Theor Appl Genet (2011) 123:431–438
DOI 10.1007/s00122-011-1595-7

ORIGINAL PAPER

Genetics and molecular mapping of genes for high-temperature resistance to stripe rust in wheat cultivar Xiaoyan 54

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Received: 19 December 2010 / Accepted: 6 April 2011 / Published online: 23 April 2011
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Abstract Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is one of the most widespread and destructive wheat diseases worldwide. Growing resistant cultivars is the preferred means of control of the disease. The winter wheat cultivar Xiaoyan 54 has high-temperature resistance to stripe rust. To identify genes for stripe rust resistance, Xiaoyan 54 was crossed with Mingxian 169, a winter wheat genotype susceptible to all Chinese races of the pathogen. Seedlings and adult plants of the parents and F_1, F_2, F_3 and F_4 progeny were tested with Chinese race CYR32 under controlled greenhouse conditions and in the field. Xiaoyan 54 has two recessive resistance genes, designated as *Yrxy1* and *Yrxy2*, conferring high-temperature resistance. Simple sequence repeat (SSR) primers were used to identify molecular markers flanking *Yrxy2* using 181 plants from one segregating F_3 line. A total of nine markers, two of which flanked the locus at genetic distances of 4.0 and 6.4 cM on the long arm of chromosome 2A were identified. Resistance gene analog polymorphism (RGAP) and SSR techniques were used to identify molecular markers linked to *Yrxy1*. A linkage group of nine RGAP and two SSR markers was constructed for *Yrxy1* using 177 plants of another segregating F_3 line. Two RGAP markers were closely linked to the locus with genetic distances of 2.3 and 3.5 cM. Amplification of a set of nullitetrasomic Chinese Spring lines with RGAP markers *M8* and *M9* and the two SSR markers located *Yrxy1* on the short arm of chromosome 7A. The SSR markers *Xbarc49* and *Xwmc422* were 15.8 and 26.1 cM, respectively, from the gene. The closely linked molecular markers should be useful for incorporating the resistance genes into commercial cultivars and combining them with other genes for stripe rust resistance.

Communicated by J. Snape.

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Introduction

Stripe rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Eriks., is a major disease of wheat worldwide, especially in China (Li and Zeng 2000; Lin and Li 1990; Wan et al. 2004). China represents the largest stripe rust epidemiologic region in the world in terms of wheat area affected by the disease, which is particularly destructive to autumn-sown wheat in the northwest and southwest of the country (Zeng 1979; Li 1980; Li et al. 1984; Stubbs 1988; Li and Zeng 2000; Wan et al. 2004). Destructive epidemics of stripe rust in China occurred in 1950, 1964, 1990 and 2002, causing yield losses of 6.0, 3.2, 1.8 and 1.3 million tonnes, respectively (Li and Zeng 2000; Wan et al. 2004). The most recent country-wide epidemic in 2002 was caused by race CYR32, first identified in 1994 (Wan et al. 2004).

The most effective, economic and environmentally friendly control of stripe rust is achieved by resistant cultivars. Seedling or all-stage resistance and adult-plant resistance, including high-temperature adult-plant (HTAP) resistance, are commonly distinguished types of resistance to stripe rust. Seedling resistance detected at the seedling

stage usually remains effective at all stages of plant growth. It is generally race specific, qualitatively inherited, and follows the gene-for-gene interaction model (Flor 1971). Because of specificity and selection most such genes are currently ineffective in China and elsewhere (Chen et al. 2002; Chen and Moore 2002; Chen 2005; Lin and Chen 2007).

In contrast, high-temperature adult-plant (HTAP) resistance, which expresses at later stages of plant development when the weather is warm, is non-race specific and durable (Qayoum and Line 1985; Chen and Line 1995a, b; Line and Chen 1995; Line 2002; Imtiaz et al. 2004; Chen 2005). Plants with only high-temperature adult-plant (HTAP) resistance are susceptible at the seedling stage at both low and high temperatures and at low temperatures at adult-plant stages of growth (Qayoum and Line 1985).

Many wheat cultivars grown in China have seedling resistance to one or more races of the stripe rust pathogen (Shang et al. 1997; Shang 1998). Another class of temperature-sensitive resistance is high-temperature resistance that is effective at the seeding stage when temperatures are higher than 18°C (Shang 1998; Wang and Shang 1996). Plants with this type of resistance are susceptible when temperatures are below 18°C. Xiaoyan 54, a winter wheat cultivar with good bread-making quality, was developed by Prof. Zhensheng Li from Xiaoyan 6 {St2422/464/Xiaoyan 96 [Fengchan No.1/ Selection 5 (Zhongnong 28/*Elytrigia elongata*//Xinong 6028//Fengshou, Biyumai]}. It has remained resistant to stripe rust since its release in 1996 (Wang et al. 2006; http://www2.cas.cn/html/Dir/2001/10/18/1937.htm).

The objectives of this study were to (1) characterize the seedling and adult-plant responses of Xiaoyan 54 to stripe rust at different temperatures, and (2) to map the resistance gene(s) to wheat chromosomes.

Materials and methods

Plant materials

Xiaoyan 54 was crossed with susceptible wheat genotype Mingxian 169 using the latter as the female parent. F_1, F_2, F_3 and F_4 progenies and two segregating F_3 (numbered -46 and -52) families were used in this study. Plants of the parents were used in seedling and adult-plant tests in a temperature-controlled greenhouse.

A set of 21 Chinese Spring (CS) nulli-tetrasomic lines was used to localize RGAP markers linked to resistance genes to chromosomes as previously described (Shi et al. 2001; Lin and Chen 2007, 2008). SSR markers from specific chromosomes were screened to position the markers and linked resistance loci to chromosomal regions.

Greenhouse experiments for characterizing stripe rust resistance

Seedling tests were conducted under controlled greenhouse conditions. Eight *P. striiformis* f. sp. *tritici* races (CYR29, CYR30, CYR31, CYR32, Su-4, Su-11, Su-14 and PST-127) were initially chosen to determine the reactions of Xiaoyan 54 and Mingxian 169. In the initial test, the resistant and susceptible parents were evaluated at both the seedling and adult-plant stages. Seedlings were grown in the greenhouse under controlled temperature, humidity and light conditions. When the first leaves were fully expanded, all seedlings were inoculated with fresh urediniospores that were increased on susceptible wheat variety Mingxian 169 using the brushing method (Li and Shang 1989). Inoculated seedlings were placed in dew chambers at 10°C for 24 h and then one set of the parents was transferred into an environmentally controlled greenhouse with a daily cycle of 16 h of light at 18°C and 8 h of darkness at 10°C for the low-temperature test, another set of parents was transferred to another greenhouse with a daily cycle of 16 h of light at 28°C and 8 h of darkness at 18°C for the high-temperature test.

For the adult-plant test, germinated seeds of Xiaoyan 54 and Mingxian 169 in Petri dishes were vernalized for 5 weeks in a 4°C refrigerator, before transplanting to pots. The conditions for growing plants before and after inoculation were as described above. One month after planting, plants of the resistant and susceptible parents at the booting to heading stages were inoculated with urediniospores mixed with talc and incubated as described above. Infection type (IT) data were recorded 18–20 days after inoculation based on a 0–4 scale, in which 0 = no visible symptoms 0; = necrotic and/or chlorotic flecks without sporulation; 0; = large chlorotic areas without sporulation; 1 = necrotic/chlorotic blotches (on seedlings) or stripes (on adult-plants), with limited sporulation; 1^+ = chlorosis and necrosis associated with limited uredinial development; 2 = moderate sporulation, with necrotic/chlorotic blotches or stripes; 2^+ = chlorosis and necrosis with abundant intermediate sporulation, 3^- = chlorosis and necrosis with increased uredinial development, 3 = abundant sporulation, with chlorotic blotches or stripes, 3^+ = occasional necrosis with abundant sporulation, and 4 = abundant sporulation without chlorosis or necrosis. Plants with ITs 0 to 2^+ were considered to be resistant and those with ITs 3^- to 4, susceptible (Li and Shang 1989).

Identification of single gene lines for resistance to stripe rust

To separate the resistance genes, homozygous resistant F_3 (-14 and -30) and their F_4 lines were inoculated at the

seedling and adult-plant stages with race CYR32 in the greenhouse in China and with race PST-127 at Washington State University. For the adult-plant test, the homozygous resistant F_3 (-14 and -30) and their F_4 lines were vernalized as described above. The conditions for growing plants before and after inoculation for the low and high-temperature tests were as described above.

Field testing of the mapping population

The field tests were conducted near Yangling, Shaanxi, China. About five seeds for F_1, 250 seeds for F_2, 20 seeds for each of 162 F_3 lines, about 200 seeds for the two segregating F_3 (-46 and -52) lines, 20 seeds for each F_4 line derived from those F_3 lines, and 20 seeds for the parents were planted in 1 m rows spaced 30 cm apart. The nursery was surrounded by Mingxian 169 as a spreader. The 162 F_3 lines were grown as three replicates. The various populations and parents were evaluated after inoculation with CYR32 at the booting stage. During the test period the average night/day temperatures in the field were 13/32°C. Following the 2007 crop season, and based on the F_3 line data two F_3 (-46 and -52) lines believed to be segregating at different single loci based on distinctive low responses and two F_3 lines (-14 and -30) believed to be homozygous resistant for those responses were chosen for further analysis. The two segregating populations and two homozygous resistant lines were evaluated at the same locations in the 2008 crop season. Infection types and rust severities were recorded at the heading-flowering, and mid-dough growth stages. During the 2009 crop season, the genotypes of the two F_3 (-46 and -52) populations were confirmed by testing their F_4 progenies. The F_4 lines were classified as homozygous resistant (showing a uniformly resistant response), segregating (with both resistant and susceptible responses) and homozygous susceptible (with a uniformly susceptible response).

DNA extraction and bulk segregant analysis

Genomic DNA was isolated from each parent and individual plants of the two selected segregating F_3 populations using the cetyltrimethyl ammonium bromide (CTAB) method (Plaschke et al. 1995). Based on phenotypic data, two sets of resistant and susceptible DNA bulks were constructed to screen for RGAP and SSR markers linked to the resistance loci. For each resistant and susceptible bulk, equal amounts of DNA from 12 resistant and 12 susceptible plants were chosen from individual plants in each segregating F_3 lines (-46 and -52). A total of 1,128 RGA primer pairs and SSR markers covering all wheat chromosomes were screened on the parents and bulks. Primer pairs generating specific bands in both Xiaoyan 54 and the resistant bulks or Mingxian 169 and the susceptible bulks were used to genotype the F_3 lines. The segregation data for RGAP and selected SSR markers together with the disease data were used to construct genetic maps.

PCR amplification, electrophoresis and silver staining

RGAP (Chen et al. 1998; Shi et al. 2001) and SSR (Röder et al. 1998) methods were followed. The 48 RGA primers used in random pairs were the same as previously described (Chen et al. 1998; Shi et al. 2001; Yan et al. 2003; Lin and Chen 2007, 2008). The SSR primers used in the study were from the GrainGenes 2.0 website (http://wheat.pw.usda.gov/cgi-bin/graingenes/browse.cgi?class=marker). PCR was performed in a PTC200 Peltier Thermo-cycler. The 15-µl reaction mixtures consisted of 30 ng of template DNA, 1.5 µl Mg-free 10× PCR buffer, 0.8 unit of *Taq* DNA polymerase, 5 mM of $MgCl_2$, 0.2 mM each of dCTP, dGTP, dTTP and dATP, and 5 µM of each primer pair. After 4 min of denaturation at 94°C, amplifications were programmed for 40 cycles each consisting of 1 min at 94°C, 1 min at 45, 50, 55 or 60°C (45°C for RGA primers and 50, 55 or 60°C for SSR primers depending on the individual primers), 2 min at 72°C, then followed by a 7 min extension at 72°C. After amplification, 6.5 µl of formamide loading buffer [98% formamide, 10 mM EDTA (pH 8.0), 0.5% (W/V) xylene cyanol and 0.5% (W/V) bromophenol blue] was added to the PCR products followed by 4 min denaturation at 94°C for electrophoresis in 5% polyacrylamide gels. Following electrophoresis, the gel was silver-stained, as described by Bassam et al. (1991).

Chromosomal locations of molecular markers and linked resistance genes

Chinese Spring (CS) and 21 nulli-tetrasomic (NT) derivatives (Sears 1966) were used to determine the chromosomal locations of RGAP markers linked to the stripe rust resistance genes and then SSR markers from the specific chromosomes were screened to position the markers and linked resistance loci to specific chromosomal locations (Lin and Chen 2007; Cheng and Chen 2010).

Data analyses

Chi-squared (χ^2) tests were used to analyze the goodness of fit for observed and expected segregation ratios. The "chitest" procedure in the data analysis of Microsoft Excel 2007 was used to calculate *P* values. Linkage analyses and map construction of the RGAP and SSR markers and resistance loci were performed with the computer program Mapmaker, version 2.0 (Lander et al. 1987). A logarithm of likelihood ratio of 3.0 was adopted for significance, and for

map construction recombination values were converted to map distances using the Kosambi mapping function (Kosambi 1944).

Results

Responses of seedlings and adult plants under greenhouse conditions

Under the low-temperature regime (10°C/18°C), seedlings of Xiaoyan 54 and the two selected homozygous resistant F_3 (-14 and -30) lines putatively possessing different resistance genes displayed high infection types (IT 4) (Table 1) similar to the susceptible parent, Mingxian 169, with each race. Under high-temperature conditions seedlings of Mingxian 169 were susceptible (IT 4), whereas those of Xiaoyan 54 and homozygous resistant lines produced IT 0; or IT 1, with those of CYR32 being slightly higher. The two homozygous resistant lines tested with PST-127, differed in that one had small necrotic blotches and the other had intermediate necrotic blotches and limited sporulation (Fig. 1).

Table 1 Infection types of Xiaoyan 54, Xiaoyan 6 and Mingxian 169 to eight prevalent *P. striiformis tritici* races at the seedling and adult-plant stages

Race	Cultivar	Seedling		Adult	
		Low temp[a]	High temp[b]	Low temp	High temp
CYR29	Xiaoyan 54	3	0;	3	0;
	Xiaoyan 6	3	0;	3	0;
	Chinese 166	4	4	4	3
	Mingxian 169	4	4	4	4
	F_3 line-14	4	0;	3	0;
	F_3 line-30	4	0;	3	0;
CYR32	Xiaoyan 54	4	1	4	1
	Xiaoyan 6	4	1	4	1
	Chinese 166	4	4	4	4
	Mingxian 169	4	4	4	4
	F_3 single line-14	4	1	3	1
	F_3 single line-30	4	1	3	1
PST-127	Xiaoyan 54	4	0;	4	0;
	Mingxian 169	4	4	4	4
	F_3 line-14	4	0;	4	0;
	F_3 line-30	4	1	4	0;

The same results as CYR29 were obtained with races CYR30, CYR31, Su-4, Su-11 and Su-14

[a] 16 h of light at 18°C and 8 h of dark at 10°C

[b] 16 h of light at 28°C and 8 h of dark at 18°C

Adult-plant tests under low-temperature conditions gave results similar to those obtained with seedlings. Inoculated under high-temperature conditions, Xiaoyan 54 was resistant (IT0; or IT1) to all eight races. Mingxian 169 had similar susceptible infection types (IT 4) under both conditions (Table 1; Fig. 1).

Genetic analysis of stripe rust resistance in Xiaoyan 54

In the field test with race CYR32, Xiaoyan 54 was resistant (IT 1), whereas Mingxian 169 was susceptible (IT 4). Five F_1 plants were susceptible (IT 3–4), and the F_2 population segregated in a 7R:9S ratio (Table 2) indicative of segregation of two independent recessive genes for resistance. The 162 F_3 lines segregated 7 homozygous resistant:8 segregating:1 homozygous susceptible (Table 2) confirming the two-gene segregation hypothesis. Progenies of lines -46 and -52 that segregated 1:3 in F_3, segregated in 1:2:1 ratios as F_4 lines supporting the single gene hypotheses (Table 2). The gene in segregating line -46 and probably homozygous line line -30 was tentatively designated *Yrxy1* and that in segregating line -52 and homozygous line -14 was designated *Yrxy2*.

Identification of molecular markers and mapping of the high-temperature resistance genes

Eight RGA primer pairs were selected to test all plants in family F_{3-46}. Of the nine RGAP markers, *M8* and *M9* were co-dominant and the others were dominant. *M1* and *M2* co-segregated with the resistance locus. Four polymorphic markers (*M2, M4, M5 and M6*) were present in the susceptible parent and susceptible bulk but not in the resistant parent and resistant bulk, and three markers *M1, M3,* and *M7* were present in the resistant parent and resistant bulk but not in the susceptible parent and susceptible bulk (Table 3).

Nulli-tetrasomic lines representing all 21 CS chromosomes were tested with RGAP markers *M8* and *M9* to identify the chromosome on which the markers are located. Marker *M8* gave a 260 bp fragment in Mingxian 169 and CS, whereas marker *M9* amplified a 184 bp fragment in Xiaoyan 54 and CS and none in Mingxian 169. All nulli-tetrasomic lines, except N7AT7B, showed the expected bands, indicating that both markers were located on chromosome 7A. SSR primers for loci on chromosome 7A were screened to confirm the chromosome location and determine the specific region. According to the wheat SSR consensus map (http://wheat.pw.usda.gov/cgi-bin/graingenes/browse.cgi?class=marker) both *Xgwm49* (168 bp) and *Xgwm422* (172 bp) are located on 7AS, thus suggesting that the resistance gene was on the short arm. All markers, including nine RGAP markers, segregated in 1:3

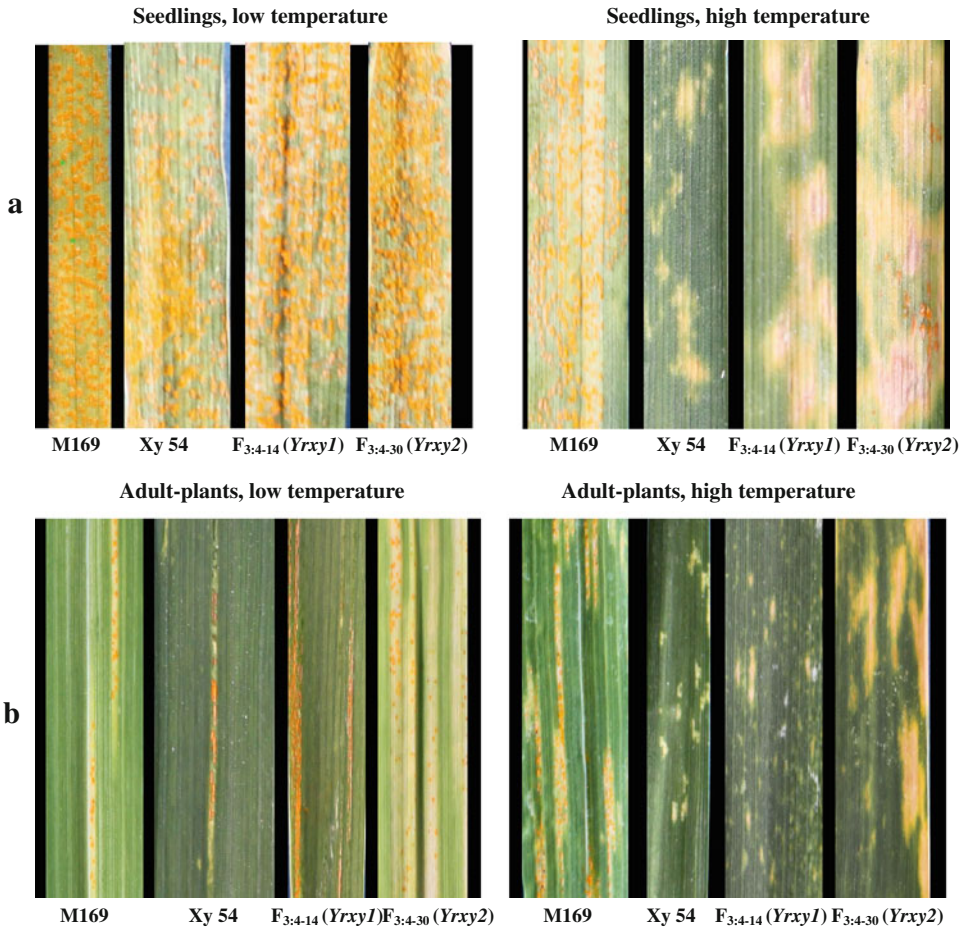

Fig. 1 Mingxian 169, Xiaoyan 54, and lines -30 (*Yrxy1*) and -14 (*Yrxy2*) single gene line are compared at the seedling (**a**) and adult-plant stages (**b**) under contrasting temperature conditions after inoculation with PST-127

Table 2 Frequencies of parental and F_2 plants, and, F_3 and F_4 lines from cross Mingxian 169/Xiaoyan 54 in response categories when tested with race CYR32 in the field

Parents and cross	Generation	Observed number of plants or lines[a]			Expected ratio (R:S)	No. of genes	χ^2 value	*P* value
		Res.	Seg.	Sus.				
Mingxian 169	P_1		–	20	–	–	–	–
Xiaoyan 54	P_2	20	–		–	–	–	–
Mingxian 169/Xiaoyan 54	F_1		–	5	–	–	–	–
	F_2	96	–	131	7:9	2	0.14	0.66
	F_3	68	81	13	7:8:1	2	0.93	0.63
	F_3 Seg. line-46	41	–	136	1:3	1	0.23	0.58
	F_3 Seg. line-52	43	–	138	1:3	1	0.09	0.70
	F_4 Seg. line-46	40	91	46	1:2:1	1	0.55	0.76
	F_4 Seg. line-52	44	86	51	1:2:1	1	0.99	0.61

[a] *Res* resistant, *Seg* segregating, *Sus* susceptible. Plants with IT 0 to 2^+ were considered resistant and plants with IT 3^- to 4 were susceptible

ratios for absence:presence, indicating that they were reliable markers for constructing the linkage map (Fig. 2a). Using the closest marker (*M1: RLRR Rev/CLRR-INV1*) to check individual F_4 plants from homozygous lines $F_{3–30}$ (*Yrxy1*) and $F_{3–14}$ (*Yrxy2*), A 320 bp band was present in the resistant parent and *Yrxy1* single gene line, but not in the susceptible parent and the *Yrxy2* homozygous resistant line (Fig. 3).

SSR markers covering all wheat chromosomes were used for identifying markers associated with the stripe rust

Table 3 Resistance gene analog polymorphism (RGAP) and simple sequence repeat (SSR) markers associated with the *Yrxy1* and *Yrxy2* loci and their primer pairs, size and presence (+) or absence (−) in Chinese Spring (CS), Xiaoyan 54, the resistant bulk, Mingxian 169 and the susceptible bulk

Marker	Primer pair	Size (bp)[a]	Present(+)/absent(−)					*P* value
			CS	RP	RB	SP	SB	
M1	RLRR Rev/CLRR-INV1	320	−	+	+	−	−	0.63
M2	RLRR Rev/CLRR-INV1	190	−	−	−	+	+	0.63
M3	S1/NLRR-INV2	218	−	+	+	−	−	0.63
M4	S2-INV/RLRR Rev	145	−	−	−	+	+	0.52
M5	AS3/S2	185	−	−	−	+	+	0.52
M6	S2-INV/S2	260	−	−	−	+	+	0.18
M7	S2-INV/Ptokin4	180	−	+	+	−	−	0.52
M8	S2-INV/LM637	255/260	+	−	−	+	+	0.46
M9	S2-INV/AS3	184/180	+	+	+	−	−	0.83
Xbarc49	BARC49	168/173	ND	A	A	B	B	0.70
Xwmc422	WMC422	172/170	ND	A	A	B	B	0.83
Xcfd168	CFD168	168/163	ND	A	A	B	B	0.97
Xwmc455	WMC455	165/170	ND	A	A	B	B	0.90
Xgwm47	GWM47	148/153	ND	A	A	B	B	0.58
Xgwm294	GWM294	105/115	ND	A	A	B	B	0.70
Xwmc819	WMC819	200/205	ND	A	A	B	B	0.97
Xgwm794	GWM794	220/215	ND	A	A	B	B	0.70
Xbarc5	BARC5	248/251	ND	A	A	B	B	0.37
Xwmc372	WMC372	205/195	ND	A	A	B	B	0.52
Xgwm328	GWM328	196/200	ND	A	A	B	B	0.76

CS Chinese Spring, *RP* resistant parent Xiaoyan 54, *RB* resistant bulk, *SP* susceptible parent Mingxian 169, *SB* susceptible bulk, + present, − absent, *A* resistance bands, *B* susceptible bands, *ND* no data

[a] Sizes of all markers were estimated based on 1-kb plus DNA marker

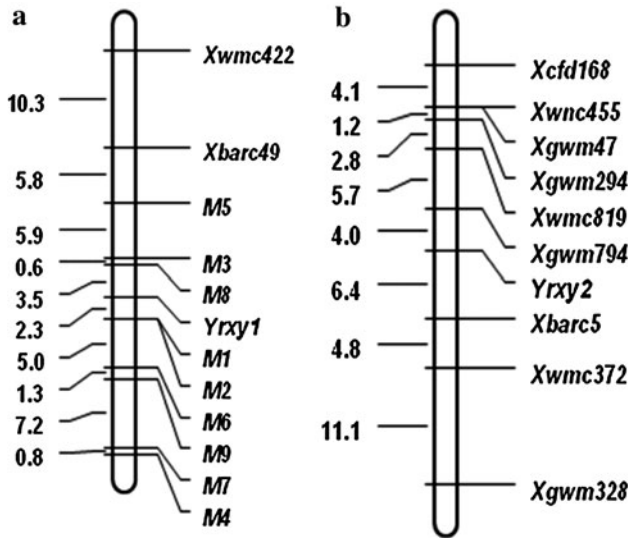

Fig. 2 Linkage maps for the recessive resistance genes *Yrxy1* on chromosome 7AS (**a**) and *Yrxy2* in chromosome 2AL (**b**). Map distances in centi-Morgans are shown on the left

resistance in Xiaoyan 54. Primer pairs showing specific bands in both Xiaoyan 54 and the resistant bulk, or Mingxian 169 and the susceptible bulk, were used to genotype 181 plants in segregating line F_{3-52}. Nine markers were polymorphic and were mapped with respect to *Yrxy2* (Table 3; Fig. 2b). The second resistance gene in Xiaoyan 54 was closely linked to SSR markers *Xgwm749* and *Xbarc5* on chromosome 2A at genetic distances of 4.0 and 6.4 cM, respectively.

Discussion

Because of its continuing effectiveness against all Chinese *P. striiformis tritici* races, the high-temperature resistance in Xiaoyan 54 may be useful for sustainable control of stripe rust. We report here the characterization of two high-temperature resistance genes for both seedling and adult plant resistance in Chinese cultivar Xiaoyan 54, a cultivar that has remained resistant under field conditions for more than 14 years.

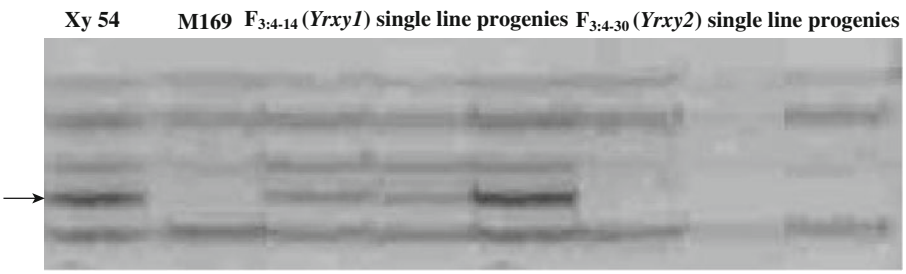

Fig. 3 The closest marker (*M1: RLRR Rev/CLRR-INV1*) to (320 bp) was present in the resistant parent and all F_4 plants of homozygous line -30 (*Yrxy1*) (indicated by an *arrow*), but not in those of line -14 (*Yrxy2*)

One gene in Xiaoyan 54 was mapped on the short arm chromosome 7A. Since no formally named stripe rust resistance gene was previously mapped to chromosome 7AS this gene in F_3 families –30 and –46 is likely to be located at a unique locus. It was temporarily designated as *Yrxy1*.

The second gene in families -14 and -52, designated *Yrxy2*, was mapped to chromosome 2AL. There are three named *Yr* genes on chromosome 2A: *Yr17* (Bariana and McIntosh 1993) is on chromosome 2AS, and *Yr32* (Eriksen et al. 2004) and *Yr1* are on 2AL (Bariana and McIntosh 1993). Because the *Yr1* carrier Chinese 166 was fully susceptible to all races used in the present study, and *Yr1* and *Yr32* (Carstens V) are conventionally identified seedling resistance genes rather than high-temperature resistance genes, the gene we identified on chromosome 2AL in Xiaoyan 54 should be different but its position relative to the *Yr1* and *Yr32* loci is yet to be determined.

The resistance genes *Yrxy1* and *Yrxy2* representing a new category of temperature-sensitive resistance genes, showed consistent responses in the field at different locations and years. Xiaoyan 54 has conferred seedling and adult-plant stage resistance under both high-temperature greenhouse testing regimes and under field conditions since it was released in 1996. The resistances of the parent line, and F_3 line -14 and -30 and their F_4 homozygous resistant lines under field conditions (13–32°C) were genetically correlated with results obtained under controlled high-temperature conditions.

In summary, we identified recessive genes *Yrxy1* and *Yrxy2* in wheat cultivar Xiaoyan 54 and mapped them on chromosomes 7AS and 2AL, respectively. *Yrxy1* is more effective than *Yrxy2*. Because of long-term effectiveness, the resistance of Xiaoyan 54 is a valuable source of resistance for use in breeding. The molecular markers closely linked to each gene should be useful in marker-assisted selection for incorporating the genes into new wheat varieties or for pyramiding them with other effective *Yr* genes to develop varieties with durable resistance to stripe rust.

Acknowledgments The authors are grateful to Dr. Xianming Chen and Dr. R.A. McIntosh for editorial review of manuscript and suggestions for its improvement. The financial support of projects "Introducing Talents of the Disciplinary Innovation Program (No. B07049)", "National Eleventh Five Year Plan Key Project" (2006BAD08A05) and "Toxicity Variation of Wheat Stripe Rust Pathogen and Demonstration of Integrated Management of Stripe Rust" (No. 200903035-02) are thankfully acknowledged.

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