected only in the Embrapa 48 x BRS 214 cross. The larger absolute values of [h] comparatively to those of [d] coupled with the predominance of D over H effects and detection of repulsion linkage in one cross suggested that the yield increasing genes were dispersed among the parents.

In experiment II, out of the 15 crosses investigated [d] gene effects were significant in 10 crosses and [h] effects in 11 crosses, with [h] effects always towards yield increase. Duplicate epistasis was detected in three crosses (FT-2 x Embrapa 48, FT-2 x BRS 214 and Embrapa 48 x BRS 214). The D estimates were significant in 8 out of 15 crosses, indicating that the genetic variability detected for yield in the presence of *P. pachyrhizi* was predominantly of the additive type. Repulsion linkage between loci expressing additive gene effects was detected on a single occasion in the BRS 184 x BRS 214 cross (D1 > D2, data not shown). No significant H estimates were obtained and significant genotype x micro-environment interaction was detected in two crosses (FT-2 x BRS 184 and Embrapa 48 x BRS 184). The main picture is that the genetic control of soybean yield in the presence of the pathogen was mostly by dispersed genes displaying additive effects.

Narrow sense heritability estimates based on F_3 family means (Table 4) were of moderate value, ranging from 0.53 to 0.80 in experiment I and from 0.52 to 0.80 in experi-

Table 2 - Genetic models of means and variances fitted for the soybean yield trait in Experiment I. All the estimates are significant at the level of 5% probability, except when specifically noted as being at the l0% level. The column headings represent the following: m = mean effects of the genes non-segregating in the cross; [d] = additive mean effects; [h] = dominance mean effects; [i] = additive by additive epistatic mean effects; [l] = dominance by dominance epistatic mean effects; χ^2 = Chi-square value; df = degrees of freedom; p = probability level; D = additive variance effects; D_1 and D_2 = additive variance effects in the presence of digenic linkage; H = dominance variance effect; E = additive environmental variance component; E1 and E2 are the additive environmental variance components of P1 and P2, respectively, in the presence of genotype x microenvironment interaction.

Crosses / parameters	m	[d]	[h]	[i]	[l]	χ^2	df	p	D	H	E or E_1 and E_2	χ^2	gl	p
FT 2 x EMBRAPA 48	26.49 ± 0.45	-	-	-	-	5.12	3	0.16	51.65 ± 15.71	-	65.52 ± 6.88	2.19	3	0.53
FT 2 x BRS 154	23.83 ± 0.80	-	12.91 ± 2.57	-	-	1.66	2	0.44	31.58 ± 12.69	-	99.17 ± 8.60	6.04	3	0.11
FT 2 x BRS 184	27.41 ± 0.85	3.11 ± 0.95	10.18 ± 2.54	-	-	0.20	1	0.66	74.83 ± 21.24	-	83.11 ± 8.92	1.79	3	0.62
FT2 x BRS 214	29.77 ± 0.98	5.59 ± 1.10	8.99 ± 3.02	-	-	0.02	1	0.88	49.48 ± 22.44	-	131.73 ± 12.36	6.24	3	0.10
FT2 x BRS 231	25.41 ± 0.80	1.67 ± 0.88[a]	4.44 ± 2.49 [a]	-	-	1.08	1	0.30	67.97 ± 21.03	-	88.76 ± 9.28	2.18	3	0.53
EMBRAPA 48 x BRS 154	24.58 ± 0.77	2.10 ± 0.85	5.63 ± 2.59	-	-	0.43	1	0.51	37.16[c] ± 10.21	-	88.47 ± 7.41	7.12	3	0.07
EMBRAPA 48 x BRS 184	28.30 ± 0.79	1.64 ± 0.91[a]	8.78 ± 2.45	-	-	0.46	1	0.50	-	-	95.08 ± 6.34	3.72	4	0.44
EMBRAPA 48 x BRS 214	29.96 ± 0.56	3.69 ± 1.01	-	-	-	1.69	2	0.43	66.70 ± 23.52	-	154.67 ± 22.92 64.43 ± 12.49	0.79	2	0.67
EMBRAPA 48 x BRS 231	27.17 ± 0.84	-	-28.00 ± 7.75	-	77.65 ± 15.10	0.10	1	0.75	-	-	-	-	-	-
BRS 154 x BRS 184	26.54 ± 0.86	3.79 ± 0.95	15.29 ± 2.76	-	-	0.00	1	0.97	62.46 ± 23.12	-	114.90 ± 11.41	5.26	3	0.15
BRS 154 x BRS 214	28.60 ± 0.99	6.11 ± 1.10	11.67 ± 3.04	-	-	0.60	1	0.44	-	-	163.96 ± 10.93	8.48	4	0.08
BRS 154 x BRS 231	20.64 ± 1.62	2.36 ± 0.87	18.96 ± 4.55	4.45 ± 1.84	-	[b]	-	-	-	-	-	-	-	-
BRS 184 x BRS 214	32.35 ± 1.01	2.36 ± 1.15	14.45 ± 3.11	-	-	0.56	1	0.45	-	-	153.58 ± 10.22	7.8	4	0.10
BRS 184 x BRS 231	28.66 ± 0.92	-	-19.10 ± 9.58	-	65.89 ± 18.74	2.34	1	0.13	109.21 ± 28.76		104.07 ± 11.49	4.56	3	0.21
BRS 214 x BRS 231	25.17 ± 1.95	3.90 ± 1.10	13.32 ± 5.16	6.18 ± 2.24	-	[b]	-	-	-	-	139.7 ± 9.29	8.97	4	0.06

[a][d] and [h] significant at the 10% probability level.
[b]Perfect fit.
[c]D estimated as 0.5 (D_1 + D_2).

Table 3 - Genetic models of means and variances fitted for the soybean yield trait in Experiment I. All the estimates are significant at the level of 5% probability, except when specifically noted as being at the l0% level. The column headings represent the following: m = mean effects of the genes non-segregating in the cross; [d] = additive mean effects; [h] = dominance mean effects; [i] = additive by additive epistatic mean effects; [l] = dominance by dominance epistatic mean effects; χ^2 = Chi-square value; df = degrees of freedom; p = probability level; D = additive variance effects; D_1 and D_2 = additive variance effects in the presence of digenic linkage; H = dominance variance effect; E = additive environmental variance component; E1 and E2 are the additive environmental variance components of P1 and P2, respectively, in the presence of genotype x microenvironment interaction.

Crosses / parameters	m	[d]	[h]	[i]	[l]	χ^2	df	p	D	H	E or E_1 and E_2	χ^2	gl	p
FT 2 x EMBRAPA 48	4.35 ± 0.26	-	6.76 ± 2.42	-	-8.84 ± 4.52	2.61	1	0.11	-	-	8.43 ± 0.56	9.42	4	0.05
FT 2 x BRS 154	5.02 ± 0.28	0.93 ± 0.31	2.24 ± 0.85	-	-	2.04	1	0.15	5.51 ± 2.02	-	10.10 ± 1.00	6.83	3	0.08
FT 2 x BRS 184	5.70 ± 0.31	1.77 ± 0.34	3.46 ± 0.93	-	-	0.15	1	0.70	6.61 ± 2.37	-	16.49 ± 2.38 6.06 ± 1.18	0.56	2	0.76
FT2 x BRS 214	4.31 ± 0.28	-	12.02 ± 2.66	-	-17.04 ± 5.23	2.68	1	0.1	-	-	-	-	-	-
FT2 x BRS 231	4.58 ± 0.76	2.43 ± 0.41	6.84 ± 2.14	1.81 ± 0.86	-	[b]			-	-	-	-	-	-
EMBRAPA 48 x BRS 154	5.70 ± 0.19	0.59 ± 0.31[a]	-	-	-	3.80	2	0.15	9.29 ± 2.96	-	17.60 ± 2.68 7.50 ± 1.47	4.4	2	0.11
EMBRAPA 48 x BRS 184	6.54 ± 0.17	1.55 ± 0.33	-	-	-	1.48	2	0.48	-	-	20.20 ± 2.14 7.06 ± 1.37	2.31	3	0.51
EMBRAPA 48 x BRS 214	4.84 ± 0.29	-	6.98 ± 2.86	-	-12.56 ± 5.46	0.05	1	0.83	4.50 ± 1.90	-	10.43 ± 1.00	4.40	3	0.22
EMBRAPA 48 x BRS 231	1.16 ± 0.57	2.02 ± 0.41	14.08 ± 1.95	5.65 ± 0.71	-	[b]	-	-	-	-	-	-	-	-
BRS 154 x BRS 184	6.83 ± 0.37	0.98 ± 0.40	3.52 ± 1.17	-	-	1.77	1	0.18	19.73 ± 5.11	-	18.21 ± 2.02	2.66	3	0.45
BRS 154 x BRS 214	5.40 ± 0.31	-	2.94 ± 0.93	-	-	2.06	2	0.36	7.85 ± 2.71	-	12.81 ± 1.29	1.57	3	0.67
BRS 154 x BRS 231	3.07 ± 0.68	1.58 ± 0.45	10.04 ± 1.98	4.18 ± 0.82	-	[b]	-	-	-	-	-	-	-	-
BRS 184 x BRS 214	6.29 ± 0.34	1.34 ± 0.38	2.63 ± 1.08	-	-	0.07	1	0.79	3.15[c] ± 0.97	-	17.73 ± 1.36	4.87	3	0.18
BRS 184 x BRS 231	8.23 ± 0.28	-	-	-	-	3.36	3	0.34	23.06 ± 6.95	-	27.42 ± 2.99	6.59	3	0.09
BRS 214 x BRS 231	6.15 ± 0.20	1.65 ± 0.40	-	-	-	4.7	2	0.09	-	-	-	-	-	-

[a][d] and [h] significant at the 10% probability level.
[b]Perfect fit.
[c]D estimated as 0.5 (D_1 + D_2).

Table 4 - Narrow sense heritability estimates ($h2_n$) based on F_3 family means from Experiments I and II.

Crosses	Experiment I	Experiment II
FT-2 x Embrapa 48	0.75 ± 0.06	*
FT-2 x BRS 154	0.54 ± 0.10	0.67 ± 0.07
FT-2 x BRS 184	0.77 ± 0.05	0.52 ± 0.11
FT-2 x BRS 214	0.58 ± 0.09	*
FT-2 x BRS 231	0.74 ± 0.06	*
Embrapa 48 x BRS 154	0.61 ± 0.09	0.58 ± 0.09
Embrapa 48 x BRS 184	0.00	*
Embrapa 48 x BRS 214	0.53 ± 0.11	0.62 ± 0.09
Embrapa 48 x BRS 231	*	*
BRS 154 x BRS 184	0.67 ± 0.07	0.80 ± 0.04
BRS 154 x BRS 214	*	0.70 ± 0.07
BRS 154 x BRS 231	*	*
BRS 184 x BRS 214	*	0.40 ± 0.14
BRS 184 x BRS 231	0.80 ± 0.05	0.76 ± 0.05
BRS 214 x BRS 231	*	*

*no estimate was possible because a genetic model could not be fitted to the data.

Table 5 - Expected percentage of random inbred lines higher yielding than BRS 231 derived from each cross in Experiments I and II.

Crosses	Experiment I (%)	Experiment II (%)
FT-2 x Embrapa 48	44.83	0.00
FT-2 x BRS 154	26.11	5.26
FT-2 x BRS 184	50.00	11.12
FT-2 x BRS 214	62.93	-*
FT-2 x BRS 231	40.13	-*
Embrapa 48 x BRS 154	31.92	15.15
Embrapa 48 x BRS 184	0.00	0.00
Embrapa 48 x BRS 214	62.17	3.01
Embrapa 48 x BRS 231	-*	-*
BRS 154 x BRS 184	45.62	32.64
BRS 154 x BRS 214	0.00	11.12
BRS 154 x BRS 231	-*	-*
BRS 184 x BRS 214	0.00	7.64
BRS 184 x BRS 231	54.78	45.22
BRS 214 x BRS 231	0.00	-*

*no estimate was possible because a genetic model could not be fitted to the data.

ment II, suggesting that selection for higher yield is likely to be successful in both cases.

Table 5 shows the genetic potential of each cross estimated as the percentage of random inbred lines expected to score higher yields than the BRS 231 cultivar in the presence and absence of *P. pachyrhizi*. The probability of generating random inbred lines superior to BRS 231 was higher in experiment I than in experiment II, but an overall picture of successful selection was portrayed in both cases.

Discussions

The extreme yield reductions for all cultivars seen in experiment II as compared with experiment I suggests that the two inoculations (one at plant growth stage V3 and the other at stage V5) with *P. pachyrhizi* spores were carried out too early in the plant growth cycles. However, as previously reported in the disease severity studies by Ribeiro *et al.*, 2007, screening cultivars, F_2 plants and F_3 families for *P. pachyrhizi* tolerance was successfully performed in experiment II using yield assessment. The genetic component analyses confirmed previous observations (Toledo, unpublished data) indicating that quantitative genes controlling yield in soybean in the presence of *P. pachyrhizi* are dispersed among the currently available Brazilian cultivars. Given the predominantly additive effect expressed by these genes, recurrent selection in the presence of the pathogen is likely to bring good results. This type of selection has been tried successfully before at Embrapa Soybean for insect resistance to stinkbugs (Souza and Toledo, 1995). Further indications of the feasibility of selection for quantitative resistance to *P. pachyrhizi* were provided by the moderate levels of heritability detected in some crosses and by the predicted potential of a few crosses to generate high yielding random inbred lines in experiment II. The experimental data clearly showed that, as expected, deriving random inbred lines with higher yields than BRS 231 is more difficult in experiment II than in experiment I. However, the predictions were rather encouraging given that at least five out of the 15 crosses showed that more than 10% of the derived lines were expected to yield higher than BRS 231 under *P. pachyrhiz* pressure and quantitative resistance, tolerance or both is likely to be durable.

Our data demonstrated that breeding soybean for resistance or tolerance to *P. pachyrhizi* does not have to rely solely on the few identified major genes already reported in the literature (Bromfield & Hartwig, 1980; Hartwig, 1986; Hartman *et al.*, 2004; Laperuta *et al.* (submitted to Genet Mol Biol); Pierozzi *et al.* (submitted to Genet Mol Biol)). This is important especially after the MT strain had defeated the resistance expressed by the *Rpp1* and *Rpp3* genes after only two years of the presence of *P. pachyrhizi* in Brazil. In spite of the low yield attained under severe pathogen pressure in experiment II, cultivars showing quantitative levels of resistance or tolerance to *P. pachyrhizi* similar to, or higher than, cultivar BRS 231 may prove an important asset for farmers since with this level of resistance or tolerance they are likely to attain adequate yield levels in well managed fields where a single fungicide spray in a season could suffice to obtain good disease control, resulting in higher economic returns and safer cropping.

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