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Optimization of breeding methods when introducing multiple resistance genes from American to Chinese wheat

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Stripe rust is one of the most destructive diseases of wheat worldwide. Growing resistant cultivars with resistance genes is the most effective method to control this disease. QuLine is a computer tool capable of defining genetic models, breeding strategies and predicting parental selection using known gene information. This paper reports the breeding process for pyramiding resistance genes to stripe rust using genetic information of American cultivars Aplowa (P1), Louise (P2), Express (P3) and Chinese cultivar Zhoumai18 (P4). The breeding objective was to transfer the stripe rust (SR) resistance genes from the three American lines to the elite Chinese wheat, without reducing its desired agronomic performance (AT). Results show that double crosses (P4×P1)//(P4×P2), (P4×P1)//(P4×P3) and (P4×P2)//(P4×P3) were efficient in improving genetic gains on traits AT and SR in selection strategy AHA, while only in HAH, cross combination (P4×P3) // (P1×P2) had the highest genetic gains on high-temperature, adult-plant resistance (HTAP). The results in this study could be important in targeted breeding for efficiently pyramiding more resistance genes to stripe rust, avoiding simplified resistance genes, and breeding novel varieties.

Key words: Breeding methods, wheat, resistance, genes.

INTRODUCTION

Wheat stripe rust, caused by *Puccinia striiformis Westend. f. sp. tritici Eriks.* is an air-borne fungal disease worldwide. The use of resistant cultivars, widely recog-nized worldwide, is the primary measure to control stripe rust due to its effective, economic, and environmentally friendly characteristics.

Race-specific and non-race-specific resistance is two major types of resistance to wheat stripe rust. Seedling resistance is generally race-specific resistance and shows qualitative inheritance (Lin and Chen, 2008; Sui et al. 2009; Li et al. 2010, Gao et al. 2011), whereas adult-plant resistance is non-race-specific, durable, and shows quantitative inheritance (Uauy et al., 2005; Lin and Chen, 2007 and 2009; Santra et al., 2008). However, resistant cultivars, after relatively short-time promoted, tend to

'loss' resistance due to the rapid virulence changes in pathogen populations. Zhoumai18, carrying *Yr9* from wheat-rye IB/IR chromosome substitution line, showed resistance to leaf rust, stem rust, stripe rust and powdery mildew, and was grown broadly in the 1970s and 1980s in China (Wu and Niu, 2000; Shi ZX et al., 2001). At the end of the 1980s, the production and development of races CYR28 and CYR29 led to *Yr9* resistance losing, wheat stripe rust epidemic in 1990 and the wheat output loss of over 20 billion kg.

Many cultivars grown in the Pacific Northwest (PNW) of the United States were reported to carry high-temperature, adult-plant resistance (HTAP) genes to stripe rust, for example, cultivars Alpowa and Louise from PNW carry major HTAP QTLs *Yr39* (Lin and Chen, 2007) and *Qyrlo.wgp-2BS* (Carter et al., 2009), respectively. Cultivar Express from PNW carries three HTAP QTLs *Qhtap.wsu-6AS*, *Qhtap.wsu-3BL* and *Qhtap.wsu-1BL* (Lin and Chen, 2009). The exploitation and utilization of these

Table 1. The location and genotypic value of resistance genes.

Cultivar	Resistance gene	Resistance type	Location	Favorable genotype value	Weighted genotype value[†]	Reference
Zhoumai18	*Yr9*	SR	1RS	100	50	--
Alpowa	*Yr39*	HTAP	7BL	21.7	16.05	Lin and Chen (2007)
Express	*Qhtap.wgp-6AS*	HTAP	6AS	13.3	9.84	Lin and Chen (2009)
	Qhtap.wgp-3BL	HTAP	3BL	12.5	9.24	Lin and Chen (2009)
	Qhtap.wgp-1BL	HTAP	1BL	6.8	5.03	Lin and Chen (2009)
Louise	*Qyrlo.wgp-2BS*	HTAP	2BS	13.3	9.84	Lin and Chen (2009)

[†]Weighted genotype value= (qualititative or quantitative genotype value ÷ total qualititative or quantitative genotype value) ×mid-parent value 50.

HTAP resistance QTLs can overcome the loss of race-specific resistance to stripe rust to the frequent variation of pathogen virulence and is very meaningful to durable resistance in wheat stripe rust breeding.

Traditional breeding techniques involve making thousands of crosses, only 2% of which in addition to qualifying as breeding goal traits, also result in the loss of other crosses considered to be eliminated in the selection process. Hence, it is hard to decide in the short-term how to utilize HTAP QTLs and select parents, and also difficult to know which is the most efficient selection strategy through traditional breeding. Nowadays, domestic and international scientists are trying to combine computer technology and quantitative genetics or breeding methods together, such as the exploitation of simulated breeding platform and software (Frisch et al., 2000), comparison of different breeding methods (Wang et al., 2003a), the optimization and modification of breeding strategy and selection strategy (Wang et al., 2007) and so on. QU-GENE is a simulation platform developed at the University of Queensland for quantitative analysis of genetic models. QuLine (previously called QuCim), the application module of QU-GENE, designed specifically for simulating CIMMYT's wheat breeding program, can simulate a breeding program under complex genetic models.

The objectives of this study were to predict hybrid performance of Alpowa, or Express or Louise crossing with Zhoumai18 based on different breeding strategy, to optimize crosses, and to establish breeding platform for pyramiding resistance genes to stripe rust.

MATERIALS AND METHODS

Definition of genetic models in QU-GENE

One environment type was defined and the genotype × environment (GE) interaction system was not considered in QU-GENE in this study. Three general traits were also defined in the models, which were seedling resistance (SR), HTAP resistance to stripe rust and adaptation (AT). Adaptation is a combined index of various breeding target traits (except SR and HTAP), such as maturity, plant height, yield and quality. Parental lines included Chinese cultivar Zhoumai18 and three American cultivars (Alpowa, Express and Louise). Resistance genes and their effects from the parents are listed in Table 1.

Assuming R and r were the two alleles at SR locus, then SR values of the three genotypes RR, Rr, and rr were 50, 25, and 0, respectively. When the mid-parent value is defined as 50, the highest SR value is 100, which indicates all the favorable alleles are fixed, and the lowest value is 0, which means no favorable alleles are present (SR values equals to genotype values plus mid-parent values). Due to the qualitative characteristics of SR, the broad-sense heritability was set at 1.

Five additive genes (*Yr39, Qhtap.wgp-6AS, Qhtap.wgp-3BL, Qhtap.wgp-1BL,* and *Qyrlo.wgp-2BS*) contribute to the expression of HTAP resistance; the distribution on wheat chromosomes are listed in Table 1. Assuming H and h are the two alleles at a HTAP locus, the genotypic values of HH, Hh, and hh are weighted (Table 1). If the mid-parent is 50, the highest HTAP value are 100 (all favorable alleles present), and the lowest HTAP value is 0 (no favorable alleles present).

A total of 210 additive genes which are evenly distributed on the 21 chromosomes were to have considered contributed to the expression of AT, and the distance between two neighboring genes was set at 10cM.

Assuming A and a are the two alleles at an AT locus, the genotypic values of AA, Aa, and aa are 1, 0, and -1, respectively. Meanwhile, we also consider the pleiotropy with which each HTAP may affect 4 AT values. Therefore, the mid-parent value is 230, the highest AT value is 460 (all favorable alleles present), and the lowest AT value is 0 (no favorable alleles present). The phenotypic value of an individual is actually defined by the frequency of favorable genes, gene combinations and some associated environmental errors in an environment. It allows the definition of different parental groups based on different gene frequencies in QU-GENE and QuLine assuming the favorable gene frequency of American cultivars is 0.3 for AT and 1 for HTAP, while favorable gene frequency of Chinese cultivar is 0.8 for AT and 1 for SR. Broad-sense heritability at the individual plant level was set at 0.6 and 0.3 for both HATP and AT, respectively.

In order to estimate environmental errors, original population with 200 individuals was created first in the QU-GENE file, and the gene frequency of population was assumed as 0.5 (Wang et al., 2003a).

Breeding process

In the simulation experiment, the single backcrossing breeding strategy was employed. The selected bulk method (SELBLK), with two options pedigree and bulk in QuLine for the generation advance method (Wang et al., 2003b), was applied in the entire breeding cycle containing 7 generations. In the SELBLK method, spikes of selected $F_2 \sim F_5$ plants within each cross are harvested in bulk and threshed together, resulting in just one cross in the next generation,

Table 2. The single backcrossing breeding strategy in the simulation study.

Generation	selected proportion[†]	Number of crosses or family grown	Individuals per cross or family	Number of selected crosses or family	Number of selected individuals in each cross or family	Generation advance method
F1	--	100	10	100	10	bulk
BC_1F_1	0.292	100	1200	100	30	bulk
BC_1F_2	0.292	100	400	100	10	bulk
BC_1F_3	0.292	100	400	100	10	bulk
BC_1F_4	0.292	100	400	100	10	bulk
BC_1F_5	0.292	100	400	1000	1	pedigree
BC_1F_6	0.215	1000	100	10	100	bulk

[†]Selected proportion = $\sqrt[A]{B}$ (A is the total number of trait selection; B= number of selected individuals in each cross or family ÷ number of individuals per cross or family)

while pedigree selection is used only in the F_6 (Table 2) (Wang et al. 2003a and 2003b). In each generation, there are different traits and selected intensities (selected proportions) for selection (Table 2).

For the selection strategy, if traits SR, HTAP, and AT in the next generation are considered, selected proportion for the generations F_2 to F_6 is 0.292, while the selected proportion for F_7 generation is 0.215; If traits SR, AT, HTAP, AT or SR, HTAP, AT, HTAP in different growth stages of the same generation are considered, selected proportions of the generations F_2 to F_6 are 0.398, the F_7 is 0.316 (Table 2).

The design of simulation experiments

It was a combined computer simulation of the selection process and known gene information to assist in parental selection for strip rust resistance breeding in this simulation experiment. Using breeding methods single-cross, double-cross, and triple-cross, a total of 12 different crosses were made as follows: $P_4 \times P_1$, $P_4 \times P_2$, $P_4 \times P_3$, $P_4//(P_1 \times P_2)$, $P_4//(P_1 \times P_3)$, $P_4//(P_2 \times P_3)$, $(P_1 \times P_2)//(P_4 \times P_3)$, $(P_1 \times P_3)//(P_4 \times P_2)$, $(P_2 \times P_3)//(P_4 \times P_1)$, $(P_4 \times P_1)//(P_4 \times P_2)$, $(P_4 \times P_2)//(P_4 \times P_3)$, $(P_4 \times P_1)//(P_4 \times P_3)$, in which P_1, P_2, P_3, and P_4 refers to parents Alpowa, Express, Louise, and Zhoumai18, respectively.

Besides the 12 crossing strategies, we also considered four selection schemes relevant to the selection order of traits HTAP and AT in different breeding stages. For example, breeders sometimes select for HTAP first, then select for AT. This strategy will be referred to as HA when breeders select for AT and then for HTAP. This is referred to AH. At other times, breeders select for HTAP first, then for AT, and finally for the HTAP. This is similar to HAH; when breeders select for AT first, then for HTAP, and finally for the AT. This is similar to AHA. HAH and AHA indicate that HTAP and AT are selected twice in a generation. We can readily define these crossing and selection strategies in QuLine, and predict their performance for best selection in future breeding.

RESULTS

Comparison of the genetic gains on traits HTAP and AT from different selection strategies

In selection strategies HA, AH, HAH, and AHA, the mean genetic values on traits HTAP and AT of recombinant inbred lines (F_7) are listed in Table 3. In selection strategies HA and AH, both HTAP and AT were selected once. However, comparing selection strategy HA with AH, mean genetic value on the same trait of the same cross was different, indicating that the selection order of AT and HTAP resulted in different genetic gains. In selection strategy HAH, HTAP was selected twice in one generation at different wheat growth stages, such as host plant resistance to stripe rust was selected at grain-filling and at maturity, and AT was selected once. The selection intensity for HTAP was higher than that for DT. Therefore, genetic gains on HTAP in selection strategy HAH were higher than that in selection strategy HA. Due to the low heritability of trait AT assumed in this simulation experiment, trait AT was selected twice in one generation at different wheat growth stages in selection strategy AHA; the mean genetic value on AT was the highest in cross combination $(P_4 \times P_2)//(P_4 \times P_3)$. The reason is that HTAP might have effected AT due to the presence of pleiotropy.

### Comparison of the genetic gains on traits HTAP and AT from different crosses

Positive mean genetic gains on HTAP were observed in four selected scenarios HA, AH, HAH, and AHA (Figure 1). In selection strategy HA, No.7 cross combination was the most efficient in improving HTAP, followed by cross combinations No.2 and No.4; in selection strategy AH, No.8 was the most efficient one, then No.7; in selection strategy HAH, the most efficient combination was No.7, next was No.2 and No.4; while in selection strategy AHA, No.8 was the best one. Meanwhile, the selection order of HTAP had a significant impact on mean genetic values; in strategy HA, No.4 was better than No.8 and No.9; however, in strategy AH, No. 8 and No.9 were better than No.4. Based on the above results, cross combination 7 was the most efficient in introducing HTAP resistance into Zhoumai18 in the selection strategy HAH.

Mean genetic values on AT was observed in four select

Table 3. Mean genetic values on traits HTAP and AT in different crosses under different selection strategies.

Selection strategy	Trait	Mean genetic values on traits HTAP and AT in different crosses											
		1	2	3	4	5	6	7	8	9	10	11	12
HA	HTAP	17.66	26.65	9.68	27.12	17.06	20.62	29.85	22.96	24.16	16.90	9.63	13.65
	AT	236.3	245.89	240.69	240.63	234.03	237.97	214.57	221.65	212.95	279.64	276.45	278.35
AH	HTAP	13.29	19.96	8.15	15.30	9.75	11.83	22.26	23.15	21.45	13.31	8.05	11.26
	AT	250.49	259.62	248.95	252.61	248.56	250.27	217.35	218.17	216.35	278.48	275.95	276.81
HAH	HTAP	17.85	26.81	10.47	27.36	17.49	21.94	29.99	23.34	26.30	17.99	11.04	15.86
	AT	234.21	243.46	235.05	239.61	232.85	236.29	213.60	219.49	211.31	273.89	269.23	271.79
AHA	HTAP	13.87	20.83	8.50	16.08	10.03	12.01	22.18	22.97	21.20	11.35	6.79	9.30
	AT	247.32	256.20	245.50	249.38	245.19	247.17	220.32	220.51	218.48	285.33	284.30	286.02

1, Cross combination $P_4 \times P_1$; 2, $P_4 \times P_2$; 3, $P_4 \times P_3$; 4, $P_4 // (P_1 \times P_2)$; 5, $P_4 // (P_1 \times P_3)$; 6, $P_4 // (P_2 \times P_3)$; 7, $(P_4 \times P_3)//(P_1 \times P_2)$; 8, $(P_4 \times P_2)// (P_1 \times P_3)$; 9, $(P_4 \times P_1)// (P_2 \times P_3)$; 10, $(P_4 \times P_1)//(P_4 \times P_2)$; 11, $(P_4 \times P_1)//(P_4 \times P_3)$; 12, $(P_4 \times P_2)//(P_4 \times P_3)$; P_1, P_2, P_3, and P_4 stand for donors Alpowa, Express, Louise, and Zhoumai18.
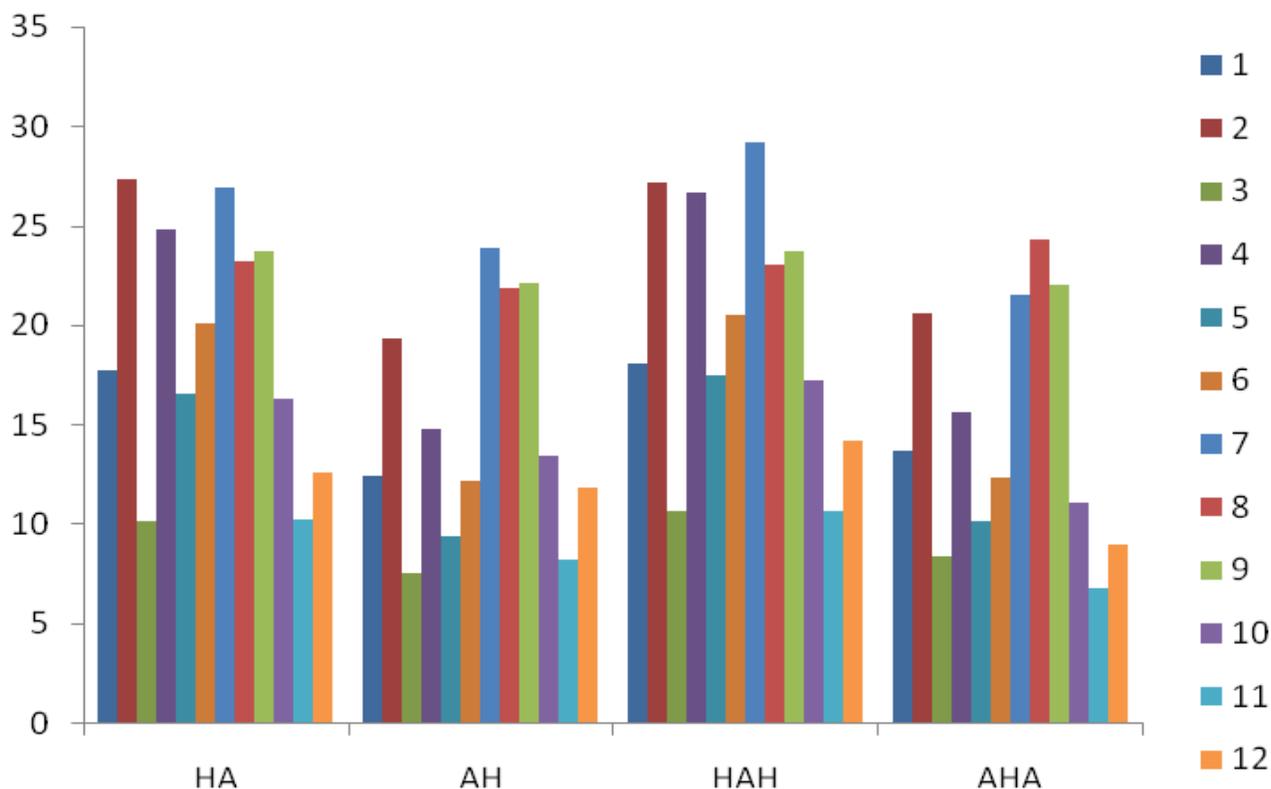
Figure 1. Mean genetic means for HTAP from different crosses. 1, cross combination $P_4 \times P_1$; 2, $P_4 \times P_2$; 3, $P_4 \times P_3$; 4, $P_4 // (P_1 \times P_2)$; 5, $P_4 // (P_1 \times P_3)$; 6, $P_4 // (P_2 \times P_3)$; 7, $(P_4 \times P_3)//(P_1 \times P_2)$; 8, $(P_4 \times P_2)// (P_1 \times P_3)$; 9, $(P_4 \times P_1)// (P_2 \times P_3)$; 10, $(P_4 \times P_1)//(P_4 \times P_2)$; 11, $(P_4 \times P_1)//(P_4 \times P_3)$; 12, $(P_4 \times P_2)//(P_4 \times P_3)$; P_1, P_2, P_3, and P_4 stand for donors Alpowa, Express, Louise, and Zhoumai18.
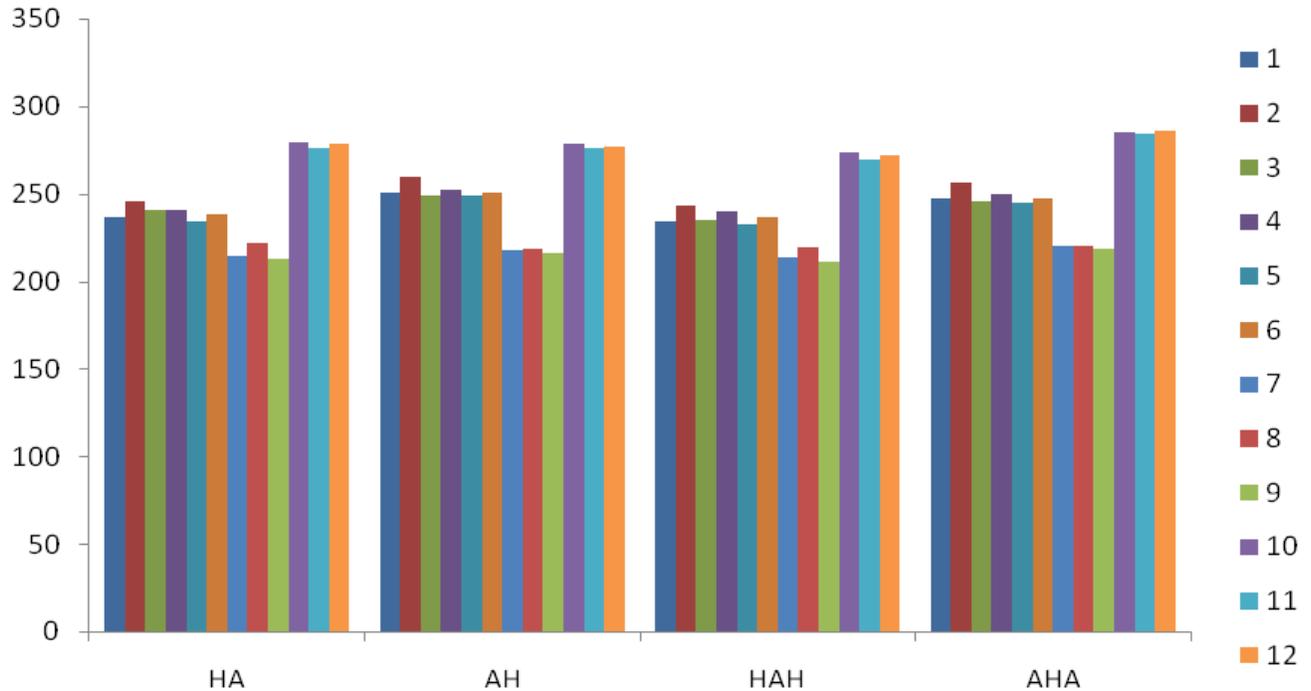
Figure 2. Mean genetic means for AT from different crosses. 1, cross combination $P_4 \times P_1$; 2, $P_4 \times P_2$; 3, $P_4 \times P_3$; 4, P_4 // $(P_1 \times P_2)$; 5, P_4// $(P_1 \times P_3)$; 6, P_4// $(P_2 \times P_3)$; 7, $(P_4 \times P_3)//(P_1 \times P_2)$; 8, $(P_4 \times P_2)//$ $(P_1 \times P_3)$; 9, $(P_4 \times P_1)//$ $(P_2 \times P_3)$; 10, $(P_4 \times P_1)//(P_4 \times P_2)$; 11,$(P_4 \times P_1)//(P_4 \times P_3)$; 12: $(P_4 \times P_2)//(P_4 \times P_3)$; P_1, P_2, P_3, and P_4 stand for donors Alpowa, Express, Louise, and Zhoumai18.

scenarios (Figure 2). Due to the high AT value of Zhoumai18 and low AT value of American cultivars assumed in this simulation experiment, cross combinations No.10, 11 and 12 were all the best options for the four selection strategies when zhoumai18 was double-crossed with American cultivars. Anyway, their mean genetic values were different (Figure 2). Mean genetic values for trait AT from cross No.10 was the highest in strategy HA, AH and HAH; in strategy AHA, the mean genetic values for AT was the highest in cross No.12 (Figure 3).

**Comparison of the genetic gains on trait SR from different selection strategies**

Zhoumai18, carrying *Yr9*, is defined as a donor with a seedling stripe rust resistance gene and American cultivars did not have seedling stripe rust resistance genes in this simulation study. Hence, after crossing, the seedling resistance only came from Zhoumai18. In all the four strategies (HA, AH, AHA, and HAH), crosses No.10, 11, and 12 showed the highest seedling resistance (Table 4).

DISCUSSION

Recently, with the production and development of

Chinese dominant races CYR31, CYR32 and CYR33, wheat varieties broadly cultivated in China face serious stripe rust resistance crisis. It has been proved that the application of varieties with pyramiding resistance genes is the effective, economical, and environmentally friendly means to control stripe rust. Sharp and Fuchs, (1982) reported that pyramided resistance genes to stripe rust had the advantages in persistent resistance. Many wheat cultivars in CIMMYT with high resistance to stripe rust carried four to five non-race-specific resistance genes to stripe rust (Singh et al., 2005). Zhoumai18 was released in 2004 (Yushenmai2004008) and cultivated broadly in Henan province and south Huanghuai wheat production areas due to its steady output and broad application. However, it lost resistance to stripe rust with the appearance of Chinese races CYR28 and CYR29. American wheat cultivars Alpowa, Express, and Louise carry HTAP resistance, and show high resistance to stripe rust at adult stage in the field. In the simulation experiment, *Yr9* in Zhoumai18 was kept and HTAP resistance in American cultivars was introduced into Zhoumai18, which was very meaningful for improving HTAP resistance in Zhoumai18, and enriching the resistance germplasm tostripe rust.

Nowadays, breeders are still not clear in wheat important trait breeding trait. Hence, both resistance to stripe rust (HTAP and SR) and adaption (AT) were considered in the study. Wang et al. (2003b) compared selected bulk method with modified pedigree method
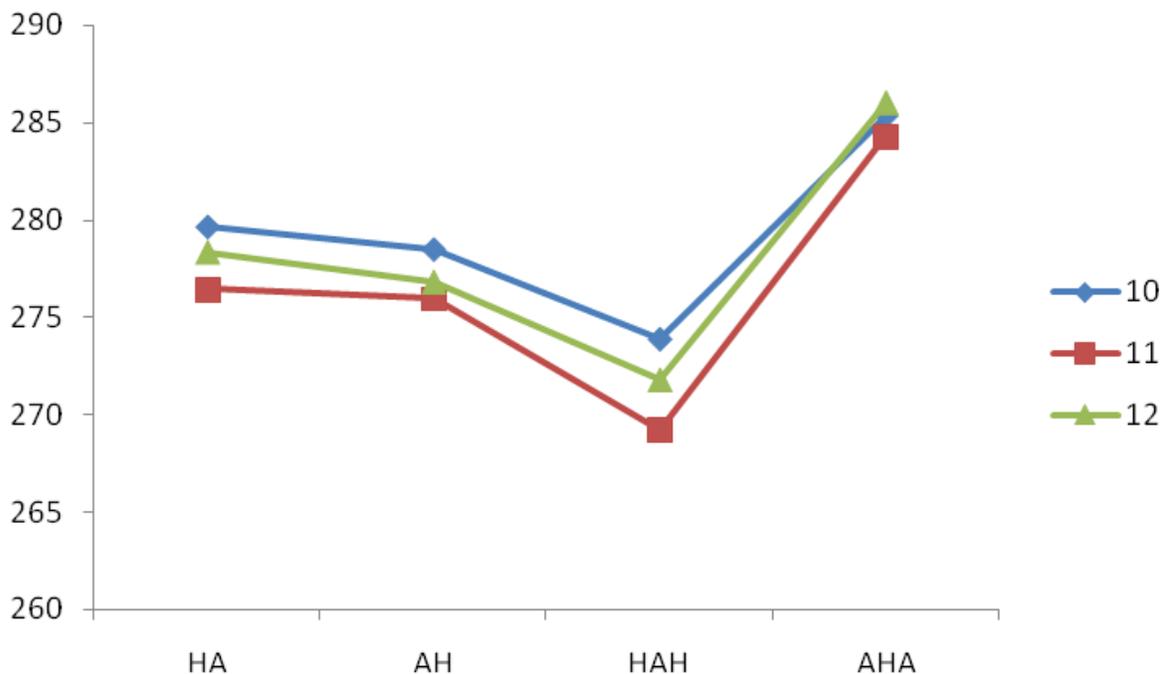
Figure 3. Mean genetic means for AT from different selection strategies. 10, $(P_4 \times P_1)// (P_4 \times P_2)$; 11, $(P_4 \times P_1)//(P_4 \times P_3)$; 12, $(P_4 \times P_2)//(P_4 \times P_3)$; P_1, P_2, P_3, and P_4 stand for donors Alpowa, Express, Louise, and Zhoumai18.

Table 4. Mean genetic values on trait SR in different selection strategies.

Selection strategy	Mean genetic values on trait SR from different crosses											
	1	2	3	4	5	6	7	8	9	10	11	12
HA	59.8	59.8	59.8	59.8	59.8	59.8	46	46	46	75.9	75.9	75.9
AH	58.6	58.6	58.6	58.6	58.6	58.6	44.7	44.7	44.7	73.2	73.2	73.2
HAH	59.8	59.8	59.8	59.8	59.8	59.8	46.2	46.2	46.2	73.5	73.5	73.5
AHA	56.8	56.8	56.8	56.8	56.8	56.8	45.5	45.5	45.5	76.4	76.4	76.4

1, Cross combination $P_4 \times P_1$; 2, $P_4 \times P_2$; 3, $P_4 \times P_3$; 4, $P_4 // (P_1 \times P_2)$; 5, $P_4// (P_1 \times P_3)$; 6, $P_4// (P_2 \times P_3)$; 7, $(P_4 \times P_3)//(P_1 \times P_2)$; 8, $(P_4 \times P_2)// (P_1 \times P_3)$; 9, $(P_4 \times P_1)// (P_2 \times P_3)$; 10, $(P_4 \times P_1)//(P_4 \times P_2)$; 11, $(P_4 \times P_1)//(P_4 \times P_3)$; 12, $(P_4 \times P_2)//(P_4 \times P_3)$; P_1, P_2, P_3, and P_4 stand for donors Alpowa, Express, Louise, and Zhoumai18.

using QuLine. Based on genetic gains on output traits, the selected bulk method was far superior to the modified pedigree method. Therefore, the selected bulk method was chosen in this simulation experiment.

Wang et al. (2009) recommend the use of the single backcrossing breeding strategy which met two conditions in our experiment: (1) individual genotypes cannot be precisely identified; (2) multiple genes govern the phenotypic traits are transferred from donor parents to adapted parents. Hence, we chose the single back-crossing breeding strategy in the stimulation experiment.

Cross combinations $(P_4 \times P_1)// (P_4 \times P_2)$, $(P_4 \times P_1)//(P_4 \times P_3)$, and $(P_4 \times P_2)//(P_4 \times P_3)$ were all efficient in improving genetic gains on traits AT and SR in the selection strategy AHA, while in HAH, only cross combination $(P_4 \times P_3) // (P_1 \times P_2)$ had the highest genetic gains on HTAP. The results in the study can provide important reference

values for efficiently pyramiding more resistance genes to stripe rust, avoiding simplified resistance genes, and breeding novel varieties. Anyway, it is necessary to combine stimulation study with genetics and breeding together. The stimulation research can be proved by breeding, while field experiments also contribute to the improvement of breeding simulation models.

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