Emerging *Yr26*-Virulent Races of *Puccinia striiformis* f. *tritici* Are Threatening Wheat Production in the Sichuan Basin, China

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Abstract

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Stripe rust, caused by *Puccinia striiformis* f. *tritici*, is one of the most destructive diseases of wheat in the world. The Sichuan Basin is one of the most important regions of wheat production and stripe rust epidemics in China. Stripe rust resistance gene *Yr26* (the same gene as *Yr24*) has been widely used in wheat breeding programs and in many cultivars grown in this region since the gene was discovered in the early 1990s. Virulence to *Yr26* has increased in frequency since its first detection in 2008. The objective of this study was to assess the vulnerability of the wheat cultivars and breeding lines in the Sichuan Basin to *Yr26*-virulent races. In total, 85 wheat accessions were tested with *Yr26*-avirulent races CYR32, CYR33, and Su11-4 and two *Yr26*-virulent races, V26/CM42 and V26/Gui22. DNA markers for *Yr26* were used to

determine the presence and absence of *Yr26* in the wheat accessions. Of the 85 wheat accessions, only 5 were resistant and 19 susceptible to all races tested, and the remaining 61 were resistant to at least one or more races tested in seedling stage. In all, 65 (76.5%) accessions were susceptible to the emerging *Yr26*-virulent race V26/Gui22. In field tests, susceptible accessions increased from 31.8% in a nursery inoculated with predominant and *Yr26*-avirulent races to 61.2% in the nursery inoculated with the predominant races mixed with V26/Gui22. Based on the results of the molecular marker and race tests, 33 (38.8%) accessions were determined to have *Yr26*, showing that the *Yr26* virulence is a major threat to wheat production in the Sichuan Basin and potentially in other regions of China.

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* Erikss., is one of the most important diseases of wheat (*Triticum aestivum* L.) worldwide (6,10,34,36). Because *P. striiformis* f. *tritici* urediniospores of the fungal pathogen can be disseminated by wind over long distances, the fungal pathogen is able to cause large-scale epidemics, resulting in huge yield losses if no control measures are taken (1). In China, nationwide stripe rust epidemics resulting in huge yield losses or wide application of fungicides occurred in 1950, 1964, 1990, and 2002, with the disease occurring more frequently in the northwestern and southwestern regions where the pathogen can overwinter or overwinter (5,15,17,30,32). Every devastating epidemic was related to the appearance and development of new *P. striiformis* f. *tritici* races. Growing resistant cultivars is the most economical and effective strategy for sustainable control of the disease (6,9,23). Currently, more than 60 permanently named genes (*Yr1* to *Yr67*) and numerous temporarily designated genes have been reported in wheat for stripe rust resistance and most of them have been used in wheat breeding programs worldwide (7,11,20,22,26). However, many of the race-specific resistance genes have been overcome by new virulent races of *P. striiformis* f. *tritici*, which have resulted in large-scale epidemics (8,9,34).

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Stripe rust resistance gene *Yr26* (the same gene as *Yr24*) (16) was initially identified in a series of wheat–*Haynaldia villosa* 6AL/6VS translocation lines, such as 92R137, 92R149, and 92R078, developed by Chen et al. (3,4,21) in Nanjing Agricultural University and released in the early 1990s. Because of its high level resistance to predominant *P. striiformis* f. *tritici* races, including CYR32 and CYR33, *Yr26* has been widely deployed in the major stripe-rust-prone regions in China, especially the Sichuan Basin. Virulence to *Yr26* was first detected on ‘Chuanmai 42’ wheat in the Sichuan Basin in 2008 (19) and subsequently in Gansu on line 92R137 and Guinong 22 (13); which have been widely used in breeding programs in these regions. In 2010, *Yr26*-virulent races were detected at low frequencies from samples collected from highly susceptible ‘Mingxian 169’ and 92R137. However, moderate to severe stripe rust was observed on cultivars with *Yr26*, including ‘Neimai 8’ and ‘Lantian 17’ in 2011. Since then, the frequency of *Yr26*-virulent races has increased from 3.4% in 2011 to 10.3% in 2013 (Z. S. Kang and associates, unpublished data). Moreover, several races virulent to *Yr26* have been detected in the recent years in many provinces, including Sichuan, Gansu, Shaanxi, Qinghai, and Ningxia. The initial *Yr26*-virulent race has a narrow virulence range but different *Yr26*-virulent races identified more recently have wider virulence spectra.

The stripe rust pathogen is capable of long-distance dispersal, and epidemiological regions can be characterized as overwintering, overwintering, or spring epidemic zones based on climatic conditions and cropping systems for the pathogen (1,5,28,38). The Sichuan Basin, which is about 260,000 km² and located in southwestern China (Fig. 1), plays an important role in stripe rust epidemics in China (12,15,17). Wheat crops in the basin are infected in the autumn by urediniospores disseminated from the surrounding mountainous *P. striiformis* f. *tritici*-overwintering areas. In the basin, the mild

and often moist winter allows wheat to grow and the *P. striiformis* f. *tritici* fungus to survive, sporulate, and even infect wheat crops in multiple cycles (12). Therefore, the basin is considered to be a reservoir of *P. striiformis* f. *tritici* inoculum for spreading to other regions, and the early occurrences of stripe rust are used to predict stripe rust epidemics for the region and other regions farther east (5,15,39). The dynamics of the pathogen population is strongly influenced by the distribution of resistance genes in the host population (2,14). Given the *Yr26*-virulent races started in the Sichuan Basin, the presence of *Yr26* in the wheat cultivars grown in the region should have affected the race structure changes in the region and other regions. Although *Yr26*-virulent races have caused only localized damage thus far, a better understanding of the potential threat by the races through determining the distribution of *Yr26* in wheat cultivars and breeding lines in the region and their resistance or susceptibility to predominant races and those virulent to *Yr26* should reduce potential risk. Therefore, the objectives of this study were to determine resistance or susceptibility of wheat cultivars and breeding lines from the Sichuan Basin to the emerging *Yr26*-virulent races and the presence and absence of *Yr26* in the cultivars and breeding lines. The results will be useful in assessing the epidemic risks posed by the new race group and will guide proper strategies for control of the disease through changing wheat cultivars in production and resistance sources in breeding programs.

Materials and Methods

Wheat materials and *P. striiformis* f. *tritici* races. A collection of 85 wheat accessions, including 70 cultivars and 15 breeding lines grown or developed in the Sichuan Basin, was obtained from Sichuan Agriculture University and tested for stripe rust reaction and presence or absence of *Yr26*. The wheat accessions and their pedigree and year of release are listed in Table 1. Five *P. striiformis* f. *tritici* races that had been determined by a set of Chinese wheat differentials were used in this study, including the three predominant races (CYR33, CYR32, and Su11-4) during 2011 to 2013 (5,13), which are avirulent to *Yr26*, and two *Yr26*-virulent races, V26/CM42 isolated from Chuanmai 42 in 2008 and V26/Gui22 isolated from Guinong 22 in 2012. The virulence or avirulence patterns of the races were determined using 17 *Yr* single-gene lines (31,35), the recurrent susceptible parent Avocet S (AvS), and *Yr26* donor lines 92R137 and Guinong 22 (Table 2).

Stripe rust tests in the greenhouse. Seedling evaluations for reaction to stripe rust were conducted in a greenhouse. Ten seeds of each accession were sown in a pot of 9 by 9 by 9 cm. Mingxian 169 was used as a susceptible control. Seedlings at the two-leaf stage

(14 days after planting) were inoculated with urediniospores of a *P. striiformis* f. *tritici* race. The inoculated plants were incubated at 10°C in a dew chamber in the dark for 24 h, then transferred to a greenhouse at 17 ± 2°C with 14 h of light (22,000 lx). Infection types (ITs) were scored 20 days after inoculation using a 0-to-9 scale described by Line and Qayoum (18). Plants with ITs 0 to 6 were considered resistant and the inoculated race avirulent; and plants with ITs 7 to 9 were considered susceptible and the race virulent. All seedling tests were repeated at least two times to confirm and clarify infection types.

Stripe rust tests in the fields. To evaluate resistance or susceptibility of adult plants of the wheat accessions to the predominant races and *Yr26*-virulent races, the evaluations for resistance in the adult plant stage were conducted in two nurseries on the Northwest A&F University research farms in Yangling, Shaanxi in the 2012–13 wheat growing season. The two nurseries were about 1 km away and surrounded by kiwifruit orchards. The nurseries were planted on 10 October 2012. In each nursery, seed of each wheat accession were planted in two rows of 100 cm in length, with a 10-cm space between the two rows and a 25-cm space between accessions for convenience of collecting rust data. Accessions in each nursery were arranged in a randomized block design with two replications. ‘Xiaoyan 22’, a local susceptible cultivar, was planted, also in two rows, between every 20 accessions as a susceptible check, and Mingxian 169 was planted at both ends of the nursery as a spreader. When flag leaves emerged, the nurseries were inoculated by spraying a mineral oil suspension of mixed urediniospores of the selected races on 10 April 2013. Nursery A was inoculated with *Yr26*-avirulent but predominant races CYR33, CYR32, and Su11-4, and nursery B was inoculated with these three races plus *Yr26*-virulent race V26/Gui22. IT and disease severity (DS) were scored three times, at weekly interval, starting when the susceptible check had at least 30% severity using the modified Cobb scale (24). DS was assessed visually using the percentage of diseased leaf area. Both IT and DS on the third assessment that gave the highest DS were used to determine resistance or susceptibility of the accessions. For each entry, one-way analysis of variance (ANOVA) was performed with two replicates to estimate environmental effects.

DNA marker analysis. Sequence-tagged site (STS) markers *WE173* and *BQ74*, which are codominant markers and about 1.4 and 0.43 centimorgans flanking the *Yr26* locus (33,40), were used to determine the presence or absence of *Yr26* in each wheat accession. DNA was extracted from leaves using the cetyltrimethyl ammonium bromide procedure (27). Polymerase chain reaction (PCR) reactions were performed in a S1000 Thermal Cycler (Bio-Rad Laboratories, Hercules, CA, USA)

Fig. 1. Location of the Sichuan Basin (shaded) in China. Area 1: the most important overwintering area of *Puccinia striiformis* f. *tritici* and the major source of inoculum for wheat infection in autumn; area 2: the overwintering and reproducing region and the major spring inoculum source of *P. striiformis* f. *tritici*; and area 3: spring epidemic zones.

in a 15- μ l volume, containing 1.0 U of *Taq* DNA polymerase (Thermo Fisher Scientific, Inc., Waltham, MA), 1.5 μ l of 10 $\times$ buffer (50 mmol KCl and 10 mmol Tris-HCl), 1.2 mmol MgCl₂, 200 μ mol each dNTP, 6 pmol each primer, and 50 to 100 ng of template DNA. The PCR condition was as follows: predenature at 94°C for 4 min; followed by 35 cycles of 94°C for 1 min, 55°C for 1 min, and 72°C for 1 min; and a final extension for 10 min at 72°C. PCR products were separated in 6% denature polyacrylamide gels. 92R137 and AvS were used as positive and negative controls, respectively.

Results

Virulence or avirulence patterns of the *P. striiformis* f. *tritici* races. The ITs of the five *P. striiformis* f. *tritici* races produced on the *Yr* gene lines are shown in Table 2. The predominant races Su11-4, CYR32, and CYR33 were all avirulent to the *Yr26* single-gene lines. In contrast, V26/CM42 and V26/Gui22 were virulent to the *Yr26* lines. The initial *Yr26*-virulent race, V26/CM42, was virulent to *Yr6*, *Yr7*, *Yr8*, *Yr10*, *Yr17*, *Yr28*, *Yr29*, *YrTr1*, and *Yr26* but avirulent to *Yr1*, *Yr5*, *Yr9*, *Yr15*, *Yr27*, *Yr32*, and *YrSP*. The later

Yr26-virulent race, V26/Gui22, had a broader virulence spectrum, because it was virulent to *Yr1*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr10*, *Yr17*, *Yr26*, *Yr27*, *Yr28*, *Yr29*, and *YrSP* but avirulent to *Yr5*, *Yr15*, *Yr32*, and *YrTr1*. These results indicate that the *Yr26* virulent population has evolved into more complex races. The results also indicate that *Yr1*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr10*, *Yr17*, *YrTr1*, and *Yr26* were not effective against the most predominant and emerging *Yr26*-virulent races.

Evaluation of wheat cultivars and lines for reaction to *P. striiformis* f. *tritici* races. In seedling tests conducted in the greenhouse, of the 85 accessions, only 5 (5.9%) were resistant and 19 (22.3%) were susceptible to all four races tested, while the remaining 61 (71.8%) were susceptible (or resistant) to one, two, or three races (Table 3). The frequency of susceptible accessions was 34.1% for race Su11-4, 36.6% for CYR33, 48.2% for CYR32, and 76.5% for V26/Gui22. The *Yr26*-virulent race V26/Gui22 made the majority of wheat accessions susceptible, including 50 (71.4%) cultivars and 15 (100%) breeding lines.

In the field trials, the analysis results by ANOVA for IT and DS of each entry showed that there were no significant differences between

Table 1. Pedigree and year of release of wheat cultivars and breeding lines from the Sichuan Basin used in this study

Number	Accession	Pedigree ^a	Year of release ^b
1	Mianyang 19	Pedigree selection from Mianyang11	1984
2	Chuanmai 24	8282-15 $\times$ Mianyang 19	1995
3	Chuanmai 28	Wanya2/2874//Gaojiasuo/2874// Mianyang19	1997
4	Mianyang 26	Mianyang20/Chuanyu9	1998
5	Chuanmai 30	77/YAA//ALD'S/3/YSZ//ST2022/ 983	1999
6	Chuanmai 32	(1900"S"Ning8439) $\times$ 1900	2001
7	Chuannong 10	78-5038/85-D.H.5015	2001
8	Chuannong 11	78-5038/85-D.H.5015	2001
9	Chuanmai 35	SW1862/2469	2002
10	Chuanmai 36	Milan/SW5193	2002
11	Chuannong 12	91S-23/A302	2002
12	Chuannong 17	91S-23 $\times$ A302	2002
13	Chuanmai 16	30020/8619-10//Jinmai30	2002
14	Chuanmai 17	Mianyang26/G295-4	2002
15	Mianyang 31	90-310 $\times$ Chuanzhi89-076	2002
16	Chuanmai 38	SynCD769/SW89-3243//Chuan6415	2003
17	Chuanmai 39	Mo444/90-7	2003
18	Chuanmai 41	91T4135 $\times$ 88Fan8	2003
19	Chuanmai 42	SynCD768/SW89-3243//Chuan6415	2003
20	Chuannong 18	Chuanmai12 $\times$ 87-429	2003
21	Chuannong 19	Qian1104A/R935	2003
22	Chuanmai 18	Chuanmai5/Mo460//94F2-4	2003
23	Chuanmai 19	Chuanmai5/Mo460//Mianyang26	2003
24	Neimai 8	Mianyang26/92R178	2003
25	Xikemai 1	Mianyang25/MoM-212	2003
26	Chuanmai 43	SynCD768/SW89-3243//chuan6415	2004
27	Chuanmai 44	96-440/Guinong21	2004
28	Chuannong 21	R843/Qianhui3	2004
29	Liangmai 2	Mianyang26/Yiyuan2	2004
30	Mianmai 37	96EW37/Mianyang90-100	2004
31	Mianmai 38	07146-12-1/Guinong19-4	2004
32	Neimai 9	Mianyang26/92R178	2004
33	Xingmai2	Mianyang26/92R178	2004
34	Chuanmai 45	GH430/SW1862	2005
35	Chuanmai 46	Ta193-6280/96-5429	2005
36	Chuanmai 47	Syn-CD786/Mianyang26// Mianyang26	2005
37	Chuannong 22	R164/86-104	2005
38	Chuannong 23	R1658/MY26	2005
39	Mianmai 39	Mianyang96-78/Guinong21-1	2005
40	Mianmai 40	Mianyang01821/Guinong19-4	2005

(continued on next column)

^a An *Yr26* or *Yr24* donor in the pedigree is indicated by underline.

^b NR denotes a breeding line that has not been released.

Table 1. (continued from preceding column)

Number	Accession	Pedigree ^a	Year of release ^b
41	Xikemai 2	Chuanmai11/Mo444	2005
42	Chuannong 26	Chuannong19/R3301	2006
43	Chuanmai 20	SW3243//35050/21530	2006
44	Mianmai 41	Mianyang01821/90-165//Guinong19-4	2006
45	Mianmai 42	Mianyang96-5/Guinong21-1	2006
46	Mianmai 43	07146-12-1(Mianyang92-8/88-304)/ Guinong19-4	2006
47	Zimai 1	Mianyang29/Chuanmai25	2006
48	Chengdianmai	MY92-8 / 91S-5-4	2007
49	Chuannong 24	Baili3/Yunfan52894-2	2007
50	Chuannong 25	961-225 $\times$ 91S-5-4	2007
51	Chuanmai 21	Zhou88114/G159	2007
52	Liangmai 4	N1491/N1071	2007
53	Mianmai 1403	Mianyang04854/Guinong21-1	2007
54	Mianmai 45	07146-12-1/Guinong19-4	2007
55	Neimai 11	Pin5 $\times$ 94-7	2007
56	Rongmai 4	96-2547/133-3	2007
57	Xikemai 3	Guinong21/5575	2007
58	Chuanmai 51	174/183//99-1572	2008
59	Chuanmai 52	Chuanmai36/SW1862	2008
60	Mianmai 185	Mianyang96-5/Liaochun10	2008
61	Mianmai 46	07242-3-1-1/Guinong21	2008
62	Neimai 836	5680/92R133	2008
63	Xikemai 4	Mo460/9601-3	2008
64	Xikemai 6	Mianyang95-325/92R-135	2008
65	Chuannong 27	chuannong19/R3301	2009
66	Mianmai 48	Mianyang01821/Guinong19-4	2009
67	Mianmai 367	Mianyang1275-1/99-1522	2010
68	Chuanmai 60	98-1231//Guinong21/Shenghe3295	2011
69	Chuanmai 104	Chuanmai42/Chuannong16	2013
70	Mianmai 51	Mian1275-1/99-1522	2013
71	Chuan 00030	88Fan8/88-309	NR
72	LTM 18	Unknown	NR
73	M9876	Unknown	NR
74	Mian 05-164	Unknown	NR
75	Mian 06-374	Unknown	NR
76	Mian 1971-98	Unknown	NR
77	Mian11-13	Unknown	NR
78	Mian11-25	Unknown	NR
79	Mian11-48	Unknown	NR
80	Mianyang 96-5	Unknown	NR
81	MR 125	Unknown	NR
82	MR 168	Unknown	NR
83	MR 71	Unknown	NR
84	MR11-12	Unknown	NR
85	MR11-20	Unknown	NR

replications in the same nursery, but obvious differences in reactions and significant differences in severity were detected for many accessions between the nurseries inoculated with races including or not including a *Yr26*-virulent race (V26/Gui22). Therefore, the final reactions and severity averaged between the two replications were presented and used to characterize the accessions (Table 3). In nursery A, inoculated with the three most predominant but *Yr26*-avirulent races (CYR33, CYR32, and Su11-4), 58 (68.2%) were resistant and 27 (31.8%) were susceptible. In nursery B, which was inoculated with the three predominant races plus *Yr26*-virulent race V26/Gui22, the number of susceptible accessions was increased by 25, reaching 52 (61.2%). All of the 25 cultivars changing from resistant to susceptible were found to have *Yr26* based on their pedigrees, greenhouse individual race tests, and the presence of the *Yr26* markers, as indicated below.

Presence and absence of *Yr26* in wheat cultivars and lines. When the 85 accessions were tested with molecular markers *WE173* and *QB-74* for *Yr26*, 33 had both markers and, therefore, were considered to have *Yr26* (Table 3). The molecular results were in consistent with the results based on the phenotypic IT data, except accessions 18 ('Chuanmai 41') and 68 ('Chuanmi 60') that did not have the marker alleles of 92R137.

Discussion

The emerging *Yr26*-virulent races, such as V26/CM42 and V26/Gui22, have overcome *Yr26* (= *Yr24*) and *Yr10*, which are effective against all previously identified *P. striiformis* f. *tritici* races and have been deployed in commercial cultivars to fight predominant races of the fungus in China. Race V26/CM42, detected in 2008, was found to be virulent to these genes. The present study confirmed the *Yr26* virulence and proved it as a race different from the predominant races CYR32, CYR33, and Su11-4. Race V26/Gui22, collected in 2012, is an even more virulent race than V26/CM42 because it has a broader virulence spectrum than V26/CM42. This race is a bigger threat to wheat production in the Sichuan Basin. It is noteworthy that all 33 *Yr26* wheat accessions were resistant in nursery A, whereas 24 of them became susceptible in nursery B and only 9 of them showed resistance to all four races used in the inoculation. These results, together with the seedling data from the greenhouse, indicated that the *Yr26*-virulent race was virulent to *Yr26* at both seedling and adult plant stages. The high numbers of susceptible accessions in the greenhouse and fields indicate that the predominant races continue posing threats and the emerging *Yr26*-virulent races pose an even greater threat to breeding programs and production of wheat in the Sichuan Basin.

More than 76% of wheat cultivars and breeding lines from the Sichuan Basin are susceptible to the *Yr26*-virulent races at the seedling stage. The emerging races could be a threat to other wheat-growing areas because *P. striiformis* f. *tritici* can spread from the Sichuan Basin to the east (5,12,15), although wheat cultivars grown in other regions were not tested in the present study. Wheat entries from many regions have been tested in the field in the Sichuan Basin but the relatively low frequencies of the *Yr26* virulence thus far may not provide adequate information. Therefore, further testing of cultivars and breeding lines from other regions with *Yr26*-virulent races under controlled conditions is needed.

In the late 1990s, *Yr26* was introduced into Sichuan wheat breeding programs as the 92R series lines (92R133, 92R137, 92R149, and 92R178) and Guinong series lines (Guinong 19, Guinong 21, and Guinong 22). Neimai 8 (Mianyang 26/92R178) was released in 2003 as the first cultivar with *Yr26*. *Yr24*, derived from *T. turgidum* var. *durum* accession K733, was introduced into Sichuan wheat breeding programs by a synthetic wheat resistance line Syn769 (AABBDD), which was developed from Decoy 1 (*T. turgidum* accession AABB) crossed with *Aegilops tauschii* 188 (DD) (16). Chuanmai 42, also released in 2003, was the first Chinese cultivar with *Yr24*. Since then, more than 30 wheat cultivars and breeding lines have been developed that have *Yr26* or *Yr24* (Table 1). Previous studies suggested that *Yr24*, *Yr26*, and *YrCH42* should be the same gene (11,16,22). In the present study, the *Yr24* and *Yr26* near-isogenic lines Guinong 22, 92R137, and Chuanmai 42 were all resistant to the *Yr26*-avirulent races and susceptible to the *Yr26*-virulent races, supporting the idea that *Yr24* and *Yr26* are the same gene. Because of the high potential yields and high resistance to predominant races CYR32 and CYR33, cultivars with *Yr26* such as Chuanmai 42, Neimai 8, and Mianmai 37 have become the major cultivars grown in the Sichuan Basin in recent years. Unfortunately, these cultivars are susceptible to the emerging *Yr26*-virulent races, and should be withdrawn from production as soon as possible to avoid devastating epidemics.

It is interesting that the *Yr26*-virulent races are also virulent to *Yr10*. However, *Yr10* is a gene different from *Yr26* and *Yr24*, as demonstrated by previous studies with virulence data and molecular markers (11,29,31). The present study shows that *Yr10* is no longer effective against the *P. striiformis* f. *tritici* population in China. *Yr10* has not been used as much as *Yr26* in wheat breeding programs in China. However, cultivars with *Yr10* are also at risk. Although we did not attempt to determine wheat cultivars and breeding lines for the presence of *Yr10* in the present study, Chuanmai 41 and

Table 2. Infection types of *Puccinia striiformis* f. *tritici* races used in the study based on 17 *Yr* single-gene lines and 3 *Yr26* (= *Yr24*) donor lines

Number	Line	<i>Yr</i> genes	Infection type				
			Su11-4	CYR32	CYR33	CM42	Gui22
1	AvSYr1NIL	<i>Yr1</i>	7	9	8	1	9
2	AvSYr5NIL	<i>Yr5</i>	0	1	0	0	1
3	AvSYr6NIL	<i>Yr6</i>	8	9	9	9	9
4	AvSYr7NIL	<i>Yr7</i>	9	9	7	9	9
5	AvSYr8NIL	<i>Yr8</i>	8	9	0	9	7
6	AvSYr9NIL	<i>Yr9</i>	8	9	8	1	9
7	AvSYr10NIL	<i>Yr10</i>	0	2	2	7	8
8	AvSYr15NIL	<i>Yr15</i>	0	0	0	0	0
9	AvSYr17NIL	<i>Yr17</i>	5	9	8	8	8
10	AvSYr24NIL	<i>Yr24</i>	1	0	2	7	9
11	AvSYr26NIL	<i>Yr26</i>	1	2	2	9	9
12	AvSYr27NIL	<i>Yr27</i>	5	9	3	6	9
13	AvSYr28NIL	<i>Yr28</i>	9	9	9	7	9
14	AvSYr29NIL	<i>Yr29</i>	9	9	9	8	9
15	AvSYr32NIL	<i>Yr32</i>	2	2	2	4	4
16	AvSYrSPNIL	<i>YrSP</i>	6	9	9	2	9
17	AvSYrTr1NIL	<i>YrTr1</i>	1	2	2	9	2
18	Avocet S (AvS)	Unknown	9	9	9	9	9
19	Chuanmai 42	<i>Yr24</i>	1	2	2	8	9
20	Guinong 22	<i>Yr26</i>	1	2	2	7	9
21	92R137	<i>Yr26</i>	1	2	1	7	9

Chuanmai 60, which were resistant to the *Yr26*-avirulent races and susceptible to the *Yr26*-virulent races, may have *Yr10* because they do not have *Yr26*. The hypothesis can be tested with molecular markers or with races that can differentiate *Yr10* and *Yr26* from other countries. The presence of *Yr10* in wheat cultivars in other regions of China also needs to be studied.

The Sichuan Basin is considered a secondary center for emerging new *P. striiformis* f. *tritici* races and stripe rust epidemics in China (12,17,39). The appearance and development of the *Yr26*-virulent races support this point, although it is still not clear where the *Yr26* virulence originated. More wheat cultivars and breeding lines with *Yr26* in the Sichuan Basin than any other region apparently selected the *Yr26* virulence. The Sichuan Basin wheat region is adjacent to the pathogen

overwintering areas. In the autumn, *P. striiformis* f. *tritici* inocula from southern Gansu, northwestern Sichuan, and other areas in the southwestern region could be blown by wind to the Sichuan Basin, where the pathogen can infect, reproduce, and spread to the regions further east and north. Similarly, urediniospores produced in the basin may be spread back to infect wheat crops in the overwintering regions. The shuttling of *P. striiformis* f. *tritici* between the overwintering and overwintering regions can spread to other regions, which makes the *Yr26*-virulent races a great concern for the whole country.

Using pedigrees, phenotype data, and molecular markers, we were able to detect *Yr26* in wheat cultivars and breeding lines in the present study. The molecular markers apparently provide accurate information about the presence and absence of the gene. Such accurate

Table 3. Seedling infection types (ITs), severity, and reactions at adult-plant stage in the field nurseries, molecular markers detected, and presence (P) or absence (A) of *Yr26* in the 85 wheat accessions

Number	Accession	Seedling IT ^a				Adult-plant severity and reaction ^b			Molecular markers ^c		
		CYR32	CYR33	Su11-4	Gui22	Nursery A ^d	Nursery B ^e	Type	WE173	QB-74	<i>Yr26</i> ^f
1	Mianyang 19	9	8	7	8	100 S	100 S	S	–	–	N
2	Chuanmai 24	8	9	9	8	30 S	80 S	S	–	–	N
3	Chuanmai 28	3	9	9	7	60 S	80 S	S	–	–	N
4	Mianyang 26	9	5	8	7	30 S	60 S	S	–	–	N
5	Chuanmai 30	9	5	7	5	60 S	80 S	S	–	–	N
6	Chuanmai 32	9	8	9	7	30 S	60 S	S	–	–	N
7	Chuannong 10	7	7	7	3	30 S	30 S	S	–	–	N
8	Chuannong 11	7	7	5	3	30 S	30 S	S	–	–	N
9	Chuanmai 35	1	1	7	1	10 R	30 MR	APR	–	–	N
10	Chuanmai 36	8	5	5	8	40 S	60 S	S	+	–	N
11	Chuannong 12	5	1	1	1	30 MR	20 MR	ASR	–	–	N
12	Chuannong 17	7	1	1	1	5 R	10 MR	APR	–	–	N
13	Chuanyu 16	8	1	1	1	10 R	30 R	APR	–	–	N
14	Chuanyu 17	9	7	1	7	1 R	1 R	APR	–	–	N
15	Mianyang 31	9	9	7	7	30 S	30 S	S	–	–	N
16	Chuanmai 38	8	8	5	7	10 MR	60 S	S	+	–	N
17	Chuanmai 39	1	9	7	7	20 S	30 S	S	–	–	N
18	Chuanmai 41	1	1	5	7	30 MR	30 R	APR	–	–	N
19	Chuanmai 42	3	1	3	9	1 R	60 S	S	+	+	Y
20	Chuannong 18	3	1	1	5	10 R	10 MR	ASR	–	–	N
21	Chuannong 19	9	7	5	1	1 R	1 R	APR	–	–	N
22	Chuanyu 18	9	9	7	7	30 S	60 S	S	–	–	N
23	Chuanyu 19	9	9	7	7	60 S	60 S	S	–	–	N
24	Neimai 8	1	1	1	7	1 R	30 S	S	+	+	Y
25	Xikemai 1	9	9	7	9	100 S	100 S	S	–	–	N
26	Chuanmai 43	1	1	5	7	1 R	80 S	S	+	+	Y
27	Chuanmai 44	1	1	1	7	1 R	1 R	APR	+	+	Y+?
28	Chuannong 21	7	9	7	7	30 S	80 S	S	–	–	N
29	Liangmai 2	7	7	7	9	60 S	80 S	S	–	–	N
30	Mianmai 37	1	5	1	7	1 R	30 S	S	+	+	Y
31	Mianmai 38	5	9	1	1	5 R	10 R	APR	–	–	N
32	Neimai 9	1	1	5	7	1 R	30 S	S	+	+	Y
33	Xingmai 2	1	1	5	7	1 R	80 S	S	+	+	Y
34	Chuanmai 45	9	5	5	1	1 R	1 R	APR	–	–	N
35	Chuanmai 46	1	1	1	3	10 MR	10 MR	ASR	–	–	N
36	Chuanmai 47	3	1	5	7	5 R	10 R	APR	+	+	Y+?
37	Chuannong 22	5	1	5	9	1 R	30 S	S	+	+	Y
38	Chuannong 23	5	1	1	7	1 R	30 S	S	+	+	Y
39	Mianmai 39	1	1	1	7	1 R	80 S	S	+	+	Y

(continued on next page)

^a Seedling ITs were based on the 0-to-9 scale (18), where ITs 0 to 6 are considered resistant and ITs 7 to 9 susceptible.

^b A field response was a combination of disease severity recorded as a single value for each accession at each site from 0 to 100% of the foliage infected using the modified Cobb scale (24), where R = resistant, MR = moderately resistant, M = moderately resistant to moderately susceptible, MS = moderately susceptible, and S = susceptible, APR = adult plant resistance, ASR = all stage resistance.

^c Symbols + and – indicate presence and absence, respectively, of the Sequence-tagged site markers.

^d Nursery A was inoculated with a mixture of three races (CYR32, CYR33, and Su11-4) that are all avirulent to *Yr26*.

^e Nursery B was inoculated with a mixture of races CYR32, CYR33, Su11-4, and a *Yr26*-virulent race, Gui22.

^f Symbol +? indicates the presence of an unknown *Yr* gene or genes in addition to *Yr26*.

^g Number of resistant accessions.

^h Number of susceptible accessions.

ⁱ Number of accessions with *Yr26*.

marker-assisted detection has been achieved by a series of studies (33,37,40). From these markers, we selected two STS markers (*WE173* and *BQ74*) to detect the presence and absence of *Yr26* in the 85 wheat cultivars and breeding lines. In the results, we conclude that 31 accessions have *Yr26* and the markers, when used in combination, are more accurate than the phenotypic data for detection of *Yr26*. Although *Yr26* is no longer effective against the new races, keeping the gene in new wheat cultivars together with other effective resistance genes still has value in protecting wheat crops against races avirulent to *Yr26* but still predominant. The markers are helpful for detecting the presence of *Yr26*. However, breeding programs should use other effective resistance genes in combination and, even better, to combine with adult-plant resistance genes that are more likely to last longer. The

use of a single gene conferring a high level of resistance, such as *Yr26* in the past, should be avoided. In the present study, some of the wheat cultivars and breeding lines with *Yr26* showed various levels of adult-plant resistance in the field tests, including 'Chuanmai 44', 'Chuanmai 47', 'Chuanmai 5', 'Neimai 11', 'Neimai 836', 'Mian 05-164', MR 71, MR 11-12, and MR 11-20. These cultivars and breeding lines could be continually grown or released if they have other required traits. However, further studies should be conducted under early and heavy infection of *Yr26*-virulent races to determine whether they have adequate resistance, because adult-plant resistance is usually affected by growth stage, temperature, and inoculum load (6,7,25).

Diligently monitoring stripe rust in the Sichuan Basin and other regions is needed to keep track of stripe rust occurrence and

Table 3. (continued from preceding page)

Number	Accession	Seedling IT ^a				Adult-plant severity and reaction ^b			Molecular markers ^c		<i>Yr26</i> ^f
		CYR32	CYR33	Su11-4	Gui22	Nursery A ^d	Nursery B ^e	Type	WE173	QB-74	
40	Mianmai 40	9	7	9	7	10 R	30 R	APR	–	–	N
41	Xikemai 2	9	7	7	7	80 S	80 S	S	–	–	N
42	Chuannong 26	9	1	9	9	1 R	10 R	APR	–	–	N
43	Chuanmai 20	9	7	3	1	10 MR	20 MR	APR	–	–	N
44	Mianmai 41	7	7	3	3	10 MR	10 MR	APR	–	–	N
45	Mianmai 42	1	1	5	7	1 R	80 S	S	+	+	Y
46	Mianmai 43	5	5	1	1	1 R	1 R	ASR	–	–	N
47	Zimai 1	7	7	7	9	60 S	80 S	S	–	–	N
48	Chengdianmai	7	9	9	9	60 S	60 S	S	–	–	N
49	Chuannong 24	9	9	9	9	10 MR	20 MR	APR	–	–	N
50	Chuannong 25	7	1	5	9	30 S	80 S	S	–	–	N
51	Chuanmai 21	7	1	1	1	1 R	1 R	APR	–	–	N
52	Liangmai 4	9	7	7	7	80 S	100 S	S	–	–	N
53	Mianmai 1403	9	9	1	1	30 S	30 S	S	–	–	N
54	Mianmai 45	9	1	1	1	10 R	30 R	APR	–	–	N
55	Neimai 11	1	1	1	7	1 R	10 MR	APR	+	+	Y+?
56	Rongmai 4	1	1	1	7	1 R	60 S	S	+	+	Y
57	Xikemai 3	9	9	9	9	100 S	100 S	S	–	–	N
58	Chuanmai 51	1	1	1	7	30 MR	60 MR	APR	+	+	Y+?
59	Chuanmai 52	5	1	1	1	10 MR	10 MR	ASR	–	–	N
60	Mianmai 185	9	1	7	7	30 S	60 S	S	–	–	N
61	Mianmai 46	9	1	5	7	5 R	10 R	APR	–	–	N
62	Neimai 836	1	1	1	7	1 R	10 MR	APR	+	+	Y+?
63	Xikemai 4	1	3	5	9	0 R	30 S	S	+	+	Y
64	Xikemai 6	1	3	3	9	0 R	40 S	S	+	+	Y
65	Chuannong 27	9	1	7	1	5 MR	10 MR	APR	–	–	N
66	Mianmai 48	7	7	9	7	10 R	30 R	APR	–	–	N
67	Mianmai 367	1	1	5	9	1 R	80 S	S	+	+	Y
68	Chuanmai 60	1	1	5	7	10 R	20 R	APR	–	–	N
69	Chuanmai 104	3	1	5	9	1 R	40 S	S	+	+	Y
70	Mianmai 51	1	3	5	9	1 R	80 S	S	+	+	Y
71	Chuan 00030	9	7	7	9	80 S	80 S	S	–	–	N
72	LTM 18	9	7	9	7	80 S	80 S	S	–	–	N
73	M9876	9	9	9	9	60 S	60 S	S	–	–	N
74	Mian 05-164	1	1	1	7	1 R	30 MR	APR	+	+	Y+?
75	Mian 06-374	1	1	5	9	1 R	80 S	S	+	+	Y
76	Mian 1971-98	1	1	5	7	1 R	60 S	S	+	+	Y
77	Mian11-13	3	3	0	7	0 R	20 S	S	+	+	Y
78	Mian11-25	3	3	0	9	0 R	60 S	S	+	+	Y
79	Mian11-48	1	3	0	7	0 R	30 S	S	+	+	Y
80	Mianmai 96-5	1	1	1	7	1 R	30 S	S	+	+	Y
81	MR 125	5	1	1	7	1 R	30 S	S	+	+	Y
82	MR 168	1	1	1	7	1 R	80 S	S	+	+	Y
83	MR 71	5	1	1	7	1 R	10 MR	APR	+	+	Y+?
84	MR11-12	3	3	0	7	0 R	5 R	APR	+	+	Y+?
85	MR11-20	1	3	0	7	0 R	5 R	APR	+	+	Y+?
CK1	Avocet S	9	9	9	9	100 S	100 S	S	–	–	A
CK2	92R137	1	1	0	9	1 R	40 S	S	+	+	P
Total R ^g		44	54	56	20	58	33	...	...	...	...
Total S ^h		41	31	29	65	27	52	...	...	...	...
Total <i>Yr26</i> ⁱ		...	...	...	...	...	...	...	...	...	20

development, cultivar reaction changes, and race changes in frequency and distribution. Accurate forecasts of stripe rust epidemics could be made from the disease monitoring and weather conditions (29,31). Whenever appropriate, fungicides can be used to prevent epidemics and reduce yield losses (6,36). Ultimately, more effective resistance genes should be identified and used in breeding programs to develop wheat cultivars with diversified genes providing high-level and durable resistance to stripe rust.

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