

Race Dynamics, Diversity, and Virulence Evolution in *Puccinia striiformis* f. sp. *tritici*, the Causal Agent of Wheat Stripe Rust in China from 2003 to 2007

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ABSTRACT

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Stripe (or yellow) rust caused by *Puccinia striiformis* f. sp. *tritici* is the most destructive foliar disease of wheat in China. The pathogen populations were analyzed for virulence evolution, complexity, phenotypic dynamics, and diversity on temporal and spatial bases. A total of 41 races were identified and characterized from 4,714 stripe rust isolates collected during 2003 through 2007 from wheat growing areas in 15 provinces in China. The races were based on avirulence/virulence patterns to 19 differential host genotypes. Chinese stripe rust population exhibited high diversity with a complex virulence structure. Comparisons using the relative Shannon's index indicated that some differences in the richness and evenness of races were present in pathogen populations within years and between regions despite a national tendency to reduced diversity over time. A noticeably increased frequency of race CYR33 (Chinese yellow rust 33) with virulence for *YrSu* was the major virulence change recorded in this study compared to the results on an annual basis. Isolates of *Puccinia striiformis* f. sp. *tritici* from different regions showed differences in the composition of races, distribution frequency, and diversity. The uneven distribution of major races and comparatively greater diversity in the Northwest and Southwest regions than that in the Huang-Huai-Hai region suggest that long-distance migrations of the pathogen occur from one or more over-summering areas eastward into over-wintering areas. This supports the hypothesis that southern Gansu and northwestern Sichuan comprises a "center of origin for virulence". Mutation of virulence or avirulence for host resistance in the stripe rust fungus may be the basic cause of the occurrence of new virulent types. The subsequent dominance of certain races will vary with parasitic fitness and the opportunities to be selected through large-scale cultivation of varieties with matching resistance genes. Implications of the center of origin for virulence variation and diversity in the pathogen population and an alternative strategy for limiting virulence evolution are discussed.

China is one of the largest producers of agricultural commodities in the world, including production and consumption of wheat. Wheat (*Triticum aestivum* L.) is annually grown on more than 22.8 million hectares, and the total wheat production exceeds 100 million metric tons (24). Stripe (yellow) rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Eriks., is an economically important disease of wheat in many regions of the world (5,15,27,28,39,40), and is considered the most destructive foliar disease of wheat in

many areas of China. Epidemics have occurred at varying intensities all over the country, and the disease is notably endemic in the Northwest and Southwest wheat growing areas since 1950. Annual losses of wheat yields due to stripe rust averaged about 1 million metric tons (3,4). The most severe epidemics, which occurred in 1950, 1964, 1990, and 2002, caused yield losses of wheat estimated at 6.00, 3.20, 2.65, and 1.40 million metric tons, respectively (2-4,14,33).

China has the largest independent epidemic region for wheat diseases in the world, with more than 20 million hectares of wheat affected by stripe rust (28). Comprehensive research of the epidemiology of wheat stripe rust, including over-summering, over-wintering areas, inter-regional dispersal of inoculum, and strategies for disease control in China, has been documented among a nationwide network

of colleagues working for more than five decades (1-4,30,45). Growing resistant cultivars is the most economical, environmentally friendly, and effective method to control stripe rust of wheat. More than 40 designated and many other temporarily designated *Yr* genes for resistance to stripe rust have been described in wheat, and some of them have been widely used in different areas worldwide (21,22). However, when resistance to an obligate parasite such as rust is determined by a single gene, it is common to observe the evolution of a new race capable of overcoming the resistance within about 5 years (36,38). This inevitably leads to disease epidemics of boom-bust cycles and has occurred in China in past years (14,30,36,38). For example, wheat lines with *Yr9* were widely used in wheat breeding programs throughout China since the 1960s, and more than 80% of the released cultivars contained *Yr9* by the late 1980s (30,33). A new race of *P. striiformis* f. sp. *tritici*, CYR29 (Chinese yellow rust 29), with virulence to *Yr9* was detected in 1985; this race led to the breakdown of resistance in wheat cultivars carrying *Yr9*, resulting in yield losses of 2.65 million tons in 1990. A similar situation occurred in 2002 as races CYR31 and CYR32 virulent to wheat variety Fan 6 and its derivatives with the resistant genes *Yr3b* and *Yr4b* appeared (33).

Monitoring the dynamics and variation of virulence in rust populations provides the basis for anticipatory breeding of cultivars with optimum resistance levels, prediction of disease epidemics, and integrated control (5,16,20). Surveys of *P. striiformis* f. sp. *tritici* races in China were first conducted in the 1940s (6,7); a total of nine races (C1 to C9) were found at that time using seven wheat genotypes. Lu et al. (17) reported 16 races from 50 samples from eastern and northern China tested with 14 differential genotypes used by Gassner and Straib (8). During 1957 through 1961, 10 races (CYR1 to CYR10) were identified from 325 samples using a Chinese differential set (35). Annual surveys of races throughout major wheat-growing areas have been conducted by the

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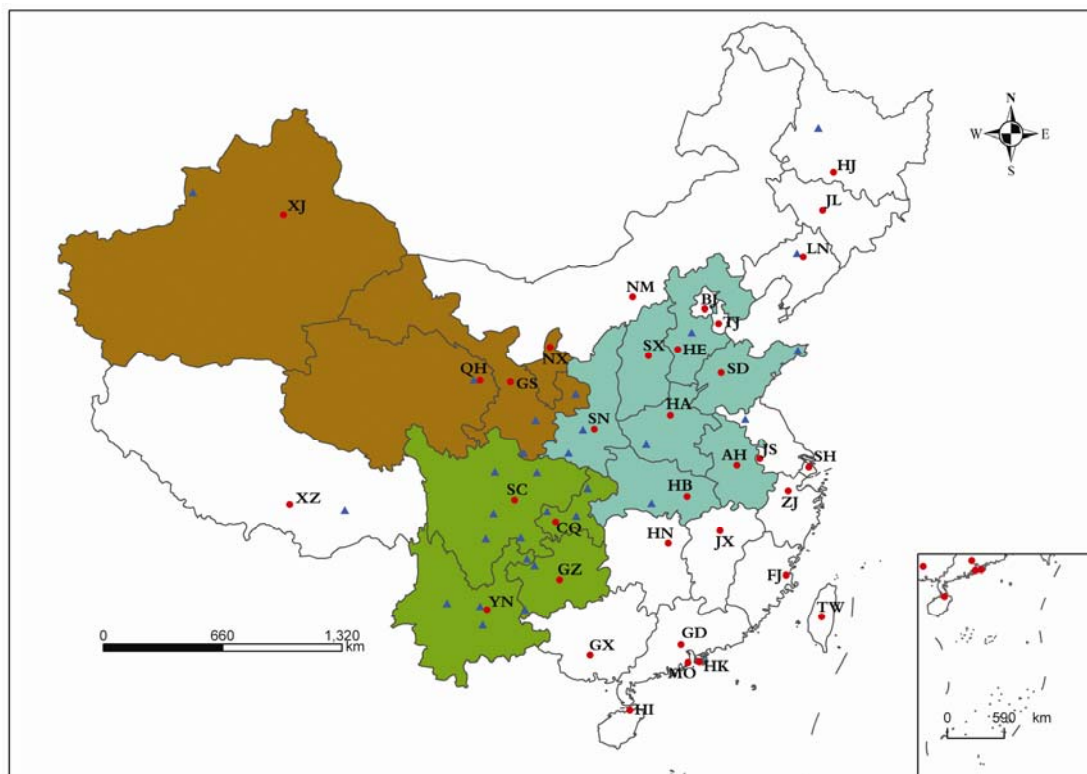
Institute of Plant Protection, Chinese Academy of Agricultural Science (IPP, CAAS) alone or with its cooperating institutes from the Chinese National Wheat Rust Collaborative Group (CNWRCG) since 1961, except for some irregularities from 1966 to 1971 (31–33,35,37,38,41). The major virulence patterns have been formally designated CYR races with sequential numbers based on their chronological appearance by the annual meeting of CNWRCG. Minor virulence patterns with low frequencies and limited distribution were temporarily nominated using the abbreviations of specific wheat differential genotypes. The composition of differential sets was supplemented and adjusted several times along with the changes of wheat commercial cultivars, but the race nomenclature system has remained relatively consistent since the 1960s. The current differential set consists of 19 wheat genotypes. By 2002, there were 32 CYR races of *P. striiformis* f. sp. *tritici* (CYR1 to CYR32) described in China using diverse sets of stripe rust differentials. Newly detected races tended to have a wider virulence spectrum than that of earlier ones (32,33).

have provided valuable data for wheat breeding programs and also helped to identify virulence evolution over time. Changes in races and their virulence have corresponded to changes in wheat cultivars deployed in commercial production

(36,38). In recent years, more cultivars with various resistance genes have been released, especially in Gansu and Sichuan provinces, the most important over-summering and inoculum-source regions of *P. striiformis* f. sp. *tritici* in China

Table 1. Wheat differential lines and their *Yr* genes used for race surveys of *Puccinia striiformis* f. sp. *tritici* in China during 2003 to 2007

^z *Yr* genes were based on Stubbs (27), Yang et al. (44), Roelfs et al. (26), Line and Chen (16), McIntosh et al. (22), and Zhao et al. (46–48).



(30,49). The objectives of this study were to characterize the virulence of *P. striiformis* f. sp. *tritici* populations in China during 2003 to 2007. General attributes within the pathogen populations, including virulence evolution, complexity, phenotypic dynamics, and diversity on the temporal and spatial bases, were examined.

MATERIALS AND METHODS

Field surveys and isolate collections.

Regular field surveys were conducted annually across wheat growing areas in China, especially in the inoculum source areas (e.g., southern Gansu and northwestern Sichuan), at seedling stage (late November to early December) and adult-plant stage (late April to early July) during 2003 to 2007. Infected wheat leaves were collected from trap nurseries and commercial wheat fields (Fig. 1). Date of collection, location, cultivar, severity, collector, and any other relevant information was recorded for each sample whenever possible. Diseased leaves were dispatched in paper envelopes for pathogenicity tests to the IPP, CAAS, and others were identified at Shaanxi, Gansu, and Sichuan provinces. Infected leaves were air-dried and stored at 4 to 5°C until spores were collected for inoculation and increase. A total of 4,714 stripe rust samples were collected from trap nurseries and wheat growing areas in 15 provinces in China from 2003 to 2007, of which 3,950 (83.8%) originated from Gansu, Sichuan, and Shaanxi, where the most frequent stripe rust epidemics occurred.

Trap nurseries. Trap nurseries contained 130 wheat genotypes, including wheat cultivars, important resistant materials, differentials, and near-isogenic *Yr* gene lines and highly susceptible lines (cv. Mingxian 169). The nurseries were planted at 29 locations in 16 provinces of Gansu, Shaanxi, Qinghai, Xinjiang, Sichuan, Yunnan, Guizhou, Chongqing, Tibet, Henan, Hebei, Shandong, Hubei, Jiangsu, Liaoning, and Helongjiang during the 2007 growing season to monitor rust development and virulence, and to determine effectiveness of resistance. Disease severity and infection type were recorded during the flowering to soft dough stages using the modified Cobb scale (26).

Identification of race and virulence.

Rust collections were assessed separately in the IPP, CAAS in Beijing and in the Academies of Agricultural Sciences of Shaanxi, Gansu, and Sichuan. Air-dried leaves with urediniospores were incubated on water-soaked tissue paper in petri dishes in the dark at 4°C for 10 to 15 h. Urediniospores from each collection were multiplied by inoculating 7-day-old seedlings of susceptible wheat genotype Mingxian 169. Inoculated plants were kept in a dew chamber overnight at 10°C and then moved to greenhouse benches at 15 to 18°C supplemented with 10,000 lx of fluo-

rescent light for 10 h per day. The second leaves were clipped when chlorotic spots appeared on leaves (~7 days postinoculation), and the plants were covered with a glass cylinder to prevent cross contamination. Urediniospores of each isolate were collected 15 days after inoculation and temporarily kept in a dryer at low temperature (3 to 4°C). A set of 19 differential wheat genotypes was used to determine races of *P. striiformis* f. sp. *tritici* (Table 1). Sets of differentials were planted in 10-cm-diameter pots containing a mixture of commercial peat moss and soil, each with four wheat genotypes (five to seven plants per line), and grown in a rust-free greenhouse. About 10 days after planting, when the first leaf was fully extended, seedlings were inoculated with fresh urediniospores by using a spatula or spraying a spore suspension (Soltrol 170, Phillips 66 Company,

OK, USA). Inoculated plants were transferred to a dew chamber and then to greenhouse benches under the same temperature and light conditions described above. Infection type (IT) data of the plant-pathogen interactions were recorded 15 to 20 days after inoculation when the disease was fully developed. Races of *P. striiformis* f. sp. *tritici* were determined by IT based on the 0 to 4 scale (27), i.e., no visible symptoms (IT 0), necrotic or chlorotic flecks (IT 1), necrotic or chlorotic blotches with very low level of sporulation (IT 1), moderate uredinia with necrosis/chlorosis (IT 2), moderate to abundant uredinia with chlorosis (IT 3), and abundant uredinia without necrosis and chlorosis (IT 4). Infection types 0 to 2 were considered avirulent, and 3 to 4 virulent. The results obtained were based mostly on single tests, but if an infection type was not

Table 2. Race frequencies of *Puccinia striiformis* f. sp. *tritici* detected in China during 2003 to 2007 and their virulence spectra on 19 Chinese differential hosts

Race group ^w	Race name ^x	Avirulence / virulence formula ^y	F (%) ^z
LvG	CYR17	3,5,8,9,10,11,12,13,14,15,16,17,18,19 / 1?,2,4?,6?,7	<1
	CYR18	1,2,4,5,7,8,10,11,12,13,14,15,16,17,18,19 / 3,6,9	<1
	CYR19	1,5,10,12,13,14,15,16,17,18,19 / 2,3,4,6,7,8,9,11	<1
	CYR21	5,12,13,14,15,16,17,18,19 / 1?,2,3,4,6,7,8?,9?,10,11	<1
	CYR22	5,12,14,15,16,17,18,19 / 1,2,3,4,6,7,8,9?,10,11,13	<1
	CYR23	5,10,12,13,14,15,16,17,18,19 / 1,2,3,4,6,7,8,9,11	<1
	CYR24	5,9,10,12,13,14,15,16,17,18,19 / 1?,2,3,4,6,7,8,11	<1
	CYR25	10,12,13,14,15,16,17,18,19 / 1?,2,3,4,5,6,7,8?,9?,11	<1
	CYR26	5,10,12,13,14,15,16,17,18,19 / 1?,2,3,6,7,8,9,11	<1
	CYR27	12,14,15,16,17,18,19 / 1,2,3,4,5,6,7,8,9,10,11,13	<1
	CYR28	10,12,13,14,15,17,18,19 / 1,2,3,4,5,6,7,8,9,11,16	<1
	CYR29	10,13,14,15,17,18,19 / 1,2,3,4,5,6,7,8,9,11,12,16	<1
	Lv10-2	4,5,10,12,13,14,15,17,18,19 / 1,2,3,6,7,8,9,11,16	<1
Lv10-3	1,5,10,12,13,14,15,17,18,19 / 2,3,4,6,7,8,9,11,16	<1	
Lv10-5	5,10,12,13,14,15,17,18,19 / 1,2,3,4,6,7,8,9,11,16	<1	
Lv10-6	5,12,13,14,15,17,18,19 / 1,2,3,4,6,7,8,9,10,11,16	<1	
Lv13-2	4,5,10,13,14,15,17,18,19 / 1,2,3,6,7,8,9,11,12,16	<1	
Lv13-3	14,15,17,18,19 / 1,2,3,4,5,6,7,8,9,10,11,12,13,16	<1	
Lv13-8	13,14,15,17,18,19 / 1,2,3,4,5,6,7,8,9,10,11,12,16	<1	
HyG	CYR30	10,13,14,15,18,19 / 1,2,3,4,5,6,7,8,9,11,12,16,17	1.1
	CYR31	10,13,15,18,19 / 1,2,3,4,5,6,7,8,9,11,12,14,16,17	3.6
	CYR32	15,18,19 / 1,2,3,4,5,6,7,8,9,10,11,12,13,14,16,17	29.6
	Hy46-4	12,15,18,19 / 1?,2,3,4,5,6,7,8,9,10,11,13,14,16,17	<1
SuG	Hy46-5	12,15,18,19 / 1,2,3,4,5?,6,7,8,9,10,11,13,14,16,17	<1
	Hy46-6	10,12,13,15,16,18,19 / 1?,2,3,4,5,6,7,8?,9?,11,14,17	1.1
	Hy46-7	1,15,18,19 / 2,3,4,5?,6,7,8,9,10,11,12,13,14,16,17	2.2
	Hy46-8	13,15,18,19 / 1?,2,3,4,5?,6,7,8,9,10,11,12,14,16,17	2.9
	Hy46-9	12,15,18,19 / 1,2,3,4,5?,6,7,8,9,10,11,13,14,17	<1
	CYR33	15,18,19 / 1?,2,3,4,5?,6,7,8,9,10,11,12,13,14,16	17.4
	Su11-1	3,4,5,6,8,9,10,11,12,13,15,16,17,18,19 / 1,2,7,14	1.6
	Su11-2	10,12,13,15,16,17,18,19 / 1,2,3,4,5,6,7,8,9,11,14	1.2
	Su11-3	12,15,16,17,18,19 / 1?,2,3,4,5,6,7,8,9,10,11,13,14	1.1
	Su11-4	1,5,11,12,15,17,18,19 / 2,3,4,6,7,8,9,10,13,14,16	6.2
	Su11-5	10,12,13,15,17,18,19 / 1,2,3,4,5?,6,7,8,9,11,14,16	4.2
	Su11-6	4,5,10,12,13,15,16,17,18,19 / 1,2,3,6,7,8,9,11,14	1.7
	Su11-7	10,13,15,17,18,19 / 1,2,3,4,5?,6,7,8,9,11,12,14,16	5.5
Su11-8	5,10,12,13,15,16,17,18,19 / 1,2,3,4,6,7,8,9,11,14	1.2	
Su11-10	1,5,10,12,,13,15,16,17,18,19 / 2,3,4,6,7,8,9,11,14	1.1	
Su11-11	5,12,15,16,17,18,19 / 1,2,3,4,6,7,8,9,10,11,13,14	2.3	
Su11-12	1,4,5,10,12,13,15,17,18,19 / 2,3,6,7,8,9,11,14,16	1.7	
Su11-13	5,12,13,15,16,17,18,19 / 1,2,3,4,6,7,8,9,10,11,14	1.8	

^w LvG = Race group virulence for Lovrin 10/Lovrin 13 (*Yr9*); HyG = race group virulence for Hybrid 46 (*Yr3b*, *Yr4b*); and SuG = race group virulence for Suwon 11 (*YrSu*).

^x CYR = Chinese yellow rust; Lv = Lovrin; Hy = Hybrid; and Su = Suwon.

^y Avirulence = infection types 0–2, and virulence = infection types 3–4; ? = segregation of resistant and susceptible plants but more susceptible.

^z Weighted average frequencies (%) of 5 years from 2003 to 2007 were calculated as $F(\%) = \sum (N_i \cdot P_i) / N \cdot 100\%$, in which P_i is frequency of races in i th year, N_i is number of isolates tested in i th year, and N is total number of isolates in 5 years.

conclusive, the test was repeated. For a new virulence pattern, urediniospores were usually separated in water agar for single spore isolates. Races were designated using CYR numbering based on the chronological order of appearance or using the abbreviations of specific wheat differential genotypes.

Race diversity measurements. Frequencies of races within the population collected during different years or diverse geographical regions of China were compared. The regions are distinguished by climatic conditions, agronomic characteristics, and pathogen life cycle features (2,45,50). The relative Shannon index (H_{SR}) was calculated from data on races of *P. striiformis* f. sp. *tritici* from different regions and years (9,23):

$$H_{SR} = -\sum (P_j \cdot \ln P_j) / \ln N_i$$

in which P_j is the frequency of the j th race in the sample and N_i is the total number of isolates in the sample.

The Shannon indices between different regions and years were compared statistically by the t test using Statistical Analysis System (SAS) software.

RESULTS

Frequencies of races. Forty-one races were identified and characterized from the 4,714 stripe rust samples based on their avirulence/virulence patterns to the 19 differential genotypes. The weighted average frequencies of each race detected in 5 years are presented in Table 2. No isolates virulent to Zhong 4 ($Yr+$), *Triticum spelta* album ($Yr5$), or Guinong 22 ($Yr+$) were found. All races were virulent to Fulhard ($Yr+$) and Early Premium ($Yr+$) except CYR18, and all were virulent to Abbonanza ($Yr+$) except Su11-1. CYR32 had the widest virulence spectrum and combined virulence for differential genotypes Lovrin 10 or Lovrin 13 ($Yr9$), Hybrid 46 ($Yr3b$, $4b$), and Suwon 11 ($YrSu$), whereas CYR18 had the narrowest virulence spectrum, possessing virulence for only three differentials, i.e., Lutescenes ($Yr+$), Abbonanza ($Yr+$), and Danish 1 ($Yr3$).

Races CYR17 to CYR27 were first detected before 1980, and the remaining 31 races were found after 1980. The latter can be classified into three race groups, i.e., Lovrin group (LvG) with 9 races, Hybrid 46 group (HyG) with 9 races, and Suwon 11 group (SuG) with 13 races according to their avirulence/virulence patterns on differential genotypes Lovrin 10, Lovrin 13, Hybrid 46, and Suwon 11. Nine of the 41 races (CYR32, CYR33, Su11-4, Su11-7, Su11-5, CYR31, Su11-11, and Hy46-7) were the most common, with frequencies of 29.61, 17.37, 6.21, 5.50, 4.20, 3.59, 2.86, 2.27, and 2.23%, respectively, during 2003 to 2007, while others remained at less than 2% (Table 2). Races CYR18, CYR19, CYR27, CYR30, Lv10-3, Lv13-2, and Hy46-4 were sporadically detected in certain years or in some regions and remained less than 1% in frequency during 2003 to 2007. The most frequently identified race in the past 5 years was CYR32, which comprised 29.61% nationwide and was distributed in all 15 sampled provinces. CYR33 was the second most frequent race and comprised 17.37% nationwide and was distributed in all sampled provinces except Shandong. Both CYR32 and CYR33 played a major role in causing the widespread epidemics of wheat stripe rust in China in recent years.

Dynamics of major races. Compared with the frequencies of the major races from year to year during 2001 to 2007, the frequencies of CYR33 and Su11-7 increased from 4.21 and 1.50% in 2001 to 26.72 and 9.46% in 2007, respectively, while the frequencies of CYR30, CYR31, and Su11-4 decreased from 7.33, 9.51, and 9.51% in 2001 to 0.51, 2.26, and 4.93% in 2007, respectively (Fig. 2). CYR32 was first detected in 1994, became predominant in 2000 with a frequency of 11%, and dramatically increased to 28.79% in 2001 and 34.60% in 2002 (33). This race later declined somewhat but remained at frequencies of 29.23 to 29.97% during 2003 to 2007. CYR33 (old Su11-14), first found in 1997 with a frequency of less than 1%,

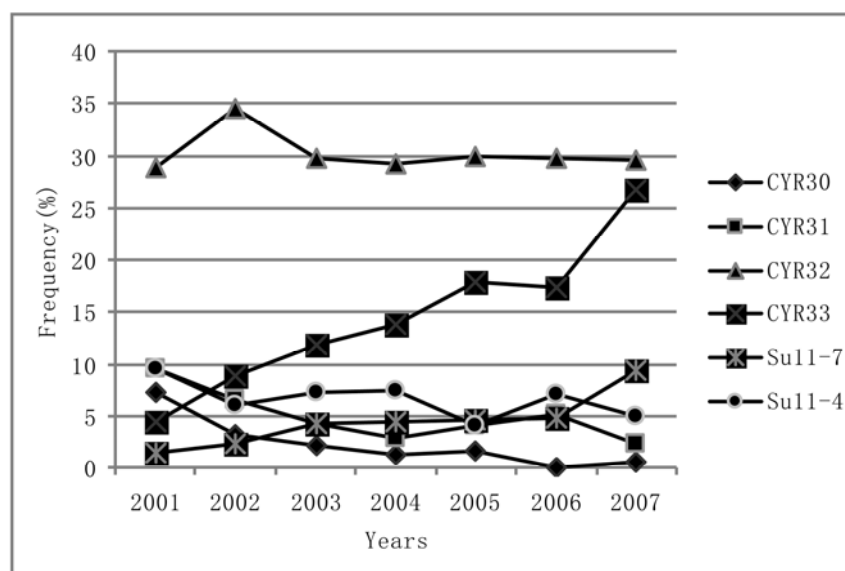


Fig. 2. Dynamics of major races of *Puccinia striiformis* f. sp. *tritici* in China from 2001 to 2007.

Table 3. Distribution of 12 prevalent races of *Puccinia striiformis* f. sp. *tritici* in areas of China identified in 2003 to 2007^a

(continued on next page)

Phenotype	Henan		Hebei		Shandong		Shanxi		Hubei		Shaanxi		Gansu	
	#	%	#	%	#	%	#	%	#	%	#	%	#	%
CYR28	0	0	0	0	0	0	0	0	0	0	8	0.7	2	0.1
CYR29	0	0	0	0	0	0	0	0	1	1.7	17	1.6	12	0.7
CYR30	0	0	0	0	0	0	0	0	0	0	3	0.3	4	0.2
CYR31	3	3.7	0	0	0	0	0	0	6	10.0	69	6.4	30	1.8
CYR32	25	30.9	5	21.7	6	54.5	5	11.4	3	20.0	402	37.2	370	21.6
CYR33	5	6.2	3	13.0	0	0	7	15.9	8	13.3	186	17.2	472	27.5
Hy46-7	4	4.9	0	0	0	0	0	0	7	11.7	10	0.9	15	0.9
Hy46-8	7	8.6	0	0	2	18.2	1	2.3	3	5.0	4	0.4	47	2.7
Su11-4	3	3.7	9	39.1	1	9.1	8	18.2	5	8.3	66	6.1	120	7.0
Su11-5	1	1.2	0	0	0	0	5	11.4	2	3.3	34	3.1	110	6.4
Su11-7	2	2.5	0	0	0	0	0	0	3	5.0	32	3.0	180	10.5
Su11-11	4	4.9	0	0	0	0	0	0	5	8.3	48	4.4	10	0.6
Others	27	33.3	6	26.1	2	18.2	18	40.9	17	28.3	203	18.8	342	20.0
Total	81		23		11		44		60		1,082		1,714	

^a Anhui (3 samples) and Ningxia (2 samples) not included in Table 4 due to the low sample sizes.

increased year by year from 4.21% in 2001 to 26.72% in 2007, and was formally named CYR33 in 2008. Su11-7 was first found in 1995 and slightly increased year by year to nearly 10% in 2007. A noticeably increased frequency of CYR33 with virulence to *YrSu* was the major virulence change recorded in this study compared with the results on an annual basis (Fig. 2) and with that before 2003 (33). During the late 1990s to early 2000s, cultivars with *YrSu* were grown in China, especially in the Northwest wheat growing areas where most likely races with virulence to *YrSu* were selected. The weighted average frequencies of Su11-5, Hy46-7, and Hy46-8 in 2003 to 2007 were 4.20, 2.86, and 2.23%, respectively, but slightly fluctuated between 0.11 and 6.28% on an annual basis (data not shown).

Distribution and diversity of races.

The distribution and frequencies of some important races in 13 sampled provinces of China in the course of this study are presented in Table 3. Anhui and Ningxia were excluded due to small sample size. Data in Table 3 show that isolates of *P. striiformis* f. sp. *tritici* from different regions displayed obvious differences in the composition, distribution, and diversity of races. Race CYR32 was widely distributed throughout all 13 provinces, with frequencies from 11.4% in Shanxi to 54.5% in Shandong, whereas CYR28 virulence for Lovrin 10 (*Yr9*) but avirulence for Lovrin 13 (*Yr9+*) was restricted to only the three provinces of Sichuan, Shaanxi, and Gansu. CYR29 with virulence to both Lovrin 10 and Lovrin 13 was evident in the four provinces of Sichuan, Shaanxi, Hubei, and Gansu, with frequencies of 0.7 to 1.8%. Su11-4 was also distributed in the 13 provinces with frequencies varying from 2.2% in Guizhou to 39.1% in Hebei. CYR33 was the third widely detected race and was distributed in all provinces except Shandong with frequencies of 2.6% in Guizhou and 27.5% in Gansu. The presence of races CYR32 and CYR33 in western provinces as well as in the wider eastern regions

suggested that some movement of stripe rust occurred from the western regions eastward into the central and eastern regions. Race Hy46-8 was detected in 11 provinces with frequencies ranging from 0.4% in Shaanxi to 15.4% in Guizhou. Su11-5 was also found in 11 provinces with frequencies from 1.2% in Henan to 11.4% in Shanxi. Both races Hy46-7 and Su11-11 were detected in nine provinces with frequencies ranging from 0.9 to 9.9% and 0.6 to 9.9%, respectively. CYR31 and Su11-7 were detected in eight provinces with frequencies ranging from 1.8 to 10.0% and from 2.5 to 10.5%. CYR30 was not found in Henan, Hebei, Shandong, Shanxi, Hubei, Chongqing, Guizhou, and Qinghai, which are generally the overwintering areas of stripe rust in China. Results indicated that there were also great differences in the composition of the predominant races in various regions (Tables 2 and 3). CYR32 was the most dominant

race with the highest frequency (above 20%) in the majority of wheat growing areas. CYR33 was also predominant with a frequency of 27.5% in Gansu. Su11-4 was especially common in Hebei and Shanxi with frequencies of 39.1 and 18.2%, respectively, although the sample sizes were small. Race group (SuG) virulence to *YrSu* consisted of 13 races (CYR33, Su11-1, Su11-2, Su11-3, Su11-4, Su11-5, Su11-6, Su11-7, Su11-8, Su11-10, Su11-11, Su11-12, and Su11-13) and comprised of 48.15% of the samples in 2003 to 2007 (Table 2 and Fig. 3). This group was most frequent in the Northwest regions, with frequencies of up to 64.15%. Nine races (CYR30, CYR31, CYR32, Hy46-4, Hy46-5, Hy46-6, Hy46-7, Hy46-8, and Hy46-9) formed the second race group (HyG) virulent to *Yr3b* and *Yr4b*, which comprised 44.21% of the samples in 2003 to 2007 and was most commonly detected in the Southwest regions with frequencies of

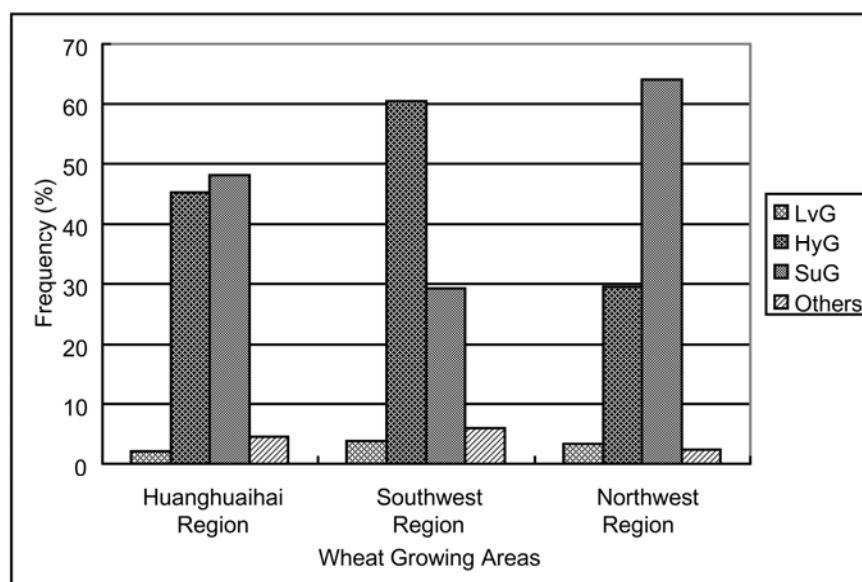


Fig. 3. Distribution of major race groups of *Puccinia striiformis* f. sp. *tritici* in China during 2003 to 2007. LvG = Race group virulence for Lovrin 10 and Lovrin 13 (*Yr9*); HyG = race group virulence for Hybrid 46 (*Yr3b*, *Yr4b*); and SuG = race group virulence for Suwon 11 (*YrSu*).

Table 3. (continued from preceding page)

Phenotype	Qinghai		Xinjiang		Sichuan		Yunnan		Guizhou		Chongqing		Total	
	#	%	#	%	#	%	#	%	#	%	#	%	#	%
CYR28	0	0	0	0	11	1.0	0	0	0	0	0	0	21	0.4
CYR29	0	0	0	0	21	1.8	0	0	0	0	0	0	51	1.1
CYR30	0	0	1	3.8	44	3.8	1	0.3	0	0	0	0	53	1.1
CYR31	0	0	1	3.8	52	4.5	6	1.9	2	5.1	0	0	166	3.5
CYR32	28	31.8	6	23.1	368	31.9	136	43.0	12	30.8	21	29.6	1387	29.5
CYR33	7	8.0	2	7.7	98	8.5	22	7.0	1	2.6	7	9.9	818	17.4
Hy46-7	6	6.8	0	0	28	2.4	31	9.8	1	2.6	7	9.9	109	2.3
Hy46-8	3	3.4	0	0	49	4.2	10	3.2	6	15.4	2	2.8	133	2.8
Su11-4	14	15.9	2	7.7	50	4.3	7	2.2	4	10.3	3	4.2	291	6.2
Su11-5	8	9.1	1	3.8	33	2.9	4	1.3	1	2.6	2	2.8	201	4.3
Su11-7	3	3.4	0	0	33	2.9	5	1.6	0	0	3	4.2	261	5.5
Su11-11	5	5.7	1	3.8	13	1.1	10	3.2	0	0	7	9.9	102	2.2
Others	14	15.9	12	46.2	354	30.7	84	26.6	12	30.8	19	26.8	1110	23.6
Total	88		26		1,154		316		39		71		4,709	

60.44% (Table 2 and Fig. 3). The third race group (LvG) was virulent to Yr9 consisting of nine races (CYR28, CYR29, Lv10-2, Lv10-3, Lv10-5, Lv10-6, Lv13-2, Lv13-3, and Lv13-8). This group was infrequently detected in all three wheat growing regions (Table 2 and Fig. 3). Different wheat genotypes planted in various wheat growing regions may be the underlying cause of the spatial variability for the distribution of races in China.

The *P. striiformis* f. sp. *tritici* population in China is highly diverse, with more than 41 races present during 2003 to 2007 (Table 4). The diversity of races within population-years and between population-regions was calculated using relative Shannon index (H_{SR}) (Tables 4). The H_{SR} value varied between 0.3329 and 0.4098 within years across all wheat growing regions. In general, H_{SR} values did not differ significantly between years in the

course of this study (0.4097 in 2003, 0.3867 in 2004, 0.3920 in 2005, 0.3918 in 2006, and 0.3329 in 2007), indicating that the richness of *P. striiformis* f. sp. *tritici* races and their relative dominance remained relatively stable in China from 2003 to 2007 despite the constant directional selection for different virulences. However, some differences in diversity were detected within population-years. The greatest Shannon index (0.4097) for diversity of races was observed in 2003, and the smallest index (0.3329) in 2007. This probably reflects a tendency toward reduction in the diversity of races over time. Comparison of relative Shannon indices indicated no greater differences in the richness and evenness of races among three regions despite the fact that the number of races detected in the Northwest and Southwest wheat growing regions was much greater than that in the Huang (Yellow) River, Huai River, and Hai River regions (Huang-Huai-Hai regions), which was probably due to considerable difference in sample sizes (Table 4). More similarity of Shannon index between the Northwest regions (0.3752) and Southwest regions (0.3615), but a little greater than that in Huang-Huai-Hai regions (0.3405), indicated that collections from the three regions had very similar diversity of races, further implying the movement of urediniospores across large distances within wheat growing areas. The climatic conditions and wheat planting system favorable for rust fungi to survive year-round in both the Southwest and Northwest regions are probably the main reasons for greater diversity than that in the Huang-Huai-Hai regions.

DISCUSSION

The wheat stripe rust population in China appears to be geographically isolated from those in other countries in terms of virulence evolution (3,4,27,28,44,45). It is presumed that mutation and local adaptation to the host resistance is the basis for the occurrence of newly virulent types of this pathogen. Empirical data suggested that several mutation events from avirulence to virulence or the opposite direction for certain resistance loci may occur independently in the *P. striiformis* f. sp. *tritici* population of China (Fig. 4). A range of races was detected during the period of this study, and each newly emerging race was closely related to pre-existing ones. For example, CYR29 possessed virulence for wheat lines that carried resistance gene Yr9, and most likely evolved from a single mutation in CYR25. Both CYR30 and Su11-7, detected in 1991 and 1994, separately displayed great similarities to CYR29 with the exception of increased virulence for Hybrid 46 and Suwon 11, respectively, which was considered to have arisen from a single mutation in CYR29. Basically, there have been two major

Table 4. Total numbers of isolates tested, races detected of *Puccinia striiformis* f. sp. *tritici*, and Shannon's index in different years, and wheat growing regions of China during 2003 to 2007

Years or regions ^y	Isolates tested	Race numbers detected	H_{SR} ^z
2003	955	41	0.4097 a
2004	1,194	40	0.3867 a
2005	871	38	0.3920 a
2006	721	36	0.3918 a
2007	973	37	0.3329 b
Huang-Huai-Hai regions	1,304	34	0.3405 b
Southwest regions	1,580	39	0.3615 ab
Northwestern regions	1,830	41	0.3752 a
Total	4,714	—	—

^y Huang-Huai-Hai region includes Henan, Hebei, Shandong, Shanxi, Shaanxi, Anhui, and Hubei provinces; Southwest region includes Sichuan, Yunnan, Guizhou, and Chongqing provinces (or cities); and Northwest region includes Gansu, Qinghai, Ningxia, and Xinjiang provinces (or municipalities).

^z Different lowercase letters indicate significant difference at $P = 0.05$.

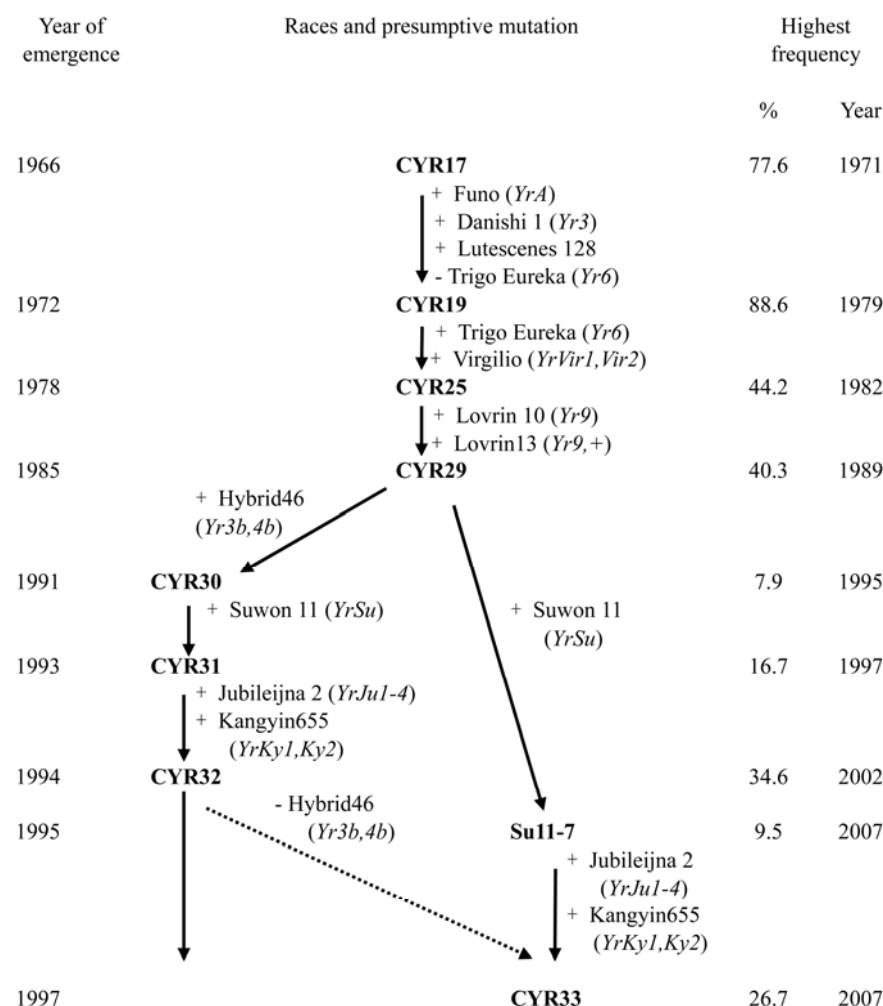


Fig. 4. Diagrammatic progress and presumed mutation events of important races of *Puccinia striiformis* f. sp. *tritici* in China in the past four decades.

courses of virulence evolution in the *P. striiformis* f. sp. *tritici* population in China since the 1990s. One was directed at the specific virulence for Hybrid 46 (group HyG) with virulence to Hybrid 46 and Suwon 11, and another was subject to the specific virulence for Suwon 11 alone (group SuG) (Fig. 4). CYR31 and CYR32 with the combined virulence to Hybrid 46, Suwon 11, and Lovrin 10/Lovrin 13 were first found in the Southwest regions in 1993 and 1994, respectively, which were consistent with CYR30. CYR33 with the combined virulence to Suwon 11 and Lovrin 10/Lovrin 13 has most likely arisen from a mutation of virulence for Jubileijna 2 and Kangyin 655 in Su11-7. Alternatively, it would be possible that CYR33 came from CYR32 with loss of virulence for Hybrid 46 based on the emerging sequence and similarity of virulence spectra. Since the 1980s, Fan6 and its derivatives with resistance from Hybrid 46 have become the leading cultivars in the Southwest region and mid-valley of the Yangtze River, simultaneously the cultivars with the same type of resistance as Suwon 11 have probably been planted in the Northwest region in recent years, which provided favorable conditions for the directional selection of new races for Hybrid 46 and Suwon 11, leading to local adaptation and widespread HyG and SuG. In conclusion, mutation of stripe rust fungus from avirulence to virulence or the opposite direction for certain loci and local adaptation to the host resistance is the basic cause of the occurrence of new virulence types. This hypothesis is consistent with the evolution in the northwest European *P. striiformis* f. sp. *tritici* population described using amplified fragment length polymorphism markers by Hovmøller and Justesen (11) and that in Australasia described by Wellings and McIntosh (39,40). In addition, parasexuality or somatic recombination events between isolates may be an alternative way to yield new races (19). Based on the results of this study, CYR32 and CYR33 became the predominant races in recent years, and this may be attributed to a relatively greater parasitic fitness of both races on leading commercial cultivars (29).

It has been found that southern Gansu and northwestern Sichuan are the most important over-summering areas of *P. striiformis* f. sp. *tritici*. These regions have important roles in providing inoculum for the autumn-sown wheat in the eastern areas (1,2,4,14,43). Historically, almost all Chinese races were first detected in these regions (31,32,35,37,41). Two main hypotheses can be proposed on the origin of rust virulence in those regions. Firstly, wheat planting systems in these zones are favorable for rust fungi to survive year-round. In southern Gansu, wheat can be grown from lowland valleys at 1,000 m to highland terraces at 2,500 m, and sowing

periods vary from early September in the highlands to late October in the lowlands, whereas harvest occurs from mid-June in the lowlands to late July in the highlands. At elevations above 1,500 m, stripe rust inoculum can over-summer on volunteer wheat seedlings that provide a “green bridge” and inoculum transfer from late-matured wheat to early-sown seedlings (2,3,14,34). Therefore, there is no restriction of inoculum transfer between successive cropping cycles. Pathogen inoculum can also over-winter at elevations below 1,800 m, where temperatures are less drastic for pathogen survival. During the spring, urediniospores would migrate from the over-wintering areas to the mountain terraces and so allow a continuing movement of viable pathogen inoculum. In northwestern Sichuan, such as the Aba district, where wheat is cultivated from 1,170 to 3,300 m, there exists a “year-round wheat” cropping cycle from August to September of the following year (42). The overlapping period between preceding and succeeding wheat crops provides an ideal condition for local over-summering of *P. striiformis* f. sp. *tritici*. The areas of altitude 1,500 to 1,800 m in southern Gansu and 1,900 to 2,500 m in northwestern Sichuan are considered the “hotspots” for the wheat stripe rust pathogen, where over-summer and over-winter occurs. A large population of *P. striiformis* f. sp. *tritici* survives the summer on the late-matured wheat or volunteer seedlings and the winter on the susceptible winter wheat in southern Gansu and northwestern Sichuan, thus creating a large reservoir for potential mutations for new virulence and subsequent selection by those cultivars with specific resistance genes. Secondly, the climatic conditions (low temperatures and high humidity) are ideal for infection and reproduction of *P. striiformis* f. sp. *tritici* urediniospores in southern Gansu and northwestern Sichuan. For example, in the half mountain areas of elevation 1,800 m in southern Gansu, the annual averages for temperature (8.5°C), annual precipitation (533.9 mm), rainy days (103.3 days), dew days (92.5 days), and foggy days (7.3 days) are ideal for stripe rust epidemics. The monthly average temperatures in the hottest July and the coldest January are 18.3 and -3.9°C, respectively (data sourced from a local weather station). In northwestern Sichuan, such as the Aba district, it is 17.5°C in July and -0.9°C in January in the areas approximating 2,400 m (42). These low temperature and high humidity conditions facilitate year-round survival of the pathogen, leading to rapid reproduction of the pathogen and consequent huge inoculum supply. It was reported that *P. striiformis* f. sp. *tritici* urediniospores could complete the reinfection of 16 to 18 generations in the areas of elevation 1,700 m during March to November annually (14).

The Chinese population of *P. striiformis* f. sp. *tritici* exhibited great diversity with a complex virulence structure, which could be mostly attributed to the existence of diversity of wheat cultivars planted in various wheat growing regions. Since the 1990s, developing wheat cultivars with slow-rusting or durable resistance to stripe rust has become a top priority in the wheat breeding programs in Sichuan, Gansu, Henan, Shaanxi, and Yunnan provinces (10,50). More than 90 wheat cultivars were planted in the Tianshui region of Gansu province, with total areas of 144,700 and 143,300 ha in 2005 and 2006, respectively (data from Tianshui Bureau of Agriculture). Cultivars with different resistance genes or gene combinations would be expected to select different virulence patterns. However, despite a multitude of *P. striiformis* f. sp. *tritici* races being detected across the country over the 5-year period of this study, only a few races such as CYR32, CYR33, Su11-4, and Su11-7 occurred with relatively high frequencies, suggesting that the situation of relatively simple resistance in leading wheat cultivars has not been dramatically improved, which is supported by the postulation of resistance genes in Chinese commercial cultivars (13,25).

Higher diversity for races in the Northwest and Southwest regions than in the Huang-Huai-Hai region has been revealed in this study. This further supports the hypothesis that the regions of southern Gansu and northwestern Sichuan are the centers of origin for new virulence variation and diversity in the Chinese *P. striiformis* f. sp. *tritici* population. Alternate strategies, such as biodiversity (genetic diversity and crop diversity), should be considered as priority strategies for developing sustainable disease control nationwide. Improving cultivar resistance and deploying resistance genes would be expected to be implemented in the near future.

The relative Shannon index was used to avoid bias in comparisons between samples of greatly different sizes, which reflects both richness (number of races) and evenness (similarity of race frequencies) in the sample. However, diversity differences among populations can be only partially explained by Shannon's index between corresponding diversities within the population. Shannon's index considers nonidentical phenotypes as equally distinct and ignores the number of differences in virulence isolates (18). Nevertheless, some isolates exhibit distinct response patterns, while others are quite similar. Kosman (12) suggested two new analyses for assessing genetic variation between and within populations that take into account both race frequencies and degrees of similarity among distinct races (12,18). In this study, a major restriction was that many of the resistance genes in Chinese differential

genotypes are unknown. Therefore, further work would be expected to survey and monitor the virulence variation of stripe rust population between years and regions using near isogenic lines or monogenic lines with different genes for stripe rust resistance as differentials, combined with their molecular polymorphisms.

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