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RESEARCH ARTICLE

Genetic analysis and location of a resistance gene for *Puccinia striiformis* f. sp. *tritici* in wheat cultivar Zhengmai 7698

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Abstract. Wheat stripe (yellow) rust, caused by *Puccinia striiformis* West. f. sp. *tritici* (*Pst*), is one of the most destructive diseases in many wheat-growing countries, especially in China, the largest stripe rust epidemic area in the world. Growing the resistant cultivars is an effective, economic and environmentally friendly way to control this disease. Wheat cultivar Zhengmai 7698 has shown a high-level resistance to wheat stripe rust. To elucidate its genetic characteristics and location of the resistance gene, Zhengmai 7698 was crossed with susceptible variety Taichung 29 to produce F_1, F_2 and BC_1 progeny generations. The genetic analysis showed that the stripe rust resistance in Zhengmai 7698 to *Pst* predominant race CYR32 was controlled by a single-dominant gene, named *YrZM*. Bulked segregant analysis and simple sequence repeat (SSR) markers were used to map the gene. Four SSR markers, *Xbarc198*, *Xwmc179*, *Xwmc786* and *Xwmc398* on chromosome 6BL were polymorphic between the parents and resistance, and susceptible bulks. A linkage genetic map was constructed using 212 F_2 plants in the sequential order of *Xwmc398*, *Xwmc179*, *YrZM*, *Xbarc198*, *Xwmc786*. As this gene is effective against predominant race CYR32, it is useful in combination with other resistance genes for developing new wheat cultivars with resistance to stripe rust.

Keywords. genetic analysis; resistance gene; simple sequence repeat; wheat stripe (yellow) rust.

Introduction

Wheat stripe (yellow) rust is a typical air-borne disease. This disease is a serious threat to wheat production in Asia, North America, Europe and other wheat-growing areas. China is the largest epidemic region of wheat stripe rust in the world and its occurrence, and damage are especially frequent and severe (Wan *et al.* 2004). Stripe rust reduces wheat yields by damaging plants and shrinking the grain. Many severe epidemics of wheat stripe rust have occurred since 1950, including the nation-wide extremely severe epidemics in 1950, 1964, 1990 and 2002 which caused multimillion tons of yield losses in these epidemic years. Highly virulent races and widely grown susceptible cultivars were attributed to the epidemics.

Due to the appearance of new races CYR30, CYR31, CYR32 and CYR33 since 1995, many wheat cultivars of the Fan 6 derivatives, Mianyang series and Shuiyuan-derived cultivars have become susceptible. In recent years, a new group of Guinong 22-virulent races that infect wheat cultivars with *Yr24* (=*Yr26*) has been rapidly increasing in frequency and distribution. The predominant races CYR32, CYR33 and new races have accelerated the turnover frequency of wheat cultivars. This has put forward higher requirement of developing wheat cultivars with effective resistance to stripe rust in China.

The use of resistance genes against stripe rust is essential in wheat breeding programmes. Stripe rust resistance genes in wheat have been designed with the symbol '*Yr*' (Lupton and Macer 1962). Numerous genes for stripe rust resistance have been identified, including 78 *Yr* permanently named genes (McIntosh *et al.* 2017) and hundreds of temporarily named genes. Many resistance genes were identified in common wheat, while some came from wheat-related species, such as *Yr5* from *Triticum spela album* (Macer 1966); *Yr7*, *Yr53*, *Yr64* and *Yr65* from *T. durum* (Macer 1966; Xu *et al.* 2013; Cheng *et al.* 2014); *Yr9* from *Secale cereale* (Macer 1975); *Yr15*, *Yr35* and *Yr36* from

T. dicoccoides (Gerechter-Amitai *et al.* 1989; Marais *et al.* 2005a; Uauy *et al.* 2005); *Yr24* (= *Yr26*) from *T. turgidum* L. (McIntosh and Lagudah 2000; Ma *et al.* 2001); *Yr8*, *Yr17*, *Yr28*, *Yr37*, *Yr38*, *Yr40* and *Yr42* from different *Aegilops* species (Riley *et al.* 1968; Robert *et al.* 1999; Singh *et al.* 2000; Marais *et al.* 2005b, 2006; Kuraparthy *et al.* 2007; Marais *et al.* 2009) and *Yr50* from *Thinopyrum intermedium* (Liu *et al.* 2013). Most of the genes with resistance to stripe rust were on B group chromosomes. Due to quick development of new races of *Puccinia striiformis* f. sp. *tritici* (*Pst*), wheat cultivars with race-specific resistance usually become susceptible about 3–5 years after release. Currently, most reported seedling resistance genes are ineffective against race CYR32 in China (Yang *et al.* 2003). Although, a lot of efforts have been made to identify genes for resistance and develop stripe rust-resistant cultivars, it is still a great challenge to have enough wheat cultivars with effective and long-lasting resistance. Therefore, the best strategy for controlling wheat stripe rust is to introduce new resistance genes into wheat-breeding programmes, broaden the genetic basis, and develop cultivars with durable resistance and many other excellent traits.

Zhengmai 7698 with high quality and yield potential was developed by the Molecular Breeding Laboratory, Wheat Research Center, Henan Academy of Agricultural Sciences. It has been grown in more than 13 million acres since its release in 2011. The cultivar has resistance to stripe rust. The objective of this study was to identify the resistance gene(s) through genetic analysis and molecular mapping.

Materials and methods

Plant materials and Pst inoculum

Stripe rust resistant cultivar Zhengmai 7698 was developed from a cross between Zhengmai 9405 and 4B269, and then crossed with Zhoumai 16. Spring wheat Taichung 29 was susceptible to all known Chinese races of *Pst*. An F_2 population derived from crossing Zhengmai 7698 with the susceptible cultivar Taichung 29 was used for genetic analysis and molecular mapping. In addition, F_1 plants were backcrossed with Taichung 29 to develop a BC_1 population to confirm the F_2 results. A highly susceptible wheat cultivar, Mingxian 169, was used as a disease spreader in the field tests.

Single urediniospore isolates of eight *Pst* races (CYR17, CYR26, CYR27, CYR29, CYR31, CYR32, CYR33 and V26) maintained at the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, China, were used for evaluating wheat cultivars. The isolate of race CYR32, which is prevalent throughout China, and virulent on all Chinese differential cultivars except for Zhong 4 and all world differential cultivars except for Moro, was used to phenotype the segregating populations for genetic analysis and molecular mapping. Fresh urediniospores of an isolate were produced on susceptible wheat cultivar Mingxian 169.

Resistance evaluation to wheat stripe rust

Seedlings of Zhengmai 7698 were grown in a greenhouse under controlled conditions of 20°C, humidity 80% and 14 h daily light. Plants at the fully expanded one-leaf stage were inoculated with fresh urediniospores suspended in aqueous solution containing 0.05% v/v Tween 20. The inoculated seedlings were placed in a dew chamber at 10°C for 24 h and then transferred into a controlled greenhouse with a diurnal cycle of 14 h of light at 18°C and 10 h of dark at 12°C. F_1, BC_1 and F_2 plants were inoculated with CYR32. After 14–15 days, when the susceptible cultivar Mingxian 169 was fully sporulating, infection type (IT) data were recorded according to the scale of 0–4 (McIntosh *et al.* 1995). ITs 0–2 were considered resistant whereas ITs 3–4 were susceptible.

Field tests were conducted in the Langfang Experimental Station in the Hebei province. F_2 plants were grown in rows with 15–20 seeds planted in a 1-m row. Mingxian 169 was planted as a susceptible control around the field and inoculated at the jointing stage with urediniospores of CYR32 suspended in 0.05% v/v Tween 20. The inoculated plants were covered with plastics overnight to facilitate dew formation for *Pst* infection. The plastics were removed in the following morning. ITs were scored when Mingxian 169 had more than 80% severity. The IT data were classified as resistant (R, IT 0–2) and susceptible (S, IT 3–4).

DNA extraction, PCR amplification, electrophoresis and gel visualization

Genomic DNA was extracted from leaf tissues of each F_2 plant and the parents using a modified method of cetyltrimethylammonium bromide (CTAB) (Rogers and Bendich 1985) and dissolved in 100 μL TE-buffer (10 mM Tris, pH 8.0, 1 mM EDTA). The DNA was quantified with a NanoDrop 1000 Spectrophotometer (Thermo Fisher Scientific, USA) and assessed in 1% agarose gel. DNA samples were diluted to a concentration of 50 ng/μL before storing at −20°C.

To identify the DNA markers that are associated with stripe rust resistance, the bulked segregant analysis (BSA) method was used. DNA samples from 10 R (IT 0 0;) and 10 S (IT 4) F_2 plants were mixed to construct the R and S bulks, respectively and then evaluated with simple sequence repeat (SSR) markers together with the parents. SSR markers in the WMC, GWM, BARC, CFA, CFD and GDM series (http://wheat.pw.usda.gov/ggpages/SSR) were chosen across the 21 wheat chromosomes according to the consensus map of Somers *et al.* (2004).

Table 1. ITs of Zhengmai 7698 and Taichung 29 inoculated with *P. striiformis* f. sp. *tritici* races.

Cultivars	CYR17	CYR26	CYR27	CYR29	CYR31	CYR32	CYR33	V26
Zhengmai 7698	0;	0;	0;	0;	0;	0;	0;	4
Taichung 29	4	4	4	4	4	4	4	4

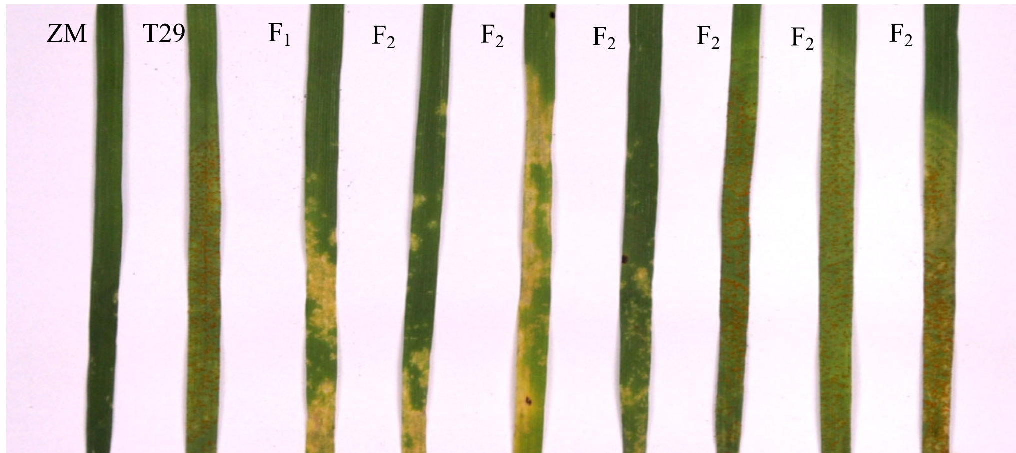

Figure 1. Seedling IT of the parents and some F_2 plants from cross Taichung 29/Zhengmai 7698 inoculated with race CYR32 of *P. striiformis* f. sp. *tritici*. ZM, Zhengmai 7698; T29, Taichung 29.

PCR was performed in a 10-μL solution containing 2 μL of 50 ng/μL template DNA, 1 μL of 10× PCR buffer, 0.2 μL of 5 U/μL *Taq* DNA polymerase, 2.5 mM of each dNTP, 5 μmol/L forward and reverse primer solutions and sterilized double distilled H_2O. Amplification was performed in a GeneAmp PCR System 9700 programmed as follows: 5 min at 94°C for initial denaturation; 35 cycles each consisting of 1 min at 94°C for denaturation, 1 min at 50°C, 55°C or 60°C for annealing depending on individual primers, 1 min at 72°C for extension and finally a 10 min extension step at 72°C. Six microlitre 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 each PCR product. After 5 min denaturation at 94°C, 5 μL of the PCR product and loading buffer mixture for each sample was loaded for electrophoresis in a 6% polyacrylamide gel in 1× TBE buffer (89 mM Tris, 89 mM boric acid, 2 mM EDTA, pH 8.3) (Bassam *et al.* 1991). Electrophoresis was carried out at 1400 V for 1.0–1.5 h. Gel staining and visualization was done as previously described (Chen *et al.* 1998). Polymorphic markers were used to genotype the F_2 population. Genotype data were used to construct a genetic map and locate the resistance gene.

Mapping and data analysis

A linkage map was established using software JoinMap ver. 3.0 (van Ooijen and Voorrips 2001). A regression mapping algorithm and Kosambi's function were utilized to convert recombination fractions into map distances and order the markers (Kosambi 1943).

Chi-square (χ^2) tests were applied to evaluate the F_2 segregation ratios of R/S plants to determine the goodness of a theoretical ratio.

Results

Response of Zhengmai 7698 to Pst races

When tested in the seedling stage in the greenhouse, Zhengmai 7698 was resistant (IT 0;) with necrotic spots without any uredinia to all tested races except for V26, while Taichung 29 was susceptible (IT 4) to all races (table 1).

Reactions of progenies to CYR32

In the progeny test with race CYR32, Taichung 29 was susceptible (4) and Zhengmai 7698 was resistant as described above. All F_1 plants were resistant and F_2 plants segregated into resistant and susceptible reactions (figure 1), indicating dominant resistance of Zhengmai 7698. The F_2 segregation fits a 3 resistant:1 susceptible ratio ($\chi^2 = 1.73$, $P = 0.19$), indicating one gene for resistance (table 2). The 32 tested BC_1 plants were divided into 15 resistant and 17 susceptible plants. The observed

Table 2. Seedling and adult plants of ITs of parents and progenies of cross Taichung 29/Zhengmai 7698 inoculated with race CYR32 of *P. striiformis* f. sp. *tritici* and chi-squared analysis.

		IT								
Stage	Generation	0	0;	1	2	3	4	R:S	χ^2 value	*P* value
Seedling	T29						30			
	ZM		14							
	F_1		19							
	F_2	4	107	6	14	20	34	3:1	1.73	0.19
	BC_1		15			2	15	1:1	0.13	0.72
Adult	T29						20			
	ZM		20							
	F_1	2	6	2						
	F_2	3	72	10	73	48	6	3:1	0.03	0.86
	BC_1	1	9	2			13	1:1	0.04	0.84

T29, Taichung 29; ZM, Zhengmai 7698.

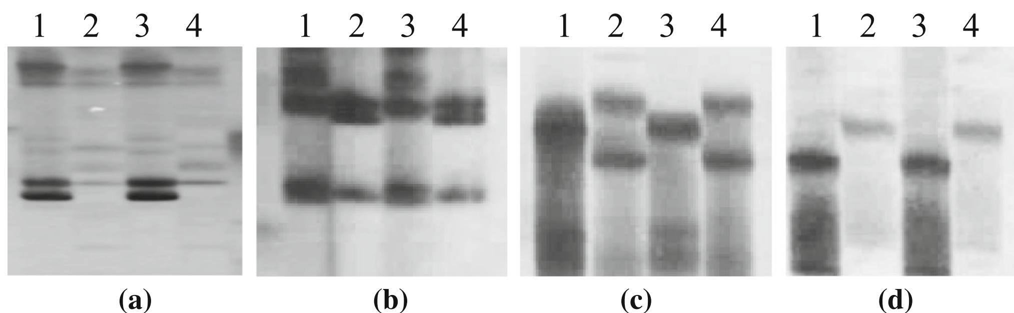

Figure 2. PAGE patterns of (a) Xwmc786, (b) Xwmc398, (c) Xwmc179 and (d) Xbarc198 on(1) Zhengmai 7698, (2) Taichung 29, (3) resistance bulk and (4) susceptible bulk.

segregation ratio was consistent with the expected ratio of 1:1 ($\chi^2 = 0.13$, $P = 0.72$). These results showed that Zhengmai 7698 has a dominant gene conferring resistance to race CYR32.

In the field evaluation, Taichung 29 was susceptible (IT 4), Zhengmai 7698 was resistant (IT 0;) and F_1 plants were also resistant (IT 0;). The 212 F_2 plants segregated into 158 resistant and 54 susceptible fitting the ratio of 3:1 ($\chi^2 = 0.03$, $P = 0.86$), indicating that resistance under field conditions was also controlled by a single-dominant gene (table 2). The segregation of resistant and susceptible BC_1 plants fit the 1:1 ratio ($\chi^2 = 0.04$, $P = 0.84$). The field results confirmed a single-dominant gene for resistance to CYR32 and the gene was tentatively designated as *YrZM*.

Screening of polymorphic markers

From 240 tested SSR markers, which were selected to cover the 21 common wheat chromosome 5 markers, Xwmc786, Xwmc398, Xwmc179, Xbarc198 and Xwmc597, were polymorphic between the parents, and between the resistant and susceptible bulks (figure 2), indicating that these markers were linked to *YrZM*. The five markers were all from chromosome 6B, suggesting that *YrZM* was likely located on chromosome 6B.

Linkage analysis and mapping resistance gene

The associations of the five polymorphic SSR markers with the resistance gene were tested with 212 F_2 plants. Because the dominant marker Xwmc597 was present in Taichung 29 and susceptible bulk, it was not used to construct the linkage map. Other four markers were present in Zhengmai 7698 and the resistant bulk. Figure 3 shows the amplification results of marker Xbarc198 for the two parents and some F_2 plants. Three of the markers were codominant and one was dominant (table 3). Codominant markers Xwmc398, Xwmc179 and Xbarc198 segregated at the expected 1:2:1 ratio for homozygous resistant, heterozygous and homozygous susceptible in the F_2 population ($\chi^2 = 0.03 - 0.46$, $P = 0.50 - 0.86$). The segregation of marker Xwmc786 fit the expected ratio 3:1 ($\chi^2 = 0.91$, $P = 0.34$) for presence and absence in the F_2 population (table 3).

A linkage map was constructed with the four segregating markers (figure 4). *YrZM* was flanked by

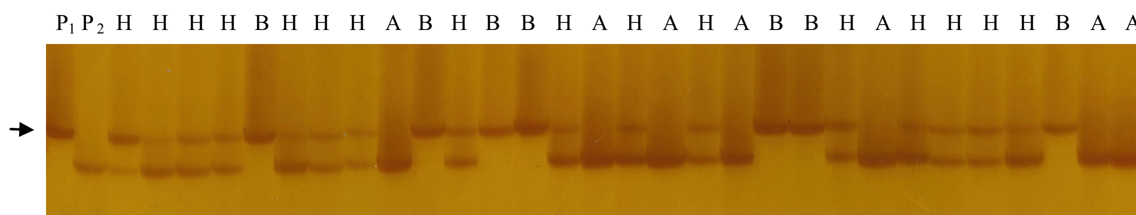

Figure 3. Amplification of F_2 plants of cross Taichung 29/Zhengmai 7698 using the primers of SSR marker Xbarc198. P_1, Zhengmai 7698; P_2, Taichung 29. A, homozygous resistant; B, homozygous susceptible; H, heterozygote. The band associated with *Yr* is indicated by the arrow.

Table 3. Segregations of SSR markers in the F_2 population of cross Taichung 29/Zhengmai 7698.

Markers	Size (bp)	Number of F_2 plants				χ^2	*P* value
		A	H	B	D		
Xbarc198	129	54	105	53		0.03	0.86
Xwmc786	154			47	165	0.91	0.34
Xwmc398	180	50	109	43		0.25	0.62
Xwmc179	380	57	103	51		0.46	0.50

A, homozygous resistant plants; H, heterozygous plants; B, homozygous susceptible plants; D, dominant A-allele plants.

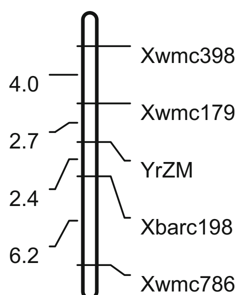

Figure 4. Genetic linkage map of stripe rust resistance gene *YrZM* on chromosome 6BL. The left side shows the map distances in centi-Morgans and the right side indicates the corresponding locations on the genetic map between the two loci and the *YrZM* locus.

markers *Xwmc179* and *Xbarc198* at genetic distances of 2.7 and 2.4 cM, respectively.

Discussion

The first requirement for breeding programmes is to have resistance sources which can be used for developing cultivars with resistance to major diseases and pests. Many genetic studies of wheat stripe rust have identified one, two or more genes with additive effects on disease resistance. Wheat cultivar Zhengmai 7698 was derived from a complex cross involving three parental varieties (Zhengmai 9405/ Zhengmai 4B269/Zhoumai 16). The cultivar is resistant to many *Pst* races, including predominant races CYR17, CYR26 and CYR32. CYR32, virulent to *Yr1*, *Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr9*, *Yr27*, *YrA*, *YrAlba*, *YrCle*, *YrCV*, *YrGaby*, *YrRes*, *YrSD*, *YrSP* and *YrSu* circumvents resistance in many wheat cultivars and has caused a severe epidemic in recent decades in China (Kang *et al.* 2010). In addition to CYR32, CYR33 has become predominant, which has made more cultivars susceptible (Kang *et al.* 2010). Only a few genes for race-specific all stage resistance, such as *Yr5* and *Yr15* are effective against Chinese *Pst* races. In this study, Zhengmai 7698 was found to be resistant to *Pst* races CYR32 and CYR33, indicating that its resistance is effective against the major predominant races. Genetic analysis indicated that resistance of Zhengmai 7698 against CYR32 was conferred by a single dominant gene, tentatively designated as *YrZM*. The closely linked SSR primers mapped *YrZM* to the long arm of chromosome wheat 6B. The two flanking markers, Xbarc198 and Xwmc179, should be useful for identifying *YrZM* in breeding programmes.

Currently, four formally named *Yr* gene loci (*Yr4*, *Yr35*, *Yr36* and *Yr78*) have been identified on chromosome 6B (Wang and Chen 2017). The typical carriers of these genes are Cappelle-Desprez (*Yr4a*), Hybrid 46 (*Yr4b*), 98M71 (*Yr35*), Glupro (*Yr36*) and PI 519805 (*Yr78*). Cappelle-Desprez was first released in France in 1946 and widely cultivated in Western Europe up to 1970s (Lupton and Macer 1962; Worland and Law 1986; Bonjean *et al.* 2001). It is known to possess the seedling resistance genes *Yr4a* (de Vallavieille-Pope *et al.* 1990) on chromosome 6B and Chen *et al.* (1996) also reported *Yr4b* in Hybrid 46 on chromosome 6B. However, their specific chromosomal location is unknown. Based on the seedling tests with different Chinese *Pst* races, Cappelle-Desprez and Hybrid 46 were susceptible to CYR32, indicating that *Yr4a* and *Yr4b* were different from *YrZM*. *Yr35* on the short arm of chromosome 6B was transferred from *T. turgidum* spp. *dicoccoides* to hexaploid wheat by Marais *et al.* (2005a). *Yr36*, also located on chromosome 6BS and from *T.turgidum* ssp. *dicoccoides*, confers high-temperature and adult-plant resistance (Uauy *et al.* 2005). Through pedigree analysis, it was concluded that *YrZM* was different from *Yr35* and *Yr36*. *Yr78* for adult-plant resistance to stripe rust was identified in PI 519805 and several other common wheat cultivars and mapped to chromosome 6BS

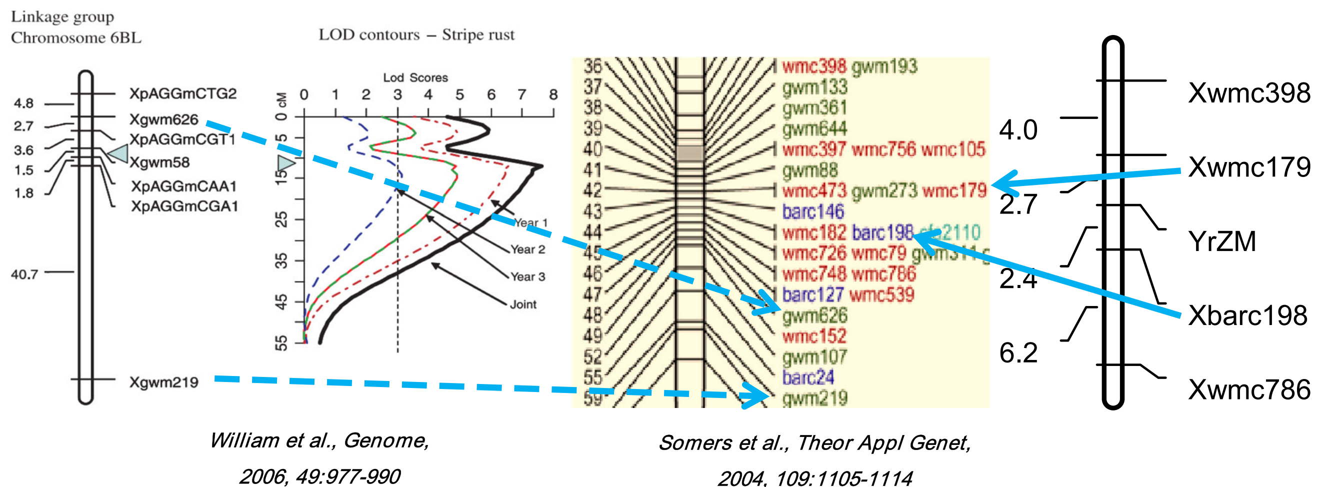

Figure 5. Comparison of the *YrZM* linkage map with the consensus map of Somers *et al.* (2004) and QTL on 6BL chromosome (William *et al.* 2006).

(Dong *et al.* 2017). As *YrZM* is located on chromosome 6BL and resistant to CYR32 and CYR33, it is different from all permanently named *Yr* genes on chromosome 6B.

There were three regions of importance in chromosome 6B for stripe rust resistance (Rosewarne *et al.* 2013): QRYr6B.1 referred to the short arm; QRYr6B.2 mainly contained *Yr36* and the final region was identified in Pastor (Rosewarne *et al.* 2012) and Pavon (William *et al.* 2006). Due to the differences in marker platforms and associated linkage maps, it was difficult to accurately compare the chromosomal location of *YrZM* with previously identified quantitative trait loci (QTL). By comparing chromosome 6B with other published SSR maps based on shared markers, the *YrZM* locus is different from previously reported QTL for stripe rust resistance (figure 5). As marker platforms will continue to be developed and improved, and more linkage maps will be published with combinations of SSR and SNP markers, we will be able to compare the *YrZM* linkage map with maps containing similar chromosomal regions.

To improve the durability of resistance in wheat cultivars and to achieve sustainability of stripe rust management, it is important to diversify the resistance gene in breeding programmes and deploy diverse effective resistance genes in wheat cultivars. As a widely grown cultivar for high yield and stripe rust resistance, Zhengmai 7698 is also a valuable cultivar to be used in breeding programmes. As its stripe rust resistance gene *YrZM* is race-specific and ineffective against the recently emerged race groups, e.g. V26, caution needs to be taken to use the gene in combinations with other effective genes and especially for nonrace specific adult-plant resistance genes. The flanking markers Xbarc198 and Xwmc179 can be used for marker-assisted selection in pyramiding *YrZM* with other resistance genes.

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