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BIOLOGY

Molecular identification and mapping of a novel stripe rust resistance gene in wheat resistance line CH5389

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ABSTRACT: *Stripe rust, caused by Puccinia striiformis is one of the most destructive diseases of wheat worldwide. CH5389 is a wheat-Thinopyrum intermedium derived line conferring stripe rust resistance. Genetic analyses of seedlings of F_2 populations and $F_{2:3}$ families developed by crossing CH5389 and susceptible common wheat revealed that stripe rust resistance in CH5389 was controlled by a single dominant gene that was designated YrCH5389. Eight SSR and EST-PCR polymorphic markers on chromosome 3AL were identified in F_2 population of CH5389/Taichung29. The YrCH5389 was flanked by EST marker BE405348 and SSR marker Xwmc388 on chromosome 3AL with genetic distances of 2.2 and 4.6 cM, respectively. Comparative genomic analysis demonstrated that the orthologous genomic region of YrCH5389 covered 990 kb in rice, 640 kb in Brachypodium, and 890 kb in sorghum. Based on the locations of the markers, the resistance gene was located to chromosome deletion bin 3AL-0.85-1.00. Because there are no officially named stripe rust resistance genes on the 3AL chromosome, the YrCH5389 should be designated as a new resistance gene. These linkage markers could be useful for marker-assisted selection in wheat resistance breeding.*
Key words: *stripe rust, genetic analysis, resistance gene, comparative genomic analysis, marker assisted selection.*

Identificação e mapeamento de um novo gene de resistência a ferrugem linear na linhagem de trigo CH5389

RESUMO: *A ferrugem linear causada por Puccinia striiformis é uma das doenças mais destrutivas do trigo no mundo. A linhagem CH5389 é derivada do cruzamento de trigo com Thinopyrum intermedium e confere resistência a ferrugem linear. Análises genéticas de indivíduos da população F2 e família F2:3 obtida a partir do cruzamento entre CH5389 e trigo comum suscetível revelaram que a resistência à ferrugem linear na linhagem CH5389 foi controlada por um único gene dominante, designado YrCH5389. Oito marcadores polimórficos SSR e EST-PCR no cromossomo 3AL foram identificados na população F2 de CH5389/Taichung29. O gene YrCH5389 foi delimitado pelos marcadores EST BE405348 e SSR Xwmc388 no cromossomo 3AL com distâncias genéticas de 2,2 e 4,6 cM, respectivamente. Análises genômicas comparativas demonstraram que regiões genômicas ortólogas do gene YrCH5389 compreendem 990 kb em arroz, 640 kb em braquipódio e 890 kb em sorgo. Com base nas localizações dos marcadores, o gene de resistência foi localizado no cromossomo 3AL-0.85-1.00. Como não há genes oficialmente nomeados de resistência à ferrugem linear no cromossomo 3AL, o YrCH5389 deve ser designado como um gene novo de resistência. Esses marcadores de ligação podem ser úteis para a seleção assistida de genótipos de trigo resistentes a ferrugem linear.*
Palavras-chave: *ferrugem linear, análise genética, gene de resistência, análise genômicas comparativas, seleção assistida por marcado.*

INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the most important crops for humans. Stripe rust (yellow rust) caused by *Puccinia striiformis* Westend. f. sp. *tritici* Eriks. (*Pst*) is a devastating disease of wheat in cold and wet regions worldwide (CHEN, 2005). The disease has occurred in six pandemics and led to serious yield losses in China. The first epidemic of wheat stripe rust occurred in China in the 1950s. Subsequently, five pandemics occurred in 1964, 1990, 2002, 2003, and 2009, resulting in yield losses of 3.2 billion, 1.8 billion, 1.3 billion, 980 million, and 810 million kilograms, respectively (XIANG et al. 2016). Among the strategies for the control of wheat stripe rust, the most effective, economic, and environment-friendly measure is the utilization and deployment of resistant varieties.

So far, more than 60 formally named stripe rust resistance genes (*Yr1-Yr78*) and many temporarily designated have been reported in wheat and its wild relatives (XIANG et al. 2016; DONG et al. 2017). However, with the rapid evolution and spread of virulence of stripe rust pathogen populations, the major resistance genes are only effective for a limited period of time. In particular, the *Pst* races CYR32 and

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CYR33 prevented most of the stripe rust resistance genes from being effective in China (CHEN et al. 2005; YANG et al. 2003). Therefore, to reduce wheat yield losses caused by epidemics of stripe rust, the discovery of new sources conferring effective and durable resistance is urgently needed.

At present, molecular markers are widely used to identify wheat resistance genes. Of these, microsatellite (SSR) markers are extensively utilized in genetic mapping of wheat stripe rust resistance genes. Resistance genes *Yr17*, *Yr18*, *Yr29*, *Yr24/Yr26*, *Yr36*, *Yr41*, *Yr43*, *Yr44*, *Yr45*, *Yr46*, *Yr47*, *Yr48*, *Yr50*, and *Yr76* were identified and localized by SSR markers. For example, a high temperature adult plant (HTAP) QTL, *QYrAlt.syau-3BS*, was flanked on the short arm of chromosome 3B with SSR markers *Xgwm389* and *Xbarc238* (ZHAO et al. 2012). There was high collinearity between the genomes of wheat, rice, *Brachypodium distachyon*, and sorghum (DRAPER et al. 2001; PATERSON et al. 2009). Based on comparative genomics, Expressed sequence tag (EST)-SSR markers are an effective approach for producing molecular marker linkage maps of target genes (LI et al. 2006; LILLEMO et al. 2008; LIU et al. 2013; XIANG et al. 2016). Using EST-SSR markers analysis, genetic linkage maps of stripe rust gene *Yr26* and powdery mildew resistance gene *Pm41* were located in wheat chromosome deletion 1BL bin 0.32-0.47 and 3BL bin 0.63-1.00, respectively (ZHANG et al. 2013; WANG et al. 2014).

CH5389 is a new wheat *Thinopyrum intermedium* derived line. It is immune to five *Pst* races CYR31, CYR32, CYR33, SY11-5, and CYR34. Here, we identify the new stripe rust resistance gene and construct a comparative genomic linkage map using SSR markers and EST-SSR markers in the wheat line.

MATERIALS AND METHODS

Materials and populations

CH5389 is a wheat-*Th. intermedium* line derived from crossing Jingchun 5/TAI7045//76216-96. Resistant donor TAI7045 of CH5389, a wheat-*Th. intermedium* partial amphiploid with 56 chromosomes,exhibited immune responses to stripe rust and powdery mildew. The resistant parent CH5389 is resistance, whereas, the susceptible wheat cultivars/lines SY95-71, Taichung 29 and Mianyang 11 are all susceptible to stripe rust. .

To examine the inheritance of stripe rust resistance, F_1 and F_2 plants derived from the cross CH5389/SY95-71, CH5389/Taichung 29, and Mianyang 11/CH5389 were used to construct segregating populations. The one hundred fifty-five $F_{2:3}$ families of CH5389/ Taichung 29 were further used for genetic analyses. The susceptible control was Chuanyu 12. The TAI7045, CH5389, SY95-71, Taichung 29, Mianyang 11, and Chuanyu 12 were maintained by Shanxi Academy of Agricultural Sciences. The Chinese Spring nullisomic-tetrasomic and ditelosomic stocks were obtained from the Wheat Genetic and Genomic Resource Center, Kansas State University.

Disease evaluation

Approximately 30 seeds of *Th. intermedium*, TAI7045, and 7 wheat cultivars/lines (76216-96, Jing 411, Taiyuan768, Jinchun 5, CH5389, Taichung 29, SY95-71, and Chuanyu 12) were planted in 10 cm pots in controlled greenhouse for seedling resistance evaluation using five *Pst* races CYR31, CYR32, CYR33, SY11-5, and CYR34. The first leaf fully expanded, seedlings were artificially inoculated with fresh spores of the *Pst* races. Inoculated plants were incubated at 9-11 °C in 100% relative humidity without light for 24 h. Seedlings were then transferred into a greenhouse with 16 h of light and 8 h of darkness with a diurnal temperature cycle of 17 °C and 12 °C, respectively. When Chuanyu 12 was heavily infected, stripe rust reactions were recorded on individual plants or lines about 20 days after inoculation. Infection type (IT) was based on 0-4 scale system, plants with ITs of 0-2 were considered to be resistant and those with IT 3-4 were determined to be susceptible.

Seedling of parents, all F_1, F_2, and $F_{2:3}$ plants were grown in controlled greenhouse. Twenty seeds of each parent and F_1 generations, about 200 seeds of the F_2 population and 15 seeds for each of the $F_{2:3}$ lines were randomly sown in large pots (54×27×20 cm). Race CYR32 was used to evaluate seedling resistance of all plants with the same method mention above.

Molecular marker analysis

Total genomic DNA of parents and F_2 individuals was extracted from uninfected seedling leaves. Bulk DNA was obtained by combining equal amounts of DNA from 10 resistant (IT 0) and 10 susceptible (IT 4) F_2 plants derived from CH5389/ Taichung 29. Six hundred and nineteen SSR primers distributed across the A, B and D genomes and 52 EST-STS markers were used to screen polymorphisms in the two parents and bulk DNA from resistant and susceptible plants.

PCR was conducted in total volumes of 15 µl containing 50 ng genomic DNA, 0.25 mM each of the primers, 0.3 mM dNTPs, 1× PCR Buffer, and 0.75U *Taq* DNA polymerase (LI. 2011). The PCR was performed at 94 °C for 5 min; followed by 34 cycles of 94 °C for 1 min; 50, 55, or 60 °C (depending on the individual primers) for 30s; 72 °C for 1 min; and a final incubation at 72 °C for 5 min. The amplification products were analyzed by separation on 8% non-denaturing polyacrylamide gels with 1×TBE buffer and visualized by silver staining.

Statistical analysis

Chi-square tests were used to determine the goodness of fit of observed and expected segregation in the F_1, F_2, and $F_{2:3}$ populations. Linkage analysis between linked markers and the resistance gene was performed using the JoinMap 4.0 software and recombination values were calculated using the Kosambi mapping function (KOSAMBI. 1944).

RESULTS AND DISCUSSION

Stripe rust responses

Seedling IT data showed that CH5389, resistance donor TAI7045, and wild parent *Th. Intermedium* were resistant to five *Pst* races CYR31, CYR32, CYR33, SY11 and CYR34 (IT 0-2), whereas the wheat parents (76216-96, Jing 411, Taiyuan 768, and Jinchun 5) were susceptible to five *Pst* races (IT 3-4). Taichung 29 was only resistant to the new virulent *Pst* race CYR34 (Table 1). These results suggested that CH5389 probably contained one or more resistance genes to stripe rust.

CH5389 was resistant, while SY95-71, Taichung 29, and Mianyang 11 were highly susceptible to CYR32 in the seeding stage. All F_1 plants of the three reciprocal crosses showed resistance similar to that of the resistant parent, indicating that the resistance gene was dominant in CH5389 (Table 2). Among the 167 plants from the CH5389/Taichung 29 F_2 population, 119 plants were resistant and 48 plants were susceptible to *Pst* race CYR32. Segregation of resistance was consistent with a ratio of 3:1 (χ^2=1.25, P=0.26). The F_2 population of Mianyang11/CH5389 segregated into 97 resistant and 40 susceptible individuals, fitting the 3:1 ratio (χ^2=1.29, P=0.26). In another 187 test plants from the CH5389/SY95-71 F_2 population, the segregation ratio of resistance to susceptibility was 3:1 (χ^2=0.29, P=0.59) (Table 2). One hundred and fifty-five $F_{2:3}$ lines were obtained when 167 F_2 plants were transplanted to the field. In $F_{2:3}$ families, the segregation ratio was 41 homozygous resistant (RR): 77 segregating (Rr): 37 homozygous susceptible (rr), which was consistent with an expected 1:2:1 ratio (χ^2=1.95, P=0.16). All finding indicated that the resistance to CYR32 was controlled by a single dominant gene in CH5389. The gene was designated temporarily as *YrCH5389* (Table 3).

Identification of markers linked to the stripe rust resistance gene

To determine the chromosomal location of the stripe rust resistance gene *YrCH5389*, a total of 619 pairs of SSR markers from the entire wheat genome were utilized. Of these, 394 markers amplified polymorphisms between the resistant and susceptible parents. Six markers (*Xgwm666*, *Xwmc173*, *Xwmc388*, *Xwmc594*, *Xwmc215*, and *Xgwm497*) were polymorphic between the resistant and susceptible bulk DNA samples as well as the parents CH5389 and Taichung 29. The F_2 mapping population from the CH5389×Taichung 29 cross was genotyped with the six polymorphic markers. All primers are co-dominant markers except for *Xwmc388* and *Xgwm497*. Results demonstrated that six primers were linked to *YrCH5389* with genetic distances ranging from 4.6 to 45.8 cM (Figure 1, Figure 3). Of the six markers linked to *YrCH5389*, *Xgwm666*, *Xwmc594*, and *Xwmc388* were previously mapped to wheat chromosome arm 3AL, *Xwmc173* was located in 1D, 3A, 4A, and 5A, *Xwmc215* was assigned to 5D, 3A, and 5A, and *Xgwm497* was mapped to 1A, 2A, 3A, 3D, and 5B (SOMERS et al. 2004). To verify the location of *YrCH5389*, these markers were further examined in CS nulli-tetrasomic and ditelosomic lines. Six microsatellite markers amplified the specific bands in CS and the CS nulli-tetrasomic lines, N3BT3A, N3DT3B, and Dt3AL, but no expected bands were produced in the nulli-tetrasomic N3AT3B, N3AT3D, and Dt3AS lines (Figure 2). Results clearly validated that the location of the resistance gene *YrCH5389* was in the long arm of chromosome 3A.

The *Xgwm666* and *Xwmc388* markers were mapped 14 cM and 4.6 cM, respectively, away from the resistance gene *YrCH5389*. Because the markers were previously assigned to the 3AL-8 deletion bin FL 0.85-1.00, we designed the EST-STS markers based on wheat EST and orthologous regions of rice. Eight markers, linked to stem rust resistance gene *Sr35*, were also developed (ZHANG et al. 2010). These markers were further tested for polymorphisms between susceptible and resistant lines. Among the EST-STS primers, two primers, BE405348 and CV775292, were also linked to *YrCH5389*. Based

Table 1 - Resistance to five *Pst races* in CH5389 and its parents.

Line	2*n*=	genome	CYR31	CYR32	CYR33	SY11	CYR34
Th.IntermedIium	42	SJJ^s	0	0	0	0	0
TAI 7045	56	ABDS+J^s	0	0	0;	0;	0
76216-96[a]	42	ABD	3	4	4	4	4
Jing 411[a]	42	ABD	3	4	3	4	4
Taiyuan768[b]	42	ABD	3	4	4	3	4
Jinchun 5[b]	42	ABD	4	4	4	4	4
CH5389	42	ABD	0	0	0	0;	0
Taichung29	42	ABD	4	4	4	4	0;
SY95-71	42	ABD	4	4	3	4	4
Mianyang 11	42	ABD	4	4	4	4	3

[a]The wheat parents of TAI7045. [b]The wheat parents of CH5389.

on these molecular markers, *YrCH5389* was located to deletion bin 3AL 0.85-1.00 and was flanked by markers BE405348 and *Xwmc388* at genetic distances of 2.2 and 4.6 cM, respectively.

Comparative genomics analysis

The wheat 3AL region of stripe rust resistance gene *YrCH5389* had the same gene order to rice 1, *Brachypodium* 2, and sorghum 3. BE405348 was orthologous to rice, *Brachypodium*, and sorghum genes *Os01g72240*, *Bd2g60930*, and *Sb03g045930*, respectively. The marker CV775292 was linked to the homologous genes of rice, *Brachypodium*, and sorghum, *Os01g73230*, *Bd2g61570*, and *Sb03g046820*, respectively. Thus, the orthologous genomic region of *YrCH5389* covered 990 kb in rice (*Os01g72240* to *Os01g73230*), 640 kb in *Brachypodium* (*Bd2g60930* to *Bd2g61570*), and 890 kb in sorghum (*Sb03g045930* to *Sb03g046820*). Orthologous genomic regions of *YrCH5389* in rice, *Brachypodium*, and sorghum genomes will be useful for the fine mapping of *YrCH5389*.

With the appearance of new *Pst* races, most stripe rust resistance genes have become ineffective. For example, since the prevalence of *Pst* race CYR29, many wheat cultivars with resistance gene *Yr9* lost resistance in China (Wan et al. 2004). Similarly, the newly identified *Pst* race CYR34 overcame the resistance of the *Yr24/Yr26* polymerization gene in wheat variety Cuanmai42 (LIU et al. 2010). Thus, it is essential to explore new stripe rust resistance genes for wheat breeding. In this study, we investigated the resistance gene in wheat line CH5389. Genetic analysis indicated that the stripe rust resistance in

Table 2 - Genetic analysis of resistance for stripe rust reactions in parents and F_1, F_2 populations.

Parent or cross	Generation	Number of tested	Resistant	Susceptible	Expected ratio	χ^2-value	Probability
CH5389	P_1	19	19				
SY95-71	P_2	18		18			
Taichung29	P_3	16		16			
Mianyang 11	P_4	17		17			
CH5389/Taichung29	F_1	17	17	0	1:0		
	F_2	167	119	48	3:1	1.25	0.26
Mianyang 11/CH5389	F_1	18	18	0	1:0		
	F_2	137	97	40	3:1	1.29	0.26
CH5389/SY95-71	F_1	16	16	0	1:0		
	F_2	187	137	50	3:1	0.29	0.59

Table 3 - resistance segregation to stripe rust race CYR32 in the F_3 lines.

	----------F_3 lines----------		----------F_3 plants---------			
	Observed	Expected	R	S	χ^2-value (3:1)	Probability
YrYr HR	41	38.25	731	0		
Yryr Seg	77	77.5	902	273	1.95	0.16
Yryr HS	37	38.25	0	556		
Total	155					
χ^2-value (1:2:1)	0.24					
Probability	0.89					

line CH5389 was controlled by a dominant gene *YrCH5389*.

The stripe rust resistance gene *Yr76* has been mapped on the short arm of chromosome 3A (XIANG et al. 2016). In our study, *YrCH5389* was located in the 3AL chromosome. Tyee carrying *Yr76* was resistant to races PSTV37, PSTV40, and PSTV79, while CH5389 was effective against *Puccinia striiformis* f. sp. *tritici* (*Bgt*) isolates CYR31, CYR32, CYR33, SY11, and PSTV26. This finding verified that *YrCH5389* was different from stripe rust resistance gene *Yr76*. To date, no stripe rust resistance gene was previously located on 3AL chromosome. There were five quantitative trait loci (QTL) *QYrst.orr-3AL*, *QYrdr.wgp-3AL*, *QyrPI182103.wgp-3AL*, *QYr.cau-3AL*, and *QYr.cim-3A* in chromosome 3AL. Among these QTL, *QYrst.orr-3AL* accounted for 6% of the phenotypic variations. The *QYrdr.wgp-3AL was* located by marker *IWA6834*, explaining 1.78-13.85% of the phenotypic variations, and *QyrPI182103.wgp-3AL* was maped with markers *IWA899* and *Xgwm2*, accounted for 5.4%-8.1% of the phenotypic variance (ROSEWAME et al. 2010; YUAN et al. 2013). Because all of the stripe rust resistant QTL belonged to minor quantitative resistance, *YrCH5389* was likely a new gene for stripe rust resistance.

Micro-collinearity of the YrCH5389 genomic region in rice, Brachypodium, and sorghum

Studies have shown that the homologous regions of wheat, rice, *Brachypodium*, and sorghum genomes are powerful tool for constructing genetic linkage maps. The powdery mildew resistant genes, *Pm36*, *Pm41*, *Pm51*, and *MlIW170*, and the stripe rust

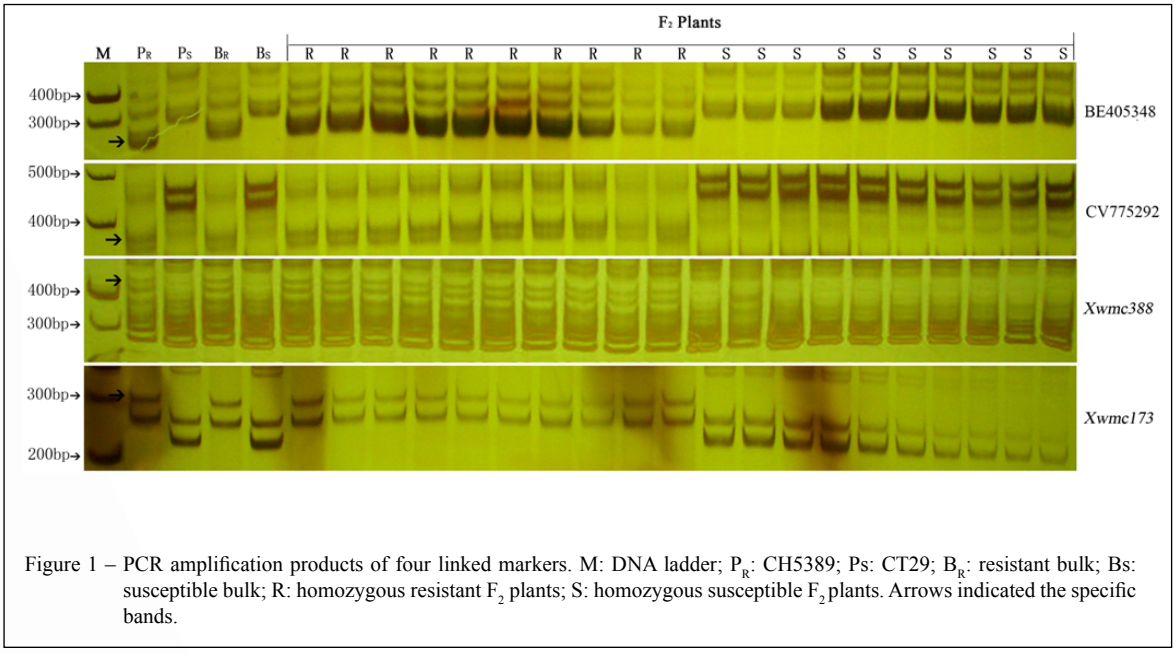

Figure 1 – PCR amplification products of four linked markers. M: DNA ladder; P_R: CH5389; Ps: CT29; B_R: resistant bulk; Bs: susceptible bulk; R: homozygous resistant F_2 plants; S: homozygous susceptible F_2 plants. Arrows indicated the specific bands.

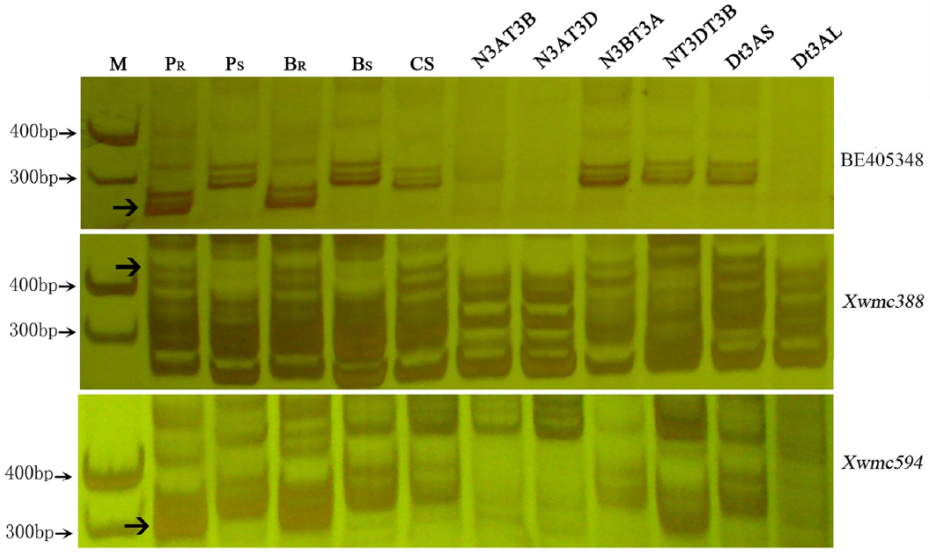

Figure 2 – PCR products of markers BE405348, Xwmc388 and Xwmc594. M: DNA ladder; PR: CH5389; Ps: CT29; BR: resistant bulk; Bs: susceptible bulk; CS: Chinese Spring; N3AT3B, N3AT3D and N3DT3B: nullisomic-tetrasomic lines; Dt3AL: ditelosomoc 3AL; Dt3AS: ditelosomic 3AS. Arrows indicated the specific bands.

resistant gene *Yr26* were identified by comparative genomics analysis, and linkage markers were also designed using the collinear regions in wheat, rice, *Brachypodium*, and sorghum (ZHANG et al. 2013; WANG et al. 2014; ZHAN et al. 2014). In the current study, collinearity was observed between wheat, rice, *Brachypodium*, and sorghum in the *YrCH5389* genomic region. Two linked markers, BE405348 and CV775292, were developed to construct the genetic linkage map of CH5389. Comparative genomic analysis showed that the orthologous genomic region of *YrCH5389* covered 990 kb in rice, 640 kb in *Brachypodium*, and 890 kb in sorghum. The recently published genome data of wild emmer and *Aegilops*

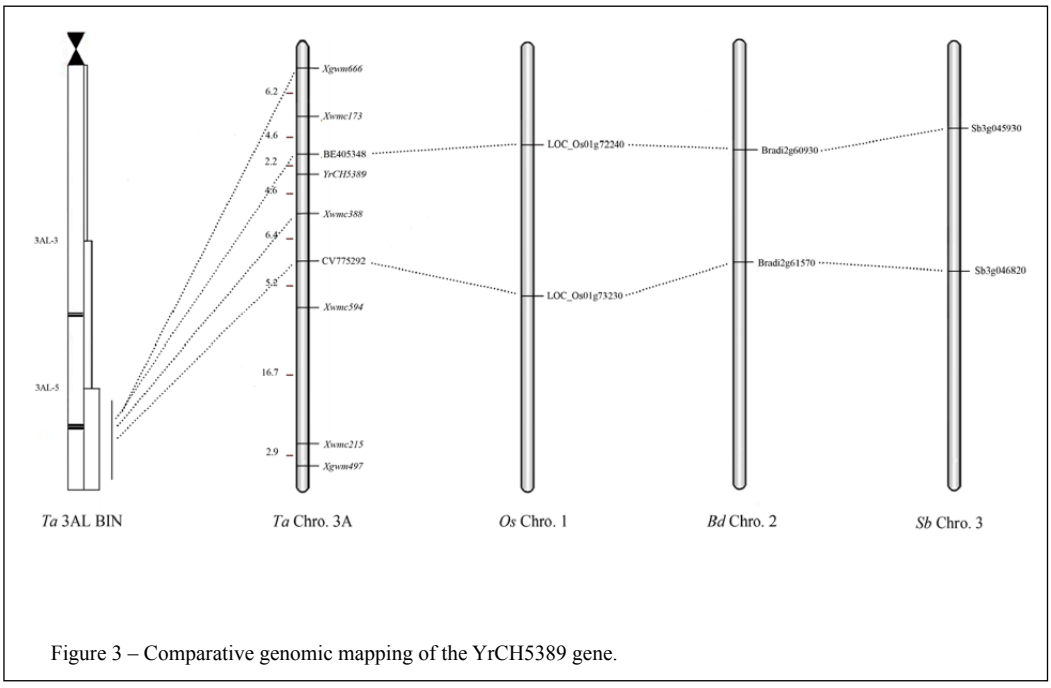

Figure 3 – Comparative genomic mapping of the YrCH5389 gene.

tauschii provide more information for identification of resistance genes (JIA et al. 2013; AVNI et al. 2017). The publication of wheat genome data could benefit further development of fine genetic linkage maps for stripe rust resistant gene *YrCH5389* (CALLAWAY 2017).

Marker-assisted selection (MAS)

The MAS was a useful tool for the specific tracking of many traits in wheat germplasm resources, such as disease resistance and drought tolerance (ELSAYED et al. 2012). Through the identification of tightly linked markers, we detected the presence of target genes and select target traits. The nearest marker linked to stripe rust resistance gene *Yr15* could distinguish between resistant and susceptible parents, accordingly, the marker was the best tool for MAS of *Yr15* (YANIV et al. 2015). In order to acquire more durable resistance, the linked markers of powdery mildew resistance gene *Pm51* were used to diagnose other resistance genes. The primer A-8, amplified specific bands associated with drought tolerance in bread wheat Giza-168 and Sham-6, was used to select tolerant genotypes in wheat breeding (ELSAYED et al. 2012). Based on the linkage map, we found that *YrCH5389* was flanked by markers BE405348 and *Xwmc388* with 2.2 and 4.6 cM genetic distances, respectively. All the examples above illustrated that BE405348 could be used for marker-assisted selection of *YrCH5389* to produce resistant wheat cultivars.

CONCLUSION

The wheat line CH5389 showed outstanding resistance to the prevalent races of stripe rust. Genetic and molecular markers analyses identified that resistance gene *YrCH5389* was located to chromosome deletion bin 3AL-0.85-1.00. The CH5389 should be used as a new source of resistance for breeding wheat resistant to stripe rust.

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