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Genetic analysis of the major gene plus polygene model in soybean resistance to *Leguminivora glycinivorella*

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ABSTRACT. In order to investigate the genetic characteristics of soybean *Leguminivora glycinivorella* resistance and to improve soybean resistance insectivorous breeding efficiency by applying the multi-generation joint analysis method of the major gene plus polygene model, 5 pedigrees and generations (P1, F1, P2, F2, and F2:3) were used as the materials to perform the soybean *L. glycinivorella* resistance multi-generation joint analysis. The results showed that soybean resistance to *L. glycinivorella* was controlled and inherited by an additive major gene plus additive, dominant polygene. The major gene had a negative additive effect (d = -0.1633). The combination of the anti-*L. glycinivorella* genes showed negative heterosis. Because the polygene additive effects were positive, the polygene effects would increase the insect herbivory rate in the F1 generation. This hybrid combination showed an insect herbivory rate polygenic heritability of 21.9556 and 54.3490% in the F2 and F2:3 pedigrees, which presented a high heritability. Therefore, it was appropriate to perform the selective breeding of the insect herbivory rate in the late generation.

Key words: Soybean; Major gene plus polygene; Insect herbivory rates; Genetic analysis

INTRODUCTION

Leguminivora glycinivorella (Mats) is the main pest that harms soybean production in the northern spring soybean area. It causes 5 to 10% loss in a normal year and up to 40% loss in a severe year in the Songliao Plain of Northeast China. It also can seriously affect the quality of the product (Yan et al., 2011). Domestic research focused on identifying the resistance methods and the insect resistance mechanisms of the *L. glycinivorella* (Xue and Cheng, 1992; Zhao et al., 1994), but few studies have investigated the heredity of the insect resistance (Sun et al., 1989). Zhang et al. (1983) found that soybean resistance against *L. glycinivorella* had quantitative heritability: the traits of F1 were between those of the parents, the F2 generation showed a continuous variation, and the future generations had gradually increased insect resistance. Sun et al. (1993) analyzed the F2 generation that resulted from the hybridization of 9 soybeans that were grown in conditions of artificial infestation. The experimental results showed that the insect resistance of the F2 generation had an asymmetrical distribution, but it did not have the quantitative trait-specific centrosymmetric distribution characteristics; therefore, the test results did not support purely quantitative trait assumptions. Liu (2004) used previously identified anti-*L. glycinivorella* materials to create the hybrid combinations. The F2 analysis showed that it was in accordance with the inheritance pattern known as the Jagger effect of 2 pairs of alleles. In order to clarify the genetic mechanism of *L. glycinivorella* resistance in the soybean and to determine whether the feature was caused by the major genetic inheritance, polygenic inheritance, or the combination of the 2 effects, we used the plant quantitative trait major gene and multi-gene mixed inheritance model as the method to analyze the genetic mechanism of *L. glycinivorella* resistance in the soybean and to provide a theoretical basis for the breeding of *L. glycinivorella*-resistant soybean.

MATERIAL AND METHODS

Materials

We selected the P1 and the EXP (P2) in the 2002 series as parents to configure a family of 5 generations. The experiment was carried out in Jilin Agricultural University in 2009. Hybridization was conducted to obtain the F1 generation seeds. The seeds were divided into 2 groups; 1 part was kept, and the other was hybridized in Hainan in the winter of 2009 to obtain the F2 seeds. In 2010, 1 part of the F2 generation seeds was planted, and the other part of the seeds was reserved to obtain the F2:3-derived lines. In 2011, 5 generations of pedigree seeds were planted in Jilin Agricultural University. Twenty-three and 29 parental materials were randomly selected from the 2002 and EXP series, respectively, 23 materials were randomly selected from the F1 population, 149 materials were randomly selected from the F2 population, and 136 families were randomly selected from the F2:3 groups (5 plants were randomly selected from each family) for a total of 360 copies of materials.

Measurement of the insect herbivory rate

The weight of *L. glycinivorella* herbivory soybean was known as the weight of soybean

after herbivory by *L. glycinivorella*, and the ratio of the insect herbivory weight to the total seed weight of each individual plant was known as the insect herbivory rate. The formula was as follows: insect herbivory rate = (weight of soybean after herbivory/seed weight per plant) x 100%.

Statistical analysis

The multi-generation joint quantitative trait separation model I was used to analyze the herbivory rate in the P1, F1, P2, F2, and F2:3 generations of the 2002 series and EXP hybrid combinations. The maximum likelihood method and iterated expectation and conditional maximization algorithm were used to estimate the related parameters, the Akaike's information criterion (AIC) and test for goodness-of-fit were used to select the most appropriate genetic model and calculate the distribution parameters. Finally, according to the selected genetic model, the heritability rate of major genes ($h_{mg}^2 = \sigma_{mg}^2/\sigma_p^2$) and heritability rate of polygenes ($h_{pg}^2 = \sigma_{pg}^2/\sigma_p^2$) were estimated. The genetic analysis software was provided by professor Zhang of Nanjing Agricultural University. In the data analysis, the insect herbivory rate measurement was presented as a percentage, and the majority of these values were less than 0.3. In order to meet the normality and mixed normality assumption in the analysis procedure, the data were arcsine-transformed for analysis.

RESULTS

Frequency distribution of the insect herbivory rate in each family and generation

The average P1, P2, and F1 insect herbivory rates were 0.7963, 1.1678, and 0.5802, respectively. The average insect herbivory rate in F1 was below the midparent value, indicating that the insect herbivory rate of this combination had negative heterosis (Figure 1). The F2 and F2:3 families and generations showed a bimodal distribution (Figures 2 and 3), suggesting that this combination may have the major genes that control the insect herbivory rate.

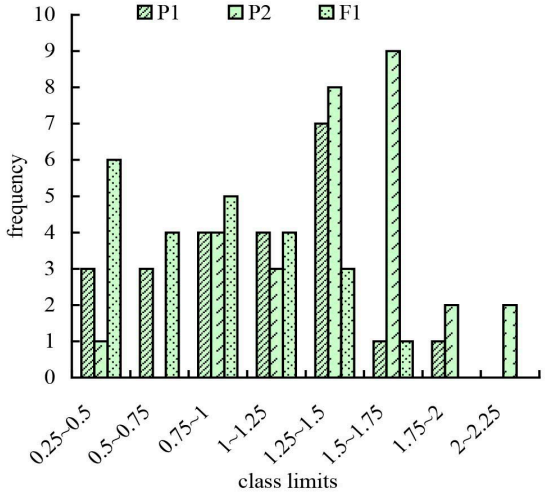

Figure 1. Insect herbivory rates of P1, F1 and P2.

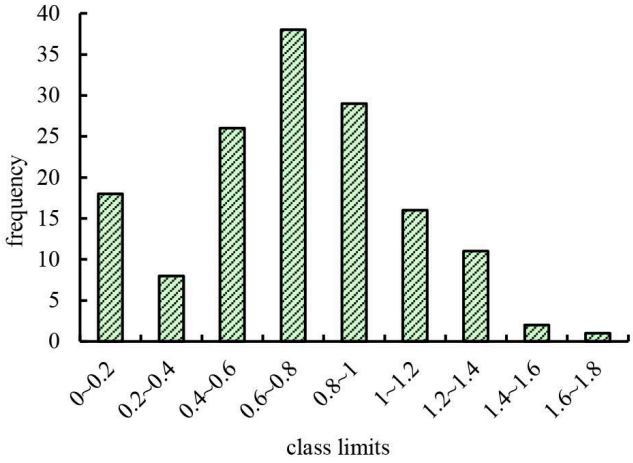

Figure 2. Insect herbivory rates in F2 generation.

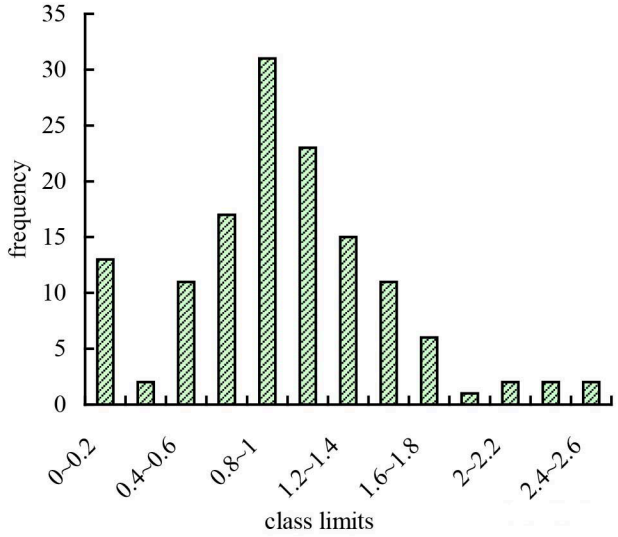

Figure 3. Insect herbivory rates in F2:3 generation.

Major gene model and polygenic model of insect herbivory rate

Genetic model

Through the major gene and polygenic genetic model and multi-generation joint analysis of the insect herbivory rate, the great values of the log-likelihood and AIC values in 24 kinds of genetic models were calculated. Among them, 3 models with the smallest AIC values were selected as the best candidate models (Table 1). The AIC values of the 3 models, D-2 (1

pair of additive major genes), D-3 (1 pair of completely dominant genes), and D-4 (1 pair of negative complete dominant major genes), were 412.3062, 416.3657, and 416.2266, respectively. These 3 models were selected as the genetic alternative models of the insect herbivory rate in the 2002 series and EXP hybrid combinations. The 3 models used 1 pair of major genes, indicating that the insect herbivory rate inheritance in this combination was controlled by 1 pair of major genes (Table 1).

Table 1. Akaike's information criterion (AIC) values in different genetic models of soybean herbivory rate.

Model	Great value of the log-likelihood	AIC value
D-2	-199.1531	412.3062
D-3	-201.1829	416.3657
D-4	-201.1133	416.2266

The 1 group fit testing of the D-2, D-3, and D-4 models was performed using 3 alternate models (U_1^2, U_2^2, U_3^2, nW^2, D_n). The statistics above were chosen, and the models with the fewest significant models was identified as the optimal model. Table 2 presented the fit test results of D-2, D-3, and D-4 models, which were not significant in 5 generations and 30 statistics using these 3 models. Then, it was necessary to perform the likelihood ratio test for D-2, D-3, and D-4. The chi-square value for D-2 and D-3 was 4.06 ($P < 0.05$), and that for D-2 and D-4 was 3.92 ($P < 0.05$), indicating that there were significant differences in the models. The D-2 model had the smallest AIC, so the D-2 model (a pair of additive genes plus an additive, dominant multi-gene model) was selected as the best genetic model for the 2002 series and EXP soybean hybrid combinations insect herbivory rate (Table 2).

Table 2. Fit test for soybean herbivory rate model.

Model	Group	U_1^2	U_2^2	U_3^2	nW^2	D_n
D-2	P1	0.126 (0.7229)	0.300 (0.5842)	0.666 (0.4144)	0.0646 (>0.05)	0.1429 (>0.05)
	F1	0.251 (0.6167)	0.364 (0.5464)	0.225 (0.6352)	0.1033 (>0.05)	0.1487 (>0.05)
	P2	0.180 (0.6713)	0.098 (0.7545)	0.154 (0.6944)	0.0726 (>0.05)	0.1532 (>0.05)
	F2	0.117 (0.7318)	0.546 (0.4599)	2.653 (0.1033)	0.1594 (>0.05)	0.0698 (>0.05)
	F2:3	0.006 (0.9367)	0.170 (0.6799)	1.804 (0.1792)	0.1477 (>0.05)	0.0659 (>0.05)
D-3	P1	0.127 (0.7220)	0.301 (0.5832)	0.667 (0.4142)	0.0647 (>0.05)	0.1430 (>0.05)
	F1	0.994 (0.3189)	1.246 (0.2643)	0.366 (0.5454)	0.1816 (>0.05)	0.1728 (>0.05)
	P2	0.181 (0.6704)	0.099 (0.7535)	0.154 (0.6947)	0.0727 (>0.05)	0.1533 (>0.05)
	F2	0.976 (0.3231)	1.875 (0.1709)	2.725 (0.0988)	0.2342 (>0.05)	0.0791 (>0.05)
	F2:3	0.110 (0.7405)	0.017 (0.8973)	3.237 (0.0720)	0.2155 (>0.05)	0.0843 (>0.05)
D-4	P1	0.187 (0.6652)	0.395 (0.5296)	0.703 (0.4017)	0.0721 (>0.05)	0.1479 (>0.05)
	F1	0.956 (0.3282)	1.202 (0.2729)	0.359 (0.5492)	0.1778 (>0.05)	0.1713 (>0.05)
	P2	0.251 (0.6165)	0.154 (0.6950)	0.138 (0.7103)	0.0809 (>0.05)	0.1588 (>0.05)
	F2	0.817 (0.3661)	1.708 (0.1913)	2.980 (0.0843)	0.2263 (>0.05)	0.0771 (>0.05)
	F2:3	0.018 (0.8925)	0.091 (0.7627)	2.996 (0.0835)	0.1957 (>0.05)	0.0769 (>0.05)

Significant threshold of nW^2 5% was 0.461. Numbers in parentheses are the theoretical probability values in columns U_1^2, U_2^2 and U_3^2, the corresponding values in parentheses of nW^2 and D_n are critical probability values.

Estimation of genetic parameters

The mean insect herbivory rate value (m = 0.7551), the major gene additive effect value (d = -0.1633), and the polygenic additive effect value (d = 0.4765) were large. The multi-gene dominant effect, which controlled the insect herbivory rate traits, was small (h =

-0.0537). The dominant effect of the major gene and the additive effect of multi-genes could decrease the insect herbivory rate value. The additive effect of multiple genes could increase the insect herbivory rate value. The major gene had a negative additive effect, indicating that the insect herbivory rate of the 2002 series x EXP combination had negative heterosis. The polygene additive effect was positive, suggesting that the insect herbivory rate increase in the F1 generation was mainly caused by the additive effect of multiple genes. The major genes in the F2 and F2:3 pedigrees showed lower heritability (8.4234 and 7.9066%, respectively). The polygene heritability rate was higher in these pedigrees (21.9556 and 54.3490%, respectively). The major gene + polygenic effects of the F2 and F2:3 pedigrees determined 30.3799 and 62.2556% of insect herbivory rate phenotypic variation, respectively. The major gene in the F2:3 pedigrees showed low heritability, but the polygene heritability was high, indicating that the insect herbivory rate in the F2:3 pedigrees may be controlled by multiple genes (Table 3).

Table 3. Estimation of genetic parameters in insect herbivory rate of the D-2 model.

First-order parameters	Estimated value	Second-order parameters	Estimated value	
			F2	F2:3
m	0.7551			
d	-0.1633	σ_p^2	0.1582	0.2919
[d]	0.4761	σ_{mg}^2	0.0133	0.0231
[h]	-0.0537	σ_{pg}^2	0.0347	0.1586
		σ_e^2	0.1102	0.1102
		h_{mg}^2	8.4243	7.9066
		h_{pg}^2	21.9556	54.3490

DISCUSSION

The quantitative traits were controlled by a group of genes with different effects. Among them, the genes with larger effects and easily perceived performance were the major genes, and the genes with small effects and less easily perceived performance were polygenes. The major gene plus polygene heritability model was a common model of quantitative traits; the pure major gene model and pure polygene model were just special cases in the quantitative trait hereditary.

As early as the 1970s, Elston and Stewart (1973) and Stewart and Elston (1973) proposed the major gene and polygene genetic model. It was applied in the genetic analysis of human pedigrees. Wang and Gai (1998), Gai and Wang (1998), and Gai et al., 2000 expanded the joint analysis of the multiple separate generations and the joint analysis of 5 generations (P1, F1, P2, F2, and F2:3) was used to make seeds that cannot be easily obtained by hybridization. Therefore, this method was suitable for the analysis of the insect herbivory rate of soybean with multiple generations. The multi-generation joint analysis method had a very important guiding significance for breeding. According to the quantitative trait major genes and polygene heritability, the corresponding effective breeding methods can be used (Gai et al., 2003).

Few studies have been conducted on the genetics of the insect herbivory rate in soybean. Liu et al. (2005) found that analysis of the F2 generation was in line with the 2 alleles genetic characteristics with independent dominant Jagger effects. Yan et al (2011) found that the soybean mode of inheritance in resistance to *L. glycinivorella* may be expressed as quantitative traits under certain conditions; it may also be expressed as a discontinuous variation of quality traits. Under the appropriate inoculation strength, the anti-*L. glycinivorella* trait can be more effective than any other quantitative traits. There were differences between our results and

the findings of Liu and Yan. Our results showed that soybean resistance to *L. glycinivorella* was controlled and inherited by 1 pair of additive major genes plus additive, dominant polygenes. The F2:3 pedigree mainly showed that the polygene quantitative trait was hereditary. Because we used limited combinations in this study, different types of anti-sense and anti-combinations should be increased in future studies to determine the specific soybean anti-*L. glycinivorella* mode. With the richness of the research materials and the deepening of the research, the genetic mechanism of soybean resistance to *L. glycinivorella* will gradually be revealed.

CONCLUSIONS

With the application of the multi-generation joint analysis method of major gene plus polygene model, we analyzed the soybean hybrid combinations 2002 series x EXP. The results showed that soybean resistance to *L. glycinivorella* was controlled and inherited by an additive major gene plus an additive, dominant polygene. The major gene had a negative additive effect (d = -0.1633). The polygene effect value was a larger positive value (d = 0.4765). The major genes in the F2 and F2:3 pedigrees showed low heritability (8.4234 and 7.9066%, respectively). The polygene showed a higher heritability in these pedigrees (21.9556 and 54.3490%, respectively). Therefore, it was appropriate to perform selective breeding for the insect herbivory rate in late generations.

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