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RESEARCH ARTICLE

Inheritance of soybean resistance to *Rotylenchulus reniformis*

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ABSTRACT

Genetic inheritance of soybean resistance to *Rotylenchulus reniformis* was studied by evaluating the phenotypic reaction of soybean plants to the nematode. The resistant (Forrest and Custer) and susceptible (BR96-25619) soybean cultivars used as parents as well as the F_1, F_2 and $F_{2:3}$ derived from their crosses were infested individually with 1,000 eggs and vermiform *R. reniformis*. About 70 days after the infestation, the nematodes were extracted from the roots and the reproduction factors and the numbers of nematodes per gram of roots were estimated, and data were adjusted for genetic models. Results suggested a predominance of additive genetic effects controlling the nematode resistance reaction. Based on mean and variance genetic models, further genetic gains are expected in the crossing Custer x BR96-25619. The effect of genetic dominance is towards susceptibility. The presence of significant epistasis indicates the existence of at least two genes controlling resistance and that they are interacting. The normal continuous distribution of frequencies of the number of individuals in different classes of resistance indicates that the resistance to the reniform nematode is inherited quantitatively.
Key words: *Glycine max,* genetic parameters, quantitative genetic, reniform nematode.

INTRODUCTION

The reniform nematode (*Rotylenchulus reniformis* Linford & Oliveira, 1940) is an important pathogen to many crop plants worldwide (Robinson et al., 1997). In soybean, this nematode has been shown to be especially important in the southeastern USA (Kinloch, 1998) and midwestern Brazil (Asmus, 2005; Dias et al., 2010). Yield losses up of to 32% have been reported in soybean in Brazil. Its status changed from being of secondary importance as a pathogen to becoming one of the most important disease problems for the crop in the last decade (Asmus et al., 2003; Asmus, 2005).

Among the options for managing the reniform nematode, the use of resistant and / or tolerant cultivars is considered to be promising, but although the literature indicates that some soybean cultivars bear high resistance to reniform nematodes (Robinson, 2002; Robbins et al., 2002; Robbins & Rakes, 2006; Asmus, 2008), few combine resistance with other desirable agronomic traits, allowing them to be recommended for cultivation (Dias et al., 2010). Knowledge of the inheritance of soybean resistance to *R. reniformis* can increase the efficiency of selection processes of soybean germplasm, especially if associated with molecular markers (Dias et al., 2010).

In the 1980's it was proposed that resistance of soybean to *R. reniformis* is a quantitative trait likely to be controlled by two pairs of genes with unequal effects (Harville et al., 1985), or that it could be recessive and controlled by alleles at a major locus, with possible effects of one or more minor genes causing intermediate reactions (Williams et al., 1981).

Considering the diversity of responses reported in the literature and the need for further knowledge on the subject, an experiment was carried out with the objective of studying the inheritance of soybean resistance to *R. reniformis*.

MATERIAL AND METHODS

Crosses between resistant (R) and susceptible (S) soybean genotypes to reniform nematodes, as well as the derived F_1, F_2 and $F_{2:3}$ generations, were performed between November 2005 and September 2007 in a greenhouse at Embrapa Soja (23º11'28''S, 51º10'41''W and 624m altitude). Cultivars Forrest and Custer were used as resistant progenitors, and BR96-25619 was used as the susceptible parent, generating three crosses: CBR (Custer x BR96-25619), FBR (Forrest x BR96-25619) and CF (Custer x Forrest). A complete control of generations, where it is possible to know the origin of each progeny since the individual F_2 plant, was applied similarly to a genealogical method or "pedigree" developed in a regular breeding program.

The CBR, FBR and CF populations were studied individually with sowings on November 19, 2007, January 4, 2008 and February 23, 2008, respectively. For each of the populations there were 30 replications of each parent, 30 of the derived F_1 generation, 110 of the F_2 generation and 700 of the $F_{2:3}$ generation (100 progeny with seven replications). The plants were sown in pots according to a totally randomized design in a greenhouse at Embrapa Agropecuária Oeste (22°16'30''S, 54°49'00''W and 408m

altitude). Three seeds of each soybean genotype were sown in a 500 mL polyethylene pot filled with 400 mL of substrate (58.5% sand, 7% silt and 34.5% clay, ammended with 0.4 g of a 2-20-20 N-P-K formula). The substrate was previously fumigated with methyl bromide (150 mL/m^3). Temperature and moisture varied from 20 to 30^{o}C and 30% to 85% along the day, respectively. Complementary artificial light was not necessary. Six days after sowing, seedlings were thinned to one per pot. Ten days after sowing, the pots were infested with 1000 eggs of *R. reniformis* (Coolen & D'Herde, 1972). The reniform population used was from a culture originating in soybean roots from Maracaju, state of Mato Grosso do Sul, maintained on passion fruit plants. Susceptible soybean BRS 239 was used to check the quality of infestation (Cardoso et al., 2009).

Ten weeks after infestation, roots were separated from the soil, gently washed on tap water and weighted. Then, eggs and vermiform nematodes were extracted from roots according to Coolen & D'Herde (1972) and counted in two aliquots of 1.0 mL using a Peters counting slide under an optical microscope (100x magnification). The number of nematodes per gram of roots (NGR) and the reproduction factor [RF = final population (Pf) / initial population (Pi)] were calculated for each pot. An RF lower than or equal to 1.0 characterizes a resistant genotype (Oostenbrink, 1966).

Data were analyzed using means and variances for the different generations (parents, F_1, F_2 and $F_{2:3}$) (Mather & Jinks, 1982). The genetic models adjusted for the means and variances were obtained with the computer programs GENFIT and QMS - Quantitative Genetics System (Toledo, 1991). The data were transformed into log x+1 for quantitative analysis.

The genetic models related to the resistant and susceptible parents and to the generations derived from crosses between them (Mather & Jinks, 1982) are:

$$\overline{P}_1 = m + [d] + [i]$$
$$\overline{P}_2 = m - [d] + [i]$$
$$\overline{F}_1 = m + [h] + [l]$$
$$\overline{F}_2 = m + 1/2[h] + 1/4[l]$$
$$\overline{F}_{2:3} = m + 1/4[h] + 1/16[l]$$

where:
m: is the mean of parental or combined genetic and environmental effect of the crossing;
[d]: is the additive genetic effect;
[h]: is the effect of genetic dominance;
[i]: is the genetic effect of additive x additive interaction;
[l]: is the genetic effect of dominance x dominance interaction;
$\overline{P}_1$: is the mean of the susceptible parent;
$\overline{P}_2$: is the mean of the resistant parent;
$\overline{F}_1$: is the mean of the F_1 generation;
$\overline{F}_2$: is the mean of the F_2 generation;
$\overline{F}_{2:3}$: is the mean of the $F_{2:3}$ generation.

The model utilized considered only the mean of the homozygous genotypes and the deviations of homozygous and heterozygous genotypes from the mean, and additive *vs.* additive epistasis. The joint scale test was used to verify if the model fitted to the experimental data (Toledo, 1991). The method consists in estimating the parameters "m", "d", "h" and "I" from available generations. Based on these estimates, the expected values for the mean of the generations are obtained. Subsequently, the fitness of the proposed model was determined by comparing the observed and expected values by the chi-square (χ^2) test (Steel et al., 1997), through the following expression:

$$\chi^2 = \Sigma\ [(obs-exp)^2/exp]$$

with n-1 degrees of freedom, and n number of phenotypic classes (generations) of the model. If the result of the test is not significant, then the proposed model explains the mean phenotypic value of each generation.

For the estimation of the parameters, the weighted least squares method was used with weights represented by the inverse rate of the mean variance of each generation.

RESULTS

In both crosses between resistant and susceptible parents (CBR and FBR), the amplitude of means for the variable NGR were 20-302 and 4.8-714 for the resistant genotypes Custer and Forrest, respectively, and 126-2138 and 132-3686 for the susceptible genotype (BR96-25619) in the CBR and FBR crossings, respectively. The amplitude of mean values of the RF were 0.05-2.7 and 0.08-8.1 for the resistant genotypes Custer and Forrest, respectively, and 3.23-71.6 and 2.45-93.4 for the susceptible genotype BR96-25619 in the CBR and FBR crossings, respectively. The standard susceptible cultivar BRS 239, used to control the quality of the infestation, had mean RF values of 28.5, 14.6 and 13.6 and mean NGR values of 1014.6, 843.8 and 494.5 for the CBR, FBR and CF crossings, respectively.

For both CBR and FBR crossings, values of variance of NGR and RF for the resistant parents were lower (P<0.05) than those for the susceptible parent (Table 1). Variance values for NGR and RF were small for all genotypes of the CF crossing, *i.e.*, environmental variance is small in resistant parents Custer and Forrest, and their variances did not differ (P<0.05).

For mean models (Table 2) there was a predominance of additive genetic effects ([d]) in all crossings, with significant differences between the parents for both NGR and RF. This was observed even in the crossing between resistant parents. The dominance ([h]) was significant for NGR and RF in the mean models for both resistant *vs.* susceptible crossings. For the CBR and FBR crossings, the mean of each F_1 generation was directional to the susceptible parent for all traits (Table 1).

In this study, epistasis or non-allelic additive *vs.* additive interaction was also significant in most of the

mean models accepted by the chi-square test for the two traits, except log (NGR+1) in the FBR crossing. For both resistant *vs*. susceptible crossings there was a prevalence of negative values, indicating an increased level of resistance. However, for the resistant *vs*. resistant crossing, the interaction of non-allelic genes led to an increase of the mean values of NGR and RF, *i.e.*, increased susceptibility (Table 2).

The F_2 generation from resistant *vs*. susceptible crossings gave six to seven resistant and approximately 103 susceptible individuals, *i.e.*, a 15:1 ratio, indicating the involvement of at least two genes controlling soybean resistance to *R. reniformis*. This is characteristic of a qualitative trait with a discontinuous frequency distribution. However, there are several classes of resistance and susceptibility to reniform nematode that have continuous

TABLE 1 - Degrees of freedom (DF), means ($\bar{X}$) and variances (S^2) of nematodes per gram of roots (NGR), decimal logarithm of nematodes per gram of roots (log NGR + 1), reproduction factor (RF) and log RF+1, on parents and F_1, F_2 and $F_{2:3}$ generations.

Generation	NGR			log NGR+1		
	DF	$\bar{X}$	S^2	DF	$\bar{X}$	S^2
Custer (R)[1]	29	81.7 a [4]	5251 A [5]	29	1.79	0.10
BR 96-25619 (S)[2]	27	611.4 b	211941 B	27	2.68	0.09
F_1	27	736.6	361980	27	2.72	0.15
F_2	108	632.6	277434	108	2.66	0.14
$F_{2:3}$	697	521.4	220641	697	2.52	0.22
BRS 239[3]		1014.6				
Forrest (R)[1]	29	129.9 a	21591 A	29	1.89	0.23
BR 96-25619 (S)	28	781.5 b	531155 B	28	2.76	0.12
F_1	25	884.9	338493	25	2.83	0.13
F_2	105	687.7	269282	105	2.69	0.16
$F_{2:3}$	681	585.2	286180	681	2.55	0.24
BRS 239		843 8				
Custer (R)	29	57.5 a	1528 A	29	1.68	0.08
Forrest (R)	29	20.3 b	1169 A	29	1.13	0.16
F_1	28	16.3	244	28	1.09	0.16
F_2	106	20.7	263	106	1.21	0.13
$F_{2:3}$	693	21.4	384	693	1.19	0.16
BRS 239		494 5				
Generation	**RF**			**log RF+1**		
	DF	$\bar{X}$	S^2	**DF**	$\bar{X}$	S^2
Custer (R)	29	1.04 a	0.44 A	29	0.29	0.02
BR 96-25619 (S)	27	16.81 b	206.43 B	27	1.15	0.09
F_1	27	15.84	163.79	27	1.12	0.10
F_2	108	14.72	197.33	108	1.07	0.11
$F_{2:3}$	697	12.22	132.19	697	0.97	0.14
BRS 239		28.54				
Forrest (R)	29	1.32 a	2.59 A	29	0.30	0.05
BR 96-25619 (S)	28	14.44 b	304.54 B	28	1.05	0.10
F_1	25	11.72	52.23	25	1.03	0.07
F_2	105	9.87	70.88	105	0.90	0.13
$F_{2:3}$	681	10.07	89.02	681	0.89	0.14
BRS 239		14.65				
Custer (R)	29	0.99 a	0.35 A	29	0.28	0.01
Forrest (R)	29	0.41 b	0.28 A	29	0.13	0.01
F_1	28	0.29	0.05	28	0.11	0.01
F_2	106	0.42	0.13	106	0.14	0.01
$F_{2:3}$	693	0.43	0.14	693	0.14	0.01
BRS 239		13.59				

[1,2]Resistant (R) and susceptible (S) soybean genotypes.
[3]Susceptible standard for inocula quality control.
[4]Parent means followed by the same letter for each cross do not differ by the t test (P<0.05).
[5]Parent variances followed by the same letter for each cross do not differ by the F test (P<0.05).

TABLE 2 - Genetic models adjusted to the means[1] and variances[2] for the traits nematodes per gram of roots (NGR), decimal logarithm of nematodes per gram of roots (log NGR+1), reproduction factor (RF) and log RF+1, evaluated for the crosses Custer x BR95-25619 (CBR), Forrest x BR95-25619 (FBR) and Custer x Forrest (CF).

Genetic parameters	CBR	FBR	CF	CBR	FBR	CF
	NGR			log NGR+1		
m	395.9 ±30.0	476.3±37.0	21.0±0.7	2.44±0.03	2.42±0.03	1.19±0.01
[d]	312.0±31.5	344.9±43.1	18.6±4.7	0.45±0.04	0.41±0.05	0.28±0.04
[h]	461.0±99.9	435.2±113.6	-	0.34±0.09	0.49±0.08	-
[i]	-	-	17.9±4.8	-0.21±0.05	-	0.22±0.05
χ^2 / df / P[3]	2.72 / 2 / 0.26	0.13 / 2 /0.94	2.95 / 2 / 0.23	2.66 / 1 / 0.10	4.88 / 2 / 0.09	2.14 / 2 / 0.34
D	-	-	-	0.14±0.02	0.12±0.02	0.05±0.01
E	-	-	-	0.10±0.01	0.14±0.01	0.12±0.01
χ^2 / df / P	-[6]	-[6]	-[6]	5.63 / 4 / 0.23	8.58 / 4 / 0.07	5.52 / 4 / 0.24
h^2[4]	-	-	-	0.41	0.30	0.17
	RF			log RF+1		
m	10.17±0.78	10.04±0.32	0.48±0.02	0.91±0.03	0.84±0.03	0.14±0.01
[d]	9.12±0.78	8.68±0.43	0.29±0.07	0.43±0.03	0.38±0.04	0.08±0.01
[h]	7.73±2.49	-	-0.17±0.06	0.25±0.07	0.16±0.07	-
[i]	-	-	0.22±0.08	-0.19±0.04	-0.17±0.04	0.07±0.01
χ^2 / df / P	1.90 / 2 / 0.39	3.22 / 3 / 0.36	0.90 / 1 / 0.34	1.67 /1 / 0.20	0.83 /1 / 0.36	2.52 / 2 / 0.28
D	-	-	0.04±0.01	0.08±0.01	0.08±0.02	-
E	-	-	-	-	0.08±0.01	0.01±0.001
E1	-	-	0.20±0.02	0.02±0.01	-	-
E2	-	-	0.04±0.01	0.10±0.01	-	-
E3	-	-	-	-	-	-
χ^2 / df / P	-[6]	-[6]	13.57 / 3 / 0.01[5]	0.44 / 3 / 0.93	3.48 / 4 / 0.48	12.33 / 5 / 0.03[5]
h^2	-	-	-	0.40	0.33	-

[1]Mean parameters include the mean of genetic and environmental effects for the cross (m), the additive genetic effect [d], dominance [h], and epistasis [i].
[2]Effect of additive genetic variance (D), additive environmental variance (E), and effect of genetic by microenvironment interaction (E1, E2 and E3).
[3]Chi-square (χ^2) value for the model fit, degree of freedom (df), probability (P) associated to the chi-square.
[4]Estimative of narrow sense heritability (h^2).
[5]Best model found.
[6]No model found for variance data.

distribution, consistent with quantitative genetic control. In this study, no clearly distinct classes were observed along the frequency distribution for the characters (Figures 1, 2 and 3).

The estimates of narrow sense heritability, considering only additive genetic variation relative to total variation for each character, were calculated only for the two characters with higher genetic variation in both crossings involving both resistant and susceptible parents (Table 2).

DISCUSSION

The mean values for NGR and RF were consistently different between the resistant and susceptible parents, indicating that the parents used allowed us to obtain a suitable database for studying the inheritance of soybean resistance to reniform nematodes. This indicates that a way of studying a quantitative character to infer on its genetic potential for genotype selection is by using special designs. Good examples are the study of phenotypic values obtained from contrasting parents and their progeny, and the simpler situation, when evaluating the performance of the contrasting P_1 and P_2 parents and their F_1 and F_2 progeny (Cruz, 2010).

The lower variance observed in resistant parents for both NGR and RF was predictable, due to less multiplication and lower counts of reniform nematodes on the roots of resistant genotypes. However, nematode multiplication in the susceptible parent was unequal, with high amplitude values, resulting in higher variances that were attributed

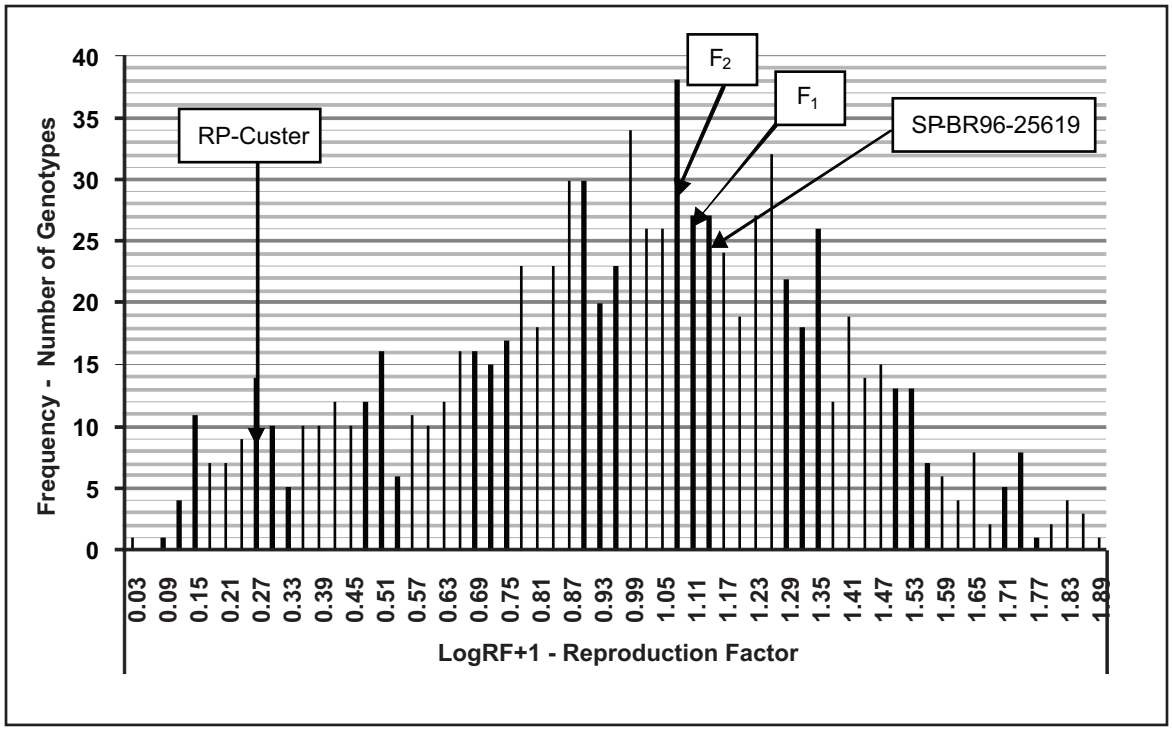

FIGURE 1 - Distribution of frequency of $F_{2:3}$ families derived from the cross Custer x BR96-25619 for the trait log of reproduction factor (log RF+1) of reniform nematodes and the relative positions of resistant (RP) and susceptible (SP) parents and of the derived F_1 and F_2 generations.

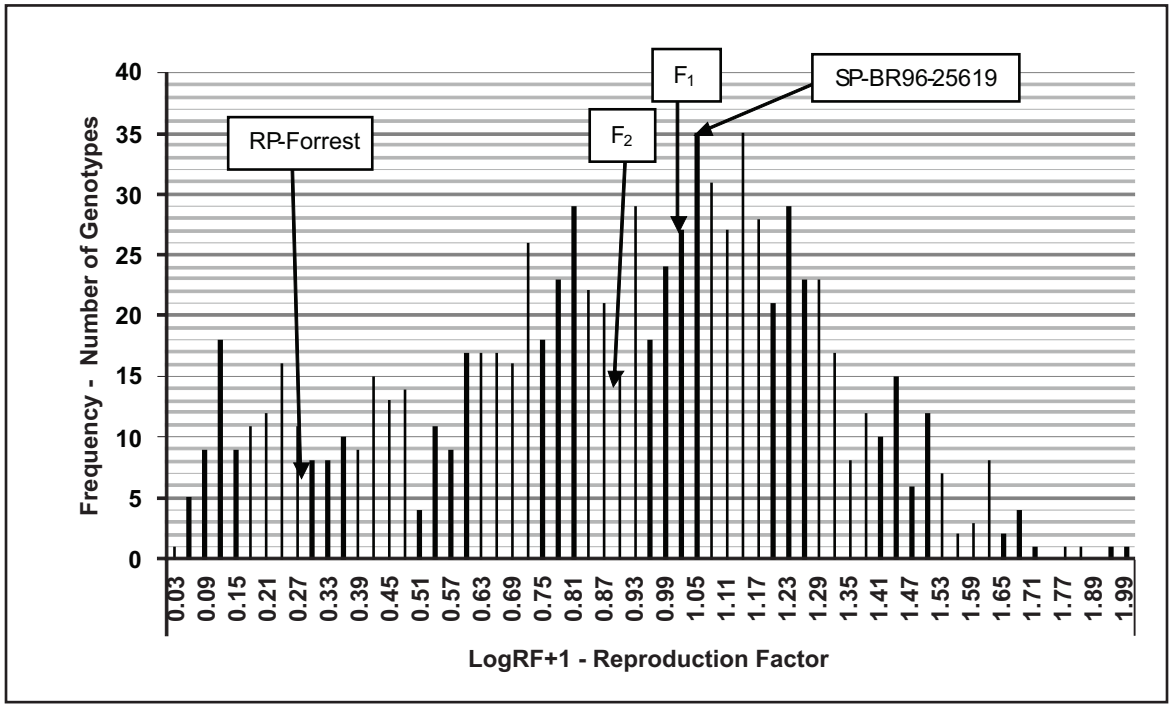

FIGURE 2 - Distribution of frequency of $F_{2:3}$ families derived from the cross Forrest x BR96-25619 for the trait log of reproduction factor (log RF+1) of reniform nematodes and the relative positions of resistant (RP) and susceptible (SP) parents and of the derived F_1 and F_2 generations.

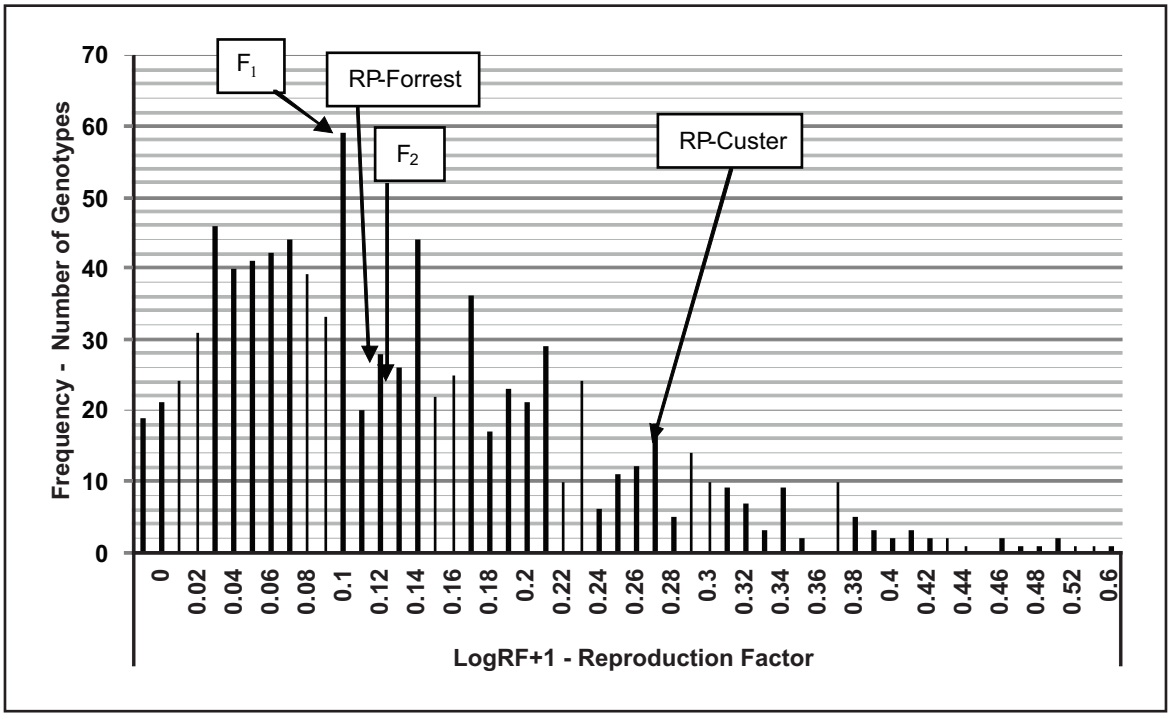

FIGURE 3 - Distribution of frequency of $F_{2:3}$ families derived from the cross Custer x Forrest for the trait log of reproduction factor (log RF+1) of reniform nematodes and the relative positions of resistant (RP) and susceptible (SP) parents and of the derived F_1 and F_2 generations.

to environmental factors. Each individual expresses a phenotypic value, but its true potential is given by the genotypic value. However, as the phenotypic value of an individual trait is the only one that can be directly measured, the proportion of the variability in the segregating population (F_2), which is genetic-based, should be assessed (Cruz, 2010).

Individuals of the F_1 generation from the FBR and CBR crossings displayed NGR and RF values similar to those of the susceptible parent BR96-25619 (Table 1), showing that the genetic effects of dominance, which is the sum of the dominance effects of several individual loci involved in the control of the trait, was directional towards susceptibility.

The log (x+1)-transformed data for NGR and RF allowed us to find genetic models, test their significance and have a better interpretation of the inheritance of resistance to *R. reniformis*, as previously reported (Ledo et al., 2001; Gravina et al., 2004).

There was a predominance of additive genetic effects for the resistance to reniform nematodes. The presence of additive genetic effects was also demonstrated through the significant estimates of additive genetic variance (D) for both variables evaluated in the three crossings, except for the character log (RF+1) in the crossing between resistant parents (CF). The occurrence of D is a guarantee that there is additive genetic variability to be exploited in selection processes for improving the level of nematode resistance in soybean cultivars. The absence of significant D in the resistant *vs.* resistant crossing was not unexpected. A low [d] value in the mean model is an indicative of low genetic divergence in this combination (R x R), which is difficult to detect in variance models in which the errors are larger than in the mean model.

Dominance indicates the behavior of F_1, F_2 and $F_{2:3}$ compared to the mean of the parents, being positive when graphically on the right and negative when on the left of the mean value of the parents. In this work, data of the three generations was positioned at the right of the mean value of the parents, indicating that the genetic effects of dominance play a role in determining the nature of resistance, and always in the direction of increasing the mean that corresponds to susceptibility. These results are similar to those obtained by Harville et al. (1985) crossing susceptible Davis and resistant Pickett 71 soybean cultivars. The authors suggested that the resistance is quantitative and controlled by two pairs of genes with unequal effects, one with complete recessiveness and another with no dominance.

Several soybean cultivars resistant to the soybean cyst nematode, *Heterodera glycines* Ichinohe, are also resistant to *R. reniformis*. Thus, the additive effect of genes in the former pathosystem was reviewed. Studies of Mendelian and quantitative genetics based on 120 $F_{2:3}$ families derived from 120 F_2 plants, 20 F_1 plants and 20

plants of each of the resistant parent cultivars E97-2502-9-3-1 and E97-2502-9-3-5 (PI437654-type), and of the susceptible parent cultivar E96-776 ('Hartwig'-type), have shown that two genes, a major one located in the linkage group A2 and strongly linked to the locus "I', and a minor one, hypostatic to the major gene, explain the resistance to race 4+ of *H. glycines* (Dias et al., 2005).

The occurrence of interaction between genes (non-allelic epistasis) is indicative of at least two genes controlling the character and that they are interacting. In this case the interaction is favorable for breeding for resistance, because the negative value indicates that the effect is directional for resistance to *R. reniformis*.

The CBR crossing showed a higher heritability (av. 40%) than the FBR crossing (av. 30%), indicating that higher genetic gains would be expected from the first one. To explore molecular markers linked to resistance genes, the CBR crossing would be the most advantageous since it has the highest D and minor E values among the variance models.

In this study, the crossing between the resistant parents Custer and Forrest as well as the evaluation of its generations were performed to check whether the genes for resistance to *R. reniformis* were the same in both resistant parents. Based on the data obtained we conclude that the genes involved in resistance to reniform nematodes are the same in both resistant parents. The likely explanation is that both resistant parents have the same origin, being descendants of Peking, which is also resistant to reniform nematodes. The number of individuals in each of the several classes and the proportions of individuals showing mean values either lower, equal or higher than the resistant parents indicates that the inheritance of soybean resistance to reniform nematodes is quantitative.

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