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Résumé de l'article

Les races CYR31 et CYR32 de la rouille jaune du blé (*Puccinia striiforis* f. sp. *tritici*), très répandues en Chine, sont virulentes pour plusieurs gènes de résistance à cette maladie (gènes *Yr*). Afin d'accroître la disponibilité d'une résistance efficace aux races CYR31 et CYR32, la résistance à la rouille jaune du blé a été transférée de l'agropyre intermédiaire (*Thinopyrum intermedium*) au blé tendre (*Triticum aestivum*). CM107, un cultivar de blé sensible, a été croisé avec l'amphiploïde AI7047 dérivé du croisement éloigné Taiyuan768/*Thinopyrum intermedium*//76(64). Deux lignées de blé provenant de ce croisement, soit YU24 et YU25, étaient résistantes aux races CYR31 et CYR32. Une analyse généalogique a démontré que la résistance à la rouille jaune du blé chez les lignées YU24 et YU25 provenait de l'agropyre intermédiaire. Des analyses génétiques ont indiqué que cette résistance était contrôlée par un seul gène dominant. Des tests d'allélisme ont révélé que le(s) gène(s) de résistance dans les lignées YU24 et YU25 étaient identiques. Le nouveau gène a temporairement été nommé *YrYU25*. Des analyses SSR et RAPD ont démontré que le gène *YrYU25* avait été introduit dans le blé tendre par translocation cryptique.

A new stripe rust resistance gene transferred from *Thinopyrum intermedium* to hexaploid wheat (*Triticum aestivum*)

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Wheat stripe rust (*Puccinia striiforis* f. sp. *tritici*) races CYR31 and CYR32, prevalent in China, are virulent to many wheat stripe rust resistance genes (*Yr* genes). To expand the availability of effective resistance to CYR31 and CYR32, stripe rust resistance was transferred from intermediate wheatgrass (*Thinopyrum intermedium*) to common wheat (*Triticum aestivum*). The susceptible wheat cultivar CM107 was crossed with amphiploid TAI7047, derived from the wide cross Taiyuan768/*Thinopyrum intermedium*//76(64). Two wheat lines originating from the cross, YU24 and YU25, were resistant to CYR31 and CYR32. Pedigree analysis showed that the resistance to stripe rust in YU24 and YU25 originated from intermediate wheatgrass. Genetic analyses indicated that the resistance to stripe rust is controlled by a single dominant gene. Allelic tests determined that the resistance gene(s) in YU24 and YU25 are identical. The new gene has temporarily been designated as *YrYU25*. SSR and RAPD analyses showed that *YrYU25* was introduced by cryptic translocation into common wheat.

Keywords: Genetic resistance, intermediate wheatgrass, *Puccinia striiformis* f. sp. *tritici*, *Thinopyrum intermedium*, wheat.

[Un nouveau gène de résistance à la rouille jaune du blé transféré de *Thinopyrum intermedium* au blé hexaploïde (*Triticum aestivum*)]

Les races CYR31 et CYR32 de la rouille jaune du blé (*Puccinia striiforis* f. sp. *tritici*), très répandues en Chine, sont virulentes pour plusieurs gènes de résistance à cette maladie (gènes *Yr*). Afin d'accroître la disponibilité d'une résistance efficace aux races CYR31 et CYR32, la résistance à la rouille jaune du blé a été transférée de l'agropyre intermédiaire (*Thinopyrum intermedium*) au blé tendre (*Triticum aestivum*). CM107, un cultivar de blé sensible, a été croisé avec l'amphiploïde AI7047 dérivé du croisement éloigné Taiyuan768/*Thinopyrum intermedium*//76(64). Deux lignées de blé provenant de ce croisement, soit YU24 et YU25, étaient résistantes aux races CYR31 et CYR32. Une analyse généalogique a démontré que la résistance à la rouille jaune du blé chez les lignées YU24 et YU25 provenait de l'agropyre intermédiaire. Des analyses génétiques ont indiqué que cette résistance était contrôlée par un seul gène dominant. Des tests d'allélisme ont révélé que le(s) gène(s) de résistance dans les lignées YU24 et YU25 étaient identiques. Le nouveau gène a temporairement été nommé *YrYU25*. Des analyses SSR et RAPD ont démontré que le gène *YrYU25* avait été introduit dans le blé tendre par translocation cryptique.

Mots clés : agropyre intermédiaire, blé, *Puccinia striiformis* f. sp. *tritici*, résistance génétique, *Thinopyrum intermedium*.

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INTRODUCTION

Stripe rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Eriks., is still one of the most devastating diseases threatening wheat yield throughout the world, especially in cool and moist environments. The disease is controlled through resistance breeding and fungicides. Stripe rust attacks wheat at the early stages of plant development, and infection can result in stunted and weakened plants, leading to yield losses as high as 50% due to shriveled grain and damaged tillers (Roelfs *et al.* 1992). Although chemical control can reduce losses caused by stripe rust, and is the preferred means of control in some regions, genetic resistance remains a major objective for wheat breeding programs. The deployment of diverse resistance cultivars is the most effective, economical and environmentally-friendly approach for controlling this disease (Line and Chen 1995; Luo *et al.* 2009a). For more than half a century, wheat stripe rust has caused periodical epidemics and severe damage in China, especially in the southwest where the widely grown varieties have become susceptible. With the prevalence of the pathotypes CYR31 and CYR32, stripe rust has become the greatest threat to wheat yield because only a few of the known resistance genes are effective against these pathotypes (Luo *et al.* 2005, 2006, 2008a; Wan *et al.* 2004; Yang and Ren 2001). Long-lasting genetic resistance can be achieved through gene pyramiding (Johnson 1988), cultivar diversification, and cultivar mixing (Finckh 2008). Such strategies depend greatly on the availability of effective resistance genes. Thus, the identification of new stripe rust resistance genes is urgently needed to control the disease.

Intermediate wheatgrass *Thinopyrum intermedium* (Host) Barkworth and D.R. Dewey (2n = 6x = 42; JJJ^{s}J^{s}SS) (syn. *Elytrigia intermedia* (Host) Nevski) has been hybridized extensively with wheat and has proven to be a useful source of disease resistance in hexaploid wheat (*Triticum aestivum* L.) (2n = 42; AABBDD) thanks to its close relationship with wheat. There is a lot of evidence suggesting that *T. intermedium* would constitute a potential tertiary gene pool for wheat resistance improvement to diseases such as wheat streak mosaic virus (Friebe *et al.* 1996), barley yellow dwarf virus (Ayala *et al.* 2001), Fusarium head blight (Fedak and Han 2005), leaf rust (Autrique *et al.* 1995), stem rust (Fedak 1999) and powdery mildew (Liu and Wang 2005; Liu *et al.* 2005). Recently, two powdery mildew resistance genes, *Pm40* and *Pm43*, were transferred from *Thinopyrum intermedium* to common wheat by cryptic translocation, and they were located on chromosomal arm 7BS and 2DL, respectively (He *et al.* 2009; Luo *et al.* 2009b).

The main purpose of this study was to identify new genes for resistance to stripe rust by transferring such resistance from *T. intermedium* to common wheat. The introgressed resistance was then characterized through genetic analysis and molecular marker studies.

MATERIALS AND METHODS

Virulence spectra of *P. striiformis* pathotypes CYR31 and CYR32

Various wheat differential lines (Table 1) carrying known *Yr* genes (kindly provided by Chen Xianming, Washington State University) as well as the main resistance genes utilized in the region were used to establish the virulence spectrum of the stripe rust pathotypes CYR31 and CYR32 and to differentiate the resistance response.

Introgression and genetic analysis of stripe rust resistance

Chuanmai107 (CM107) was pollinated with octoploid *Trititrigia* TAI7047, derived from the wide cross Taiyuan768/*T. intermedium*//76(64). Two wheat lines, Yuan24 (YU24) and Yuan25 (YU25) (*Triticum aestivum*, 2n = 6x = 42, AABBDD), were selected from the F_5 population of the cross (CM107/TAI7047) (Luo *et al.* 2009b). The two lines were characterized by a hypersensitive response to both races of *P. striiformis* f. sp. *Tritici*, CYR31 and CYR32, following natural infection. To study the genetic composition and nature of the resistance, three F_2 populations were derived from the F_1 population originating from the crosses MY11/YU24, MY11/YU25 and YU24/YU25. The F_1 hybrids were also backcrossed to both parents. The backcross to the susceptible parent ($BC_1^sF_1$) and the backcross to the resistant parent ($BC_1^RF_1$) were allowed to self-pollinate, and both sets of F_1 and F_2 populations were genetically analyzed.

Stripe rust resistance screening

Puccinia striiformis f. sp. *tritici* pathotypes CYR31 and CYR32, which are the predominant strains in southwest China, were used to screen and assess the resistance response of homogeneous genotypes. To test the resistance of segregating populations, plants were inoculated with CYR32 because it has the same virulent factors as CYR31 (Wan *et al.* 2004).

The various wheat genotypes, including differential lines, main resistance lines and parental lines, were grown in a temperature- and moisture-controlled glass enclosure (25 m x 10 m; 1.6 m in height) at the Experimental Station of Sichuan Agriculture University. At the three-leaf stage, 20 seedlings per genotype were inoculated with single isolates of both CYR31 and CYR32 according to Luo *et al.* (2005). The inoculated seedlings were misted through an inlet until sufficient dew was formed and incubated at 14°C in the dark for 12 h and in the light for 24 h. They were then grown under natural daylight at 16-20°C. When the stripe rust pustules were fully developed, the infection types (ITs) were recorded on a 0 to 4 scale described by Wellings *et al.* (1988): IT0 = no visible symptoms; IT0+ = visible necrotic flecks without uredia; IT1 = small sporulating uredia surrounded by necrotic tissue; IT2 = small-size uredia with chlorosis and necrosis; IT3 = moderately-sized sporulating uredia surrounded only by chlorotic tissue; and IT4 = abundantly sporulating uredia without chlorosis.

Table 1. Virulence testing of wheat stripe rust physiological strains CYR31 and CYR32 on stripe rust differential wheat lines and on main resistance cultivars in China

Genotype	Genes	Infection type (IT)[a]		Season
		CYR31	CYR32	
Chinese 166	*Yr1*	4	4	Winter
Leda	*Yr2*	3	3	Winter
Heines II	*Yr2, YrH*II, *Yr25*	3	3	Winter
Bon Fermier	*Yr3a*	4	4	Winter
Capelle Desprez	*Yr3a, Yr4a, Yr16*	3	3	Winter
Avalon	*Yr3b, Yr4b, Yr14*	4	4	Winter
Minstre	*Yr3c, YrMin*	2	2	Winter
Vilmorin 23	*Yr4a, YrV23*	3	3	Winter
Hybrid 46	*Yr4b, YrH46*	3	3	Winter
Opal	*Yr4b*	3	3	Spring
AVS/6* *Yr5*	*Yr5*	0	0+	Spring
T. spelta var. *album*	*Yr5*	0	0	Winter
Fielder	*Yr6, Yr20*	3	4	Spring
Heines Kolben	*Yr6, YrHK*	4	4	Winter
Lee	*Yr7, Yr22, Yr23*	3	4	Spring
Thatcher	*Yr7*	4	4	Spring
Maris Widgeon	*Yr8*	3	4	Winter
Compair	*Yr8, Yr19*	1	1	Spring
Aurora	*Yr9*	3	3	Winter
Benno	*Yr9*	3	3	Winter
Moro	*Yr10, YrMor*	0+	0+	Winter
PI178383	*Yr10*	0+	0+	Winter
Joss Cambier	*Yr11*	3	3	Winter
Mega	*Yr3a, Yr4a, Yr12*	3	3	Winter
Armada	*Yr3a, Yr4a, Yr12*	3	3	Winter
Mardler	*Yr1, Yr2, Yr3a, Yr4a, Yr13*	1	1	Winter
Kador	*Yr14*	3	3	Winter
AVS/6* *Yr15*	*Yr15*	0+	0+	Spring
Hybrid de Bersee	*Yr16*	3	3	Winter
AVS/6* *Yr17*	*Yr17*	3	3	Spring
Jupetico R	*Yr18*	3	3	Spring
Lemhi	*Yr21*	4	4	Spring
Yr24	*Yr24*	4	4	Spring
TP981	*Yr25*	4	4	Winter
Yr26	*Yr26*	3	4	Spring
R212	*YrR212*	0	0	Winter
AIM6	*YrCN19*	0	0	Winter
R185	*YrR212*	0	0	Winter
Ciano79	*Yr27*	3	3	Winter
Pastor	*Yr31*	3	3	Winter
R88	*YrCN19*	0	0	Winter
R57	*YrCN17*	1	1	Winter
R59	*YrCN17*	1	1	Winter
R25	*YrCN17*	1	1	Winter
AIM5	*YrCN19*	0	0	Winter
Spolding Prolifie (M)	*Yrsp*	3	3	Winter

[a] 0 = no visible symptoms; 0+ = visible necrotic flecks without uredia; 1 = small sporulating uredia surrounded by necrotic tissue; 2 = small-size uredia with chlorosis and necrosis; 3 = moderately-sized sporulating uredia surrounded only by chlorotic tissue; and 4 = abundantly sporulating uredia without chlorosis.

Genomic DNA extraction and analysis

DNA was extracted using 1 g of fresh wheat leaves from 5-wk-old seedlings (Tai and Tanksley 1990). DNA of intermediate wheatgrass and of wheat genotypes Chinese Spring (CS), MY11, CM107, YU24, YU25 and octoploid *Trititrigia* TAI7047 was used to screen for the presence of foreign DNA segments using wheat-specific microsatellites markers (SSR) and random amplified polymorphic DNA (RAPD). For SSR analysis, PCR reactions were carried out in an MJ RESEARCH (PTC-200) thermocycler using publicly available *Xgwm* primer pairs. For each PCR reaction, the 20 µL volume mixture contained 200 nM of each primer, 0.2 mM deoxynucleotides, 50 mM KCl, 10 mM Tris-HCl, 1.5 mM $MgCl_2$, 1 unit Taq polymerase (Pharmacia) and 50 ng template DNA. After 3 min denaturation at 94°C, 43 cycles were performed with 1 min denaturation at 94°C, 1 min annealing at temperatures varying from 50-60°C (depending on the primer sequence), and a 2 min extension at 72°C. A final extension step of 10 min at 72°C was performed (Roder *et al.* 1998).

RAPD analysis was performed in 20 µL reaction volumes as described by Williams *et al.* (1990). In total, 520 primers were screened from Operon primer kits A-Z. The amplified fragments were run on 3% agarose (FMC brand) in 0.5X TBE at a voltage of 120 V (4V cm^{-1}) and were then visualized using ethidium bromide staining methods.

RESULTS

Virulence of *P. striiformis* pathotypes CYR31 and CYR32 on main known resistance genes

Inoculation tests showed that CYR31 and CYR32 are virulent on most of the described wheat stripe rust resistance genes (Table 1). CYR31 and CYR32 are virulent to *Yr1, Yr2, Yr3a, Yr3b, Yr3c, Yr4a, Yr4b, Yr6, Yr7, Yr8, Yr9, Yr11, Yr12, Yr14, Yr16, Yr17, Yr18, Yr20, Yr21, Yr22, Yr23, Yr24, Yr25, Yr26, Yr27, Yr31, YrHVII, YrMin, YrV23, Yrsp, YrH46* and *YrHK.* Only *Yr5, Yr10, Yr15, YrCN19* and *YrR212* were effective against CYR31 and CYR32, while *Yr13, Yr19* and *YrCN17* were partially effective (Table 1).

The resistance response of different genotypes to CYR31 and CYR32

The parental genotypes CS, CM107, MY11, Taiyuan768 and 76(64) were susceptible, with high infection types ranging between 3 and 4. *Thinopyrum intermedium* wheatgrass, YU24, YU25 and TAI7047 were resistant, with low infection type IT=0+ (Table 2). Their leaves produced obvious large necrotic lesions between the veins of adult plants after inoculation (Fig. 1).

Genetic analyses of *Thinopyrum intermedium*-derived stripe rust resistance

The data obtained following evaluation of the seedlings of parental lines and cross progenies with isolates CYR31 and CYR32 are summarized in Table 2. Towards the end of growth, there were still no visible symptoms on the leaves of intermediate wheatgrass. The F_1 MY11/YU24 and MY11/YU25 were also highly resistant (Table 3), indicating the presence of one or more dominant resistance genes in YU24 and YU25. The two F_2 populations (crosses MY11/YU24 and MY11/YU25) each showed 3 resistant:1 susceptible segregation of a single dominant resistance gene (Table 3). Single gene segregation was also confirmed in the two $BC_1{}^{S}F_1$ populations, which fitted the expected 1:1 ratio. Segregation in the backcross F_2 populations also fitted the expected segregation of a single dominant resistance gene. All F_1 and F_2 populations produced from the cross YU24/YU25 were resistant (Tables 2 and 3), suggesting that the same gene was present in both parents.

Determination of foreign DNA segments in YU24 and YU25

In an attempt to determine the chromosome location of the introgressed foreign chromatin, 294 pairs of wheat microsatellite primers that amplify repeat sequences distributed over all wheat chromosomes were used. The results showed that wheat genotypes YU24, YU25 and octoploid TAI7047, as well as

Table 2. Reaction of various wheat and intra-specific hybrids to *Puccinia striiformis* f. sp. *tritici* physiological strains CYR31 and CYR32

Genotype	Pedigree	Infection type (IT)[a]	
		CYR31	CYR32
CS		3	3
MY11		4	4
YU24	CM107/TAI7047	0+	0+
YU25	CM107/TAI7047	0+	0+
CM107		4	4
TAI7047	Taiyuan768/*Th. intermedium*//76(64)	0+	0+
Intermediate wheatgrass		0	0
Taiyuan768		3	4
76(64)		4	4

[a] 0 = no visible symptoms; 0+ = visible necrotic flecks without uredia; 1 = small sporulating uredia surrounded by necrotic tissue; 2 = small-size uredia with chlorosis and necrosis; 3 = moderately-sized sporulating uredia surrounded only by chlorotic tissue; and 4 = abundantly sporulating uredia without chlorosis.

Figure 1. The different infection types of wheat stripe rust resistance to physiological strain CYR32 in various wheat genotypes.

common wheat controls MY11, CM107 and CS, amplified wheat-specific SSR products that did not occur in intermediate wheatgrass. In addition, 520 primers (Operon groups A to Z) were used in an attempt to identify amplicons specific to intermediate wheatgrass. Thirteen RAPD primers (B2, F9, I17, M8, N11, P6, Q18, R1, R10, R16, R19, U5 and Z20) produced amplified products in wheat genotypes YU24 and YU25 and octoploid *Trititrigia* TAI7047, and these products had the same length as those in intermediate wheatgrass. The PCR results amplified by R1 are shown in Figure 2.

DISCUSSION

Although many stripe rust resistance genes have been identified to date and incorporated into high-yield wheat cultivars, most of them are no longer effective against the stripe rust pathotypes prevalent in southwest China (Wan *et al.* 2004; Yang *et al.* 2003). Wheat lines YU24 and YU25 have a high level of resistance (IT = 0+) to stripe rust pathotypes CYR31 and CYR32, which was associated with large necrotic spots on the leaves (Table 2 and Fig. 1). Although the genotypes Moro (*Yr10* and *YrMor*), PI178383 (*Yr10*) and AVS/6**Yr15* (*Yr15*) had similar infection types (IT = 0+), they produced less necrosis. Moreover, YU24 and YU25 were derived from a wide cross between wheat cultivar CM107 and octoploid *Trititrigia* TAI7047 (Taiyuan768/*Th. intermediate* wheatgrass//74(64)). In these pedigrees, all common wheat lines were susceptible to stripe rust pathotypes CYR31 and CYR32 (Table 2); hence, the resistance factors were derived from intermediate wheatgrass and they therefore represent a new source of wheat stripe rust resistance. This also confirms that intermediate wheatgrass is an accessible source of disease resistance genes.

Genetic analysis of the resistance in YU24 and YU25 showed that segregation in the segregating populations complied with the expected segregation as a single dominant factor (Table 2), thus suggesting

Table 3. Resistance segregation of YU24 and Yu25 in various genetic backgrounds

Pedigree	Generation	CYR32		Expected ratio	χ^2	*P*
		R	S			
MY11/YU25 (F_1)	F_1	21	0			
MY11/YU24 (F_1)	F_1	19	0			
YU24/YU25 (F_1)	F_1	23	0			
MY11/Yu25	F_2	136	47	3:1	0.05	0.83
MY11/YU24	F_2	133	39	3:1	0.50	0.48
MY11/YU25//YU25	$BC_1^RF_1$ [a]	68				
	$BC_1^RF_2$	128	22	7:1	0.64	0.42
MY11/YU24//YU24	$BC_1^RF_1$	73				
	$BC_1^RF_2$	132	23	7:1	0.78	0.38
MY11/YU25//MY11	$BC_1^SF_1$ [a]	41	46	1:1	0.29	0.59
	$BC_1^SF_2$	64	112	3:5	0.10	0.76
MY11/YU24//MY11	$BC_1^SF_1$	39	44	1:1	0.30	0.58
	$BC_1^SF_2$	59	104	3:5	0.12	0.73
YU25/YU24	F_2	253	0			

[a] R and S refer to backcrosses made to the resistant and susceptible parents, respectively.

the presence of a dominant resistance gene. The results of allelic tests for resistance (Tables 2 and 3) revealed that the resistance genes to stripe rust in both parents are identical. None of the resistance genes published for wheat stripe rust originated from intermediate wheatgrass (Luo *et al.* 2008b), and the stripe rust resistance gene in YU24 and YU25 is different from the wheat stripe rust resistance genes published so far; it is therefore a new gene, which has temporarily been designated as *YrYU25*.

Chromosomal translocation is a classic and useful method for transferring alien genes from wild relatives to common wheat (Ren and Zhang 1997). Most of these translocations, despite carrying useful alien genes, have a questionable value for wheat improvement because the large transferred chromosome segments do not adequately compensate for the wheat genes they replace or they carry additional genes conferring undesirable traits. However, in a few instances, traits of interest were transferred to recipient genotypes without inducing detectable cytological or genetic changes (Dong *et al.* 2004; He *et al.* 2009; Kuraparthy *et al.* 2007; Luo *et al.* 2009b; Multani *et al.* 1994; Ren and Zhang 1997). The results of the SSR analysis showed that YU24 and YU25 amplified wheat-specific products evenly distributed over all chromosomal arms. This indicates that there is no whole foreign chromosomal arm in YU24 and YU25. Previous cytological studies have shown that YU24 and YU25 are genetically stable (2n = 42, 21II), and agronomical trait observation over the past several years has also proven that they are homogeneous (Luo *et al.* 2009b; Ma *et al.* 2007). The resistance segregation of YU24 and YU25 behaved as a normal Mendelian unit. Moreover, we could not detect hybridization signals *in situ* using *Th. intermedium* genomic DNA as a probe (data not shown). This evidence persuaded us to conclude that wheat resistance genotypes YU24 and YU25 do not have an entire foreign chromosomal arm and, therefore, that the new stripe rust resistance source could be used to expand resistance genetic diversity in common wheat.

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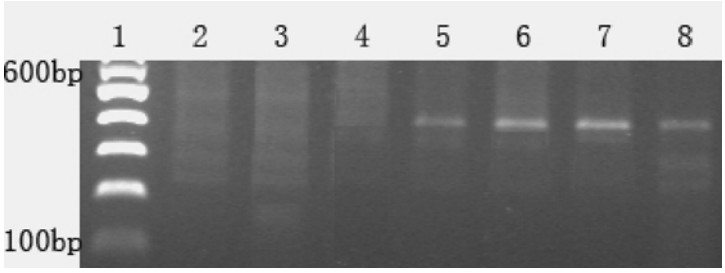

Figure 2. PCR results of various genomic DNA amplified by RAPD primer R1. Lane 1 = Marker; 2 = Chinese Spring; 3 = MY11; 4 = CM107; 5 = TAI7047; 6 = *E. intermedium*; 7 = YU24; 8 = YU25.

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