Molecular Mapping of Stripe Rust Resistance Gene *Yr76* in Winter Club Wheat Cultivar Tyee

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ABSTRACT

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Tyee, one of the wheat cultivars used to differentiate races of *Puccinia striiformis* f. sp. *tritici* in the United States, was identified to have a single gene for all-stage resistance, tentatively named *YrTyee*. To map the gene, Tyee was crossed with 'Avocet Susceptible' (AvS). Genetic analysis of the F₁, F₂, F_{2,3}, and BC₁ progenies confirmed a single dominant gene for resistance to race PSTv-37 that is avirulent to *YrTyee*. A mapping population of 135 F₂ plants was phenotyped with PSTv-37 and the derived F_{2,3} lines were tested with races PSTv-37, PSTv-40, and PSTv-79. The F₂ mapping population was genotyped with simple sequence repeat (SSR) markers. A genetic map comprising 13 SSR markers located *YrTyee* in chromosome

3AS flanked distally by SSR marker *wmc11* and proximally by *wmc532* at 2.6 and 3.4 cM, respectively. Amplification of Chinese Spring 3A deletion lines placed the gene in the distal bin 3AS4-0.45 to 1.00. Because *YrTyee* is different from all formally named *Yr* genes in chromosomal location, we permanently name the gene *Yr76*. A near-isogenic line of spring common wheat was developed and selected by testing F₃ lines derived from a AvS*4/Tyee cross with Tyee-avirulent and virulent races and the flanking markers. The specific SSR alleles flanking *Yr76* were validated using cultivars and breeding lines with and without the gene, and showed high polymorphisms. The specificity of *Yr76* is useful in differentiating *P. striiformis* f. sp. *tritici* races, and its tightly linked markers will be useful in developing resistant cultivars when combining the gene with other genes for resistance to stripe rust.

Additional keywords: *Triticum aestivum* sp. *compactum*, yellow rust.

Stripe rust (yellow rust), caused by *Puccinia striiformis* Westend. f. sp. *tritici* Erikss., is one of the most important and damaging diseases of wheat in all wheat production regions in the world (Chen 2005; Chen et al. 2014; Stubbs 1985; Wellings 2011). In the Pacific Northwest of the United States, where climatic conditions and cropping systems are favorable for stripe rust, the disease occurs every year. Based on experimental data from 1975 to 2012, stripe rust can cause yield losses on susceptible varieties ranging from 3% to more than 90%, with a mean of 36% for winter wheat and 30% for spring wheat (Chen 2014; Sharma-Poudyal and Chen 2011). Throughout the United States, severe epidemics of wheat stripe rust occurred in 2001, 2003, 2005, 2010, and 2012, causing yield losses estimated as 1.08, 2.42, 2.00, 2.61, and 1.49 million metric tons, respectively, even after millions of dollars were spent on fungicides to reduce the damage (Chen 2014; <http://striperust.wsu.edu>).

Resistant cultivars are the most effective, economical, easy-to-use, and environmentally friendly approach to control stripe rust (Chen 2013; Line and Chen 1995). Resistance to stripe rust is generally classified as two types, all-stage resistance (also called seedling resistance) and adult-plant resistance (Chen 2005, 2013).

Both types of resistance have advantages and disadvantages. All-stage resistance often provides high levels of protection, but is usually race-specific and not durable (Chen 2005; Chen and Line 1995; Johnson 1981). In contrast, adult-plant resistance, with some exceptions, is usually non-race-specific, but often provides partial protection that may be inadequate when the disease starts early, temperatures remain low, and inoculum loads are high (Chen 2005, 2013, 2014). When the two types of resistance are combined, they can be complementary and provide high levels of protection as well as durability. To search for wheat germplasm for either type of resistance, it is important to differentiate *P. striiformis* f. sp. *tritici* races using wheat lines with clearly characterized resistance genes and to use selected races to characterize new resistance sources and breeding lines for releasing new resistant cultivars.

'Tyee' (CItr 17773) is a soft white winter club wheat cultivar released by the U.S. Department of Agriculture-Agricultural Research Service (USDA-ARS) and Washington State University in 1979 (Allan et al. 1980). Before and when it was released, it was highly resistant to all U.S. *P. striiformis* f. sp. *tritici* races identified at that time. However, Tyee became susceptible and was added to the differential set in 1983 (Line and Qayoum 1992). Since then, 130 races avirulent and 25 races virulent to Tyee have been identified in the United States (Chen 2005; Chen et al. 2002, 2010; Line and Qayoum 1992; Wan and Chen 2012, 2014; Wan et al. 2016). Variation in the response of Tyee was also observed among *P. striiformis* f. sp. *tritici* isolates from Australia, Canada, Chile, China, Ecuador, Hungary, Italy, Kenya, Nepal, Turkey, and Uzbekistan (Sharma-Poudyal et al. 2013; Zhan et al. 2012; A. M. Wan and X. M. Chen, *unpublished data*).

In order to provide clearer information on races, Wan and Chen (2014) adopted a new set of differentials comprising 18 lines each with a single *Yr* gene for stripe rust resistance. The set includes Tyee, the only winter wheat cultivar and not an established

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First and second authors made equal contribution to this study.

*The e-Xtra logo stands for "electronic extra" and indicates that one supplementary figure is published online.

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near-isogenic line. Using the new differential set, 53 races avirulent and 35 races virulent to Tyee were identified in the United States, and 43 races avirulent and 12 races virulent were identified among isolates from other countries since 2010 (Wan and Chen 2014; Wan et al. 2016; A. M. Wan and X. M. Chen, *unpublished data*). The races virulent on Tyee were predominant in the U.S. Pacific Northwest from the middle 1980s and the middle 1990s, disappeared until 2006, and new races virulent to Tyee emerged and became predominant from 2007 to 2012 (Chen 2005; Chen et al. 2010; Line and Qayoum 1992; Wan and Chen 2012, 2014; Wan et al. 2016). It is interesting that the *P. striiformis* f. sp. *tritici* population in the United States can be separated into two major groups based on virulence or avirulence to *YrTyee*, and that the two

major virulence groups correspond to two major genetic groups determined using molecular markers (Cheng and Chen 2014; Wan and Chen 2014; Wan et al. 2016). In general, the frequencies of virulence to Tyee were low in other countries compared with the United States (Sharma-Poudyal et al. 2013; Zhan et al. 2012; A. M. Wan and X. M. Chen, *unpublished data*).

Previous genetic studies have determined that Tyee has a single gene for resistance to stripe rust, temporarily named *YrTyee* (Chen and Line 1992a, b; Chen et al. 1995). *YrTyee* was tentatively located on chromosome 6D by monosomic analysis (Chen et al. 1995). However, the specific chromosomal region of *YrTyee* was unknown, and there were no molecular markers available for the resistance gene. The objectives of this study were to map *YrTyee*, determine its relationships with other stripe rust resistance genes, identify and validate markers closely linked to the gene, and develop a near-isogenic line for the gene in a spring common wheat background.

TABLE 1. Infection types on seedlings of Avocet Susceptible (AvS) and Tyee produced by races of *Puccinia striiformis* f. sp. *tritici* under controlled greenhouse conditions

Race ^a	Virulence/avirulence formula on <i>Yr</i> genes ^b	Infection type	
		AvS	Tyee
PSTv-4	1,6,9,17,27,SP,Tye/5,7,8,10,15,24,32,43,44,Tr1,Exp2	8	8
PSTv-11	1,6,7,8,9,17,27,43,44,Exp2,Tye/5,10,15,24,32,SP,Tr1	8	8
PSTv-14	1,6,7,8,9,17,27,43,44,Tr1,Exp2,Tye/5,10,15,24,32,SP	8	8
PSTv-17	1,6,7,8,9,17,27,43,44,SP,Exp2,Tye/5,10,15,24,32,Tr1	8	8
PSTv-30	6,7,8,9,44,Tr1,Exp2/1,5,10,15,17,27,24,32,43,SP,Tye	8	2
PSTv-34	6,7,8,9,17,27,44,Tr1,Exp2/1,5,10,15,24,32,43,SP,Tye	8	2
PSTv-37	6,7,8,9,17,27,43,44,Tr1,Exp2/1,5,10,15,24,32,SP,Tye	8	2
PSTv-40	6,7,8,9,10,24,27,32,43,44,Tr1,Exp2/1,5,15,17,SP,Tye	8	1
PSTv-41	6,7,8,9,10,17,24,27,32,43,44,Tr1,Exp2/1,5,15,SP,Tye	8	2
PSTv-51	1,6,7,8,9,10,17,24,27,32,43,44,SP,Tr1,Exp2,Tye/5,15	8	8
PSTv-55	1,6,7,17,Exp2/5,8,9,10,15,24,27,32,43,44,SP,Tr1,Tye	8	2
PSTv-61	10,24,32,Tr1/1,5,6,7,8,9,15,17,27,43,44,SP,Exp2,Tye	8	2
PSTv-79	1,7,9,44/5,6,8,10,15,17,24,27,32,43,SP,Tr1,Exp2,Tye	8	2

^a PSTv races were differentiated using a set of wheat *Yr* single-gene lines as described in Wan and Chen (2014) and confirmed in the present study.
^b The 18 *Yr* single-gene line differentials are listed in Wan and Chen (2014).

MATERIALS AND METHODS

Development of a mapping population and a near-isogenic line. To map *YrTyee*, the winter club wheat Tyee was crossed with susceptible spring wheat genotype ‘Avocet Susceptible’ (AvS). Seedlings of Tyee and later F₂ plants were vernalized in a growth chamber at 4°C for 4 to 5 weeks before growing in the greenhouse for selfing and crossing. F₁, F₂, F_{2:3}, BC₁, and later generation progenies were generated either in a greenhouse or the field.

A near-isogenic line (NIL) BC₃F₃ was developed by backcrossing to AvS. Resistant BCF₁ plants were selected using race PSTv-37 which is avirulent on Tyee. Resistant BC₃F₁ and BC₃F₂ plants and BC₃F₃ lines were selected by stripe rust tests and flanking markers.

Evaluation of stripe rust reactions. Seedling tests were conducted under controlled greenhouse conditions as previously described (Chen and Line 1992a, b). Thirteen *P. striiformis* f. sp. *tritici* races (PSTv-4, PSTv-11, PSTv-14, PSTv-17, PSTv-30, PSTv-34, PSTv-37, PSTv-40, PSTv-41, PSTv-51, PSTv-55, PSTv-61, and PSTv-79) were used to test the responses of Tyee and AvS. These

Fig. 1. Reactions of Tyee and Avocet Susceptible (AvS) to different races of *Puccinia striiformis* f. sp. *tritici*.

races represented predominant races and/or various race groups (Wan and Chen 2014; Wan et al. 2016; A. M. Wan and X. M. Chen, unpublished data). PSTv-37, the most frequently identified race throughout the United States in the recent years, was used to test the F₂ and F_{2:3} populations derived from AvS × Tyee. The F_{2:3} lines were also tested with PSTv-40 and PSTv-79, both also avirulent on Tyee. Urediniospores of each race were increased on AvS, and their identities were confirmed by testing on the 18 differentials following previously described procedures (Wan and Chen 2014).

Seedlings of parents and F₂ and F_{2:3} populations were grown in the greenhouse. About 15 seeds of each parent, 135 seeds F₂, and 135 F_{2:3} lines each with about 15 seeds were planted in plastic pots (6 × 6 × 6 cm) filled with a potting medium (6 liters of peat moss, 2 liters of perlite, 3 liters of sand, 3 liters of potting soil mix, 4 liters of vermiculite, 300 ml of Osmocote, and 2 liters of water). Inoculations were conducted at the two-leaf stage as described by Chen and Line (1992a, b). Inoculated seedlings were kept in a dew chamber at 10°C for 24 h without light, and then grown in a growth chamber operating at 16 h light and 8 h darkness with diurnal temperatures gradually

TABLE 2. Seedling reactions of parents, F₁ plants, F₂ population, F_{2:3} lines and BC₁ plants from cross Avocet Susceptible (AvS) × Tyee to *Puccinia striiformis* f. sp. *tritici* race PSTv-37

Generation	No. of observed plants or lines			Expected ratio (Res: Seg: Sus)	P
	Resistant	Segregating	Susceptible		
AvS	0	–	15	–	–
Tyee	15	–	0	–	–
F ₁	5	–	0	–	–
F ₂	103	0	32	3: 1	0.73
F _{2:3} ^a	34	69	32	1: 2: 1	0.94
BC ₁	19	0	18	1: 1	0.87

^a The F_{2:3} population tested with races PSTv-40 and PSTv-79 produced the same numbers of resistant, segregating, and susceptible lines as in the test with race PSTv-37.

changing from 4°C at 2:00 a.m. to 20°C at 2:00 p.m. Infection type (IT) data were recorded 18 to 21 days after inoculation based on the 0 to 9 scale described by Line and Qayoum (1992).

DNA extraction and SSR marker analysis. Genomic DNA was extracted from leaf tissue of each F₂ plant and the parents using the method described by Riede and Anderson (1996). DNA was dissolved in TE buffer (10 mM Tris-HCl and 1 mM EDTA, pH 8.0). DNA quality was determined using 0.8% agarose gel electrophoresis, and the DNA concentration was measured using a NanoDrop ND-1000 (Thermo Scientific, Wilmington, DE). The stock DNA solution was diluted to 25 ng/μl with sterile deionized distilled (dd) H₂O for use as template in polymerase chain reaction (PCR).

TABLE 3. Amplicons of simple sequence repeat (SSR) markers flanking the *YrTy* locus in wheat genotype Tyee, Avocet Susceptible (AvS), Chinese Spring (CS), and 21 nulli-tetrasomic (NT), and nine deletions (Del) lines of CS

Wheat genotype	Amplicon of SSR marker (bp)	
	<i>wmc11</i>	<i>wmc532</i>
Parents and CS		
AvS	200	178
Tyee	204	182
CS	201	196
NT lines		
N3AT3D	Absent	Absent
All other 20 NT lines	201	196
Deletion lines		
Del 3AS-1	Absent	Absent
Del 3AS-2	Absent	Absent
Del 3AS-4	Absent	Absent
Del 3AL-3	201	196
Del 3AL-4	201	196
Del 3AL-5	201	196
Del 3AL-6	201	196
Del 3AL-7	201	196
Del 3AL-8	201	196

Fig. 2. Linkage map of Tyee/Avocet Susceptible (AvS) F₃ population showing *Yr76* (*YrTy*) on B, chromosome 3A and comparisons of the SSR markers in the consensus chromosome 3A maps of A, Song et al. (2005) and C, Somers et al. (2004) and D, Chinese Spring 3AS deletion map from the Kansas State University Wheat Genetics Resource Center (<http://www.k-state.edu/wgrc/Germplasm/Deletions/grp3S.html>).

Bulk segregant analysis (Michelmore et al. 1991) was used in screening simple sequence repeat (SSR) markers. Based on the IT data for individual F_2 plants and corresponding $F_{2,3}$ lines, a resistant bulk (RB) and a susceptible bulk (SB) were made with equal amounts of DNA sampled from 10 homozygous resistant (HR) and 10 homozygous susceptible (HS) F_2 plants. The DNA samples from Tyee, AvS, and the two bulks were used in screening 650 markers covering all chromosomes.

PCR were performed in volumes of 12 μ l comprising 4 μ l (100 ng) of template DNA, 1.2 μ l of 10 $\times$ buffer (with 1.5 mM $MgCl_2$), 0.48 μ l of $MgCl_2$ (25 mM), 0.96 μ l of mixed dNTP with 2.5 mM each, 0.24 μ l of M13 primer (10 μ M) with fluorescent dye, 0.12 μ l of *Taq* DNA polymerase (5 unit/ μ l), 0.06 μ l of forward primer with M13 tail (10 μ M), 0.3 μ l of reverse primer (10 μ M), and 4.64 μ l of sterilized ddH₂O. Buffer, dNTP, and *Taq* DNA polymerase were supplied by Promega Inc. (Madison, WI), and M13 fluorescent primers from Applied Biosystems (Grand Island, NY). SSR primers developed by Röder et al. (1998), Somers et al. (2004), and Song et al. (2005) were synthesized by Sigma-Aldrich Inc. (St. Louis, MO). PCR were performed in an ABI-9700 thermal cycler, programmed for 5 min of initial denaturation followed by 42 cycles, each cycle consisting of 1 min at 94°C, 1 min at 50 to 65°C annealing temperature depending on primers, and 1 min at 72°C, followed by extension of 10 min at 72°C. PCR products were detected on an ABI capillary DNA sequencer 3730 (Applied Biosystems, Foster City, CA), and the genotypes were analyzed using GeneMarker V2.2 (SoftGenetics, LLC, State College, PA).

Data analysis and molecular mapping. χ^2 tests were used to evaluate the goodness of fit of observed segregations to expected inheritance ratios. A linkage map including the molecular markers and stripe rust response as a qualitative trait was constructed with software JoinMap 4.0 (Voorrips 2002). Markers were placed in a linkage group with a minimum LOD (logarithm of odds) threshold of 3.0, and the most likely order of linked markers was determined by three-point linkage analysis. Map distances in centiMorgans (cM) were calculated from recombination fraction using the Kosambi mapping function (Kosambi 1943). The genetic map was drawn using software Mapdraw V2.1 (Liu and Meng 2003).

Chromosomal location of *YrTyee*. The chromosomal location of *YrTyee* was determined by the locations of SSR markers linked to the gene based on the consensus maps of Somers et al. (2004), Song et al. (2005), and the wheat chromosome information available at the GrainGenes website (<http://wheat.pw.usda.gov/GG3/maps-short>). To confirm the chromosomal location and map *YrTyee* to a chromosomal bin, Chinese Spring (CS), a complete set of 21 nulli-tetrasomic lines, and nine deletion lines of chromosome 3A were tested with SSR markers flanking the *YrTyee* locus based on the deletion maps of the Wheat Genetics Resource Center of Kansas State University (<http://www.k-state.edu/wgrc/Germplasm/Deletions/grp3S.html>).

Validation of markers flanking *YrTyee* and determination of their polymorphisms in wheat genotypes. A total of 140 wheat genotypes were used to validate the markers and to determine marker polymorphisms in various wheat cultivars and breeding lines. These genotypes included club wheat and common wheat cultivars and breeding lines developed and/or grown in the U.S. Pacific Northwest. These genotypes, together with AvS and Tyee, were tested at the seedling stage under controlled conditions as described above with three *P. striiformis* f. sp. *tritici* races (PSTv-37, PSTv-40, and PSTv-79) avirulent to Tyee and three races (PSTv-4, PSTv-14, and PSTv-51) virulent to Tyee. The genotypes were also tested with two markers flanking the resistance gene locus.

RESULTS

Inheritance of stripe rust resistance in Tyee. When tested with the thirteen races at the seedling stage and diurnal temperature (4 to 20°C) cycle, Tyee was resistant (IT 2) to PSTv-30, PSTv-34, PSTv-37, PSTv-40, PSTv-41, PSTv-55, PSTv-61, and PSTv-79, but susceptible (IT 8) to PSTv-4, PSTv-11, PSTv-14, PSTv-17, and

PSTv-51 (Table 1; Fig. 1). In contrast, AvS was susceptible (IT 8) to all of these races. Of the 135 F_2 plants from cross AvS/Tyee tested with PSTv-37 at the seedling stage, 103 were resistant (IT 0 to 2) and 32 were susceptible (IT 8 to 9) ($\chi^2_{3,1} = 0.12$, $P_{1df} = 0.73$) with an absence of intermediate types, indicating a single dominant gene for resistance (Table 2). Of the 135 $F_{2,3}$ lines, 32 were homozygous susceptible and all derived from susceptible F_2 plants; and 34 were homozygous resistant and 69 segregating, which were all from resistant F_2 plants. The segregation of $F_{2,3}$ lines fitted a 1 HR: 2 Seg: 1 HS ratio ($\chi^2_{1,2,1} = 0.13$, $P_{2df} = 0.94$). Tests of the $F_{2,3}$ lines with races PSTv-40 and PSTv-79 gave the same results. When 37 BC₁F₁ plants were tested with PSTv-37, 19 were resistant (IT 0 to 2) and 18 were susceptible (IT 7 to 9), fitting a 1:1 segregation ratio ($\chi^2_{1,1} = 0.03$, $P_{1df} = 0.97$). These results indicated that Tyee has a dominant gene for resistance to stripe rust.

Molecular mapping of *YrTyee*. Among 650 SSR markers covering all chromosomes initially screened, *wmc11* and *barc321* on chromosome 3AS were polymorphic between the two parents and bulks (Supplementary Fig. S1). To further delimit the position of *YrTyee* on chromosome 3A, additional 41 SSR markers on chromosome 3A were screened, 11 were found polymorphic between the parents and bulks. Segregation at all 13 marker loci in the mapping populations fitted single gene ratios. A linkage map for chromosome 3A based on the chromosomal location of the SSR markers compared with earlier maps (Somers et al. 2004; Song et al. 2005) is provided in Figure 2. The *YrTyee* locus was flanked by *wmc11* (2.6 cM distal) and *wmc532* (3.4 cM proximal).

To determine physical location of *YrTyee*, the two flanking markers were tested on CS and 21 nulli-tetrasomic lines representing all chromosomes and nine 3A deletion lines (Table 3). The CS alleles of the two markers were detected in all lines except N3AT3D-CS, Del 3AS-1, Del 3AS-2, and Del 3AS-4. Thus, *YrTyee* was located in the distal bin 3AS4-0.45 to 1.00 (Fig. 2). Because no any formally named *Yr* genes was located on chromosome 3AS, we designated *YrTyee* as *Yr76*.

Validation of flanking markers and their polymorphisms in various wheat genotypes. The reactions of 140 wheat genotypes to six *P. striiformis* f. sp. *tritici* races and amplicons at the *wmc11* and *wmc532* loci, together with those of AvS and Tyee, are presented in Table 4. Twenty-nine lines were resistant to the three Tyee-avirulent races (PSTv-37, PSTv-40, and PSTv-79) and therefore possibly carried *Yr76*. When tested with the flanking markers, five cultivars (ARS-Amber, ARS-Chrysal, Cara, Chukar, and Hyak), all with Tyee in their pedigrees, had the Tyee alleles of both markers, whereas 135 genotypes had either only one or neither Tyee allele.

Among the 135 wheat genotypes which do not have *Yr76*, 14 (10.37%) had the Tyee allele at the *wmc11* locus and 14 (10.37%) had the Tyee allele at the *wmc532* locus, but none has the Tyee alleles at both the marker loci. The results indicate that when the two markers are used together, the presence or absence of *Yr76* can be accurately determined.

Development of a NIL for *Yr76*. A homozygous spring habit F_3 line (AvS*4/Tyee F_3 -1) was selected from the AvS*4/Tyee cross based on stripe rust response and the presence of the flanking markers. The line closely resembles AvS morphology and responds to an array of *P. striiformis* f. sp. *tritici* races and can be used to replace Tyee in the differential set.

DISCUSSION

Due to its unique quality characteristics, club wheat is an important market class almost exclusively grown in the U.S. Pacific Northwest (Allan 2014). Prior to and when released in 1979, Tyee was highly resistant to stripe rust. So far, only a single gene, temporarily named *YrTyee*, has been identified in Tyee with U.S. *P. striiformis* f. sp. *tritici* races (Chen and Line 1992a, 1992b; Chen et al. 1995). The resistance is believed to be derived from Cltr 7805 (selection from PI 58787), a tetraploid introduction from Ethiopia (Allan 2014). This hypothesis can be accepted by the similar reactions to Tyee when tested with races avirulent or virulent to Tyee by early scientists in the USDA-ARS stripe rust program in

TABLE 4. Infection types produced by *Puccinia striiformis* f. sp. *tritici* on Avocet Susceptible (AvS), Tyee and 140 wheat cultivars or breeding lines and fragments amplified by primers for simple sequence repeat (SSR) markers *wmc11* and *wmc532*

Wheat	Growth habit or type ^a	Infection type produced by <i>P. striiformis</i> f. sp. <i>tritici</i> races						Size of fragment (bp)		
		PSTv-4	PSTv-14	PSTv-37	PSTv-40	PSTv-51	PSTv-79	<i>wmc11</i>	<i>wmc532</i>	Yr76
AvS	Spring	8	8	8	8	8	8	200	178	No
Tyee	Club	8	8	2	1	8	2	204	182	Yes
ARS-Amber	Winter	8	8	2	2	2	2	204	182	Yes
ARS-Chrysal	Club	2	8	2	2	2	2	204	182	Yes
Cara	Club	2	2	2	2	2	2	204	182	Yes
Chukar	Club	2	2	2	2	2	2	204	182	Yes
Hyak	Club	8	8	2	2	8	2	204	182	Yes
ARS010762-2C	Club	1	2	1	8	8	1	204	178	No
Buck Pronto	Spring	8	8	8	8	8	8	204	178	No
Cabernet	Spring	8	8	8	1	8	8	204	178	No
DH02-18-69	Winter	8	8	8	8	8	8	204	178	No
Eddy	Winter	8	8	8	8	8	8	204	178	No
Espresso	Spring	1	1	1	1	1	1	204	178	No
JD	SC	2	8	2	8	2	1	204	178	No
Louise	Spring	8	8	8	8	8	8	204	178	No
Otis	Spring	8	8	8	2	8	2	204	178	No
Solano	Spring	8	8	8	8	8	8	204	178	No
WA8163	Spring	2	2	2	2	2	2	204	178	No
WA8164	Spring	2	5	2	8	8	1	204	178	No
WB-1035CL+	Spring	8	8	8	8	8	8	204	178	No
WB-Rockland	Spring	1	1	1	1	1	1	204	178	No
Alum	Spring	8	8	8	2	8	8	184	182	No
SY605 CL	Spring	8	8	8	8	8	8	184	182	No
Zak	Spring	8	8	8	8	8	8	184	182	No
Boundary	Winter	8	8	8	8	8	8	184	182	No
IDO663	Winter	8	8	2	8	8	5	184	182	No
IDO816	Winter	2	2	5	8	8	2	184	182	No
Finley	Winter	2	2	8	8	8	2	184	182	No
Ladd	Winter	8	2	8	2	8	5	184	182	No
Kaseberg	Winter	8	8	8	8	8	8	184	182	No
ORCF-103	Winter	8	8	8	8	8	8	184	182	No
UI Silver	Winter	2	2	5	8	5	2	184	182	No
WA8153	Winter	8	8	8	8	8	8	184	182	No
WA8156	Winter	1	2	8	1	1	2	184	182	No
Lassik	Spring	2	2	2	2	2	2	200	182	No
LCS-Albany	Spring	8	8	8	8	8	8	180	178	No
Malbec	Spring	2	8	2	2	8	2	182	178	No
Mary	Winter	8	8	8	8	8	8	182	178	No
OR2080227H	Winter	2	2	2	2	5	5	182	178	No
ARS970161-2L	Club	2	8	2	8	8	1	184	178	No
ARS970277L	Club	1	2	8	2	5	5	184	178	No
ARS990077-1C	Club	1	8	2	6	2	1	184	178	No
ARS010780-3C	Club	1	2	3	8	2	1	184	178	No
ARS-Crescent	Club	2	8	8	8	5	1	184	178	No
Barbee	Club	2	2	1	8	8	2	184	178	No
Bruehl	Club	2	2	2	2	2	2	184	178	No
Coda	Club	2	2	2	8	2	1	184	178	No
Crew	Club	4	8	5	2	3	1	184	178	No
Hiller	Club	2	8	5	5	4	1	184	178	No
Rely	Club	2	8	1	5	2	1	184	178	No
Rohde	Club	2	1	2	8	5	1	184	178	No
Alpowa	Spring	8	8	8	8	8	8	184	178	No
Alturas	Spring	8	8	8	8	8	8	184	178	No
ARS03173LS	Spring	2	8	8	8	8	2	184	178	No
ARS03174CS	Spring	8	8	8	8	8	1	184	178	No
BR7030	Spring	5	2	8	5	8	2	184	178	No
Bullseye	Spring	8	8	8	2	8	8	184	178	No
Dayn	Spring	5	5	5	2	5	2	184	178	No
Glee	Spring	8	8	8	2	8	8	184	178	No
Hank	Spring	8	8	8	2	8	1	184	178	No
Hollis	Spring	2	8	8	2	8	2	184	178	No
IDO669	Spring	5	2	2	8	8	2	184	178	No
IDO671	Spring	8	8	8	8	8	8	184	178	No
IDO686	Spring	8	2	8	8	8	8	184	178	No
IDO687	Spring	8	8	8	8	8	8	184	178	No
IDO694	Spring	8	8	8	8	8	2	184	178	No
Jedd	Spring	8	2	2	2	5	2	184	178	No
Jefferson	Spring	8	2	8	2	8	8	184	178	No
Kelse	Spring	8	1	8	2	8	5	184	178	No
LCS-Powerplay	Spring	8	8	8	8	8	8	184	178	No

(continued on next page)

^a For the purpose of this study, the wheat entries are listed as either spring or winter of common wheat, or club wheat; all club entries are winter habit except JD, which is a spring type (SC).

TABLE 4. (continued from preceding page)

Wheat	Growth habit or type ^a	Infection type produced by <i>P. striiformis</i> f. sp. <i>tritici</i> races						Size of fragment (bp)		
		PSTv-4	PSTv-14	PSTv-37	PSTv-40	PSTv-51	PSTv-79	wmc11	wmc532	Yr76
Nick	Spring	8	8	8	8	8	8	184	178	No
Scarlet	Spring	8	8	8	8	8	5	184	178	No
Seahawk	Spring	1	1	1	1	1	1	184	178	No
Tara 2002	Spring	8	8	8	2	8	8	184	178	No
UI-Stone	Spring	8	8	8	8	8	8	184	178	No
UI-Winchester	Spring	2	8	8	2	8	1	184	178	No
Volt	Spring	8	2	2	2	2	2	184	178	No
WA8124	Spring	2	2	8	8	5	2	184	178	No
WA8160	Spring	2	2	8	8	8	2	184	178	No
WA8161	Spring	2	2	2	2	2	2	184	178	No
WA8165	Spring	8	8	8	2	8	2	184	178	No
WA8167	Spring	1	2	1	2	2	1	184	178	No
WA8168	Spring	8	8	8	8	8	2	184	178	No
Wakanz	Spring	8	8	8	2	5	8	184	178	No
WB-Fuzion	Spring	8	8	8	8	8	8	184	176	No
WB Hartline	Spring	8	8	8	2	8	2	184	178	No
Whit	Spring	8	8	8	8	8	8	184	178	No
ARS-Selbu	Winter	2	8	2	2	2	1	184	178	No
Azimut	Winter	3	2	5	8	2	2	184	178	No
Bauermeister	Winter	8	8	8	8	8	8	184	178	No
Curiosity CL+	Winter	2	2	5	5	2	2	184	178	No
Eltan	Winter	8	8	8	8	8	8	184	178	No
Genesi	Winter	8	8	8	8	8	2	184	178	No
LWW-04-4009	Winter	5	8	8	8	5	5	184	178	No
MDM	Winter	2	8	8	8	8	8	184	178	No
Mela CL+	Winter	2	8	8	8	8	2	184	178	No
OR08047P94	Winter	3	2	1	3	4	3	184	178	No
OR2080229H	Winter	8	5	2	8	5	8	184	178	No
OR2080236H	Winter	8	1	1	1	8	2	184	178	No
OR2701071	Winter	7	8	2	5	5	5	184	178	No
Raeder	Winter	2	2	1	8	5	3	184	198	No
Rod	Winter	8	2	3	5	8	8	184	178	No
Stephens	Winter	8	8	8	8	8	8	184	178	No
UICF-Grace	Winter	8	8	2	8	8	8	184	178	No
WA8092	Winter	3	8	2	8	2	2	184	178	No
WA8116	Winter	2	8	1	2	5	3	184	178	No
WA8136	Winter	5	8	5	8	2	2	184	178	No
WA8137	Winter	8	8	8	8	8	8	184	178	No
WA8151	Winter	8	8	5	8	8	5	184	178	No
WA8152	Winter	8	8	8	8	8	8	184	178	No
Xerpha	Winter	8	8	8	8	8	8	184	178	No
UI SRG	Winter	2	2	2	8	8	1	188	178	No
CW 515	Spring	2	1	2	2	2	2	200	178	No
Patwin 515	Spring	1	2	2	1	1	1	200	178	No
V272	Spring	2	8	8	8	8	2	200	178	No
Altigo	Winter	8	8	5	8	5	2	200	178	No
DH02-18-88	Winter	8	8	8	8	8	8	200	178	No
Madsen	Winter	8	2	2	2	8	2	200	178	No
Masami	Winter	8	8	8	8	8	8	200	178	No
Norwest 553	Winter	5	8	8	8	8	8	200	178	No
OR2080 156H	Winter	8	8	5	2	5	5	200	178	No
ORCF-102	Winter	8	8	8	8	8	8	200	178	No
Skiles	Winter	8	8	8	8	8	8	200	178	No
Tubbs 06	Winter	8	8	8	5	8	8	200	178	No
WA8061-10	Winter	2	5	8	8	5	2	200	178	No
WA 8115	Winter	8	8	8	8	8	2	200	178	No
WA8134	Winter	8	2	8	2	8	4	200	178	No
WA8135	Winter	8	8	8	8	8	5	200	178	No
WA8142	Winter	7	8	5	5	2	2	200	178	No
WA8157	Winter	5	8	2	8	8	2	200	178	No
WA8158	Winter	2	2	2	5	2	2	200	178	No
WA8159	Winter	5	8	2	8	5	2	200	178	No
WB-528	Winter	8	8	8	8	8	8	200	178	No
Babe	Spring	8	8	8	8	8	8	202	178	No
Diva	Spring	5	8	8	5	8	8	202	178	No
WA8131	Spring	2	2	2	2	2	2	202	178	No
Esperia	Winter	8	8	8	8	8	8	202	178	No
Farnum	Winter	2	8	8	8	8	3	202	178	No
Sprinter	Winter	2	8	2	2	2	2	202	178	No
WA8139	Winter	8	8	8	8	8	5	202	178	No
NSA06-2153A	Winter	5	8	5	8	5	2	202	196	No
WA8154	Winter	8	8	8	2	8	2	202	178	No
Percent (%) polymorphism for marker locus								89.6	89.6	
Percent (%) polymorphism for both marker loci								100.0		

1984 (<https://npgsweb.ars-grin.gov/gringlobal/accessiondetail.aspx?id=1041287>). Tyee was one of the major winter club wheat cultivars grown in the U.S. Pacific Northwest in the 1980s, and its derivative cultivars have been continually used for developing wheat cultivars especially club wheat. Based on the results of the present study, *YrTyee* is present only in winter club wheats, except ARS-Amber (PI 665047), a soft white common winter wheat cultivar (<https://npgsweb.ars-grin.gov/gringlobal/accessiondetail.aspx?id=1901441>) also developed in the USDA-ARS club wheat breeding program (K. Garland-Campbell, *unpublished data*). The resistance gene from Tyee is still useful when combined with other major or minor rust resistance genes. In fact, the high level and broad-spectrum resistance in several recently released club wheat cultivars, such as Chukar, Cara, and ARS-Crystal, and common wheat ARS-Amber shown in the present study, were achieved by combining the Tyee gene with other all-stage resistance genes and/or high-temperature adult-plant (HTAP) resistance genes (Garland-Campbell et al. 2005, 2013).

We confirmed that Tyee has a single gene for resistance to the majority of *P. striiformis* f. sp. *tritici* races. We constructed a genetic map with 13 SSR markers covering 100.9 cM, with the closest flanking markers being 2.6 proximal and 3.4 cM distal to *YrTyee*. Using CS 3A deletion lines, we located the gene in bin 3AS4-0.5 to 1.00. This study corrected the previous report suggesting the gene on chromosome 6D (Chen et al. 1995).

Only four temporarily named stripe rust resistance genes or quantitative trait loci (QTL) have been reported on chromosome 3A. *YrTr2* was located to chromosome 3A in club wheat cultivar Tres along with a second gene (*YrTr1*) for all-stage resistance. *YrTr2* alone provides resistance to only few races, and its chromosomal location is unknown (Chen et al. 1995). Because *YrTr1* confers resistance to more races than *YrTr2* and an NIL line in the AvS background has been developed for this gene (Wellings et al. 2004), the *YrTr1* NIL is included in the current set of *Yr* single-gene line differentials (Wan and Chen 2014). *YrTyee* and *YrTr1* display different race specificities (Wan and Chen 2014). Thus, *Yr76* (*YrTyee*) is different from either *YrTr1* or *YrTr2*. Lillemo et al. (2008) identified an unnamed QTL associated with adult-plant resistance to stripe rust on chromosome 3AS and linked to SSR marker *Xbarc310* in wheat cultivar Saar. Based on the map for this QTL, it is located 11.1 and 14.4 cM from *Xwmc11* and *Xwmc532*, respectively. Because of different types of resistance, *YrTyee* should be different from this QTL. *Yrq2* was mapped on chromosome 3AS in wheat line Xichang 76-9 but confers slow rusting (Cao et al. 2012), and therefore should be different from *YrTyee*. Through genome-wide association mapping, Jighly et al. (2015) reported a QTL on 3AS to confer seedling resistance, but neither the gene nor its location has been validated. Because of no any formally named *Yr* gene was previously located on chromosome 3AS (McIntosh et al. 2014), we named *YrTyee* as *Yr76*.

Marker-assisted selection is a powerful tool for pyramiding genes of important traits, including multiple genes for resistance to a single disease (Mallick et al. 2015; Yaniv et al. 2015). The value of any marker for breeding depends upon the closeness of linkage of a marker and gene of interest and on the uniqueness of the association between marker allele and gene source. In the present study, we identified flanking SSR markers, *wmc11* and *wmc532*, to *Yr76*; and these markers were highly polymorphic among different wheat varieties used in validation. Thus, the markers can be used to incorporate *Yr76* into various wheat backgrounds. As *Yr76* is race-specific, it should not be used alone. Therefore, combinations of this gene with other widely effective all-stage resistance genes such as *Yr5*, *Yr15*, *Yr45*, *Yr53*, *Yr61*, *Yr64*, *Yr65*, and *YrSP* (Chen et al. 2003; Cheng et al. 2014; Feng et al. 2015; Li et al. 2010; Murphy et al. 2009; Xu et al. 2013; Zhou et al. 2014a), and/or with genes for HTAP resistance such as *Yr36*, *Yr39*, *Yr52*, *Yr59*, *Yr62*, and many temporarily named QTL (Carter et al. 2009; Chen 2013; Lin and Chen 2007, 2009; Lu et al. 2014; Ren et al. 2012; Uauy et al. 2005; Zhou et al. 2014b) are recommended.

Tyee is an excellent differential for identifying *P. striiformis* f. sp. *tritici* races as it provides very clear low and high responses

with low probability of misclassification (Sharma-Poudyal et al. 2013; Wan and Chen 2014; Wan et al. 2016; Zhan et al. 2012). Race groups separated by virulence and avirulence on Tyee correspond to genetic groups separated by molecular markers (Cheng and Chen 2014; A. M. Wan and X. M. Chen, *unpublished data*). Because Tyee is the only winter wheat used in the current *Yr* single-gene differentials (Wan and Chen 2014), it often cannot be compared with other differential lines in the field for monitoring *P. striiformis* f. sp. *tritici* virulence. We developed a near-isogenic line of spring common wheat (AvS*4/TyeeF₃-1) carrying *Yr76*. Our preliminary result of this line is equal to Tyee in differentiating races. This spring wheat line with *Yr76* can be added to the AvS series and can be more easily used in stripe rust research worldwide.

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