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Full Length Article

Inheritance Analysis of "Major Genes + Polygenes" of Adult-Plant Stripe Rust Resistance in New Wheat Germplasm N07168

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Abstract

In order to clarify the genetic characteristics of resistance to stripe rust in new wheat germplasm N07168 and lay the preliminary foundation for the subsequent QTL fine mapping and the cloning of resistance genes, this experiment used N07168 as the male parent, crossed with the susceptible wheat cultivar Xinong979, to obtain the F_2 and $F_{2:3}$ segregating populations. The mixed inheritance model analysis method based on plant quantitative traits was applied to analyze five basic populations (P_1, P_2, F_1, F_2 and $F_{2:3}$). The results showed that the optimal inheritance model for stripe rust resistance at the adult plant stage in new wheat germplasm N07168 was D-3 model, which is a mixed inheritance model of "one pair of major genes with completely dominant effect plus polygenes with additive-dominant effect". The heritability of major resistance genes was 74.88 and 73.05% in the F_2 and $F_{2:3}$ populations, respectively. The polygenes' heritability was 3.92 and 3.49%, respectively, with an additive-dominant effect. The proportions of the environmental variance to the phenotypic variance were 21.2 and 23.06%, respectively, indicating that environmental effects also had an influence on the resistance expression of the major gene. Finally, using a set of nulli-tetrasomic lines of "Chinese Spring", we confirmed that this pair of completely dominant major genes was located on chromosome 1B. © 2019 Friends Science Publishers

Keywords: Wheat; Stripe rust resistance; Quantitative traits; Inheritance model

Introduction

Wheat stripe rust caused by *Puccinia striiformis* f. spp. *tritici*, may induce a serious damage to wheat production (Chen *et al*., 2002). Its high frequency of occurrence, wide spread distribution and strong ability to spread spores generally lead to 10–30% reduction in wheat production, which could be as high as 60% or more in severe cases, seriously threatening the safety of wheat production in the world's major wheat-producing countries (Wellings, 2011). At the same time as causing a significant reduction in wheat production, it will also seriously degrade wheat quality and cause huge economic losses. In the prevention and control of wheat stripe rust, breeding and application of resistant varieties is undoubtedly the most economical and ecologically safe method (Chen, 2013, 2014). Therefore, it is an important basic research work to continuously discover new stripe rust resistance genes and realize the diversification and rational layout of disease-resistance genes.

At present, most reports on the genetic analysis of adult-plant stripe rust resistance are based on Mendelian inheritance law for ratio analysis of disease-resistant plants to susceptible plants and then chi-square analysis method is used for suitability test. Because there were many intermediate infection types in the hybrid-derived progeny of N07168 and Xinong979 in this experiment, the simple identification of resistant plants and susceptible plants is often more error-prone. The mixed inheritance model analysis method based on plant quantitative traits (Gai and Wang, 1998; Zhang *et al*., 2000; Gai *et al*., 2003) can identify the major genes' and polygenes' effects, estimate the epistasis between genes, and involve the interaction between genes and environment. Therefore, we used IEMC algorithm (Zhang and Gai, 2000) to analyze the genetic characteristics of stripe rust resistance in new wheat germplasm N07168 through the jointly segregating analysis method of five basic populations (P_1, P_2, F_1, F_2 and $F_{2:3}$).

The new wheat germplasm N07168 was selected from the cross of Shaanyou225 and synthetic wheat SE5799. We continuously observed its resistance to stripe rust in the field from 2016 to 2019 and found that N07168 always showed near immunity to the stripe rust physiological races CYR32 and CYR33. Therefore, genetic analysis of resistance was carried out to determine disease-resistance genes' number, heritability and ways of interaction, which laid the preliminary foundation for the subsequent QTL fine mapping and cloning of the target gene. It is also of great significance for the future scientific use of this resistant germplasm.

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Materials and Methods

Plant Material

The new wheat germplasm N07168, which is highly resistant to the stripe rust physiological races CYR32 and CYR33, was selected from the cross of Shaanyou225 and synthetic wheat SE5799. The susceptible parent Xinong979 is the main winter wheat cultivar in China. The above two parents were provided by Prof. Ji Wanquan and Associate Professor Wang Yajuan of the Laboratory of Wheat Remote Hybridization and Chromosome Engineering at the College of Agronomy of Northwest A&F University. The F_1, F_2 and $F_{2:3}$ derived lines obtained by crossing N07168 as the male parent and Xinong979 as the female parent were preserved by our laboratory.

A set of nulli-tetrasomic lines of "Chinese Spring" N1BT1D, N1AT1B, N1DT1A, N2BT2D, N2AT2B, N2DT2A, N3BT3D, N3AT3B, N3DT3A, N4BT4D, N4AT4B, N4DT4A, N5BT5D, N5AT5B, N5DT5A, N6BT6D, N6AT6B, N6DT6A, N7BT7D, N7AT7B and N7DT7A were used to determine the chromosomal location of the simple sequence repeat (SSR) markers linked with major resistance genes.

Evaluation of Parents and Progeny of N07168/Xinong979 for Reaction to Stripe Rust

Stripe rust resistance of five basic populations (P_1, P_2, F_1, F_2 and $F_{2:3}$) was identified in 2018 and 2019 at the Experimental Field of the College of Agronomy, Northwest A&F University, Yangling, Shaanxi, China. P_1, P_2, and F_1 were each sown in 1 row, with a length of 1 m and 20 seeds per row. F_2 segregating populations were sown in the form of 20 seeds per row, and a row of Xinong979 was added every 10 rows as a susceptibility control. $F_{2:3}$ segregating populations were sown in the form of 1 line per row and a row of Xinong979 was added every 10 rows as a susceptibility control.

Stripe rust was inoculated in the field in late March 2018 and 2019 and the survey of single-plant infection types of P_1, P_2, F_1, F_2 and $F_{2:3}$ populations was carried out in early May. We observed 2 times, 7 days apart. According to the method of Li (1995), the infection types were divided into immunity (0), near immunity (0;), high resistance (1), moderate resistance (2), moderate susceptibility (3), high susceptibility (4) a total of 6 classes.

Molecular Marker Analysis (DNA Extraction, PCR Amplification, Polyacrylamide Gel Electrophoresis, Gel Visualization)

Genomic DNA was extracted from leaf tissue of parents and 309 plants of F_2 population using the CTAB method (Song *et al*., 1994).

A total of 369 synthesized SSR primers based on the sequences published in the Grain Genes database were screened and primers with polymorphic DNA bands in the parents and F_2 populations were selected for nulli-tetrasomic analysis. PCR was performed in a reaction volume of 10 μL containing 1 μL 10×Buffer, 0.8 μL dNTPs, 1 μL primer, 0.06 μL Taq DNA polymerase, 1 μL DNA and 6.14 μL ddH_2O. Reactions were performed using the following program: 94℃ for 3 min, 94℃ for 30 s, 50–65℃ (depending on the different primers) for 45 s, 72℃ for 1 min, 72℃ for 10 min and 12℃ forever. PCR products were electrophoresed using 8% SDS-PAGE, and gel visualization was achieved by silver nitrate staining and formaldehyde development (Chen *et al*., 1998).

Statistical Analysis

The experimental data were analyzed through the jointly segregating analysis method of five basic populations (P_1, P_2, F_1, F_2 and $F_{2:3}$) based on plant quantitative traits (Gai and Wang, 1998; Zhang *et al*., 2000; Gai *et al*., 2003). The theoretical basis is the mixed distribution theory, which regards the distribution of segregating populations as a mixture of multiple normal distributions of major genes under the modifications between polygenes and environment. The distribution parameters of the relevant components in the mixed distribution were estimated through the maximum likelihood method and the IECM (iterated expectation and conditional maximization) algorithm (Zhang and Gai, 2000) and then tested by AIC (Akaike's information criterion) values and a set of suitability test. The optimal model could be selected, with the corresponding variances, effect values of major genes plus polygenes, and related genetic parameters estimated accordingly.

Results

The Frequency of Infection Types in Parents and Hybrid Progeny

The identification result of stripe rust resistance in five basic populations (Fig. 1 and Table 1) showed that the coefficient of variation of infections types in each population was not higher than 15%, which satisfied the requirement of the genetic experiment based on plant quantitative traits. For the distribution of infections types (Fig. 2), the F_2 and $F_{2:3}$ populations exhibit multimodal skewed distribution that was not completely consistent with the classical quantitative traits. Therefore, the resistance to stripe rust of new wheat germplasm N01768 was a quantitative trait with the effects of major genes.

Selection and Testing of Optimal Inheritance Models

We jointly analyzed the five basic populations (P_1, P_2, F_1, F_2 and $F_{2:3}$) of N07168/Xinong979 and the AIC values and maximum likelihood values (MLV) of 22 inheritance

Table 1: Basic parameters of the five basic populations (P_1, P_2, F_1, F_2 and $F_{2:3}$) of N07168/Xinong979

Population	Sample size	Average value	Variance	Coefficient of variation
P_1	20	1.25	0.51	0.56
P_2	20	3.60	0.67	0.23
F_1	20	1.40	1.20	0.78
F_2	309	2.18	1.90	0.63
$F_{2:3}$	305	2.32	1.73	0.57

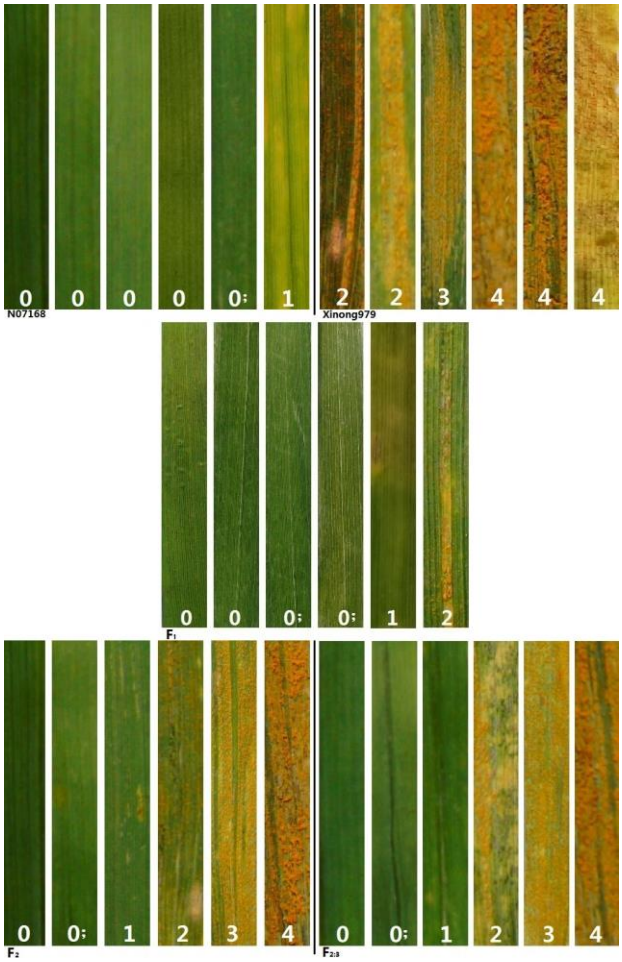

Fig. 1: Resistance reactions to stripe rust of different single plant in five basic populations (P_1, P_2, F_1, F_2 and $F_{2:3}$) of N07168/Xinong979

models were obtained through the IEMC algorithm (Table 2). Several sets of models with small AIC values that were not far from each other were selected as candidate models which were then tested for suitability (Table 3). The less the number of statistical indicators that reach significant differences, the better the model.

According to the principle of minimum AIC value, three sets of inheritance models D-0, D-1 and D-3 were selected as candidate models and tested for suitability. It could be seen from Table 3 that 11 statistical indicators of the D-0 model had reached significant differences and 2 had reached extremely significant differences; 9 statistical

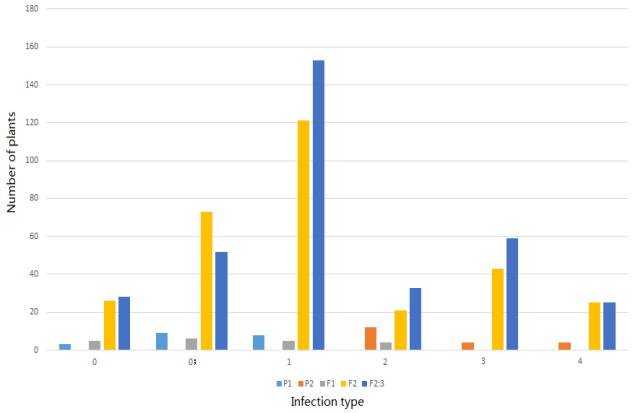

Fig. 2: The frequency of infection types in P_1, P_2, F_1, F_2 and $F_{2:3}$ populations

indicators of the D-1 model had reached significant differences and 1 had reached extremely significant differences; there were 10 statistical indicators in the D-3 model that had reached significant differences, but no extremely significant differences. Therefore, the D-3 model was chosen as the optimal model, which is a mixed inheritance model of "one major gene with completely dominant effect plus polygenes with additive-dominant effect".

Estimation of Genetic Parameters in the Optimal Model

The estimated values of the first-order genetic parameters and second-order genetic parameters in the D-3 model are shown in Table 4. In the mixed inheritance model of "one major gene with completely dominant effect plus polygenes with additive-dominant effect", the dominant effect of the major gene is equal to its additive effect (Gai *et al*., 2003), therefore both dominant and additive effect values of the major gene resistant to stripe rust of the new wheat germplasm N07168 were 1.35, which was a positive effect. The estimated values of the dominant effect and additive effect of polygenes were 0.63 and 0.18, respectively.

In the D-3 model, the major genes' variances of F_2 and $F_{2:3}$ populations were 1.42 and 1.26, respectively. The major genes' heritability is 74.88 and 73.05%, respectively. The polygenes' variances are 0.07 and 0.06, respectively. The polygenes' heritability is 3.92 and 3.49%, respectively. The ratio of environmental variances to phenotypic variances was 21.2 and 23.06%, respectively.

This showed that the resistance to stripe rust of new wheat germplasm N07168 was mainly controlled by a pair of completely dominant major genes, and the resistance gene could be stably inherited. Although the contribution rate of micro-effect polygenes' resistance was not high, it existed and had an additive effect. Environmental factors also had a certain impact on the expression of the major gene and should be properly considered in the actual breeding process.

Table 2: MLV and AIC values for each inheritance model

Model code	Model implication	AIC	MLV
A-1	One additive-dominance major gene	2193.05	-1092.53
A-2	One additive major gene	2285.77	-1139.88
A-3	One dominance major gene	2191.28	-1092.64
A-4	One negative dominance major gene	2317.81	-1155.91
B-1	Two additive-dominance-epistasis major genes	2199.68	-1089.84
B-2	Two additive-dominance major genes	2197.01	-1092.50
B-3	Two additive major genes	2287.67	-1139.83
B-4	Two dominance major genes	2193.29	-1092.65
C-0	Additive-dominance-epistasis polygenes	2279.41	-1129.70
C-1	Additive-dominance polygenes	2277.00	-1131.50
D-0	One additive-dominance major gene + additive-dominance-epistasis polygenes	2165.64	-1072.82
D-1	One additive-dominance major gene + additive-dominance polygenes	2185.40	-1084.70
D-2	One additive major gene + additive-dominance polygenes	2200.10	-1093.05
D-3	One completely dominance major gene + additive-dominance polygenes	2175.11	-1080.55
D-4	One negative dominance major gene + additive-dominance polygenes	2240.68	-1113.34
E-0	Two additive-dominance-epistasis major genes + additive-dominance-epistasis polygenes	2291.40	-1129.70
E-1	Two additive-dominance-epistasis major genes + additive-dominance polygenes	2211.46	-1091.73
E-2	Two additive-dominance major genes + additive-dominance polygenes	2204.10	-1092.05
E-3	Two additive major genes + additive-dominance polygenes	2271.29	-1127.64
E-4	Two equal additive major genes + additive-dominance polygenes	2270.07	-1128.03
E-5	Two dominance major genes + additive-dominance polygenes	2201.05	-1092.52
E-6	Two equal dominance major genes + additive-dominance polygenes	2245.25	-1115.63

Table 3: Suitability test for alternative inheritance models

Model code	Population	U_1^2	U_2^2	U_3^2	${}_nW^2$	D_n
D-0	P_1	0.036(0.8492)	0.225(0.6356)	1.343(0.2464)	0.3319*	0.2813
	P_2	0.032(0.8583)	0.722(0.3956)	16.723(0.0000)**	0.4351*	0.2857
	F_1	0.655(0.4182)	0.036(0.8488)	5.628(0.0177)*	0.6175*	0.4278*
	F_2	0.152(0.6963)	0.035(0.8513)	0.580(0.4461)	2.1960*	0.2323*
	$F_{2:3}$	5.586(0.0181)*	7.894(0.0050)**	4.345(0.0371)*	3.2870*	0.2822*
D-1	P_1	0.032(0.8585)	0.141(0.7072)	0.659(0.4168)	0.2669	0.2371
	P_2	2.439(0.1183)	0.796(0.3723)	6.153(0.0131)*	0.4515*	0.3594*
	F_1	0.507(0.4765)	0.375(0.5405)	0.096(0.7570)	0.4675*	0.3744*
	F_2	1.536(0.2152)	0.566(0.4520)	3.211(0.0731)	2.1821*	0.2294*
	$F_{2:3}$	0.979(0.3225)	2.677(0.1018)	7.356(0.0067)**	2.7476*	0.2485*
D-3	P_1	0.006(0.9400)	0.016(0.9006)	0.626(0.4289)	0.2649	0.2333
	P_2	2.658(0.1030)	0.908(0.3406)	6.260(0.0124)*	0.4713*	0.3648*
	F_1	0.229(0.6323)	0.184(0.6678)	0.019(0.8913)	0.4378*	0.3579*
	F_2	2.164(0.1413)	1.020(0.3125)	2.744(0.0976)	2.2573*	0.2367*
	$F_{2:3}$	0.038(0.8453)	0.462(0.4965)	3.858(0.0495)*	2.6362*	0.2290*

U_1^2、U_2^2、U_3^2 are the statistic of equality test. ${}_nW^2$ is the statistic of Smirnov test. D_n is the statistic of Kolmogorov test. The values before the parentheses are statistic values, and the values in parentheses represent the corresponding probabilities. * indicates a significant difference at the 0.05 level; ** indicates a significant difference at the 0.01 level

Table 4: The Estimated Values of Genetic Parameters in the D-3 Model

First-order parameter	Estimated value	Second-order parameter	Estimated value	
			F_2	$F_{2:3}$
m	2.5207	σ_p^2	1.90	1.73
d	1.3540	σ_{mg}^2	1.42	1.26
[d]	0.1790	σ_{pg}^2	0.07	0.06
[h]	0.6259	h_{mg}^2	74.88%	73.05%
		h_{pg}^2	3.92%	3.49%
		$1-(h_{mq}^2+h_{pq}^2)$	21.20%	23.06%

Nulli-tetrasomic Analysis

Through the above experimental methods, four SSR molecular markers (Table 5) with stable polymorphic DNA bands in the parents and F_2 populations were selected. They were Xgpw5195, Xbarc55, Xwmc597 and Xwmc230. In order to further determine which chromosome the disease-resistance gene was located on, we made the following nulli-tetrasomic analysis.

It could be seen from the results in the Fig. 3 that the SSR primers Xgpw5195, Xbarc55 and Xwmc597 did not amplify the target bands between 100–250 bp on the N1BT1D material compared with Chinese Spring, N07168 and Xiong979; Xwmc230 did not amplify the target bands between 250–500 bp on the N1BT1D material either. Therefore, it could be considered that the stripe rust resistance gene of the new wheat germplasm N07168 was located on chromosome 1B.

Table 5: Information about SSR Primers Xgpw5195, Xbarc55, Xwmc597, and Xwmc230

Primer	Sequence (5'-3')	Annealing temperature	Size (bp)
Xgpw5195F	CGACTCTCGCTTCAGCTTG	58°C	100-250 bp
Xgpw5195R	GGTTCTTCACGCCATTGATT		
Xbarc55F	GCGGTCAACACACTCCACTCCTCTCTC	55°C	100-250 bp
Xbarc55R	CGCTGCTCCCATTGCTCGCCGTTA		
Xwmc597F	AACACACCTTGCTTCTCTGGGA	61°C	250 bp
Xwmc597R	GACTAGGGTTTCGGTTGTTGGC		
Xwmc230F	AGAAGCGAGCAGGTGTGTTTGA	61°C	250-500 bp
Xwmc230R	CTGCTTCCTCCCACAACAGATG		

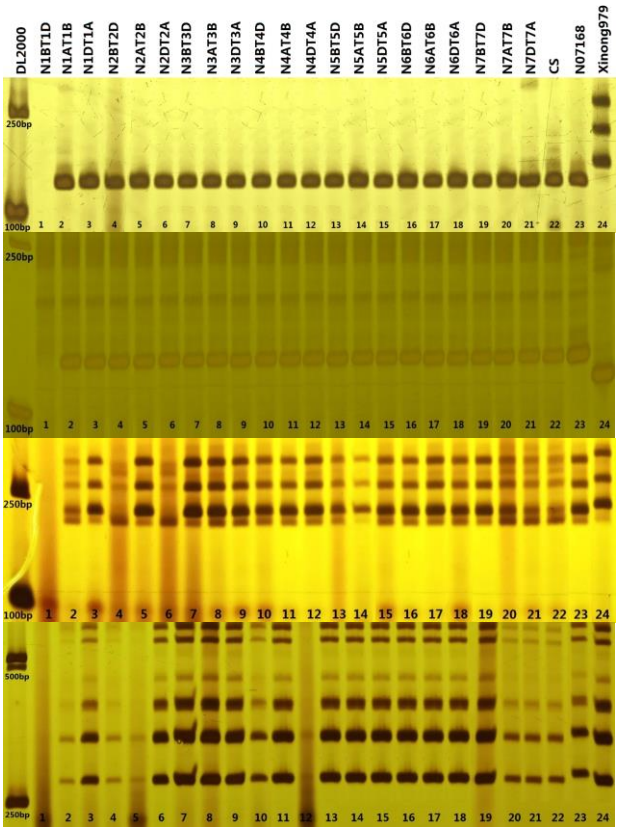

Fig. 3: DNA Amplification Results of SSR Primers Xgpw5195, Xbarc55, Xwmc597, and Xwmc230 in Nulli-tetrasomic Analysis

Discussion

Previous studies have shown that most of the disease resistance in wheat has the genetic characteristics of quantitative traits. For example, the resistance to sharp eyespot of ARZ wheat was a quantitative trait, which was regulated by two pairs of linked major genes (Ren *et al.*, 2005); The fusarium head blight resistance trait of Sumai3 wheat was controlled by three pairs of major genes, and the interaction effect among major genes was significant (Yao *et al.*, 2011); The resistance to take-all fungus of peculiar wheat germplasm H9021 was controlled by two pairs of major genes with an additive-dominant-epistatic effect (Wei *et al.*, 2009).

For wheat stripe rust, 49 disease-resistance genes have been officially named in 47 loci, most of which are dominant or incompletely dominant, while Yr2, Yr6 and Yr9 genes are recessive (Kang and Chen, 2017). The inheritance of resistance to stripe rust was diverse in different wheat varieties. According to research, the resistance of Zhengmai7698 wheat to the Pst predominant race CYR32 was controlled by a single-dominant gene (Li *et al.*, 2018); the inheritance of stripe rust resistance in Chuanmai45 wheat was conferred by two genes (Yang *et al.*, 2016); the adult-plant resistance to the stripe rust physiological races CYR30 and CYR32 in wheat cultivar Xiaoyan6 was controlled by two pairs of recessive genes with additive effect (Ma, 2013); the stripe rust resistance of hybrid progeny in cross Bakhiawar/Frontana was controlled by two major genes with additive-dominant-epistatic effect plus polygenes with additive-dominant-epistatic effect (model E-0) (Irfaq and Ajab, 2009).

Van Der Plank believed that the quantitative disease resistance of plants controlled by micro-effect polygenes had no obvious specificity to the physiological races and might remain effective for a long time (Plank, 1975). This argument has been accepted by many researchers and at least no clear evidence has yet been found that the disease resistance controlled by micro-effect polygenes was overcome by certain stripe rust physiological races. Singh *et al.* (2011) analyzed the composition of adult-plant resistance genes in a series of CIMMYT wheat resistant to stripe rust, and found that these cultivars had at least 10–12 minor polygenes possessing additive effects that regulated slow rust, except for the major gene Yr18. As these polygenes accumulated, the disease resistance gradually increased (Singh and Rajaram, 1993; Singh *et al.*, 2000). Since 1957, he has used polygenes that regulate slow-rusting traits for long-term breeding of spring wheat resistant to stripe rust and finally based on the combination of 4 or 5 minor polygenes, a number of varieties resistant to stripe rust were selected and their disease resistance reached near-immune levels which remained effective for a long time (Singh *et al.*, 2011). Therefore, the quantitative disease resistance of micro-effect polygenes can improve the persistence of major genes, and the combination of major genes and polygenes should be applied to breed new wheat germplasm with broader resistance spectrum.

The results of this experiment showed that the resistance to stripe rust of new wheat germplasm N07168

was controlled by one completely dominant major gene and additive-dominant polygenes. Both dominant and additive effect values of the major gene were 1.35, which was a positive effect. The estimated values of the dominant effect and additive effect of polygenes were 0.63 and 0.18, respectively. The major genes' heritability was 74.88 and 73.05% in F_2 and $F_{2:3}$ populations, respectively. The polygenes' heritability was 3.92 and 3.49%, respectively. The proportions of the environmental variance to the phenotypic variance were 21.2 and 23.06%, respectively, indicating that environmental effects also had an influence on the resistance expression of the major gene. The major resistance gene was located on chromosome 1B through nulli-tetrasomic analysis. Further research work is still needed to obtain the genetic map by developing molecular markers that are tightly linked to the major gene and achieve the cloning of the target gene.

Conclusion

In this research, the inheritance model of stripe rust resistance in new wheat germplasm N07168 was studied. It was confirmed that the resistance trait was controlled by one major gene plus polygenes. The major gene located on chromosome 1B showed complete dominance and the polygenes showed additive dominance (model D-3).

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