Identification, Chromosome Location, and Diagnostic Markers for a New Gene (*YrCN19*) for Resistance to Wheat Stripe Rust

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Accepted for publication 28 June 2005.

ABSTRACT

Luo, P. G., Ren, Z. L., Zhang, H. Q., and Zhang, H. Y. 2005. Identification, chromosome location, and diagnostic markers for a new gene (*YrCN19*) for resistance to wheat stripe rust. *Phytopathology* 95:1266-1270.

Several wheat lines and cultivars of wheat (*Triticum aestivum*) originating from the southwestern region of China were found to be highly resistant to stripe rust by inoculation with the prevalent races (CYR30, CYR31, and CYR32) and newly emerged races (H46-4, SY11-4 and SY11-14) of the pathogen. An inheritance study of the resistance to stripe rust was carried out by crossing resistant AIM6 with susceptible BeiZ76. Results indicated that the resistance to stripe rust was controlled by a

single dominant gene. The 112 F₂ plants chosen from the cross BeiZ76/ AIM6 were analyzed with 218 pairs of microsatellite primers to determine the map location of the resistance gene. A simple sequence repeat marker on chromosome arm 2BS, *Xgwm410*, showed polymorphism and co-segregation between stripe rust resistant and susceptible plants. From the pedigree, inheritance, molecular marker, and resistance response, it is concluded that the stripe rust resistance gene in wheat cv. Chuan-nong19 (CN19) and wheat lines AIM5 and AIM6 is a novel gene, designated *YrCN19*. The microsatellite primer *Xgwm410* is a diagnostic marker of the resistance gene *YrCN19*, which has potential for application in the marker-assisted breeding of wheat.

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is a major limitation for wheat (*Triticum aestivum* L.) production throughout the world. The application of resistance genes in wheat breeding is the most effective, economical, and environmentally friendly approach for controlling this disease. A number of stripe rust resistance genes have been identified and incorporated into commercial cultivars. To date, 35 loci for stripe rust resistance have been published officially and 21 other genes have been named provisionally (6,8,10,13,18,24; available online from the U.S. Department of Agriculture).

In China, especially in southwest China, stripe rust is the most commonly occurring disease due to temperate environmental condition in wheat growing season. Yield loss of wheat can be as high as 20 to 30% in the years when stripe rust occurs only moderately epidemic on susceptible cultivars (22,26–28,30). In recent years, stripe rust has become the most devastating disease in southwestern China due to the epidemics of new physiological races of the pathogen, CYR30, CYR31, and CYR32. Almost all of the resistance genes used in wheat breeding program of southwestern China (*Yr1*, 2, 3, 4, 6, 7, 8, 9, 17, 18, *Sp*, *Sk*, and *Sd*) have become ineffective to the three races (22,27,28). Therefore, introducing new sources of resistance to stripe rust is essential. Unfortunately, most of the described genes for resistance were not effective against the three physiological races of stripe rust in the region of southwest China (22,28).

Molecular marker techniques have been demonstrated to be an effective method for differentiating germ plasm resources in many crop species. Various molecular markers, especially restriction fragment length polymorphism, random amplified polymorphism

DNA, amplified fragment length polymorphism, and microsatellite markers, have been employed to detect different genes of wheat (1–4,11,14,21,23). Molecular markers linked to many stripe rust resistance genes, such as *Yr5*, *Yr10*, *Yr15*, *Yr17*, *Yr26*, *Yr28*, *Yr29*, *Yr34*, *YrH52*, and *Yrns-B1*, have been reported by different authors (1,3,4,6,8,12,15,18–20,23–25; available online from the U.S. Department of Agriculture). In hexaploid wheat, simple sequence repeats are more informative and useful than any other marker system in molecular mapping because of their high polymorphism (2,7,9,14,16,17). The purpose of the present study is to identify novel resistance genes to stripe rust in wheat by using microsatellite markers.

MATERIALS AND METHODS

Plant materials. Wheat lines AIM5 and AIM6 and cvs. Chuan-nong19 (CN19), Chinese Spring, Pastor, and Ciano79 were screened for resistance to stripe rust. The wheat lines AIM5 and AIM6 were provided by A. M. Zhang, Institute of Genetics, Chinese Academy of Science, Beijing. Wheat cv. CN19, a widely grown commercial cultivar in the region of southwest China and developed by the authors, has resistance to stripe rust derived from a local variety collected from Guizhou, a province of southwest China. Wheat cvs. Pastor and Ciano79 were used to determine linkage relationships, because they carried known stripe rust resistance genes on chromosome arm 2BS (available online from the U.S. Department of Agriculture). Chinese Spring was used as control in this study. The wheat line AIM6 was crossed with susceptible BeiZ76, and the resulting 16 F₁ hybrids were self-pollinated and backcrossed to each parent to produce the F₂ and two BC₁F₁ populations. The plants of two BC₁F₁ combinations were self-pollinated to produce B₁C₁F₂ (BeiZ76/AIM6//AIM6) and B₂C₁F₂ (BeiZ76/AIM6//BeiZ76) populations, respectively. Altogether, 422 F₂, 132 B₁C₁F₂, and 80 B₂C₁F₂ random individuals were used for genetic analysis.

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DOI: 10.1094/PHYTO-95-1266

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Pathogen materials. Six physiological races of *P. striiformis* f. sp. *tritici*, including CYR30, CYR31, and CYR32, which are currently epidemic in southwest China, and H46-4, SY11-4, and SY11-14, which are newly emerged and provisionally named, were used to screen and assess the resistance of the F₁, F₂, BC₁F₂, parents, and control plants at seedling and adult stages. These physiological races exhibit virulence to almost all of the described genes for resistance to wheat stripe rust (22,26,28).

Testing for resistance. The seeds of all above plant materials were sown in a controlled test plot (25 × 10 m) isolated by glass enclosure (1.6 m in height) at the Experimental Station of Sichuan Agriculture University. Seedlings were inoculated at the three-leaf stage, using an equivalent mixture of urediospores of the above races, mixed with talcum powder at 1:1 rate. The different wheat genotypes in the present study were inoculated also with the single isolates of the above six races, respectively, for elucidating their resistances. When the pustules of stripe rust were fully developed and easily discerned at the seedling stage and after the ear emergence, the infection types (ITs) were recorded according to the standard classification system with 6 classes from 0 to 4. IT 0 represented no visible symptoms; 0+, necrotic flecks; 1, small sporulating uredia surrounded by necrotic tissue; 2, small to medium uredia with chlorosis and necrosis; 3, moderately sized sporulating uredia surrounded only by chlorotic tissue; and 4, abundantly sporulating uredia without chlorosis.

Preparation of plant DNA. DNA was extracted from 2 g of fresh wheat leaves from 5-week-old seedlings according to Zhang et al. (29).

Polymerase chain reaction (PCR) amplification and electrophoretic separation of PCR products. PCRs were performed in a volume of 25 µl in a thermocycler (PTC-200; MJ Research, Watertown, MA), using publicly available GWM primer pairs (2,16,17). For each PCR, the 25-µl volume mixture contained 200 nM of each primer, 0.2 mM deoxynucleotide, 1.5 mM MgCl₂, 1 unit of *Taq* polymerase, and 80 ng of template DNA. After 3 min denaturing at 94°C, 43 cycles were performed with 1 min denaturation at 94°C, 1 min annealing at 55°C, and 2 min extension at 72°C. A final extension step was 10 min at 72°C.

Analysis of amplified products was carried out with electrophoresis on 3% agarose (FMC brand, Spain). The fragments were run in 0.5 Tris-borate-EDTA with 120 v (4 v/cm) and visualized using ethidium bromide staining methods. Fragment sizes were calculated using the computer program Fragment Manager version 1.2 (Pharmacia, Sweden) by comparison with internal size standards from 100 to 600 bp.

Linkage map construction. Linkage distance was computed using MAPMAKER version 3.0. The resistance gene was localized into published wheat maps (16; available online from the U.S. Department of Agriculture).

RESULTS

Resistance response of the analyzed wheat lines and cultivars. The wheat cultivars and lines CN19, AIM5, and AIM6 were

highly resistant, whereas wheat cultivars and lines BeiZ76, Chinese Spring, Pastor, and Ciano79 were susceptible to CYR30, CYR31, CYR32, H46-4, and a mixture of stripe rust races CYR30, CYR31, CYR32, H46-4, SY11-4, and SY11-14 at both seedling and adult stage.

Inheritance of the stripe rust resistance in AIM6. In the cross BeiZ76/AIM6, all F₁ plants displayed a high level of resistance to all inoculated races of stripe rust at either the seedling or the adult stage, indicating a dominant resistance gene carried by wheat line AIM6. In the 422 tested F₂ plants from the cross BeiZ76/AIM6, 325 individuals were highly resistant to all stripe rust races and 97 individuals were susceptible. The segregation of phenotypes is accorded with an expected 3:1 resistant/susceptible ratio ($\chi^2 = 0.814$, $P \geq 0.34$). Furthermore, in the two BC₁F₂ populations, the resistant/susceptible segregation ratios corresponded with expected values 7 resistant/1 susceptible ($\chi^2 = 0.268$, $P = 0.500$) for the backcross BeiZ76/AIM6//AIM6 F₂, and 3 resistant/5 susceptible ($\chi^2 = 1.16$, $P = 0.24$) for the BeiZ76/AIM6//BeiZ76 F₂. The results suggested that wheat line AIM6 carried a single dominant gene for resistance to stripe rust.

Microsatellite marker linkages with resistance gene in wheat line AIM6. In the present experiment, 218 microsatellite primer pairs were screened, in which one primer pair *Xgwm410* showed polymorphism between stripe rust resistant and susceptible plants. Twenty-four DNA samples, extracted from two parents (AIM6 and BeiZ76), 13 resistant and 8 susceptible F₂ individuals, were detected for resistances to stripe rust and for microsatellite marker *Xgwm410* (Fig. 1). The results show that the marker co-segregated with the resistance gene in wheat line AIM6.

The genetic map of the resistance gene to stripe rust in wheat line AIM6. For mapping the resistance gene in wheat line AIM6, 112 F₂ individuals chosen from the cross BeiZ76/AIM6 were analyzed for resistance responses to the inoculated stripe rust races, and for microsatellite marker *Xgwm410*. The AIM6 marker was associated with resistance in 71 plants, and the BeiZ76 marker was associated with susceptibility in 41 plants. The result indicated that *Xgwm410* was a diagnostic marker for the resistance gene in AIM6 because no crossover between the resistance gene and *Xgwm410* locus was detected in the present study. The resistance gene in AIM6 was localized (Fig. 2) by use of the microsatellite map of wheat published by Röder et al. (16) and the available data from the graingenes database (available online from the U.S. Department of Agriculture).

Marker diagnosis. The DNA samples extracted from seven wheat lines and cultivars (Table 1) were amplified by PCR and analyzed for presence of microsatellite locus *Xgwm410*. The result (Fig. 3) revealed that cv. CN19 and wheat lines AIM6 and AIM5, which display high resistance to stripe rust races CYR30, CYR31, CYR32, H46-4, SY11-4, and SY11-14, produced the amplicon *Xgwm410*/391, while wheat cvs. Pastor, Ciano79, and Chinese Spring, which are susceptible to stripe rust races CYR30, CYR31, CYR32, H46-4, and the mixture of CYR30, CYR31, CYR32, H46-4, SY11-4, and SY11-14, produced no amplicons with *Xgwm410*.

Fig. 1. The analysis results of microsatellite locus *Xgwm410*: lanes 1, 2, 7, 8, 10, 12, 14, and 18 for susceptible F₂ plants; lanes 3, 4, 5, 6, 9, 11, 13, 15, 16, 17, 19, 20, and 21 for resistant F₂ plants; lane 22 for susceptible bulk; lane 23 for BeiZ76; lane 24 for resistance bulk; and lane 25 for AIM6. The marker size ranged from 100 to 600 bp.

DISCUSSION

The gene for resistance to stripe rust in cultivar and wheat lines CN19, AIM5, and AIM6. In the present study, CN19, AIM5, and AIM6 displayed high resistance to the mixture of stripe rust races CYR30, CYR31, CYR32, H46-4, SY11-4, and SY11-14, while BeiZ76, Chinese Spring, Ciano79, and Pastor are susceptible to mixed races (Table 1). Resistance tests by inoculating with single isolates showed that CN19, AIM5, and AIM6 were resistant to all races tested, while BeiZ76 and Chinese Spring were susceptible to all races tested. Though Pastor was resistant to SY11-4 and Ciano79 was resistant to SY11-4 and SY11-14 at some degree, both Pastor and Ciano79 were susceptible to the mixture of CYR30, CYR31, CYR32, and H46-4.

Fig. 2. The map location of *YrCN19* in relation to microsatellite marker in chromosome 2B.

Therefore, CN19, AIM5, and AIM6 should carry a resistance gene different from *Yr27* and *Yr31*. According to the pedigree of the cv. CN19, its resistance to stripe rust originated from the parent Qian1104, which was derived from a local variety in Guizhou province in southwestern China. The stripe rust resistance of wheat lines AIM5 and AIM6 could have the same origin as CN19 (A. M. Zhang, *personal communication*). The genetic analyses suggested that a single dominant gene carried by wheat line AIM6 is responsible for resistance to stripe rust. In addition, CN19, AIM5, and AIM6 exhibited resistance to stripe rust races and possessed the same diagnostic marker for the resistance gene. It is likely that CN19, AIM5, and AIM6 could contain the same gene for resistance to stripe rust.

Microsatellite marker and map location of the stripe rust resistance gene in wheat line AIM6. In the present study, a gene for resistance to stripe rust in wheat line AIM6 was mapped by using microsatellite markers. Primer pair *Xgwm410*, out of the 218 tested primer pairs, showed polymorphism and co-segregation between resistant and susceptible plants. In the 112 analyzed F_2 plants derived from the cross BeiZ76/AIM6, all 71 F_2 resistant individuals and the parent AIM6 showed the amplicons *Xgwm410*/391, while the other 41 F_2 susceptible individuals, and BeiZ76, as well as the control cultivar, Chinese Spring, did not display the amplified DNA fragment with primer *Xgwm410* (Fig. 1). Because no crossover between the resistance gene and *Xgwm410* locus was detected in the study, it is concluded that the resistance gene in AIM6 was closely linked with the microsatellite marker *Xgwm410*, located on chromosome arm 2BS. No stripe rust resistance gene has been reported in this region (10; available online from the U.S. Department of Agriculture). The results also indicated that *Xgwm410* was a diagnostic marker for the resistance gene to stripe rust in AIM6.

The gene in wheat line AIM6 for resistance to stripe rust is a new gene. A number of genes for resistance to rust are located on chromosome 2B, such as leaf rust resistance genes *Lr13*, *Lr16*, *Lr23*; stem rust resistance genes *Sr9*, *Sr10*, *Sr19*, *Sr23*, *Sr28*, *Sr36*; and stripe rust resistance genes *Yr5*, *Yr7*, *Yr27*, *Yr31*, *YrSte*, *YrV23*, and *YrSp* (5,10, <http://wheat.pw.usda.gov>). In the present study, the gene for resistance to stripe rust in wheat line AIM6

Fig. 3. The results of diagnosis with *Xgwm410* for existence of *YrCN19*: lane 1 = Chinese Spring; lane 2 = Ciano79; lane 3 = Pastor; lane 4 = CN19; lane 5 = AIM6; and lane 6 = AIM5.

TABLE 1. Infection type (IT) of different wheat lines and cultivars inoculated as seedlings with six stripe rust races, CYR30, CYR31, CYR32, H46-4, SY11-4, SY11-14, and their mixture^a

Genotypes	Mixture	CYR30	CYR31	CYR32	H46-4	SY11-4	SY11-14
AIM6	0	0	0	0	0	0	0
BeiZ76	4	4	4	4	4	3	3
Chinese Spring	4	4	4	4	4	4	3
AIM5	0	0	0	0	0	0	0
Chuan-nong19	0	0	0	0	0	0	0
Pastor (<i>Yr31</i>)	3	4	4	4	4	1	3
Ciano79 (<i>Yr27</i>)	3	3	4	4	3	2	1

^a IT: 0 = no visible symptoms, 0; = necrotic flecks, 1 = small sporulating uredia surrounded by necrotic tissue, 2 = small to medium uredia with chlorosis and necrosis, 3 = moderately sized sporulating uredia surrounded only by chlorotic tissue, and 4 = abundant sporulation without chlorosis.

was located on chromosome arm 2BS. The genes *Yr27* and *Yr31* are also located on the short arm of chromosome 2B, but linked closely with *Lr13* and *Lr23*, respectively, which are abutted on the centromere region (available online from the U.S. Department of Agriculture). Furthermore, the result of diagnosis with *Xgwm410* revealed that the resistance gene in wheat line AIM6 was different from *Yr27* as well as *Yr31*, because the marker *Xgwm410/391* was not amplified in either Ciano79 (*Yr27*) or Pastor (*Yr31*). In addition, wheat cvs. Ciano79 and Pastor were susceptible to CYR30, CYR31, CYR32, H46-4, and the mixture of stripe rust races CYR30, CYR31, CYR32, H46-4, SY11-4, SY11-14, while CN19, AIM5, and AIM6 were resistant to all isolates inoculated and their mixture. Moreover, the pedigrees of both Pastor and Ciano79 contain *Triticum timopheevii* and originated in Mexico (GenBank available online from the National Center for Biotechnology Information [NCBI]). CN19, AIM5, and AIM6 do not have *T. timopheevii* in their pedigree and they originated in China. It is clear that the gene in wheat line AIM6 for resistance to stripe rust could not be an allele for either *Yr27* or *Yr31*.

The resistance gene in AIM6 is not an allele of the genes *Yr5* or *Yr7*, because *Yr5* and *Yr7* are located on the chromosome arm 2BL. Other genes, such as *YrSte* and *YrV23*, which are allelic and in wheat cvs. Stephens and Vilmorin23, are located on chromosome 2B (5). The gene *YrSp* in Spalding Prolific is located on chromosome 2BS (available online from the U.S. Department of Agriculture). However, the *YrSte*, *YrV23*, and *YrSp* had different geographical origins from the resistance gene in CN19, AIM5, and AIM6 (GenBank available online from the National Center for Biotechnology Information [NCBI]). Vilmorin23 (*YrV23*) and Stephens (*YrSte*) originated from the United Kingdom and the United States, respectively. Spalding Prolific originated from Europe, whereas CN19, AIM5, and AIM6 originated from southwest China. These genes are currently not located on genetic maps. It was reported that the genes, *YrSte*, *YrV23*, and *YrSp*, were not effective against the stripe rust race CYR32 (22,27), while the gene for resistance in CN19, AIM5, and AIM6 was highly resistant to the stripe rust race CYR32. These results indicate that the resistance gene in CN19, AIM5, and AIM6 is different from genes *YrSte*, *YrV23*, and *YrSp*. From the above results in this study, it is reasonable to consider that the resistance gene to stripe rust in wheat cultivar and lines CN19, AIM5, and AIM6 was a novel gene on chromosome arm 2BS, named *YrCN19*.

The utilization of *YrCN19* in wheat resistance breeding. Many genes for resistance to stripe rust of wheat have been identified to date and incorporated into commercial cultivars. However, most of the resistance genes have been rapidly overcome by epidemics of new predominant virulent races of the pathogen. In recent years, several physiological races of stripe rust, CYR30, CYR31, and CYR32, have become prevalent in southwestern China. The three races are virulent to almost all of the cultivars released in this region. In the present study, a new resistance gene, *YrCN19*, was identified in several Chinese wheat cultivars and lines. The gene *YrCN19* displays a high resistance at seedling and adult stages not only to the currently prevalent races, CYR30, CYR31, and CYR32, but also to the races H46-4, SY11-4, and SY11-14, which are newly emerged and virulent to almost all described genes for resistance to stripe rust (27). Therefore, the stripe rust resistance of *YrCN19* would possess practical value for resistance breeding of wheat. A new commercial cv. CN19, developed by us and released in 2003, contains the resistance gene *YrCN19*. The primer pair *Xgwm410* was demonstrated to be tightly linked to *YrCN19* and it should be an excellent diagnostic marker in wheat marker-assisted breeding for resistance to stripe rust.

ACKNOWLEDGMENTS

We thank The National Natural Science Foundation of China, the "863" Nation Program of China, and Wheat Breeding Program of

Province Sichuan for financial support; R. A. McIntosh, University of Sydney, for valuable comments on the manuscript; X. M. Chen, Washington State University, for granting seeds of Ciano79 and Pastor; A. M. Zhang, Institute of Genetics and Development, Academy of Sciences of China, for granting seeds of AIM5 and AIM6; and T. Zhongxiang for technical assistance.

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