Identification of Stripe Rust Resistance Genes in Common Wheat Cultivars From the Huang-Huai-Hai Region of China

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Abstract

Wheat stripe (yellow) rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is a serious fungal disease worldwide, especially in the Huang-Huai-Hai region, a main wheat production area in China. Gene postulation, molecular testing, and pedigree analysis were conducted to determine the presence of stripe rust resistance genes to 15 *Pst* races in 66 selected commercial wheat cultivars released from 2000 to 2016. In addition, races CYR32, CYR33, and CYR34 were used to evaluate resistance to *Pst* at the adult-plant stage of wheat in the field. Four *Yr* genes (*Yr9*, *Yr10*, *Yr26*, and *Yr32*) were postulated in 24 wheat cultivars either singly or in combination. Thirty-six cultivars might contain unknown *Yr* genes, whereas no identified *Yr* gene

was postulated in six cultivars. *Yr9* was detected at a frequency of 28.8%, and no cultivars carried *Yr5*, *Yr15*, or *Yr18*. Ten cultivars (15.2%) exhibited adult-plant resistance in the field tests with three predominant races. Three cultivars (Langyan 43, Xinong 889, and Yunfeng 139) had all-stage resistance. These results are useful to growers selecting cultivars and to breeders aiming to use more resistance genes to develop new cultivars with effective resistance in order to reduce stripe rust damage.

Keywords: adult-plant resistance, gene postulation, molecular marker test, wheat stripe rust, *Yr* gene

Wheat (*Triticum aestivum* L.) is the second most commonly grown food crop in China and is frequently affected by stripe rust, which is caused by *Puccinia striiformis* Westend. f. sp. *tritici* Erikss (*Pst*) (Wellings 2011). Destructive epidemics in 1950, 1964, 1990, 2002, and 2017 caused yield losses exceeding 6.0, 3.2, 1.8, 1.3, and 1.5 million metric tons, respectively, in China (Chen et al. 2009; Ma 2018; Wan et al. 2007). Severe outbreaks of wheat stripe rust occur as a result of susceptible cultivars, virulent races, and disease-favorable weather conditions (Chen et al. 2014). In 2009, a new *Pst* race virulent on wheat line G22 was detected in Sichuan Province, China (Liu et al. 2010). The G22 races were virulent to wheat cultivars with *Yr10* and *Yr26*, among other stripe rust resistance (*Yr*) genes and other resistant lines or cultivars such as the Guinong and 92R lines, Moro, and Chuanmai 42 (Liu et al. 2015). The frequency of the G22-virulent races has increased rapidly and spread to other regions of China (Li et al. 2016; Liu et al. 2012; Wang et al. 2017), owing to the high infection fitness and aggressiveness of G22 on commercial wheat cultivars (Bai et al. 2018). Among G22 races, G22-9 (formerly V26) emerged as a new predominant race and was formally named race CYR34 (Bai et al. 2018; Liu et al. 2017). CYR34, CYR32, and CYR33 are currently the predominant races in China. Planting resistant cultivars is the most economic, effective, environmentally friendly, and easy-to-use method for controlling wheat stripe rust (Chen 2005). Therefore, developing wheat cultivars

with durable resistance is critical for sustainable control of this disease.

Adult-plant resistance (APR) and seedling resistance are two major types of resistance to stripe rust (Johnson and Taylor 1972). APR is expressed at the postseedling stage, and the level of resistance increases as the plant matures. Seedling resistance genes are expressed at all stages, which follow the gene-for-gene relationships (Flor 1971). This hypothesis states that interactions between a host and a specific pathogen depend on the presence of resistance genes in the host and the corresponding avirulence genes in the pathogen. The hypothesis provides the foundation for gene postulation. Dubin et al. (1989) proposed six steps of gene postulation for wheat resistance to stripe rust, which have been widely used in the wheat-*Pst* pathosystem (Feng et al. 2009; Li et al. 2006). By 2019, 82 *Yr* genes had been permanently named (Feng et al. 2018; Gessese et al. 2019; McIntosh et al. 2017; Nsabiya et al. 2018; Pakeerathan et al. 2019), and some have been cloned and their linked molecular markers have been identified. These markers made it possible to improve the accuracy and reliability of gene postulation (Bai et al. 2010).

Wheat produced in the Huang-Huai-Hai region of China fulfills the food needs of more than 200 million people (Tang and Li 2012). In 2016, wheat was grown on 14.1 million hectares in these regions (58.3% of the total wheat production area in China) and produced 87 million tons of grain (67.5%). Stripe rust frequently causes big yield losses in the Huang-Huai-Hai region; therefore, there is an urgent need to control wheat stripe rust in this region. However, there is not enough information on *Yr* genes in the released cultivars, which makes it difficult for growers in the region to choose a cultivar. Hence, the objective of this study was to identify *Yr* genes in 66 wheat cultivars that are widely grown in the Huang-Huai-Hai region of China. The evaluation of resistance in wheat cultivars to the predominant races of *Pst* at the adult-plant stage could also provide useful information for growers selecting cultivars to plant and for breeders aiming to use more effective genes to develop new wheat cultivars with adequate and durable resistance to stripe rust.

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Materials and Methods

Plant material. Sixty-six wheat cultivars (Table 1) that were widely grown in the Huang-Huai-Hai region of China during 2000

Table 1. Pedigrees of cultivars, stripe rust reactions at the adult-plant stage, and amplifications by *Yr* gene-specific molecular markers

Line	Cultivar	Pedigree	Released number	Score at adult-plant stage ^a			Molecular marker test ^b						
				CYR32	CYR33	CYR34	Yr5	Yr9	Yr10	Yr15		Yr18	Yr26
										KinI	KinII		
1	Gaoyou 9618	8515-4/8901-11-14	Jishenmai 2005007	10R	40S	0R	–	+	–	–	–	–	–
2	Han 00-7086	Han 93-4572/Tai 9115-3	Guoshenmai 2007014	60MS	40MS	10R	–	+	–	–	–	–	–
3	Heng 0628	Heng 71-3/Han 6172	Jishenmai 2008010	60S	40S	40MS	–	+	–	+	–	–	–
4	Heng 6599	94-4277/Heng 4041	Jishenmai 2006002	40S	40MS	80S	–	–	–	–	–	–	–
5	Henong 6049	Jimai 38/Henong 91459	Guoshenmai 2009019	80MS	60S	80S	–	+	–	–	–	–	–
6	Henong 827	Linyuan 95-3091/Shi 4185	Jishenmai 2008011	60S	60S	80S	–	+	–	–	–	–	–
7	Huaimai 16	Tal (Ms2) recurrent selection	Guoshenmai 2001004	10R	10R	10MR	–	–	–	–	–	–	–
8	Huaimai 18	Yan 1064/Zhengzhou 891	Guoshenmai 2001005	40MS	20MS	60S	–	+	–	–	–	–	–
9	Ji 5265	Shi 4185/Ji 6023//9204	Guoshenmai 2009016	80S	60S	100S	–	+	–	–	–	–	–
10	Jifeng 703	Linfen 118/Shixin 163	Jishenmai 2005001	60S	60S	10R	–	+	–	+	–	–	–
11	Jimai 19	Lumai 13/Linfen 5064	Guoshenmai 2003014	30S	40MS	20MR	–	–	–	–	–	–	–
12	Jimai 21	865186/Chuannongda 84-1109//Ji 84-5418	Lunongshenzi [2004]022	40S	40MS	20MR	–	–	+	–	–	–	–
13	Jining 16	[Yan 1934/82(4)046]F1// (Liao 83-1/2114)F1	Lunongshenzi [2004]028	40MS	10MS	0R	–	–	–	–	–	–	–
14	Jining 17	Laizhou 953/Shi 90-4005	Lunongshending [2004]029	40S	40MS	10S	–	+	–	–	–	–	–
15	Jinmai 1	Xiaoyan 22// Lankaoaizaoba	Jishenmai 2005009	0R	40S	10MS	–	+	–	–	–	–	–
16	Kenong 199	Shi 4185×Kenong 9204	Guoshenmai 2006017	60S	40S	80S	–	+	–	–	–	–	–
17	Kexin 9	Yumai 18-64 lines/PH82-2-2	Lunongshen 2009060	40MS	40MS	20MS	–	–	+	–	–	–	–
18	Lai 95021	Jinan 13/Yanzhong 144// wheat- <i>Elytrigia intermedia</i> (Host) Nevski/Yanzhong 153	Lunongshenzi [2001]003	60MS	60MS	60S	–	–	–	–	–	–	–
19	Langyan 43	0591//Youmangbai 4/ Lovrin 10//Aiganzao	Jishenmai 2005013	0R	0R	0R	–	+	–	–	–	–	–
20	Liangxing 99	Ji 91102/Lumai 14// PH85-16	Guoshenmai 2006016	40S	5R	0R	–	–	–	–	–	–	–
21	Linmai 4	Lumai 23/Lin 9015	Lunongshen 2006046	60S	60S	40S	–	–	+	–	–	–	–
22	Luohan 6	Yumai 49/Shannong 45	Guoshenmai 2006020	10S	60S	60S	–	–	–	–	–	–	–
23	Luohan 8	Wenmai 6/Yumai 48	Yushenmai 2008013	0R	40S	40S	–	–	–	–	–	–	–
24	Qifeng 1	Chang 95-8//Aurora/ Mentana/ (Baihuomai+Baiyupi+ Xiaobaimai)// Xiannong 39//Xinong 64/Yanda 24/Yannong 14	Lunongshen 2009056	60S	40MS	40S	–	+	–	–	–	–	–
25	Qingnong 2	Lumai 14/Yannong 15/ Aiganmai	Lunongshen 2010070	10R	40MS	10R	–	–	+	–	–	–	–
26	Shannong 12	828006/PH85-4	Lushenmai 2005045	40MS	40MS	10MS	–	–	–	–	–	–	–
27	Shannong 15	Jinan 17/Jihe 916	Lunongshen 2006057	40MS	40S	40S	–	–	–	–	–	–	–
28	Shannong 17	L156/Laizhou 137	Guoshenmai 2009015	60S	80S	40S	–	–	–	–	–	–	–
29	Shannong 18	L156/Laizhou 137	Guoshenmai 2009015	40S	30MS	20MS	–	–	–	–	–	–	–
30	Shannong 21	Laizhou 137/Yanfu 188	Lunongshen 20100071	1R	10R	5R	–	+	–	–	–	–	–
31	Shannong 23	Tal (Ms2) recurrent selection	Lunongshen 2011034	60S	40S	40S	–	+	–	+	–	–	–
32	Shannong 29	Linmai 6/J1781	Guoshenmai 2016024	60S	60S	80S	–	–	–	–	–	–	–
33	Shannong 664	520627/Nannong 871	Lunongshenzi [2002]022	40MS	0.5MR	10MR	–	+	–	+	–	–	–
34	Shannongzimai 1	The total DNA of the Honggaoliang was introduced into the Jihe 916 through the pollen tube channel	Lunongshen 2010072	40MS	40MS	10R	–	–	–	–	–	–	–

(Continued on next page)

^a Values indicate percent severity. R = resistant, S = susceptible, MS = moderately susceptible, and MR = moderately resistant.^b + = positive amplification by PCR; – = negative amplification by PCR.

Table 1. (Continued from previous page)

Line	Cultivar	Pedigree	Released number	Score at adult-plant stage ^a			Molecular marker test ^b						
				CYR32	CYR33	CYR34	Yr5	Yr9	Yr10	Yr15		Yr18	Yr26
										KinI	KinII		
35	Shanrong 3	Jinan 177, <i>Thinopyrum elongatum</i> and <i>Agropyron elongatum</i> somatic cell fusion	Lunongshenzi [2004]030	60S	60S	60S	-	+	-	+	-	-	-
36	Shi 4185	Tal/Zhi 8094/Yumai 2/3/Jimai 26(Aiganzao/Lovrin 10/Jinfeng 1)	Guoshenmai 2006017	80S	40S	80S	-	+	-	-	-	-	-
37	Shijiazhuang 8	Shi 91-5096/Shi 9306(GS Jimai 38)	Jishenmai 2007011	60MS	40MS	10MS	-	+	-	-	-	-	-
38	Shimai 15	(GS Jimai 38/92R137)/GS Jimai 38	Guoshenmai 2009025	60S	60MS	20MS	-	+	-	-	-	-	-
39	Shimai 16	Yumai 31/Shi 96-4495	Jishenmai 2005002	60MS	60MS	60MS	-	+	-	-	-	-	-
40	Shimai 18	Shi 4185/(92 Jian 3/T447) F2 superior individual	Jishenmai 2008004	60S	80S	100S	-	+	-	-	-	-	-
41	Shixin 616	Damuzhai//6069/Jinfeng 1//9831	Jishenmai 2008001	60S	80S	80S	-	+	-	-	-	-	-
42	Shixin 618	4512/523/735-10	Jishenmai 2008001	80S	60S	20MS	-	+	-	-	-	-	-
43	Shixin 828	422/Shixin 163//612	Jishenmai 2013012	40MS	40MS	20MS	-	-	+	-	-	-	-
44	Shiyu 17	Ji 935-352/Lumai 21	Jishenmai 2007007	40S	60S	40S	-	-	+	-	-	-	-
45	Taishan 21	26744/Taishan 10//Lovrin 10/Weier/Ruluo/Youbaomai/3/Lumai 18	Guoshenmai 2003015	10MR	5MR	5R	-	-	+	-	-	-	-
46	Taishan 22	Lumai 18/Lumai 14	Guoshenmai 2004013	0R	10R	20MR	-	-	+	-	-	-	-
47	Taishan 24	904017/Zhengzhou 8329	Lushenmai [2005]044	20MR	10R	5MR	-	-	-	-	-	-	-
48	Tanmai 98	Jining 13/942	Guoshenmai 2010011	60S	40MS	5R	-	-	-	-	-	-	-
49	Weimai 7	Linfeng 550/Qianni/Zhongyin 2	Lunongshenzi [2001]032	40S	40MS	40MS	-	+	-	-	-	-	-
50	Weimai 8	88-3149/Aus621108	Lunongshenzi [2003]028	40MS	40MS	20MR	-	+	-	+	-	-	-
51	Wennong 5	Lumai 21/Taishan 5	Lunongshenzi [2003]031	40MS	40MS	20MR	-	-	-	-	-	-	-
52	Wennong 6	915021/Lumai 18/876161	Lunongshen 2006056	40S	30MS	5R	-	-	-	-	-	-	-
53	Xiaoyan 22	Xiaoyan 6//775-1/Xiaoyan 107	Guoshenmai 2003034	30S	40MS	40S	-	+	-	-	-	-	-
54	Xiaoyan 81	Xiaoyan 54/8602	Jishenmai 2005006	20MR	40MS	0R	-	-	+	-	-	-	-
55	Xin 2899	[Lovrin 13x71(17)6-1]/Laiyang 584/Linfen 5064/Lumai 14	Lunongshen 2009059	80S	60MS	40MS	-	+	-	-	-	-	-
56	Xinong 889	Xiaoyan 6/Xiaoyan 8335-2//E Han-4	Yuyinmai 2006005	0R	0R	0R	-	-	+	-	-	-	-
57	Yan 99102	(Yanhangxuan 2/Lin 9511)F1//Yan BLU 14-15	Guoshenmai 2016012	60S	60S	40S	-	-	-	-	-	-	-
58	Yannong 0428	Yan 1668/Lumai 21	Lunongshen 2008058	40S	20MR	10R	-	-	-	-	-	-	-
59	Yannong 19	Yan 1933/Shaan 82-29	Lunongshenzi [2001]001	60S	40MS	10R	-	-	-	-	-	-	-
60	Yannong 21	Yan 1933/Shaan 82-29	Guoshenmai 2004016	40S	60MS	40MS	-	-	-	-	-	-	-
61	Yannong 22	Lumai 14//Yu 132/"87chu 20"	Lunongshenzi [2002]024	40S	40S	20MS	-	+	-	-	-	-	-
62	Yannong 836	Shannong 721511///Predgornaya/Anhui 9/Hongkeouroubai/Bainimo 62///Yumai 54(space breeding)	Lunongshen 2010073	40S	40MS	1R	-	-	-	-	-	-	-
63	Yunfeng 139	Xiaoyan 22/6/[<i>Triticum turgidum</i> L. var. <i>dicoccoides</i> (Koern.) Bowd AS846//Shaanmai 8003/Shaanmai 8007]F4/3/Shaan 229/4/Aiganzao] F3/5/N9134	Wanmai 2011006	0R	0R	5R	-	-	+	-	-	-	+
64	Zhouheimai 1	Zhoumai 9/Luozhen 1	Yushenmai 2011013	40MS	10R	10R	-	+	-	-	-	-	-
65	Zhoumai 24	Bainong 791/65(14)3/Kanghuihong//Aifeng 3//Mengxian 201/Neuzuch/Yanshi 4///Zhou 8425B///Xiaoyan 6/NS2761	Yushenmai 2009002	1R	10MR	0R	-	+	-	-	-	-	-
66	Zi 12	73-110Yexuan 1//03201/3/73-1104/Yexuan 1/4/Guionong 35-2	Lunongshenzi [2001]030	5R	1MR	20MR	-	-	+	-	-	-	-

to 2016 were used in this study. Twenty-one near-isogenic lines (NILs) with the Avocet S background and susceptible variety Mingxian 169 (Table 2) were also included in the study as *Yr* gene references and a susceptible check, respectively. These seeds were provided by the State Key Laboratory for Biology of Plant Diseases and Insect Pests (SKLBPI) at the Institute of Plant Protection, Chinese Academy of Agricultural Sciences (IPPCAAS).

***Pst* races.** Fifteen *Pst* races (Table 2), including seven from China (66E26, 72E66, 70E10, 63E254, 111E239, 111E222, and 127E255) and eight from Europe (66E74 [DK], 98E26 [DK], 66E10 [DK], 66E154 [DK], 86E90 [UK], 70E72 [DK], 114E26 [DK], and 98E90 [DK]), were propagated and multiplied at SKLBPI and IPPCAAS from single uredinia.

Seedling tests. The 15 *Pst* races were used to inoculate the wheat cultivars, *Yr* gene NILs, and the susceptible check. Thirty cultivars with six to eight seeds for each cultivar were planted in a plastic box (20 × 30 × 10 cm) filled with soil mixture, and the boxes were placed in a greenhouse. Seedlings were inoculated by spraying a suspension of 10 mg of fresh urediniospores in 1 ml of Isopar L lightweight mineral oil (ExxonMobil Chemical Co. Ltd., Irving, TX) using an atomizer pressured by an air pump (20 kPa) when the seedlings were 10 cm high, approximately 7 days after sowing (Liu et al. 2015). After the mineral oil evaporated, the plants were placed in a sealed barrel to maintain moisture and held at 10°C for a day in the dark and then transferred to the greenhouse at 14 to 18°C with 16 h of light each day. Approximately 15 days after inoculation when rust was fully developed on Mingxian 169 and Avocet S, the infection types (ITs) were recorded based on a 0 to 9 scale (Line and Qayoum 1992). Plants with IT 0 to 6 were considered resistant, whereas those with IT 7 to 9 were considered susceptible.

Molecular marker tests. Genomic DNA from 10 mg of leaves of each cultivar was extracted using the cetyltrimethylammonium bromide method. The DNA concentration was measured with an ND-1000 NanoDrop spectrophotometer (Thermo Fisher Scientific, Waltham, MA) and diluted to 100 ng/μl with ddH₂O. Seven molecular markers (Tables 3 and 4) linked to *Yr5* (*Yr5*-KASP) (Marchal et al. 2018), *Yr9* (AF1/4) (Francis et al. 1995), *Yr10* (SC200) (Shao et al. 2001),

Yr15 (KinI and KinII) (Klymiuk et al. 2018), *Yr18* (csLV34) (Lagudah et al. 2006), and *Yr26* (We173) (Wang et al. 2008) were used to test all cultivars. The PCRs were performed in a 25-μl reaction mixture containing 12.5 μl of EasyTaq PCR SuperMix (TransGen Biotech, Beijing, China), 1 μl (10 ng/μl) of each forward and reverse primer, 1 μl (100 ng/μl) of template DNA, and 9.5 μl of ddH₂O. The PCR products were separated on a 2.0% agarose gel, and images were taken under a WSE-5200 integrated gel imaging system (Atto Corporation, Tokyo, Japan).

Field tests. The 66 wheat cultivars were evaluated for stripe rust reactions after inoculation separately with races CYR32, CYR33, and CYR34 in field nurseries at the Langfang Station, Hebei Province. In early October, seeds (5 g) of each cultivar were sown in a single row (1 m length and 0.33 m between rows). Susceptible cultivar Mingxian 169 was planted between each of the 20 tested wheat cultivars and perpendicular to the nursery to aid the spread of spores. Each nursery was surrounded by a barrier of winter wheat to minimize the unintentional spread of spores (Hovmöller 2007). Mingxian 169 plants were inoculated by spraying a suspension of 1 g of fresh urediniospores in 300 ml of Isopar L lightweight mineral oil in mid-April when the plants were in the jointing stage. After the oil evaporated for 1 to 2 h, the plants were sprayed with 1:2,000 Tween 20 and water solution and covered with plastic overnight to maintain moisture in the spreader rows. Irrigation was applied every 10 days to maintain moisture in order to promote stripe rust development. Stripe rust IT and severity were recorded twice in late May and early June using the method of Chen et al. (2007) when the plants were in the milk stage and Mingxian 169 was completely infected. Disease severity was assessed visually using the percentage of diseased leaf area covered by stripe rust.

Data analysis. Gene postulations were carried out based on the method of Dubin et al. (1989). SAS 9.1.3 software (Statistical Analysis Systems, Cary, NC) was used for statistical analysis (Wamishe and Milus 2004; Wamishe et al. 2004). According to the gene-for-gene hypothesis, cultivars that have high ITs (susceptible) to a specific race cannot have a *Yr* gene to which the race produces a low IT (avirulent). For each cultivar, the first step of the program was to summarize the

Table 2. Infection types of 21 *Yr* near-isogenic lines inoculated with 15 races of *Puccinia striiformis* f. sp. *tritici*

Cultivar ^a	Infection type ^b														
	66E74	98E26	66E10	66E154	86E90	70E72	114E26	98E90	66E26	72E66	70E10	127E255	63E254	111E239	111E222
AvS/ <i>Yr1</i>	1	1	2	5	2	3	1	2	1	1	1	7	7	7	7
AvS/ <i>Yr3</i>	7	6	7	7	7	7	7	7	7	3	7	7	7	7	7
AvS/ <i>Yr4</i>	7	7	7	7	7	7	7	7	7	7	7	8	4	7	7
AvS/ <i>Yr5</i>	2	1	1	0	1	2	1	1	1	0	0	2	0	0	1
AvS/ <i>Yr6</i>	7	7	7	7	5	3	7	7	7	7	7	7	7	7	7
AvS/ <i>Yr7</i>	7	7	7	7	7	4	8	7	7	7	7	7	7	7	7
AvS/ <i>Yr8</i>	7	7	6	7	7	4	7	7	7	5	7	8	7	7	7
AvS/ <i>Yr9</i>	3	1	3	5	0	1	3	0	1	0	1	7	7	7	7
AvS/ <i>Yr10</i>	3	2	0	0	1	1	7	1	1	1	1	7	7	4	4
AvS/ <i>Yr15</i>	2	1	1	5	0	7	4	1	2	1	2	0	0	2	0
AvS/ <i>Yr17</i>	1	7	7	7	5	7	2	6	5	4	7	7	7	7	7
AvS/ <i>Yr24</i>	3	3	7	2	5	1	2	2	1	2	2	7	7	4	4
AvS/ <i>Yr25</i>	3	6	2	1	1	1	7	7	4	1	3	7	7	7	7
AvS/ <i>Yr26</i>	1	2	4	1	5	2	4	3	1	2	3	8	8	0	2
AvS/ <i>Yr27</i>	7	7	7	7	6	6	7	6	7	5	7	7	7	7	7
AvS/ <i>Yr30</i>	7	7	7	7	5	7	7	7	7	6	5	7	7	4	4
AvS/ <i>Yr32</i>	3	4	6	5	6	2	1	4	1	6	7	7	7	7	3
AvS/ <i>YrA</i>	7	7	7	7	7	7	2	7	7	7	7	7	7	7	7
AvS/ <i>YrSp</i>	4	1	6	2	1	1	7	5	3	6	2	7	7	7	7
AvS/ <i>YrSk</i>	5	6	7	5	6	7	7	7	3	3	7	8	7	7	7
AvS	7	7	7	7	7	7	7	7	7	7	7	7	7	8	8
Mingxian 169	7	8	8	8	7	7	7	8	7	8	7	8	8	8	7

^a AvS = Avocet S.

^b 0 = no visible signs or symptoms; 1 = necrotic and/or chlorotic flecks, no sporulation; 2 = necrotic and/or chlorotic blotches or stripes, no sporulation; 3 = necrotic and/or chlorotic blotches or stripes, trace amounts of sporulation; 4 = necrotic and/or chlorotic blotches or stripes, light sporulation; 5 = necrotic and/or chlorotic blotches or stripes, intermediate sporulation; 6 = necrotic and/or chlorotic blotches or stripes, moderate sporulation; 7 = necrotic and/or chlorotic blotches or stripes, abundant sporulation; 8 = chlorosis behind sporulating area, abundant sporulation; and 9 = no necrosis or chlorosis, abundant sporulation.

results from races showing high ITs on a cultivar to eliminate *Yr* genes from the cultivar; this elimination led to a short list of *Yr* genes that could exist in the cultivar. The second step of the program was to use the data from races showing low ITs on the cultivar; the output listed the low ITs produced on the cultivar and the isolines with corresponding *Yr* genes that were not determined in the first step. The results from the second step were compared visually, from which an *Yr* gene was determined to be present if the low IT produced on the cultivar by the races matched the low IT on the matching NIL; otherwise, the *Yr* gene was considered not present. In addition, if the IT of a cultivar was lower than that tested on any of the NILs listed in the second step, then the cultivar was considered to possess an unknown gene that conditions a lower IT that is epistatic to the identified *Yr* gene.

Results

***Yr* genes in wheat cultivars based on gene postulation and molecular marker tests.** At seedling stage, the *Yr* genes were postulated in the 66 wheat cultivars based on the comparisons of their ITs with those of the 21 *Yr* NILs. ITs of 20 NILs were segregated when tested with the 15 *Pst* races (Table 2), indicating the ability to postulate 20 *Yr* genes: namely, *Yr1*, *Yr3*, *Yr4*, *Yr5*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr10*, *Yr15*, *Yr17*, *Yr24*, *Yr25*, *Yr26*, *Yr27*, *Yr30*, *Yr32*, *YrA*, *YrSp*, and *YrSk*. The results showed that cultivars containing *Yr5* expressed low ITs to all *Pst* races. Cultivars containing *Yr15* had low ITs to 14 *Pst* races except race 70E72. The susceptible check Mingxian 169 and Avocet S conferred high ITs to all 15 *Pst* races. The molecular marker results showed that 31 cultivars, 12 cultivars, and one cultivar were successfully amplified with primers AF1/4 for *Yr9*, SC200 for *Yr10*, and We173 for *Yr26*, respectively, indicating the possible presence of these genes in the respective cultivars. However, no PCR products were generated by primers *Yr5*-KASP (*Yr5*), csLv34 (*Yr18*), and both KinI and KinII (*Yr15*), suggesting that these genes are not present in the cultivars studied here.

Four genes (*Yr9*, *Yr10*, *Yr26*, and *Yr32* either singly or in combination) were postulated in 24 wheat cultivars. No *Yr* genes were finalized or postulated in six cultivars, whereas 36 cultivars might contain an unknown *Yr* gene or genes (Table 4). *Yr9* was postulated in 19 cultivars, five of which (Weimai 7, Shanrong 3, Shixin 616, Shijiazhuang 8, and Xiaoyan 22) might contain only *Yr9* because they were susceptible to four *Yr9* virulent races (127E255, 63E254, 111E239, and 111E222) and resistant to all other races, which was consistent with the ITs of *Yr9*. Five cultivars (Shannong 664, Xin 2899, Qifeng 1, Henong 6049, and Shixin 618) displayed low ITs consistent with races avirulent to differentials Avocet*S/*Yr9* and Avocet*S/*Yr32*,

indicating that they might contain *Yr9* and *Yr32*. Jinmai 1 was resistant to all races avirulent to cultivars containing *Yr9*, *Yr32*, and a race (127E255) that was virulent to those cultivars containing *Yr9* and *Yr32*, suggesting that it might contain *Yr9*, *Yr32*, and an unknown *Yr* gene(s). Six cultivars (Shannong 23, Kenong 199, Shi 4185, Ji 5265, Zhouheimai 1, and Zhoumai 24) might contain *Yr9* and an unknown *Yr* gene(s) because cultivars containing *Yr9* were susceptible to 127E255, 63E254, 111E239, and 111E222 but resistant to other races. Cultivars Shannong 23, Kenong 199, Shi 4185, Ji 5265, and Zhouheimai 1 containing *Yr9* showed ITs lower than that of Avocet*S/*Yr9* tested with race 66E154; thus, they should contain an unknown *Yr* gene(s) in addition to *Yr9*. Zhoumai 24 was susceptible to races 127E255, 63E254, and 111E222 but resistant to 111E222 and some other races, indicating that this cultivar contains *Yr9* and an unknown *Yr* gene(s). Taishan 21 and Zi 12 might contain *Yr10* based on their susceptibility to races 114E26, 127E255, and 63E254 and their resistance to the other 12 races, consistent with the ITs of *Yr10*. Three cultivars (Langyan 43, Xinong 889, and Yunfeng 139) had low ITs for all races tested but did not have the *Yr5* linked marker. Langyan 43 was postulated to contain *Yr9* and an unknown *Yr* gene(s), Xinong 889 contained *Yr10* and an unknown *Yr* gene(s), and Yunfeng 139 contained *Yr10*, *Yr26*, and an unknown *Yr* gene(s) according to the molecular marker tested.

Field reactions. According to the field reactions, the 66 cultivars could be classified into three groups based on the characteristics of resistant and moderately resistant or susceptible and moderately susceptible reactions (Table 1). In group 1, 10 cultivars (15.2%) (Huaimai 16, Langyan 43, Shannong 21, Taishan 21, Taishan 22, Taishan 24, Xinong 889, Yunfeng 139, Zhoumai 24, and Zi 12) were resistant in all field tests. Group 2 consisted of 21 cultivars (31.8%) that were resistant to one or two races in the field tests. Group 3 had 35 cultivars (53%) that were susceptible in all field tests.

Discussion

In this study, 66 wheat cultivars that were widely grown in the Huang-Huai-Hai region of China during 2000 to 2016 were postulated for *Yr* genes based on seedling tests with a series of *Pst* races and also tested with linked markers for some *Yr* genes. The results of the molecular tests and gene postulations were consistent for many of the cultivars. However, in some cases, conflicts were observed between the postulated genes and molecular proofs. For example, cultivar 95-111-6-3-10 (line 58) had the target product of the 1BL/1RS molecular marker but no postulated *Yr9* gene (Li et al. 2006).

Table 3. Specific primer sequences for stripe rust resistance genes *Yr5*, *Yr9* (1BL/1RS), *Yr10*, *Yr15*, *Yr18*, and *Yr26*

<i>Yr</i> gene	Primer name	Primer sequence (5' to 3')	Distance (cM)	PCR program
<i>Yr5</i>	<i>Yr5</i> -KASP	CTCACGCATTGACCATATACAAC	Cloned	94°C 5 min; 94°C 30 s, 60°C 45 s, and 72°C 45 s, 35 cycles; 72°C 7 min; 4°C continuous
<i>Yr9</i> (1BL/1RS)	AF1/4	TATTGCATAACATGGCCTCCAGT	Rye chromosome specific	94°C 3 min; 94°C 60 s, 60°C 60 s, and 72°C 90 s, 35 cycles; 72°C 10 min; 4°C continuous
		GGAGACATCATGAAACATTG		
<i>Yr10</i>	SC200	CTGTGTGTTGGGCAGAAAG	0.5	94°C 5 min; 94°C 60 s, 57°C 60 s, and 72°C 90 s, 35 cycles; 72°C 10 min; 4°C continuous
		CTGCAGAGTGACATCATACA		
<i>Yr15</i>	KinI	TCGAACTAGTAGATGCTGGC	Cloned	94°C 5 min; 94°C 30 s, 58°C 60 s, 72°C 60 s, and 30 cycles; 72°C 10 min; 4°C continuous
		GGAGATAGAGCACATTACAGAC		
	KinII	TTTCGCATCCCACCCTACTG		
<i>Yr18</i>	CsLV34	TGCACGCGGATATTAGGTAGG	0.4	94°C 5 min; 94°C 30 s, 60°C 60 s, and 72°C 60 s, 30 cycles; 72°C 10 min; 4°C continuous
		TGATGAAGAGGACCAACGCA		
		GTTGGTTAAGACTGGTGATGG		
<i>Yr26</i>	We173	TGCTTGCTATTGCTGAATAGT	1.4	95°C 5 min; 95°C 30 s, 57°C 30 s, and 72°C 50 s, 35 cycles; 72°C 7 min; 4°C continuous
		GGGACAAGGGGAGTTGAAGC		
		GAGAGTTCCAAGCAGAACAC		

Similarly, *Yr9* was postulated in 19 cultivars but the specific molecular marker for the 1RS chromosome was detected in 31 cultivars. Previous studies suggested that many independent genes, such as yield and quality genes, are present on 1RS (Mago et al. 2005). Thus, *Yr9* might have been lost during the yield or quality trait selection

although there were positive amplifications in PCR reaction with the chromosome 1RS specific AF1/4 primers. In another case, one new *Yr* gene named *YrCn17* located on 1RS led to the mimetic effects of *Yr9* in breeding lines (Ren et al. 2009). Because of the unavoidable crossover between target genes and linked molecular markers, such

Table 4. Seedling infection types in 66 common wheat cultivars from the Huang-Huai-Hai region of China tested with 15 races of *Puccinia striiformis* f. sp. *tritici*

Line	Cultivar	Infection type at the seedling stage ^a															Yr gene postulated ^b
		66E74	98E26	66E10	66E154	86E90	70E72	114E26	98E90	66E26	72E66	70E10	127E255	63E254	111E239	111E222	
1	Gaoyou 9618	7	3	4	4	1	0	1	0	1	0	0	7	7	7	7	+
2	Han 00-7086	0	1	0	7	0	0	0	0	0	0	0	7	7	7	7	+
3	Heng 0628	0	1	0	7	0	0	0	0	1	0	0	7	7	7	7	+
4	Heng 6599	4	3	1	3	3	4	4	3	1	2	2	7	7	7	7	+
5	Henong 6049	5	1	0	6	0	0	0	0	1	4	1	7	8	7	2	Yr9, Yr32
6	Henong 827	0	1	1	7	0	0	1	3	3	0	0	7	8	7	3	+
7	Huaimai 16	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	–
8	Huaimai 18	3	1	1	7	0	1	1	0	1	1	1	8	7	7	7	+
9	Ji 5265	0	0	0	1	0	0	0	0	1	0	1	7	7	7	7	Yr9, +
10	Jifeng 703	7	1	1	7	3	0	1	0	1	1	1	7	7	5	7	+
11	Jimai 19	7	7	6	6	7	5	0	7	7	1	1	7	7	7	6	+
12	Jimai 21	7	7	5	5	7	6	6	5	6	7	7	7	7	7	7	+
13	Jining 16	7	7	7	7	7	7	7	7	7	7	7	7	7	8	7	–
14	Jining 17	7	0	7	7	7	0	1	0	0	0	1	8	8	7	7	+
15	Jinmai 1	6	0	1	6	0	0	0	0	0	0	1	4	7	7	2	Yr9, Yr32, +
16	Kenong 199	0	1	0	0	0	0	0	0	0	0	0	7	7	7	7	Yr9, +
17	Kexin 9	7	7	7	7	7	7	7	7	7	7	7	6	7	4	0	+
18	Lai 95021	7	7	7	7	7	7	7	7	7	7	7	7	7	7	6	+
19	Langyan 43	2	0	0	4	0	1	0	0	1	1	0	5	6	2	2	Yr9, +
20	Liangxing 99	1	0	1	7	0	5	0	0	1	1	1	7	8	8	7	+
21	Linmai 4	7	7	7	7	7	7	7	7	7	7	7	7	7	7	0	+
22	Luohan 6	7	7	7	7	7	7	7	7	7	7	7	8	7	7	7	–
23	Luohan 8	5	1	0	7	1	1	1	1	1	1	1	7	7	7	7	+
24	Qifeng 1	1	1	0	4	1	0	0	1	1	0	1	7	7	7	0	Yr9, Yr32
25	Qingnong 2	1	5	3	5	3	4	3	2	1	1	0	6	7	7	0	+
26	Shannong 12	7	7	7	7	7	7	7	7	7	7	7	8	7	7	7	–
27	Shannong 15	1	1	0	0	0	5	2	2	1	4	7	5	8	8	5	+
28	Shannong 17	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	–
29	Shannong 18	3	2	3	4	4	6	3	2	4	4	5	4	7	7	4	+
30	Shannong 21	0	0	1	7	0	2	0	1	1	1	1	7	7	7	0	+
31	Shannong 23	0	1	1	0	1	0	0	0	6	0	0	7	8	7	7	Yr9, +
32	Shannong 29	5	0	0	7	0	6	0	1	0	5	1	7	0	7	3	+
33	Shannong 664	0	1	1	0	0	1	0	4	1	1	1	7	7	7	4	Yr9, Yr32
34	Shannongzimai 1	5	6	5	5	5	3	3	5	6	5	7	6	7	7	7	+
35	Shanrong 3	1	1	1	5	0	1	1	1	1	1	0	8	7	7	7	Yr9
36	Shi 4185	0	1	1	1	0	0	0	0	0	0	1	7	8	7	7	Yr9, +
37	Shijiazhuang 8	0	0	0	6	0	3	2	0	0	0	0	7	7	7	7	Yr9
38	Shimai 15	0	0	0	6	0	0	0	1	1	0	0	7	7	0	2	Yr9, +
39	Shimai 16	0	1	1	7	0	0	2	0	0	4	1	7	7	5	7	+
40	Shimai 18	0	1	1	7	0	0	0	0	0	0	0	8	8	7	7	+
41	Shixin 616	6	1	0	6	1	3	2	1	1	1	0	7	8	7	7	Yr9
42	Shixin 618	6	1	1	0	1	0	1	3	1	3	0	7	7	7	2	Yr9, Yr32
43	Shixin 828	3	1	1	7	0	7	1	7	0	7	0	7	7	2	2	+
44	Shiyou 17	7	5	6	4	6	6	7	6	4	5	7	7	7	7	7	+
45	Taishan 21	1	1	1	3	1	3	7	1	1	1	1	7	7	5	3	Yr10
46	Taishan 22	7	7	7	7	7	7	7	7	7	7	7	5	7	7	2	+
47	Taishan 24	7	7	7	7	7	7	6	7	7	7	7	7	7	7	0	+
48	Tanmai 98	0	1	0	3	1	3	1	7	1	1	7	7	7	5	5	+
49	Weimai 7	0	1	1	5	1	1	0	0	2	1	1	7	7	7	7	Yr9
50	Weimai 8	0	0	1	7	5	0	1	1	1	1	1	7	7	5	4	+
51	Wenong 5	0	3	1	2	6	6	2	6	1	2	1	7	7	7	4	+
52	Wenong 6	7	7	7	6	7	7	7	6	6	7	7	7	7	8	7	+
53	Xiaoyan 22	1	1	0	1	1	3	1	0	1	0	1	8	7	7	7	Yr9
54	Xiaoyan 81	7	7	7	7	7	7	7	7	7	7	7	7	7	7	4	+
55	Xin 2899	0	1	0	5	3	1	0	0	1	0	0	7	7	7	0	Yr9, Yr32
56	Xinong 889	1	3	1	3	1	1	1	2	1	1	1	1	3	4	2	Yr10, +
57	Yan 99102	6	2	1	7	1	0	0	1	3	0	1	7	7	8	7	+
58	Yannong 0428	3	3	7	7	3	6	2	3	3	0	5	7	7	7	0	+
59	Yannong 19	7	7	7	7	7	7	7	7	7	7	7	7	7	7	0	+
60	Yannong 21	7	7	7	7	7	7	7	7	7	7	7	8	8	7	7	–
61	Yannong 22	0	1	0	7	0	1	1	0	1	0	1	7	7	7	3	+
62	Yannong 836	6	6	4	5	6	1	3	6	3	5	7	7	7	7	0	Yr32
63	Yunfeng 139	1	1	1	1	1	2	1	1	1	1	1	2	6	2	5	Yr10, Yr26, +
64	Zhouheimai 1	1	1	0	2	1	0	1	0	1	1	0	8	7	7	8	Yr9, +
65	Zhoumai 24	1	1	0	1	0	0	2	1	1	1	1	7	7	0	7	Yr9, +
66	Zi 12	1	2	1	1	1	1	7	1	3	2	2	7	7	5	0	Yr10

^a 0 = no visible signs or symptoms; 1 = necrotic and/or chlorotic flecks, no sporulation; 2 = necrotic and/or chlorotic blotches or stripes, no sporulation; 3 = necrotic and/or chlorotic blotches or stripes, trace amounts of sporulation; 4 = necrotic and/or chlorotic blotches or stripes, light sporulation; 5 = necrotic and/or chlorotic blotches or stripes, intermediate sporulation; 6 = necrotic and/or chlorotic blotches or stripes, moderate sporulation; 7 = necrotic and/or chlorotic blotches or stripes, abundant sporulation; 8 = chlorosis behind sporulating area, abundant sporulation; and 9 = no necrosis or chlorosis, abundant sporulation.

^b A plus sign indicates an unknown *Yr* gene, whereas a minus sign indicates that no *Yr* gene was postulated.

conflicts may occur when linked markers are used in nonsegregated populations (Wu et al. 2007). This is a very complicated process, and scientists need to make additional efforts to identify the mechanisms. To improve the reliability of the results, only the results consistent between the molecular marker tests and gene postulations are presented in our research.

For example, no PCR product was generated by primer We173 (*Yr26*) for Shimai 15, although Shimai 15 showed the same seedling resistance spectrum as Avocet S/*Yr26* and 92R173 (*Yr26*) was in the pedigree of this cultivar. Thus, our results suggest that Shimai 15 did not contain *Yr26*, which was consistent with the results of Zhang et al. (2014). Xu et al. (2011) reported that Taishan 21 and Zi 12 did not contain *Yr10*, but our results showed that these cultivars might have *Yr10* because the target fragments were successfully amplified and the cultivars showed consistent ITs with Avocet S/*Yr10*. Zi12 might have *Yr10* inherited from the Guinong lines because Guinong 35-2 was in the pedigree of this cultivar. In addition, Marchal et al. (2018) and Klymiuk et al. (2018) developed molecular markers *Yr5*-KASP for *Yr5* and KinI and KinII for *Yr15* based on the target gene sequences, respectively. Li et al. (2008) reported that Yunfeng 139 (also known as Shaanmai 139) carried *Yr5*, *Yr10*, *Yr15*, and *Yr26*. However, our results showed that Yunfeng 139 might carry *Yr10*, *Yr26*, and unknown *Yr* genes. Yunfeng 139 does not have *Yr5* or *Yr15* because no PCR products were generated using primers *Yr5*-KASP or KinI and KinII, even though Yunfeng 139 showed resistance to all 15 *Pst* races. Zhang et al. (2016) reported that Yunfeng 139, which exhibited resistance to the majority of *Pst* isolates, possessed an unknown *Yr* gene located on the 1B chromosome that was different from *Yr5*, *Yr10*, *Yr15*, and *Yr26*. Although *T. turgidum* var. *dicoccoides* was in the pedigree of Yunfeng 139, the cultivar does not necessarily have *Yr15*, because either the *T. turgidum* var. *dicoccoides* line may not have *Yr15* or *Yr15* may have been lost during selection. The introgression of a target gene from a wild wheat is complicated as a result of several backcrossing and selection steps that were needed to reduce linkage drags (Yaniv et al. 2015). Similar results were observed for Langyan 43 and Xinnong 889.

Of all postulated genes, *Yr9* from the translocation of 1BL/1RS containing resistance to other diseases, yield, and quality traits is widely used in breeding programs all over the world (Wieser et al. 2000). In the early 1970s, 1BL/1RS lines such as Avorora, Lovrin 10, Lovrin 13, Predgornaya 2, Kavkaz, and Neuzucht were introduced in China and intensively used in Chinese wheat breeding programs (He et al. 2001), which caused a high frequency of *Yr9* (Gebrewahid et al. 2017; Ren et al. 2015). Our results showed that 19 (28.8%) of 66 cultivars carried *Yr9*. According to the pedigree, the presence of *Yr9* in Xin 2899 might be from Lovrin 13. *Yr9* in Jimai 1, Xiaoyan 22, and Shannong 664 might be from Lovrin 13 and/or Lumai 14 (Ge et al. 2009) because these two cultivars carry *Yr9* (Niu et al. 2000). Cultivars Shi 4185, Ji 5265, and Langyan 43 most likely inherited the *Yr9* gene from Lovrin 10. Henong 6049, Shimai 15, and Shijiazhuang 8 carry *Yr9*, possibly from Lovrin 10 and/or Avorora because these *Yr9* donors were present in the pedigree of these Chinese cultivars (Huang et al. 2017). The presence of *Yr9* in Zhouheimai 1 and Zhoumai 24 might be from Predgornaya 2 and/or Neuzucht because the two Chinese cultivars have these *Yr9* varieties in their pedigrees. Ren et al. (2015) reported that Jimai 21 contained *Lr26* based on the *Lr26F/R*:IB-267 molecular marker test and gene postulation. However, our results demonstrated that Jimai 21 did not possess *Yr9* because 66E74, 98E26, 86E90, 72E66, and 70E10 were virulent to Jimai 21 but avirulent to Avocet S/*Yr9*. In addition, no PCR products were successfully amplified by primer AF1/4 in Jimai 21. Moreover, the 1BL/1RS lines are not present in the Jimai 21 pedigree. Yannong 19 and Yannong 21 have the same pedigree but show different ITs to 11E222 (Yannong 19 was resistant to race 11E222 [IT = 0], whereas Yannong 21 was susceptible [IT ≥ 7]), suggesting that phenotypic selection played a critical role in breeding (Niu et al. 2000).

In the early 2000s, the utilization and development of wheat stripe rust APR was increasingly popular in breeding programs in China

(He et al. 2006), but efforts made by Chinese breeders were slightly less than those in other countries (He et al. 2011). In our study, only 10 wheat cultivars showed resistance to all races (CYR32, CYR33, and CYR34) at the adult-plant stage in the field and no cultivars contained the *Yr18* gene, which is an APR gene widely used in breeding programs in many parts of the world. Thus, the wheat cultivars widely grown in the Huang-Huai-Hai region in recent years still have a low level of APR against stripe rust. Inheritance studies conducted by scientists from the International Maize and Wheat Improvement Center showed that combinations of three to five APR genes resulted in a high level of resistance, although individual nonhypersensitive-type genes had little resistance to *Pst* (Singh et al. 2000). The Huang-Huai-Hai region is thought to have spring epidemics of stripe rust, and planting cultivars with APR in this region is the first option and a vital strategy for controlling stripe rust. Therefore, employing APR genes such as *Yr36* (Chhuneja et al. 2008) and *Yr52* (Ren et al. 2012), especially APR gene clusters such as *Yr18/Lr34/Pm38* (Lillemo et al. 2008), *Yr29/Lr46/Pm39* (Lillemo et al. 2008), and *Yr46/Lr67* (Herrera-Foessel et al. 2011), would be needed in resistance pyramiding programs for developing resistant cultivars to control stripe rust.

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