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Mapping stripe rust resistance gene *YrSph* derived from *Tritium sphaerococcum* Perc. with SSR, SRAP, and TRAP markers

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Abstract Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is one of the most devastating foliar diseases of common wheat (*Triticum aestivum* L.) worldwide. Growing resistant cultivars is the most effective approach to control the disease. To determine inheritance of stripe rust resistance and map the resistance gene in a common wheat line D31, developed from *Triticum sphaerococcum* Perc. (accession number AS348), F_1, F_2, and BC_1 progenies derived from the Taichung 29 × D31 cross were firstly inoculated with Chinese PST race CYR32 during whole growth stages under the field conditions. Genetic analysis indicated that the resistance to CYR32 in the line D31 was conferred by one recessive gene, temporarily designated as *YrSph*. A total of 400 simple sequence repeat (SSR), 315 pairs of sequence-related amplified polymorphism and 42 pairs of target region amplified polymorphism markers were screened, and four SSR markers and three TRAP markers were found to be polymorphic between the resistant and susceptible DNA bulks as well as their parents. Genetic linkage was tested on segregating F_2 population and indicated that all of the ten markers were linked to the resistance gene, two of which flanked the locus at 8.5 and 6.9 cM, respectively. The SSR markers mapped the resistance gene on chromosome arm 2AS. The results of chromosome location and pedigree analysis indicate that *YrSph* was probably a novel stripe rust resistance gene.

Keywords *Triticum sphaerococcum* Perc. · *Puccinia striiformis* · Resistant gene · Simple sequence repeat (SSR) · Sequence-related amplified polymorphism (SRAP) · Target region amplified polymorphism (TRAP)

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Introduction

Stripe (yellow) rust, caused by *Puccinia striiformis* f. sp. *tritici* Eriks., is one of the most damaging diseases of common wheat (*Triticum aestivum* L.) worldwide, especially in many cool and moist environments (Stubbs 1985; Wellings and McIntosh 1990; Wellings

et al. 2003; McIntosh and Brown 1997; Chen 2005, 2007). So far, breeding and release of resistant cultivars has been the most effective and economical approach to control the disease. Currently, more than 49 officially named *Yr* genes at 49 loci (*Yr1–Yr49*) and many temporarily designated genes have been reported (McIntosh et al. 2003, 2007; Herrera-Foessel et al. 2011; Lagudah 2011). The varietal resistances, however, are usually short-lived because of rapid virulence changes in pathogen populations. In China, especially southwest China, stripe rust is one of the most destructive diseases of wheat (Li and Liu 1957; Li et al. 1984; Li and Zeng 2000; Wan et al. 2004) and has been considered the most important disease of wheat since the first major epidemic in 1950. China also has the largest epidemic region in the world (Stubbs 1988). More unfortunately, the recent appearance and spread of new stripe rust races CYR31, CYR32, and CYR33 have caused breakdown of numerous formerly resistant sources of stripe rust resistance or *Yr* genes, studies have shown that *Yr5*, *Yr10*, *Yr11*, *Yr12*, *Yr13*, *Yr14*, *Yr15*, *Yr24*, *Yr26*, *YrZH84*, and some other genes are still effective while *Yr1*, *Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, and certain other genes have lost their effectiveness (Wan et al. 2007). Therefore, exploring new and effective stripe rust resistance genes and transferring to the existing cultivars has become an important task for the breeding wheat with stripe rust resistance (Yang et al. 1994; McIntosh and Brown 1997).

Molecular marker, including random amplified polymorphic DNA (RAPD), restriction fragment length polymorphism (RFLP), amplified restriction fragment polymorphism (AFLP), simple sequence repeat (SSR), and resistance gene analog polymorphism (RGAP), have been widely used for tagging resistance genes to stripe rust in wheat during the past years (Sun et al. 1997; Chague et al. 1999; Peng et al. 1999; Robert et al. 1999; Ma et al. 2001; Shi et al. 2001; Sun et al. 2002; Wang et al. 2002; Suenaga et al. 2003; Yan et al. 2003; Eriksen et al. 2004; Luo et al. 2005; Bariana et al. 2006; Chicaiza et al. 2006; Lin and Chen 2007; McIntosh et al. 2010). Sequence-related amplified polymorphism (SRAP) markers, which are PCR-based markers that amplify open reading frames and produce a number of co-dominant markers per amplification, were recently developed as a useful molecular marker system (Li and Quiros 2001). SRAP markers are more consistent and repeatable than RAPDs, and are less labor-intensive and time-consuming to produce than AFLP techniques (Welsh and McClelland 1990; Li and Quiros 2001; Ferriol et al. 2003; Budak et al. 2004; Gulsen et al. 2005). It is easily adapted to efficiently perform high throughput data collection from thousands or even millions of individuals, which is critical to any large-scale plant breeding program. It has been successfully applied in several species for different purposes (Budak et al. 2004; Ferriol et al. 2003; Sun et al. 2007; Rahman et al. 2007; Li et al. 2010). The other useful PCR-based markers technique namely, target region amplification polymorphism (TRAP) which amplify intragenic polymorphism has been reported by Hu and Vick (2003). TRAPs are amplified by a forward or fixed primer using gene/EST sequence information in the database and a reverse or arbitrary primer that is similar to that of a SRAP primer except for AT- or GC-rich cores that anneal with introns and exons, respectively. TRAPs were effectively used in assessing genetic diversity among wild sunflower (*Helianthus annuus* L.) and spinach (*Spinacia oleracea* L.) (Hu et al. 2003; 2007), genetic fingerprinting of lettuce (*Lactuca sativa* L.) (Hu et al. 2005), tagging gene in sunflower (Rojas-Barros et al. 2005), and constructing genetic linkage maps in wheat, common bean (*Phaseolus vulgaris* L.), cultivated sugarcane (*Saccharum officinarum* L.) (Liu et al. 2005; Miklas et al. 2006; Alwala et al. 2008).

Triticum sphaerococcum Perc. ($2n = 6x = 42$, AABBDD), including 17 varieties, is a member of the primary gene pool and mainly distributed into the northwestern of India with dry and hot climate (Dong 1982). Lan et al. (2003) demonstrated that *T. sphaerococcum* (accession number AS348) were highly resistant in both seedling and adult-plant stages to stripe rust races prevalent (including CYR32) in the field of China. Wheat new line D31, derived from the cross between AS348 and a susceptible line 94-3854, also is an excellent resistance to stripe rust race CYR32 (which is currently prevalent in China) in the field. The objective of the present study was to identify the stripe rust resistance gene in D31 and map the gene using molecular markers.

Materials and methods

Wheat materials

An F_2 population with 144 plants and 43 BC_1 plants, derived from the cross between a resistant wheat line

D31 and a susceptible variety Taichung 29, were used for the mapping of stripe rust resistance gene. D31, a new wheat line and highly resistant to a mixture of predominant Chinese PST races (including CYR31, CYR32, and CYR33) at both the seedling and adult stages under field conditions, was developed from the cross AS348/2/94-3854 by Triticeae Research Institute, Sichuan Agricultural University. Furthermore, *T. sphaerococcum* accession number AS348 and wheat line 94-3854, the parents of wheat line D31, were used for comparing the responses to confer the sources pedigree of the resistance gene.

Evaluations for stripe rust resistance

The parents and genetic populations were inoculated in the field with PST isolate CYR32, which provided by the Plant Protection Institute of Gansu Academy of Agricultural Sciences, Gansu, China. The spreader rows (SY95-71, a susceptible line, was used as check in the field) were artificially inoculated in the seedling of the two-leaf stage. To ensure precision of stripe rust resistance, we follow-up investigated rust responses of per plant from the seedling to the adult-plant stages. At last, when rust was fully developed on the susceptible check, SY95-71, infection types (IT) were scored based on a scale of 0, 0;, 1, 2, 3, and 4, where 0 = immunity, 0; = necrotic flecks, and 1–4 = highly resistant, resistant, susceptible, and highly susceptible, respectively (Liu 1988).

Molecular markers analyzes

Genomic DNA of individual plant was extracted from the third or fourth healthy leaf using cetyltrimethylammonium bromide (CTAB) method as essentially described by Saghai et al. (1984). Resistant and susceptible bulks comprising equal amounts of DNA from ten resistant and ten susceptible F_2 plants, respectively, were used for bulked segregant analysis (Michelmore et al. 1991). The primers sequences of 400 SSR markers were obtained from grain genes (website) and published by Röder et al. (1998) and Pestsova et al. (2000). A total of 315 primer combinations (15 forward primers in combination with 21 reverse primers) of SRAP reported by Li et al. (2010), and 42 primer combinations (six fixed primers in combination with seven arbitrary primers) of TRAP reported by Hu and Vick (2003), were synthesized. All of the SSR, SRAP and TRAP primers were screened on the two parents and the resistant and susceptible bulks. The candidate markers subsequently identified in DNA of each of the F_2 population.

Statistical analyzes and genetic mapping

Chi-squared (χ^2) analyzes were performed to check goodness of fit of observed segregations for stripe rust response with the expected ratios. Linkage between DNA markers and the resistance gene was established with MAPMARKER/EXP 3.0b (Lander et al. 1987). Markers were placed with a LOD threshold of 3.0 and a maximum distance of 30 cM. The Kosambi function was applied to convert recombination fractions into map distances (Kosambi 1944). The genetic map was drawn with the software Mapdraw V2.1 (Liu and Meng 2003).

Results

Inheritance of stripe rust resistance in D31

At both seedling and adult-plant stages, D31 and AS348 showed highly resistant reaction (IT 0;) against CYR32, whereas 94-3854 and Taichung 29 were susceptible (IT 3–4) by follow-up investigating rust responses of per plant. When the F_1, F_2, and BC_1 progenies of Taichung 29/D31 were tested with CYR32, all 15 F_1 plants were susceptible (IT 3–4). The 144 F_2 plants segregated into 38 resistant (IT 0–2) and 106 susceptible (IT 3–4), which conformed to 1R:3S segregation ratio ($\chi^2 = 0.148$, 1 *df*, $P \geq 0.05$). Moreover, the BC_1 population (backcross with D31) segregated into 20 resistant (IT 0–0;) and 23 susceptible (IT 3–4), which is shown to 1R:1S segregation ratio ($\chi^2 = 0.093$, 1 *df*, $P \geq 0.05$). Comprehensive analyzes above data suggested that the stripe rust resistant in D31 derived from *T. sphaerococcum* Perc. (accession number AS348), and was conferred by a single recessive gene, tentatively designated *YrSph* (Table 1).

Linkage analysis and genetic map

Bulked segregant analysis was used to identify SSR markers linking to the gene *YrSph*. Among screened 400 SSR markers, four SSR markers *Xwmc149*, *Xwmc246*, *Xwmc198*, and *Xgwm372* were polymorphic

Table 1 Resistance of the Taichung 29 × D31 F_1, F_2, and BC_1 population infected by PST race CYR32 at the seedling and adult stages

Parents and crosses	Generation	Infection type						Total number of plants	Expected (R:S)	χ^2 value
		0	0;	1	2	3	4			
AS348		0	11	0	0	0	0	11		
94-3854		0	0	0	0	2	12	14		
D31	P1	0	18	0	0	0	0	18		
Taichung 29	P2	0	0	0	0	0	18	18		
Taichung 29/D31	F_1	0	0	0	0	2	13	15		
Taichung 29/D31	F_2	6	6	20	6	57	49	144	1:3	0.1481[a]
Taichung 29/D31// D31	BC_1	8	12	0	0	9	14	43	1:1	0.093[b]

[a] $\chi^2_{0.05,1} = 3.84$

[b] $\chi^2_{0.01,1} = 6.33$

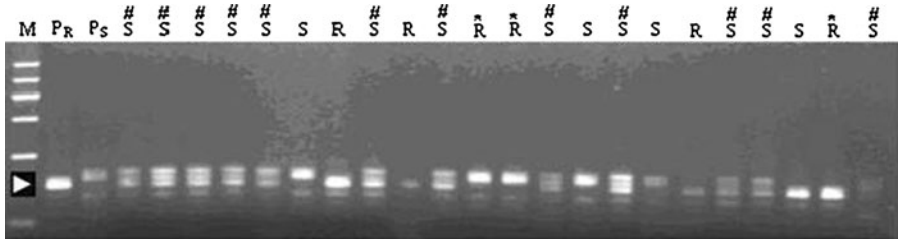

Fig. 1 Agarose gel electrophoresis detection result of microsatellite DNA products amplified by primer *Xwmc*246 among individuals of F_2. *M* marker, P_R resistance parent D31, P_S susceptible parent Taichung 29, *R* resistance individual, *S* susceptible individual, *asterisk notes* exchange between marker and agronomic trait, *pound notes* heterozygote, *arrow notes* polymorphic bands

between the resistant and susceptible DNA bulks. Subsequent linkage analysis based on the phenotype and genotype data of the 144 F_2 population plants with the four polymorphic SSR markers, indicated that the resistance gene *YrSph* was linked to the four SSR loci with genetic distances ranging from 8.5 to 38.5 cM, in which the closest flanking SSR loci was Xwm246-2AS (Figs. 1, 3). According to the SSR genetic linkage map of common wheat (Somers et al. 2004), the four SSR markers were all located on the short arm of the chromosome 2A, suggesting that *YrSph* is on the short arm of 2A. In addition, three SSR markers, *Xwmc246*, *Xwmc198*, and *Xgwm372* exhibited co-dominant inheritance and a 1:2:1 segregation ratio, whereas another SSR allele *Xwmc149* showed dominant and a 1:3 segregation ratio in the F_2 population (Table 2).

Two molecular marker techniques, SRAP and TRAP have been further used to detect molecular markers for *YrSph* to obtain more nearly direct markers. Of a total of 315 primer pairs from combinations of 15 forward and 21 reverse SRAP primers reported by Li et al. (2010), and 42 combinations of six arbitrary and seven fixed TRAP primers reported by Hu and Vick (2003), respectively, screened between the resistant and susceptible DNA bulks as well as their parents. Six primer combinations that generated strong and repeatable polymorphic bands were selected to test F_2 population plants (Fig. 2). As an example, Fig. 2 showed the banding pattern of F_2 population plants screened with SRAP primers *F-me15* and *R-me6* for marker *F-me15/R-me6*. In addition, all six markers, including three SRAP markers, *F-me15/R-me6*, *F-me14/R-me10*, and *F-me4/R-me1*, and three TRAP markers, *FIX1/Sa12-700*, *FIX5/Sa4-700*, and *FIX5/Ga5-800* exhibited dominant inheritance and a 1:3 segregation ratio in the F_2 population (Table 2). Mapmaker/EXP version 3.0b at minimum LOD of 3.0 was used for the linkage analysis. All of these six markers were linked to the resistance gene *YrSph*, in which the closest flanking marker was *F-me15/R-me6* with a genetic distance of 6.9 cM (Fig. 3).

Discussion

To date, more than 40 permanently and many temporarily designated *Yr* genes have been reported

Table 2 Genetic analysis of *YrSph* and its linked molecular markers in an F2 population of Taichung 29 × D31

Marker types	Marker	Resistant plant				Susceptible plant				Total	Expected ratio	χ^{2e}
		A[a]	H[b]	B[c]	C[d]	A[a]	H[b]	B[c]	C[d]			
Co-dominant marker	*Xwmc246*	29	9			3	67	36		144	A:H:B = 1:2:1	0.77
	Xwmc198	19	17	2		9	58	39		144	A:H:B = 1:2:1	3.16
	Xgwm372	22	16			8	57	41		144	A:H:B = 1:2:1	1.71
Dominant marker	*Xwmc149*	32			6	13			93	144	A:C = 1:3	2.36
	F-me15/R-me6	33			5	8			98	144	A:C = 1:3	0.34
	F-me14/R-me10	34			4	13			93	144	A:C = 1:3	3.00
	F-me4/R-me1	34			4	27			89	144	A:C = 1:3	21.33
	FIX1/Sa12-700	33			5	13			93	144	A:C = 1:3	1.81
	FIX5/Sa4-700	30			8	16			90	144	A:C = 1:3	2.36
	FIX5/Ga5-800	34			4	31			75	144	A:C = 1:3	27.00

[a] Homozygous in co-dominant markers or the allele in dominant markers from D31

[b] Heterozygous in co-dominant markers

[c] Homozygous allele in co-dominant markers from Taichung 29

[d] The allele in dominant markers from Taichung 29

[e] Value for significance at $P = 0.05$ is 5.99

Fig. 2 Polyacrylamide gel electrophoresis detection result of SRAP DNA products amplified by primer combinations *F-me15/R-me6* among individuals of F_2. *M* marker, P_R resistance parent D31, P_S susceptible parent Taichung 29, *Rp* resistant pool, *Sp* susceptible pool, *R* resistance individual, *S* susceptible individual, *arrow notes* polymorphic bands

(Chen 2005; McIntosh et al. 2007; Herrera-Foessel et al. 2011; Lagudah 2011). Due to the new races emerging and lacking effective resistance genes, exploring new and more effective stripe rust resistance genes has become an important task for wheat breeders and pathologists. Here we identified a stripe rust resistance gene *YrSph* in wheat line D31 and mapped it on the short arm of chromosome 2A. Classical genetic analysis showed that D31 was controlled by a single recessive gene and conferred effective all-stage resistance against Chinese PST race CYR32 and other current pathogen populations, including CYR31 and CYR33. Therefore, the *YrSph* gene should be useful for developing cultivars with stripe rust resistance. Besides *YrSph*, three other stripe rust resistance genes *Yr1*, *Yr17*, and *Yr32* have been previously located on wheat chromosome 2A as well. The *Yr1* gene was first found and named in Chinese 166, and genetic analysis showed that it was a single dominant gene (Lupton et al. 1962). The *Yr17* gene was report in VPM1 (Maia et al. 1967), which was supposed to have been introgressed from *Aegilops ventricosa* ($2n = 4x = 28$, $D^VD^VM^VM^V$) (Bariana et al. 1994) and located on the short arm of 2A using RFLP analysis (Robert et al. 1999) and displayed yellow rust resistance at the seedling stage (Bariana et al. 2006). The *Yr32* gene, originally derived from the common wheat cultivars Senat, was located on the long arm of 2A (Eriksen et al. 2004). In this study, although *YrSph* is also located on the short arm of 2A, we conclude that it is different from *Yr1*, *Yr17*, and *Yr32* from pedigree analysis and chromosome locations and maybe a novel stripe rust resistance gene.

As wheat new line D31, derived from *T. sphaerococcum* (accession number AS348), has the same genome with common wheat, it is an excellent bridge

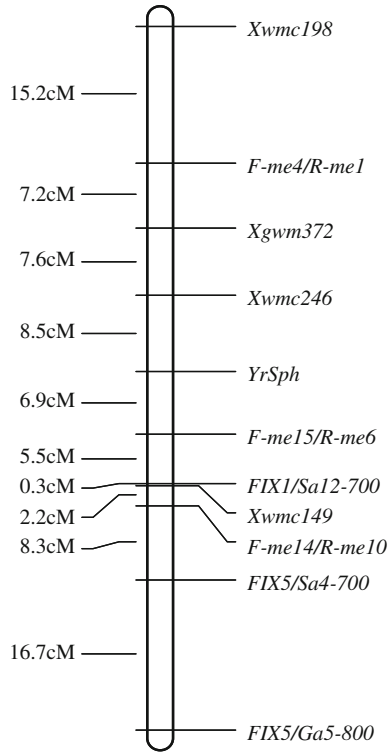

Fig. 3 A linkage map for *YrSph* on chromosome 2AS based on 144 F_2 plants from Taichung 29/D31, including four SSR markers *Xwmc149*, *Xwmc246*, *Xwmc198* and *Xgwm372*, three SRAP markers *F-me4/R-me1*, *F-me14/R-me10*, *F-me15/R-me6*, and three TRAP markers *FIX1/Sa12-700*, *FIX5/Ga5-800*, *FIX5/Sa4-700*

parent to transferring its resistance gene into different wheat cultivars. Highly resistance at both seedling and adult-plant stages to stripe rust races prevalent (including CYR32) after nearly 5 years of field test evaluation in the southwestern of China, and common wheat background makes D31 a desirable resistant donor to wheat breeding programs. Based on epidemiological considerations in China, it has been suggested that different resistance genes for controlling wheat stripe rust should be deployed in the defined over-summering, over-wintering, and eastern spring epidemic regions (Li and Zeng 2002; Wan et al. 2007). This would be best achieved by the use of resistant cultivars with multiple or different resistance genes, or effective multilines capable of reducing the build-up of inoculum. So far, growing multiple-resistance-genes cultivars by pyramiding of *YrSph* and other efficient resistance genes (including *Yr5*, *Yr10*, *Yr11*, *Yr12*, *Yr13*, *Yr14*, *Yr15*, *Yr24*, *Yr26*, *YrZH84*) in China, would promote utilization of the resistance gene. In fact, we have used D31 in breeding programs in recent years in Triticeae Research Institute, Sichuan Agricultural University by crossed or backcrossed with the main wheat cultivars (such as Chuannong 16 and Shumai 482) in Sichuan province, and obtained some resistance lines with good agronomic traits. More fortunately, we have demonstrated *YrSph* to a new gene and identified its flanking SSR and SRAP markers in this study. These results should accelerate its application in our breeding programs.

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