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Molecular mapping of a stripe rust resistance gene in wheat cultivar Wuhan 2

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Abstract Stripe rust (or yellow rust), caused by *Puccinia striiformis* f. sp. *tritici*, is one of the most destructive diseases of wheat worldwide. Growing resistant cultivars is the best approach to control the disease. To identify and map genes for stripe rust resistance in wheat cultivar 'Wuhan 2', an F_2 population was developed from a cross between the cultivar and susceptible cultivar Mingxian 169. The parents, 179 F_2 plants and their derived $F_{2:3}$ lines were evaluated for responses to Chinese races CYR30 and CYR31 of the pathogen in a greenhouse. A recessive gene for resistance was identified. DNA bulked segregant analysis was applied and resistance gene analog polymorphism (RGAP) and simple sequence repeat (SSR) techniques were used to identify molecular markers linked to the resistance gene. A genetic map consisting of five RGAP and six SSR markers was constructed. The recessive gene, designated *Yrwh2*, was located on the short arm of chromosome 3B and flanked by SSR markers *Xwmc540* and *Xgwm566* at 5.9 and 10.0 cM, respectively. The chromosomal location of the resistance gene and its close marker suggest that the locus is different from previously reported stripe rust resistance genes *Yr30*, *QYr.ucw-3BS*, *Yrns-B1*, *YrRub* and *QYrex.wgp-3BL* previously mapped to chromosome 3B. *Yrwh2* and its closely linked markers are potentially useful for developing stripe rust resistance wheat cultivars if used in combination with other genes.

Keywords Gene mapping · Yellow rust · *Puccinia striiformis* f. sp. *tritici* · Resistance

Introduction

Stripe rust (or yellow rust), a worldwide wheat disease caused by fungus *Puccinia striiformis* Westend. f. sp. *tritici* Erikss. (*Pst*), significantly reduces wheat yields and grain quality when developed to an epidemic (Smith et al. 1986; Dimmock and Gooding 2002). Like other rust fungi, uredospores of *Pst* can be disseminated by wind in a long distance, leading to large-scale epidemics. Stripe rust is a major biological disaster affecting food security in all wheat production regions (Li and Zeng 2000; Chen 2005). The disease often causes 10–30 % yield loss, and under favorable conditions for the fungus the loss can even be 100 %. In China, stripe rust epidemics caused yield losses of more than one million tons in 1950, 1964, 1990 and 2002 (Wan et al. 2004, 2007).

X. L. Zhou and D. J. Han have made equal contributions towards this study.

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Table 1 Infection types on wheat genotypes Wuhan 2 and Mingxian 169 tested with races of *Puccinia striiformis* f. sp. *tritici* in the seedling and adult-plant stages

Races	Virulence characterization[a]	Infection type	
		Wuhan 2	Mingxian 169
CYR25	1, 2, 3, 4, 5, 6, 7, 8, 9, 11	2	9
CYR29	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 12, 16	8	9
CYR30	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 12, 16, 17	2	9
CYR31	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 12, 14, 16	2	9
CYR32	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17	8	9
CYR33	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16	2	9
PST-Su5	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 14, 16	2	9
PST-CH42	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13, 14, 19	2	9

[a] Chinese differential genotypes: 1, Trigo Eureka; 2, Fulhard; 3, Lutescens 128; 4, Mentana; 5, Virgilio; 6, Abbondanza; 7, Early premium; 8, Funo; 9, Danish 1; 10, Jubilejina 2; 11, Fengchan 3; 12, Lovirn13; 13, Kangyin 655; 14, Shuiyuan 11; 15, Zhong 4; 16, Lovirn 10; 17, Hybrid 46; 18, *Triticum spelta ablum*; 19, Guinong 22

Growing resistant cultivars is the most effective way to control wheat stripe rust. However, seedling resistance (also called all-stage resistance) is usually race-specific and can be overcome by new races of the pathogen. Growing cultivars with a race-specific resistance gene accelerates the selection of new *Pst* races (Chen et al. 2010; Wang et al. 2012). Since the 1950s, several large-scale cultivar replacements occurred in China due to the appearance of virulent races which rendered previously resistant cultivars susceptible. This phenomenon also explains the lack of stripe rust resistant germplasm sources in China (Yang et al. 2003; Wan et al. 2007). Exploring new sources with resistance genes and developing new cultivars with different types of resistance, stripe rust can be effectively controlled.

Molecular markers closely linked to resistance genes can be used in gene pyramiding, facilitating breeding resistant cultivars (Young 1996). To date, over 50 genes for stripe rust resistance have been officially named (McIntosh et al. 2011; Xu et al. 2013). Only few of the genes are effective against the recent Chinese *Pst* population (Li and Zeng 2000; Wan et al. 2004; Zhou et al. 2011) (Table 1). Therefore, it is urgent to identify new genes for resistance to stripe rust and to develop molecular markers for efficient incorporation and pyramiding of new genes into wheat cultivars.

Cultivar 'Wuhan 2' was resistant to most tested *Pst* races, but which gene(s) control the resistance to stripe rust in this cultivar were not identified. The objective of this study was to characterize the gene(s) conferring resistance in Wuhan 2 through genetic analysis and molecular mapping.

Materials and methods

Plant material

Wuhan 2, a hexaploid winter wheat (*Triticum aestivum* L.) cultivar exhibited resistance to all tested Chinese *Pst* races, when tested in the seedling and adult-plant stage in the greenhouse (Kang et al. unpublished data). It was also resistant in the field tests at Yangling (Shaanxi province) and Tianshui (Gansu province) under natural infections since 2008 (Kang et al. unpublished data). Mingxian 169 (M169) is a Chinese winter wheat cultivar that is susceptible to all *Pst* races in China. Wuhan 2 as the male parent was crossed with M169. In 2010, F_1 plants were grown and selfed to produce F_2 seeds in a field, and 179 F_2 plants from a single F_1 plant were grown in the greenhouse and tested with race CYR30. After scoring stripe rust data, the F_2 plants were transferred into the open during the 2011–2012 winter for vernalization, and subsequently transplanted in the field with five plants per row of 1.0 m in length spaced 20 cm apart for seed production in 2012. One hundred and seventy nine plants were successfully harvested to produce enough $F_{2:3}$ seeds. The 179 $F_{2:3}$ lines were tested with race CYR31 for confirming the phenotypes and determine the genotypes of the F_2 plants.

Evaluation of stripe rust response phenotype

To determine reactions of Wuhan 2 to various *Pst* races at the seedling and adult-plant stages, eight races (CYR25, CYR29, CYR30, CYR31, CYR32, CYR33, PST-Su5 and PST-CH42) predominant from 1980s to 2010 (Wan et al. 2007; He et al. 2011) were used in this study (Table 1). For the seedling tests, the inoculations were done at the two-leaf stage and for the adult-plant tests, the inoculations were done at the heading stage in a greenhouse. The 179 F_2 plants together with the parents were inoculated with CYR30. Because of the failure for increasing spores of CYR30, the 179 $F_{2:3}$ lines together with the parents were inoculated with CYR31 at the seedling stage in the greenhouse. About 20 seeds each of the $F_{2:3}$ lines and the parents were planted in 8 × 8 × 8 cm^3 pots. The plants were dust-inoculated with a mixture of fresh uredospores and talc at a 1:50 ratio and kept in a dew (humid) chamber at 10 °C without light. After 24 h, the inoculated plants were transferred into an environmentally controlled greenhouse with a daily cycle of 16 h of light at 16 °C and 8 h of darkness at 12 °C. Infection type (IT) on a 0–9 scale (Line and Qayoum 1992) was recorded at 16 days after inoculation. To distinguish homozygous and heterozygous lines, a single IT was recorded if all plants of a $F_{2:3}$ line had uniform IT; whereas different ITs on plants of a line showing segregation of $F_{2:3}$ plants within a line indicated the heterozygosity of their parental F_2 plant (Zhou et al. 2011).

During the 2012 crop season, Wuhan 2 and M169, together with other wheat germplasm, were tested for stripe rust resistance at two field locations at Yangling. On March 20, one of the field nurseries was inoculated with CYR32 and another with a mixture of CYR31, CYR32, CYR33 and PST-CH42.

DNA extraction, PCR amplification, electrophoresis and silver staining

Genomic DNA was extracted from fresh leaves of the parents and each F_2 plant using the CTAB method (Yan et al. 2003). DNA quality and concentration were determined using a NanoDrop ND-1000 (Thermo scientific, Wilmington, DE, USA). Stock DNA solutions were diluted to 50 ng/μl as templates for use in PCR amplification. Twenty-seven RGA primers (Table 2) designed by Dr. Meinan Wang, Washington State University based on cereal resistance gene sequences were used in random pairs. Resistance gene analog polymorphism (RGAP) reaction mixtures were made as described by Chen et al. (1998). PCR amplification, electrophoresis and gel visualization were done following the standard procedures and conditions previously described (Chen et al. 1998). The primer sequences and chromosomal location information of simple sequence repeat (SSR) markers were obtained from the Graingenes website (http://wheat.pw.usda.gov/) and the application conditions specific for individual primer pairs were followed.

Bulk segregant analysis

Based on phenotypic data of F_2 plants and their single-seed descent $F_{2:3}$ lines, the five most resistant (IT 2 and DS 5 %) and the five most susceptible (IT 9 and DS 90–100 %) F_2 plants were selected for bulk segregant analysis to screen for RGAP and SSR markers potentially linked to the resistance locus (Michelmore et al. 1991; Chen et al. 1998). Resistant and susceptible bulks were constructed with equal amount of DNA from each selected F_2 plant. Polymorphic bands specific to the resistant parent and the resistant bulk, or the susceptible parent and the susceptible bulk, were used to genotype the 179 F_2 plants.

Chromosomal locations of molecular markers and the linked resistance gene

Chinese Spring (CS) and 21 nulli-tetrasomic (NT) lines were used to determine the chromosomal locations of RGAP markers linked to the stripe rust resistance gene. If the target band was present in CS, the complete set of CS nulli-tetrasomic lines was tested with the markers. The chromosome absent in the nulli-tetrasomic line not showing the band was determined to carry the RGAP marker locus. SSR markers (http://wheat.pw.usda.gov/) for the specific chromosomes were chosen to screen for more markers using bulk segregant analysis, and selected linkage markers were tested with DNA of the 179 F_2 plants.

Map construction

Using software quantitative trait locus (QTL) IciMapping V3.2 (Wang 2009; http://www.isbreeding.net/download_software_ICIM.aspx), a genetic map was

Table 2 Resistance gene analog (RGA) and simple sequence repeat (SSR) primers linked with the stripe rust resistance gene in Wuhan 2

Primer[a]	Sequence (5′–3′)	Tm (°C)[b]	Reference
RGA			
rga54	gcaggaaaaacaacg	45	
rga56	ggaaagacaactttt	45	
rga57	ttgggcaagaccact	45	
rga59	ccatatatcatcgat	45	
rga66	tgtggtcattattac	45	
rga67	acgagttgttgtcaa	45	
rga70	tgtggtgattagccg	45	
rga72	aaggtcaaaataaca	45	
rga75	tggtaggtccttgta	45	
SSR			
Xwmc540F	cggggTccTAAcTAcggTgA	55	Röder et al. (1998)
Xwmc540R	ccTgTAATggAggAcggcTg	55	Röder et al. (1998)
Xgpw376F	GGGCTAGAAAACAGGAAGGC	60	Sourdille et al. (2005)
Xgpw376R	TCTCCCGGAGGGTAGGAG	60	Sourdille et al. (2005)
Xcfd4F	TGCTCCGTCTCCGAGTAGAT	58	Somers et al. (2004)
Xcfd4R	GGGAAGGAGAGATGGGAAAC	58	Somers et al. (2004)
Xwmc182F	gTATcTcAcgAgcATAAcAcAA	52	Somers et al. (2004)
Xwmc182R	gAAAgTgTATggATcATTAggc	52	Somers et al. (2004)
Xwmc366F	TAccTcTcTAcgATgAAgcc	51	Somers et al. (2004)
Xwmc366R	TggAgTcTTAgTgTggTgTT	51	Somers et al. (2004)
Xgwm566R	TCTGTCTACCCATGGGATTTG	60	Röder et al. (1998)
Xgwm566F	CTGGCTTCGAGGTAAGCAAC	60	Röder et al. (1998)

[a] *rga54*, *rga56*, *rga57*, *rga59*, *rga66*, *rga67*, *rga70*, *rga72* and *rga75* are RGA primers designed by Dr. Meinan Wang and the remaining are SSR primers

[b] Annealing temperature

developed using the marker and stripe rust data of the 179 F_2 plants. The Kosambi map function was applied to calculate genetic distances in centiMorgans (cM) (Kosambi 1944). A LOD threshold of 3.0 was used for grouping, and the algorithm "nnTwo Opt" was used for ordering. Linkage groups were assigned to chromosomes and compared with previously published wheat consensus map (Somers et al. 2004; http://wheat.pw.usda.gov).

Results

Stripe rust evaluated in the greenhouse

Under controlled greenhouse conditions, M169 was consistently susceptible (IT 9) with abundant uredia in all of the race tests at seedling and adult-plant stages. Wuhan 2 was resistant (IT 2) to all races except CYR29 and CYR32 (IT 8) at seedling and adult-plant stages (Table 3).

Stripe rust evaluated in the fields

Results from the field test with race mixture showed that Wuhan 2 was resistant (IT 2-4) with disease severity of 30–50 %, with spot necrosis and short stripes, and with some sporulation on leaves at adult-plant tests in Yangling 2012. It was fully susceptible (IT 8-9) to race CYR32 and had disease severity of 60–100 % at every note-taking at another field location in Yangling. The field and greenhouse data were consistent. The results indicated that Wuhan 2 has race-specific resistance to most tested *Pst* races.

Table 3 Mingxian 169/Wuhan 2 F_2 plants and $F_{2:3}$ lines segregation for seedling resistance to races CYR30 and CYR31of *Puccinia striiformis* f. sp. *tritici*

CYR30	CYR31			Total
IT of F_2	No. of $F_{2:3}$ lines			
	Resistance	Segregating	Susceptible	
1	0	0	0	0
2	13	0	0	13
3	17	8	0	25
4	2	2	1	5
5	6	11	0	17
6	0	15	1	16
7	2	37	2	41
8	0	18	22	40
9	0	6	16	22
Total	40	97	42	179

Inheritance of stripe rust resistance in Wuhan 2 investigated on the 179 F_2 plants

Of the 179 F_2 plants from cross M169/Wuhan 2 were tested with CYR30 at seedling stage in the greenhouse as mentioned in above. The numbers of F_2 plants and $F_{2:3}$ lines with different infection types or categories are presented in Table 3. The 179 F_2 plants segregated in 43 resistant (IT 1–4) and 136 susceptible (IT 5–9) ones, fitting a 1:3 ratio ($\chi^2 = 0.3$, $P = 0.53$), suggesting that Wuhan 2 has a recessive gene conferring resistance. Of the 179 $F_{2:3}$ lines, 40 were homozygous resistant, 97 segregated and 42 were homozygous susceptible, fitting a 1:2:1 ratio ($\chi^2 = 1.3$, $P = 0.52$), confirming one gene for resistance. Almost all $F_{2:3}$ lines derived from resistant F_2 plants were homozygous resistant and most $F_{2:3}$ lines from F_2 plants with intermediate (IT 5–6) or susceptible (IT 7–9) reactions segregated (Table 3). Both the F_2 and $F_{2:3}$ phenotypes indicate a recessive gene, which is temporarily designated as *Yrwh2*, for resistance to both races CYR30 and CYR31.

Mapping of the all-stage resistance gene

A total of 205 RGA primer pairs were screened on the parents and bulks. Five primer pairs produced strong and repeatable bands which appeared to be associated with the resistance gene locus in the bulked segregant analysis. When the five RGAP markers (*Xwgp5475*, *Xwgp6670*, *Xwgp5467*, *Xwgp5672* and *Xwgp5759*) were used to genotype the 179 F_2 plants, they were found to be linked to the resistance gene in Wuhan 2. *Xwgp6670* and *Xwgp5759* were co-dominant and the remaining three (*Xwgp5475*, *Xwgp5672* and *Xwgp5467*) were dominant (Table 4). To determine the chromosomal location of the resistance gene, three RGAP markers, *Xwgp5467*, *Xwgp5759* and *Xwgp6670*, which were also present in CS, were used to test the 21 CS nulli-tetrasomic lines. *Xwgp5467*, *Xwgp5759* and *Xwgp6670* amplified the target fragments of 148, 152 and 477 bp in CS (Table 4). The three markers produced the target bands in all 21 nulli-tetrasomic lines, except N3B/T3A, indicating that the resistance gene was located on chromosome 3B. As an example, marker *Xwgp5759* was shown in Fig. 1. After the resistance gene was localized on chromosome 3B using the nulli-tetrasomic CS lines tested with RGAP markers, 66 SSR markers on chromosome 3B were screened in bulk segregant analysis to enrich the marker density. Six markers showed clear polymorphisms associated to the resistance locus. Linkage analysis using the six markers tested with the 179 F_2 plants indicated that they were linked to the resistance gene locus. Of the six SSR markers, five (*Xwmc540*, *Xgwm566*, *Xwmc366*, *Xgwm376* and *Xcfd4*) were located on the short arm and one (*Xwmc182*) on the long arm of chromosome 3B. All of the markers including five RGAP and six SSR markers fit a 3:1 (for dominant markers) or 1:2:1 (for co-dominant markers) ratio with *P* values ranging from 0.36 to 0.96 (data not shown). As examples, RGAP marker *Xwgp5467* and SSR marker *Xwmc366* are shown in Fig. 2. Using these markers, a linkage group spanning 122.34 cM was constructed around the resistance gene locus (Fig. 3a). The gene was mapped on the short arm of chromosome 3B, flanked by SSR markers *Xwmc540* and *Xgwm566* at distances of 5.9 and 10.0 cM, respectively (Fig. 3a).

Discussion

In this study, we identified a gene conferring all-stage race-specific resistance to stripe rust and mapped it to the short arm of chromosome 3B in Wuhan 2. The order of six linked SSR markers was the same as in the previously published wheat chromosome 3B consensus map (Somers et al. 2004; http://wheat.pw.usda.gov).

Table 4 Resistance gene analog polymorphism (RGAP) and simple sequence repeat (SSR) markers linked to the stripe rust resistance locus and their primer pairs, size, presence (+) and absence (−) in Wuhan 2, Mingxian169 (M169) and Chinese Spring (CS) and marker heredity bands (HetBand)

Marker	Primer pair	Size (bp)[a]	Presence (+)/absence (−)[b]			HetBand
			Wuhan 2	M169	CS	
RGAP						
Xwgp5475	Yr10_P-loop_F/Lr35_GLPL_revcom	425	425	–	–	Dominant
Xwgp6670	Lr10_NBS-B_revcom/Mla1_NBS-B_revcom	475/477	475	477	477	Co-dominant
Xwgp5759	Mla1_P-looP_F/Lr10_Kin2_revcom	150/152	150	152	152	Co-dominant
Xwgp5672	Lr1_P-loop_F/Lr10_GLPL_revcom	165	165	–	–	Dominant
Xwgp5467	Yr10_P-loop_F/Pm3b_NBS-B_revcom	148	148	–	148	Dominant
SSR						
Xwmc540	WMC540	260	260	–	NT	Dominant
Xgwm376	GWM376	160/165	160	165	NT	Co-dominant
Xcfd4	CFD4	582/590	582	590	NT	Co-dominant
Xwmc182	WMC182	335/337	335	337	NT	Co-dominant
Xwmc366	WMC366	114/112	114	112	NT	Co-dominant
Xgwm566	GWM566	145/147	145	147	NT	Co-dominant

NT not tested

[a] Fragment sizes were visually estimated based on the 100-bp DNA ladder

[b] Dominant (+, −) markers with or without the polymorphism bands in the resistant parent Wuhan 2, the susceptible parent M169 and Chinese Spring (CS)

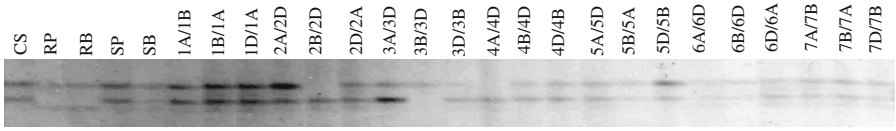

Fig. 1 Polyacrylamide gels showing resistance gene analog polymorphism (RGAP) marker *Xwgp5759* amplified in the resistance parent (RP, Wuhan 2), resistant bulk (RB), susceptible bulk (SB), susceptible parent (SP, M169) of cross M169/Wuhan 2; Chinese Spring (CS); and 21 CS nulli-tetrasomic lines

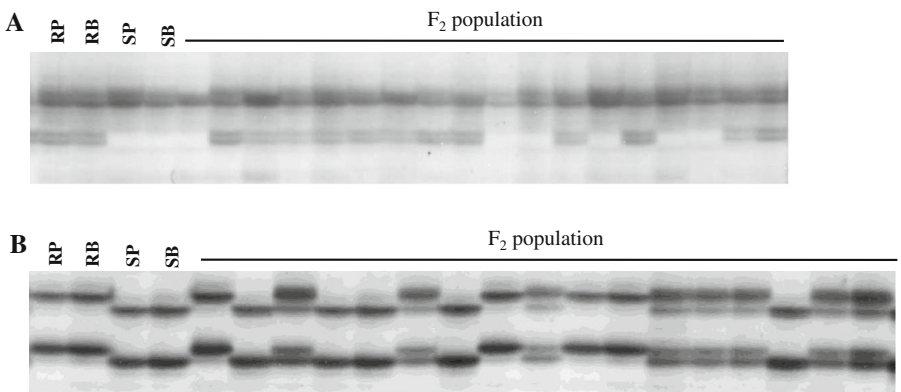

Fig. 2 Silver stained polyacrylamide gels showing resistance gene analog polymorphism (RGAP) marker *Xwgp5467* (**a**) and simple sequence repeat (SSR) marker *Xwmc366* (**b**) flanking the *Yrwh2* locus. *RP* resistance parent Wuhan 2, *SP* susceptible parent Mingxian 169 (M169), *RB* resistant bulk and *SB* susceptible bulk

Several genes for adult-plant or high-temperature adult-plant (HTAP) resistance to stripe rust were previously mapped to the short arm of chromosome 3B in other wheat genotypes. Börner et al. (2000) reported *Yrns-B1* on 3BS determining non-race specific adult-plant resistance against stripe rust, and

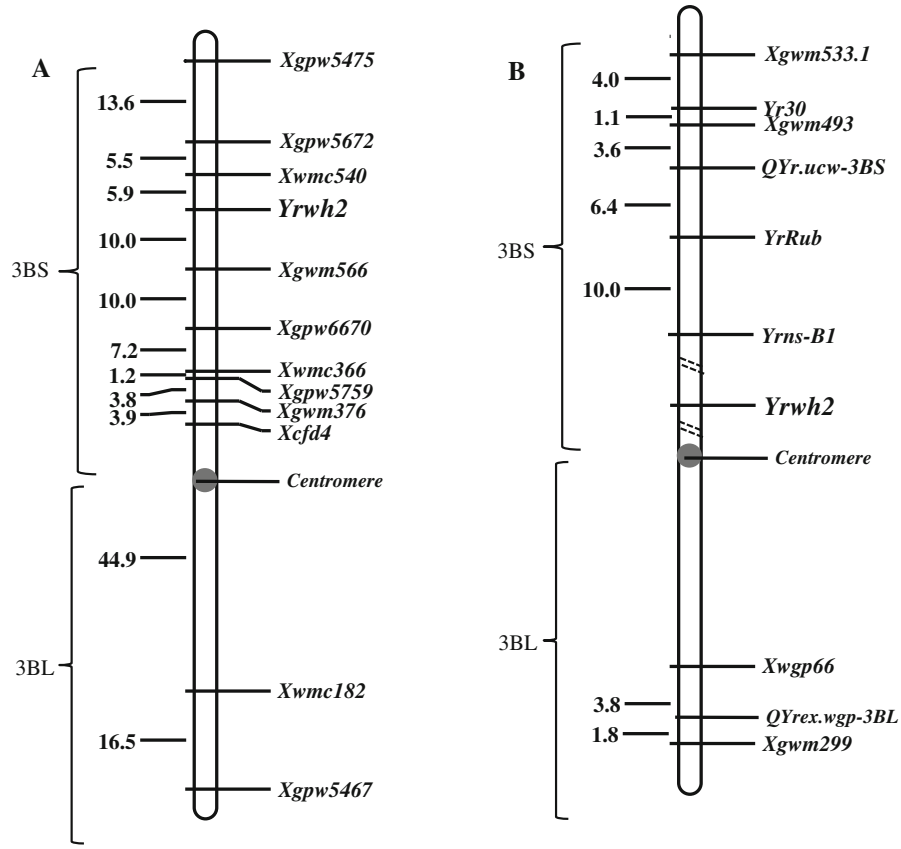

Fig. 3 Genetic map showing the location of the *Yrwh2* locus on the short arm of wheat chromosome 3B based on 179 F_2 plants with their phenotypes confirmed and genotypes determined by the single-seed descent $F_{2:3}$ lines of cross M169/Wuhan 2 (**a**). The location of *Yrwh2* in relation to previously identified genes on chromosome 3B based on molecular markers (**b**). References: *Yrns-B1* (Börner et al. 2000), *Yr30* (Suenaga et al. 2003), *YrRub* (Bansal et al. 2010), *QYr.ucw-3BS* (Loweet et al. 2011), and *QYrex.wgp-3BL* (Lin and Chen 2009)

marker *Xgwm533.1* was linked to *Yrns-B1*. *Yr30* confers adult-plant resistance to stripe rust (McIntosh et al. 2001). In contrast, *Yrwh2* confers all-stage resistance. *Sr2*, a slow-rusting stem rust resistance gene associated with *Yr30*, was completely linked to *Xgwm533.1* (Singh et al. 2000). *Yr30* was closely linked to *Xgwm389* and *Xgwm533.1* (Suenaga et al. 2003), but these markers were not polymorphic in the mapping population in the present study. A QTL for stripe rust resistance in cultivar Rubric (*YrRub*) was mapped to the distal region of chromosome 3BS (Bansal et al. 2010). However, *YrRub* was mapped 10.1 ± 4.2 cM distal of *Xgwm533.1*, and the distance suggests that the location of *YrRub* is outside of the *Yrwh2* region described in the present study. Lowe et al. (2011) reported *QYr.ucw-3BS* on chromosome 3BS. It was mapped 3.6 cM distal of *Xgwm493* (Fig. 3b). In our study, we could not determine the distance between *Yrwh2* and *Xgwm493* as the marker was not polymorphic. Lin and Chen (2009) detected a QTL on 3BL (*QYrex.wgp-3BL*) for HTAP resistance to stripe rust in spring wheat cultivar Express. *Yrwh2* and *QYrex.wgp-3BL* should be different because they confer different types of resistance and are located on different arms of chromosome 3B. *QYrex.wgp-3BL* was located between *Xgwm299* and *Xwgp66* (Fig. 3b), while *Yrwh2* was not linked with these markers. Therefore, *Yrwh2* is likely different from all previously reported genes for resistance to stripe rust in wheat genotypes. However, the genetic distances of *Yrwh2* with these genes on chromosome 3BS need further studies.

In the year 2000, stripe rust occurred at an epidemic level in China, mainly by races CYR32 and CYR33, which are virulent on most previously reported resistance genes (Xia et al. 2007; Chen et al. 2009). Among officially named *Yr* genes, only a small number of genes (e.g. *Yr5*, *Yr10*, and *Yr15*) provide effective resistance in China (Yang et al. 2003; Han et al. 2010; Zhan et al. 2012). Because *Yr24*/*Yr26*, which are now considered to be the same gene, are effective against CYR32, CYR33 and against those identified before the two races, the gene has been widely used in breeding programs in China and as a

result, many Chinese wheat cultivars carry *Yr24*/*Yr26* (He et al. 2011; Zhang et al. 2013). Since 2008, wheat cultivars Chuanmai 42 that carry *Yr26* have become susceptible due to the appearance of a new *Pst* race PST-CH42 (or PST-V26). This race would likely overcome resistance in many cultivars with *Yr26*. Therefore, any genes conferring resistance to PST-CH42 will be useful. In the present study, we identified a gene, *Yrwh2*, effective against this new race.

Although the gene *Yrwh2* in Wuhan 2 is ineffective against races CYR29 and CYR32, it is effective against the currently most predominant race, CYR33 and the new emerging race, PST-CH42. Therefore, *Yrwh2* should be used in combination with genes effective against CYR29 and CYR32, or more preferably with genes effective against all races or genes for non-race specific resistance. The closely linked molecular markers can be used in marker-assisted selection for pyramiding genes for resistance to stripe rust in wheat breeding programs. Because of its race-specificity, *Yrwh2* should be useful also in monitoring different races of the stripe rust pathogen.

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