Whole-Genome Mapping of Stripe Rust Resistance Quantitative Trait Loci and Race Specificity Related to Resistance Reduction in Winter Wheat Cultivar Eltan

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ABSTRACT

Winter wheat cultivar Eltan has been one of the most widely grown cultivars in the U.S. Pacific Northwest. It has shown variable levels of resistance to stripe rust in different years since it was released in 1990. To map all currently effective and defeated resistance genes in Eltan and understand the factors causing the resistance changes, 112 F_{2:5} recombinant inbred lines (RILs) were developed from a cross of Eltan with cultivar Avocet S. The RILs were evaluated in fields of Pullman, Washington in 2015, 2016, 2017, and 2018 and Mount Vernon, Washington in 2016 and 2017 under natural infections; they were also evaluated in the greenhouse with races PSTv-4 and PSTv-40 of *Puccinia striiformis* f. sp. *tritici*. The RILs were genotyped with the 90K Illumina iSelect wheat single-nucleotide polymorphism chip. A total of five quantitative trait loci (QTLs) were identified in Eltan. Two major QTLs

on chromosome arms 2BS and 4AL were detected in the greenhouse tests, explaining up to 28.0 and 42.0% of phenotypic variation, respectively. The two race-specific QTLs were also detected in some field experiments but with reduced effects. A minor QTL on 5BS was detected in the greenhouse and field tests, explaining 10.0 to 14.8% of the phenotypic variation. The other two minor QTLs were mapped on 6AS and 7BL and detected only in field experiments, explaining up to 20.5 and 13.5% of phenotypic variation, respectively. All stripe rust samples collected in the experimental fields in 2015 and 2016 were identified as *P. striiformis* f. sp. *tritici* races virulent on seedlings of Eltan. The resistance reduction of Eltan was caused by changes of the *P. striiformis* f. sp. *tritici* population from avirulent to virulent, overcoming the race-specific all-stage resistance in Eltan.

Stripe rust (also called yellow rust), caused by *Puccinia striiformis* Westend. f. sp. *tritici* Erikss., is one of the most devastating and economically important diseases across major wheat-growing regions in the world (Wellings 2011). In the United States, this disease was first observed in 1915 (Carleton 1915), and it has caused epidemics in the western United States since the late 1950s. Since the 1980s (especially the year 2000), wheat stripe rust has become increasingly more frequent and caused major damages in the regions east of the Rocky Mountains, making it an important disease throughout the inland United States (Chen et al. 2002; Line and Qayoum 1992). Under favorable conditions for the disease development, stripe rust can cause complete yield losses on susceptible cultivars in the U.S. Pacific Northwest (PNW) (Chen 2005). Based on experimental data, the long-term average yield loss

from 1975 to 2001 was 36% for susceptible winter wheat and 27% for susceptible spring wheat cultivars (Sharma-Poudyal and Chen 2011). However, the estimated average yield losses increased to 43.7 and 20.7% on susceptible winter and spring wheat varieties, respectively, for the period from 2002 to 2017 (Chen 2014; Chen et al. 2015, 2016, 2017, 2018). Although stripe rust resistance in wheat cultivars commercially grown during the same period was able to reduce potential yield losses to an average of 8.5%, chemical control to further reduce yield losses cost growers multimillions of dollars.

Epidemics of stripe rust usually occur with new virulent races and favorable weather conditions (Chen 2005; Wan et al. 2004). The long-distance migration, high rate of mutation, somatic recombination, and cultivar selection contribute to the constant change of *P. striiformis* f. sp. *tritici* populations (Chen 2005; Hovmöller and Justesen 2007; Lei et al. 2017). In the PNW, new races have been identified every year, and race composition is more diverse than in any other regions of the United States (Wan and Chen 2012, 2014; Wan et al. 2016). Traditionally, wheat breeders have selected breeding lines with strong all-stage resistance (ASR), which is usually controlled by a major gene and easy to incorporate into new cultivars. However, ASR is mostly race specific and can be easily overcome by new virulent races. If cultivars with race-specific ASR are widely grown, new virulent races may become widespread and cause large-scale epidemics. This was the case for the stripe rust epidemics in the United States in the early 2000s when races virulent to *Yr9* occurred in high frequency (Chen 2005, 2007; Chen et al. 2002, 2010). In contrast to ASR, adult plant resistance (APR) and high-temperature adult plant (HTAP) resistance to stripe rust are often nonrace specific and therefore, durable. However, APR and HTAP resistance are usually controlled by minor effect genes, and they are relatively difficult to incorporate into new cultivars. Also, because of the partial resistance and influences by temperature,

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plant growth stage, and disease pressure, APR and HTAP resistance may not provide adequate control (Chen 2005, 2013, 2014). For example, the cloned APR genes *Yr18* (Krattinger et al. 2009) and *Yr46* (Moore et al. 2015) and the HTAP resistance gene *Yr36* (Fu et al. 2009; Gou et al. 2015) are all nonrace specific and provide partial resistance. The best strategy is to combine several genes for effective ASR with APR or HTAP resistance to achieve high-level and durable resistance (Chen 2007, 2013, 2014).

Winter wheat cultivar Eltan (PI 536994) was developed from the cross Luke//BR-70443-4 (PI 167822/CI 013438) and released in 1990 (Peterson et al. 1991). Eltan was the most widely grown cultivar in the PNW from the late 1990s to the early 2000s. For example, Eltan was grown on 22.8% of winter wheat acreage in the state of Washington during the period of 2002 to 2012 (Chen 2014). Because of its wide adaptation in low- and intermediate-rainfall areas, Eltan has been one of the most important elite cultivars used in winter wheat breeding programs in the PNW. At the time of release, Eltan was moderately susceptible to some *P. striiformis* f. sp. *tritici* races but resistant to snow mold, common bunt, and dwarf bunt (Peterson et al. 1991). In field tests at various locations in the state of Washington, Eltan was highly resistant (mostly infection type [IT] = 0 to 3 and severity 0 to 10%; occasionally, IT = 5 to 8 and severity up to 50%) from 1999 to 2009. It had more frequent IT = 5 and severity readings in the range of 30 to 50% from 2010 to 2015. It has become more susceptible, with IT = 7 to 8 and severity in the range of 30 to 60% in more locations since 2016; these values were still much lower than the severity values of 90 to 100% of the susceptible checks (Chen et al. 2015, 2016, 2017, 2018) (X. M. Chen, unpublished data). Based on greenhouse tests, Eltan has both race-specific ASR and nonrace-specific HTAP resistance. The level of HTAP resistance seemed lower to the predominant races (with mostly IT = 5) in the tests from 2012 to 2018 than those from 2000 to 2011 (X. M. Chen, unpublished data). The Eltan resistance to stripe rust has become less effective in the last 20 years. However, the genes for stripe rust resistance in Eltan were not known, and it was not clear which genes are still effective and which are not. Therefore, this study was conducted to further characterize the stripe rust resistance in Eltan, determine the genetics of resistance, map all possible effective and defeated genes, and determine the factors causing the resistance changes in this important wheat cultivar. The information obtained in this study should be useful for breeding new wheat cultivars with durable, high-level resistance to stripe rust.

MATERIALS AND METHODS

Plant materials. Susceptible spring wheat cultivar Avocet S (AvS), Eltan, and 112 F_{2.5} recombinant inbred lines (RILs) of AvS × Eltan developed through single-seed decent were used for the tests for stripe rust phenotypes in the greenhouse and fields and DNA extraction for marker genotyping.

Characterization of stripe rust resistance in Eltan. Seedlings and adult plants of Eltan were tested in the greenhouse at both low- and high-temperature (HT) profiles as described in a four-way test (seedling: low temperature [LT], seedling: HT, adult: LT, and adult: HT) by Chen (2013). Five *P. striiformis* f. sp. *tritici* races were used in the test, including PSTv-4 (isolate 13-445), PSTv-14 (12-116), PSTv-37 (12-114), and PSTv-40 (09-78), which have been predominant races since 2000, and PSTv-18 (11-281-2G), which was the predominant race in the 1990s (Liu et al. 2017; Wan and Chen 2014). For seedling tests, six plants each of AvS and Eltan at the two-leaf stage were uniformly dust inoculated with a mixture of urediniospores of a specific race and talc at a ratio of 1:20 (Chen and Line 1992). Inoculated plants were kept in a dew chamber at 10°C for 24 h without light and then placed into two separate growth chambers: one with an LT diurnal cycle (4 to 20°C), and the other with an HT diurnal cycle (10 to 30°C); both had a 16-h light/8-h dark photoperiod (Chen 2013; Chen and Line 1995). For

adult plant tests, three plants each of AvS and Eltan were used for each race and each temperature profile. Flag leaves were dust inoculated, and plants were tested in the same conditions as described above. IT was recorded for each plant 18 to 20 days after inoculation based on a 0 to 9 scale (Line and Qayoum 1992).

Evaluating RILs for stripe rust reaction in the greenhouse. Races PSTv-4 and PSTv-40 were used for testing the RIL population in the greenhouse, because Eltan showed resistance and moderate resistance to the two races, respectively; by contrast, AvS was susceptible to both races. Around 15 plants of each RIL at the two-leaf stage were tested at LT (4 to 20°C). The inoculation method and test conditions were the same as in the seedling test described above. To identify HTAP resistance quantitative trait loci (QTLs), three plants for each RIL at the heading stage were tested with PSTv-4 at HT (10 to 30°C). The inoculation method and test conditions were the same as in the adult plant test described above. The parents AvS and Eltan were included in each test.

Evaluating RILs for stripe rust reaction in fields. The parents and F_{2.5} RILs were planted in the fields of Pullman (eastern Washington) and Mount Vernon (western Washington) in October 2014. The two locations are ~500 km apart and have different *P. striiformis* f. sp. *tritici* race composition as well as different weather conditions. The wheat lines were arranged in a randomized block design with three replications. Each replication consisted of one row of each F_{2.5} RIL and both parents, with the susceptible check PS279 included every 20 rows. Approximately 30 seeds of each F_{2.5} line were planted in a 50-cm row and spaced 20 cm apart in October 2014. The fields were managed with fertilizers and herbicides in the practice typical for each region. Stripe rust IT and disease severity (DS) data were recorded three times at late jointing-booting (Zadoks 39 to 45), heading-flowering (Zadoks 50 to 60), and milk-soft dough (Zadoks 75 to 85) stages (Zadoks et al. 1974) in June and July 2015 as previously described (Liu et al. 2018). DS data were used to calculate the area under the disease progress curve (AUDPC) (Chen and Line 1995), which was then converted to the relative area under the disease progress curve (rAUDPC) as the percentage of the AUDPC of the susceptible parent AvS (treated as 100% rAUDPC). The experiment was repeated in the 2015 to 2016 growing season the same way as in the previous year. An F_{2.6} RIL population was obtained by harvesting seeds from a single F_{2.5} plant for each line grown in the greenhouse for both DNA extraction and generation advancement. The F_{2.6} RILs and the parents were evaluated at both Pullman and Mount Vernon locations in the 2016 to 2017 crop season with three replications in each location. From the F_{2.6} plants grown in the Pullman location, a single head for each line was randomly harvested to obtain seeds of the F_{2.7} generation. In the 2017 to 2018 growth season, F_{2.7} RILs and parents were evaluated at Pullman without replications.

Statistical analyses of the phenotypic data. Analyses of variance (ANOVA) were performed for the rAUDPC and IT data using the “aov” function in R 3.5.1 (R Foundation for Statistical Computing, Vienna, Austria; <http://www.R-project.org/>) to determine the effects of genetic and environmental factors and their interaction. Broad-sense heritabilities (H^2) of phenotypic traits were calculated using the formula

$$H^2 = \sigma_G^2 / [(\sigma_G^2 + \sigma_{GE}^2/e) + \sigma_E^2/(e \times r)] \quad (1)$$

where σ_G^2 , σ_{GE}^2 , and σ_E^2 were genetic, genetic × environment, and error variances, respectively, whereas e and r represented the numbers of environments and replications, respectively (Lu et al. 2014). ANOVA and H^2 calculation were performed using the 2015, 2016, and 2017 field data, whereas the greenhouse tests and 2018 field experiment were not used in these analyses, because no replications were available. Pearson’s correlation coefficients of pairwise environments were calculated using both IT and rAUDPC data. Because the RILs were developed from a spring by winter

wheat cross, spring and winter wheat lines were compared for their reactions to stripe rust using Student *t* tests to determine whether the growth habits would affect stripe rust reactions.

Evaluating stripe rust samples for virulence. Ten leaf samples bearing stripe rust uredinia were randomly collected from RILs in both Pullman and Mount Vernon in 2015 and 2016. For each sample, urediniospores from one pustule were transferred onto AvS seedlings using a paint brush. Inoculated plants were kept in a dew chamber at 10°C for 24 h without light and then transferred to a growth chamber at the LT profile as described above. Urediniospores were collected 16 to 20 days after inoculation and used to inoculate seedlings of the *Yr* single-gene differentials: *Yr1*, *Yr5*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr10*, *Yr15*, *Yr17*, *Yr24*, *Yr27*, *Yr32*, *Yr43*, *Yr44*, *YrSP*, *YrTr1*, *YrExp2*, and *Yr76* (Wan and Chen 2014; Wan et al. 2016). The inoculation method and test conditions were the same as in the seedling tests at LT for Eltan as described above. IT data recorded 18 to 20 days after inoculation were used to obtain a formula of avirulent (IT = 0 to 6) and virulent (IT = 7 to 9) reactions on the set of differentials to identify the race for each stripe rust sample using a previously described method (Wan and Chen 2014; Wan et al. 2016). Eltan was included in the seedling tests to determine if it is resistant or susceptible to each of the stripe rust samples.

DNA extraction and molecular marker genotyping. Seedling leaves were collected from one single plant of each F_{2:5} RIL, AvS, and Eltan at two-leaf stage, and genomic DNA was extracted from each sample using the CTAB method (Clarke 2002). Quality and quantity of DNA were determined using 0.8% agarose gel electrophoresis and a spectrophotometer (NanoDrop ND-1000; Thermo Scientific, Wilmington, DE), respectively.

AvS, Eltan, and 112 RILs were genotyped using the 90K (81,587 markers) Illumina iSelect wheat single-nucleotide polymorphism (SNP) chip (Wang et al. 2014) at the U.S. Department of Agriculture Agricultural Research Service Biosciences Research Laboratory (Fargo, ND). SNP marker calling and clustering were performed using the GenomeStudio v2011.1 software package (Illumina, San Diego, CA), and manual correction was performed when calls were not correctly clustered by the clustering algorithm.

Linkage map construction and QTL analysis. Polymorphic SNP markers with <10% missing data were used for linkage map construction using JoinMap 4.1 (Van Ooijen 2006). Additional marker filter was conducted in JoinMap 4.1, including elimination of markers that did not fit a 1:1 segregation ratio at *P* > 0.01 and treating cosegregating markers as one. The regression mapping algorithm was used to assign linkage groups, and the Kosambi mapping function was used to convert genetic distances to centimorgans. Linkage groups were selected using a minimum logarithm (base 10) of odds (LOD) score of 3.0, and they were assigned to corresponding chromosomes based on the reported chromosomal locations of SNP markers (Wang et al. 2014). Linkage maps were drawn using MapChart v2.3 (Voorrips 2002).

Phenotypic data from nine greenhouse and field tests were used for QTL analysis. The greenhouse data included the IT data of seedling tests at LT with races PSTv-4 (PSTv-4_seedling low temperature [SLT]) and PSTv-40 (PSTv-40_SLT) and the adult plant test at HT with race PSTv-4 (PSTv-4_HTAP). The field data included IT and rAUDPC data of the field tests at Pullman in 2015, 2016, 2017, and 2018 and at Mount Vernon in 2016 and 2017. The data of the Mount Vernon location in 2015 were discarded, because many lines did not have plants owing to the spot flooding problem.

Fig. 1. Stripe rust reactions of cultivar Eltan at seedling stage to races A, PSTv-18, B, PSTv-4, C, PSTv-40, D, PSTv-14, and E, PSTv-37 of *Puccinia striiformis* f. sp. *tritici* tested at the low-temperature (4 to 20°C) profile and F, the adult plant stage inoculated with PSTv-4 in the greenhouse at the high-temperature (10 to 30°C) profile; they were recorded at the adult plant stage in fields of Pullman in G, 2015, H, 2016, I, 2017, and J, 2018 under natural *P. striiformis* f. sp. *tritici* infection.

When phenotypic data were recorded multiple times, the highest IT scores recorded were used in QTL analysis. QTL analysis was conducted using the “cim” function for composite interval mapping in the R/QTL 3.5.1 software package (Broman et al. 2003). A significance LOD threshold was calculated for each environment using 1,000 permutations at $P = 0.05$ (Churchill and Doerge 1994), and the threshold values ranging from 3.07 to 3.40 were used to declare significant QTLs in different environments. The phenotypic variation and additive effect of each QTL were determined using the “fitqtl” function. No significant interactions between QTLs were observed in any environments.

Amplification of Eltan with markers for stripe rust resistance genes previously mapped to the same chromosomes. To determine the relationships of Eltan QTL with previously reported resistance genes and QTL, sequence-tagged site (STS), simple sequence repeat (SSR), and Kompetitive allele-specific polymerase chain reaction (KASP) markers linked to the previously reported stripe rust resistance genes were tested on AvS and Eltan. These markers included KASP markers *660K-AN3*, *660K-AN21*, *660K-AN57*, and *660K-AN65* for *Qyrmap.nwafu-2BS* on 2BS (Wu et al. 2017); STS marker *Xsun104* for *Yr51* (Randhawa et al. 2014) and SSR markers *Xwmc219*, *Xwmc313*, and *Xwmc776* for *Yr60* (Herrera-Foessel et al. 2015) on 4AL; and SSR markers *Xgwm234* and *Xcjb309* for *Yr47* on 5BS (Bansal et al. 2011). KASP assays were conducted following the standard protocols provided by LGC Genomics (<https://www.lgcgroup.com/products/kasp-genotyping-chemistry/#.XC0HBIVKjcs>). Winter wheat Luke, which is in the pedigree of Eltan, was also evaluated with the four KASP markers on 2BS. Primers of the STS and SSR markers including the M13 tail were synthesized by Sigma-Aldrich (Atlanta, GA), and polymerase chain reaction (PCR) was conducted using the conditions described by Hou et al. (2015). PCR products were separated on an ABI3730 DNA fragment analyzer (Applied Biosystems, Grand Island, NY) and scored with the software GeneMarker v4.0 (SoftGenetics, LLC, State College, PA). Polymorphic SSR markers were tested on the RIL population and mapped to the linkage groups.

RESULTS

Stripe rust resistance in Eltan. In the four-way tests, Eltan was resistant at seedling stage to PSTv-4 (IT = 3) and moderately resistant to PSTv-40 (IT = 6), but it was susceptible to PSTv-14 (IT = 8) and PSTv-37 (IT = 8) at LT (Fig. 1). When adult plants were tested at HT, the cultivar had a higher level of resistance to PSTv-4 (IT = 2) and PSTv-40 (IT = 3) and became moderately resistant (IT = 5) to PSTv-14 and PSTv-37 (Table 1). Because both Eltan and AvS were resistant to PSTv-18 at seedling stage, this race was not included in additional analyses. When tested in fields, Eltan plants at heading-flowering stages were moderately resistant (IT = 4 to 6) to susceptible (IT = 7) but with relatively low DS values (DS = 30

TABLE 1. Infection types of seedling and adult plants of cultivar Eltan tested with four *Puccinia striiformis* f. sp. *tritici* races at the low-temperature (4 to 20°C) and high-temperature (10 to 30°C) profiles^a

Growth stage and temperature (°C)	Infection type				
	PSTv-4	PSTv-14	PSTv-18	PSTv-37	PSTv-40
Seedling					
4–20	3	8	2	8	6
10–30	3	8	2	8	5
Adult plant					
4–20	3	7	NT	8	4
10–30	2	5	NT	5	3

^a For comparison, cultivar Avocet S had infection types 8 to 9, but it had infection types 3 and 2 when tested with PSTv-18 at seedling stage at low- and high-temperature profiles, respectively. NT, not tested (because seedlings of Eltan were highly resistant).

to 60%) compared with the susceptible parent (AvS) and susceptible winter wheat check PS279 (DS = 95 to 100%) (Table 2). These results indicated that Eltan had race-specific ASR and a moderate level of HTAP resistance.

Reactions of RILs to stripe rust in the greenhouse and fields. In the seedling LT tests conducted in the greenhouse, the distribution of RIL responses was skewed toward high IT (Fig. 2). In contrast, a normal to skewed distribution toward low IT was observed in the adult plant HT test in the greenhouse. In the greenhouse tests, the population medium value of IT was high when tested with both PSTv-4 (6.5) and PSTv-40 (6.7) at SLT but became much lower (3.5) when tested with PSTv-4 at HTAP. Under the field conditions, the distributions of RILs responses were skewed toward high IT and rAUDPC, with the medium value ranging from 6.3 (MT17) to 7.8 (Pullman in 2015) for IT and from 63.1 (Pullman in 2015) to 86.8 (Mount Vernon in 2016) for rAUDPC.

Based on the ANOVA results, genetic and environmental factors and their interaction had significant effects on the observed phenotypic variations ($P < 0.001$) (Table 3). H^2 values were calculated as 0.90 and 0.89 using rAUDPC and IT data, respectively. Significant correlations ($P < 0.01$) were observed among all environments (Table 4). Correlation coefficients between pairwise environments ranged from 0.25 to 0.81 for the IT data and from 0.31 to 0.80 for the rAUDPC data. Relatively low correlation coefficients were observed between the pairwise greenhouse and field environments. No significant differences were detected between winter and spring RILs with both IT and rAUDPC data (Supplementary Table S1), indicating that growth habit did not influence the responses of RILs to stripe rust.

Virulence of stripe rust samples. Races, including their virulence formulae and octal codes, for the samples collected from the fields in 2015 and 2016 were summarized in Table 5. Eleven races were identified from a total of 40 samples. PSTv-37 (70%) was the most predominant race at Pullman in 2015, PSTv-37 (50%) and PSTv-39 (40%) were predominant at Mount Vernon in 2015, PSTv-37 (40%) and PSTv-52 (30%) were predominant at Pullman in 2016, and PSTv-75 (40%) and PSTv-131 (30%) were predominant at Mount Vernon in 2016. Race PSTv-37 was detected in all four environments, and PSTv-14 was detected only at Pullman in both 2015 (20%) and 2016 (10%). Because all of the races were virulent (IT = 7 to 8) on seedlings of Eltan, the resistance observed in the fields was attributed to APR.

TABLE 2. Mean infection type (IT) and disease severity (DS) of cultivar Avocet S (AvS) and cultivar Eltan tested with *Puccinia striiformis* f. sp. *tritici* at different growth stages in various environments^a

Environment	Growth stage		AvS		Eltan	
	Common term	Zadaks	IT	DS	IT	DS
Pu15	Heading-flowering	50–60	8	95	7	50
Pu16	Heading-flowering	50–60	8	100	4	50
MV16	Heading-flowering	50–60	8	100	4	60
Pu17	Heading-flowering	50–60	8	100	5	50
MV17	Heading-flowering	50–60	8	100	4	30
Pu18	Heading-flowering	50–60	8	100	6	50
PSTv-4_SLT	Two-leaf seedling	10	8	NR	3	NR
PSTv-40_SLT	Two-leaf seedling	10	8	NR	6	NR
PSTv-4_HTAP	Heading-flowering	50–60	8	NR	2	NR

^a The environments were field tests in Pullman 2015 (Pu15), Pullman 2016 (Pu16), Mount Vernon 2016 (MV16), Pullman 2017 (Pu17), Mount Vernon 2017 (MV17), and Pullman 2018 (Pu18) under natural infection and greenhouse tests at the seedling stage with *P. striiformis* f. sp. *tritici* races PSTv-4 (PSTv-4_seedling low temperature [SLT]) and PSTv-40 (PSTv-40_SLT) at the low-temperature (4 to 20°C) profile and the adult plant stage with *P. striiformis* f. sp. *tritici* race PSTv-4 at the high-temperature (10 to 30°C) profile (PSTv-4_high-temperature adult plant [HTAP]). In addition to AvS, winter wheat PS279 was included in the field tests as a susceptible check and had 95 to 100% DS at the adult plant stage. NR, not recorded.

Linkage map construction. After eliminating markers with >10% missing data, 13,853 polymorphic SNP markers generated by 90K SNP genotyping were used in the filtering process. After filtering out the markers with distorted segregation and cosegregating markers, 2,812 SNP markers were used to construct linkage groups. A total of 27 linkage groups were constructed, which spanned 2,418.46 cM. These linkage groups were assigned to corresponding chromosomes based on the chromosomal locations of SNP markers, with 16 chromosomes (1A, 1B, 1D, 2A, 2B, 3A, 3B, 4A, 4B, 4D, 5A, 5B, 6A, 6B, 7B, and 7D) each represented by a single linkage group, 4 chromosomes (3D, 5D, 6D, and 7A) each represented by two linkage groups, and chromosome 2D represented by three linkage groups. Markers in all linkage groups without cosegregating markers are given in Supplementary Table S2, and the cosegregating markers are provided in Supplementary Table S3. Figure 3 only shows the parts of linkage groups containing the mapped QTLs for stripe rust resistance.

QTL mapping for resistance at seedling stage. Three QTLs (*QYrel.wgp-2BS*, *QYrel.wgp-4AL*, and *QYrel.wgp-5BS*) were detected in the seedling tests with races PSTv-4 and PSTv-40 (Fig. 3 and Table 6). The major seedling resistance QTL *QYrel.wgp-2BS* was mapped to the centromeric region of chromosome 2BS, and it explained 5.8 and 28.0% of the phenotypic variation observed in the tests with PSTv-4 and PSTv-40, respectively. The other major QTL,

QYrel.wgp-4AL, was mapped to the distal region of chromosome 4AL with the closest marker *IWB45728*, and it explained 42.0% of the phenotypic variation detected in the seedling test with PSTv-4 and 21.0% when tested with PSTv-40. *QYrel.wgp-5BS* in the distal region of chromosome 5BS was a minor effect QTL detected only in the test with PSTv-4, and it explained 10.0% of the observed phenotypic variation. *QYrel.wgp-2BS* was more effective to PSTv-40, and *QYrel.wgp-4AL* was more effective to PSTv-4.

QTL mapping for resistance at adult plant stage. The ASR QTLs *QYrel.wgp-2BS*, *QYrel.wgp-4AL*, and *QYrel.wgp-5BS* that were detected in the greenhouse seedling tests at LT with PSTv-4 were also detected in the greenhouse adult plant test with the same race (Fig. 3 and Table 7). These QTLs also showed minor effects in some of the field experiments. In addition, two additional QTLs, *QYrel.wgp-6AS* and *QYrel.wgp-7BL*, were detected in some of the field experiments.

QYrel.wgp-2BS was detected with the IT data of the field experiments at Pullman in 2015, 2016, and 2017 and the greenhouse HTAP test with PSTv-4, explaining 7.2 to 15.8% of the phenotypic variation. *QYrel.wgp-4AL* was detected with the IT data of the Pullman 2016 and Mount Vernon 2016 field experiments and the greenhouse HTAP test, explaining 9.5 to 17.2% of the observed phenotypic variation. *QYrel.wgp-5BS* was detected in the field

Fig. 2. Box plot distributions of **A**, stripe rust infection type and **B**, relative area under the disease progress curve (rAUDPC) data for the cultivar Avocet S (AvS) × cultivar Eltan recombinant inbred line population tested in different environments. The solid horizontal lines show the median values. The top and bottom box edges show the first and third quartile values, respectively. Whiskers show the largest and smallest values within 1.5 times the interquartile range. Dots represent the values out of 1.5 times the interquartile range. The environments were field tests in Pullman 2015 (Pu15), Pullman 2016 (Pu16), Mount Vernon 2016 (MV16), Pullman 2017 (Pu17), Mount Vernon 2017 (MV17), and Pullman 2018 (Pu18) under natural infection and the greenhouse tests at the seedling stage with *Puccinia striiformis* f. sp. *tritici* races PSTv-4 (PSTv-4_seedling low temperature [SLT]) and PSTv-40 (PSTv-40_SLT) at the low-temperature (4 to 20°C) profile and the adult plant stage with PSTv-4 at the high-temperature (10 to 30°C) profile (PSTv-4_HTAP).

experiments at Mount Vernon in 2016 and 2017 and Pullman in 2018 as well as in the greenhouse HTAP test, explaining 10.4 to 14.8% of the phenotypic variation. *QYrel.wgp-6AS* was located in the distal region of chromosome 6AS, and it was only detected in the field experiments at Pullman in 2015, 2016, and 2018, with the rAUDPC data explaining 13.5, 11.6, and 20.5% of the phenotypic variations, respectively. *QYrel.wgp-7BL* was mapped close to the centromere on chromosome 7BL and detected only with the rAUDPC data from the field experiments at Pullman in 2016 and 2017 and Mount Vernon 2016, with the explained percentage of observed variation ranging from 8.6 to 13.5%.

In summary, relatively low QTL effects were detected in the field experiments and the HTAP test in the greenhouse. *QYrel.wgp-2BS* and *QYrel.wgp-4AL*, detected in the seedling tests, were only effective for the IT data from the field experiments. *QYrel.wgp-6AS*

and *QYrel.wgp-7BL*, detected only in field tests, were only effective for the rAUDPC data. The additive effects of the five QTLs detected in the RIL population differed with IT and rAUDPC data across the different environments (Table 7).

QTL comparison. When Eltan, Luke, and AvS were genotyped by KASP markers for *Qyrnap.nwafu-2BS* (Wu et al. 2017), *660K-AN3*, *660K-AN21*, *660K-AN57*, and *660K-AN65* produced the same haplotype (C; A; T; T) in both Eltan and Luke and a different haplotype (C; A; C; C) in AvS. The segregating KASP markers *660K-AN57* and *660K-AN65* were mapped close to the peak of *QYrel.wgp-2BS*, 1.3 and 0.4 cM away, respectively (Fig. 3), indicating that the QTL could be the same as *Qyrnap.nwafu-2BS*. STS marker *Xsun104* produced a 391-bp amplicon in Eltan and a 394-bp amplicon in AvS, significantly different from the 225-bp allele diagnostic for *Yr51*, which indicates that *QYrel.wgp-4AL* is different from *Yr51*. For the

TABLE 3. Analysis of variance for stripe rust infection type (IT) and relative area under the disease progress curve (rAUDPC) data in the cultivar Avocet S × cultivar Eltan recombinant inbred line (RIL) population tested in various environments

Source of variation	IT				rAUDPC			
	df ^a	MS ^b	F	P value	df ^a	MS ^b	F	P value
RIL	111	13.16	39.23	<0.0001	111	3,485.00	40.26	<0.0001
Environment	4	124.72	371.87	<0.0001	4	26,227.00	302.94	<0.0001
RIL × environment	441	1.51	4.50	<0.0001	441	446.00	5.15	<0.0001
Replication	2	0.25	0.75	0.47	2	396.00	4.57	0.01
Residual	1,089	0.34			1,089	87.00		

^a df = degree of freedom.

^b MS = mean square.

TABLE 4. Correlation coefficients (*r*) of stripe rust infection type and relative area under the disease progress curve (rAUDPC) data of the cultivar Avocet S × cultivar Eltan recombinant inbred line population tested in various environments^a

Environment	Correlation coefficient ^b								
	Pu15	Pu16	MV16	Pu17	MV17	Pu18	PSTv-4_SLT	PSTv-40_SLT	PSTv-4_HTAP
Pu16	0.61 (0.80)	1.00							
MV16	0.51 (0.45)	0.71 (0.43)	1.00						
Pu17	0.71 (0.69)	0.80 (0.70)	0.75 (0.59)	1.00					
MV17	0.55 (0.62)	0.78 (0.73)	0.78 (0.46)	0.81 (0.70)	1.00				
Pu18	0.54 (0.63)	0.65 (0.68)	0.46 (0.31)	0.59 (0.54)	0.58 (0.65)	1.00			
PSTv-4_SLT	0.25	0.58	0.50	0.45	0.51	0.43	1.00		
PSTv-40_SLT	0.32	0.54	0.47	0.50	0.49	0.35	0.65	1.00	
PSTv-4_HTAP	0.31	0.61	0.53	0.52	0.58	0.37	0.53	0.59	1.00

^a The environments were field tests in Pullman 2015 (Pu15), Pullman 2016 (Pu16), Mount Vernon 2016 (MV16), Pullman 2017 (Pu17), Mount Vernon 2017 (MV17), and Pullman 2018 (Pu18) under natural infection and greenhouse tests at seedling stage with *Puccinia striiformis* f. sp. *tritici* races PSTv-4 (PSTv-4_seedling low temperature [SLT]) and PSTv-40 (PSTv-40_SLT) at the low-temperature (4 to 20°C) profile and the adult plant stage with PSTv-4 at the high-temperature (10 to 30°C) profile (PSTv-4_high-temperature adult plant [HTAP]).

^b The *r* values based on rAUDPC data are given in parentheses when data are available. All correlation coefficients were significant at *P* < 0.01.

TABLE 5. Races of *Puccinia striiformis* f. sp. *tritici* identified from samples collected from the cultivar Avocet S × cultivar Eltan recombinant inbred lines tested in the fields in Pullman and Mount Vernon, Washington during the 2015 and 2016 growing seasons

Location/year	Number of isolates	Race	Octal code	Virulence formula ^a	Frequency (%)	IT ^b on Eltan seedlings
Pullman, 2015	10	PSTv-37	171266	6,7,8,9,17,27,43,44,Tr1,Exp2	70	8
Pullman, 2015	10	PSTv-14	571267	1,6,7,8,9,17,27,43,44,Tr1,Exp2,76	20	8
Pullman, 2015	10	PSTv-47	571266	1,6,7,8,9,17,27,43,44,Tr1, Exp2	10	8
Mount Vernon, 2015	10	PSTv-37	171266	6,7,8,9,17,27,43,44,Tr1,Exp2	50	8
Mount Vernon, 2015	10	PSTv-39	175266	6,7,8,9,10,17,27,43,44,Tr1,Exp2	40	8
Mount Vernon, 2015	10	PSTv-283	171264	6,7,8,9,17,27,43,44,Tr1	10	8
Pullman, 2016	10	PSTv-37	171266	6,7,8,9,17,27,43,44,Tr1,Exp2	40	8
Pullman, 2016	10	PSTv-52	171262	6,7,8,9,17,27,43,44,Exp2	30	8
Pullman, 2016	10	PSTv-14	571267	1,6,7,8,9,17,27,43,44,Tr1, Exp2,76	10	8
Pullman, 2016	10	PSTv-76	571262	1,6,7,8,9,17,27,43,44,Exp2	10	8
Pullman, 2016	10	PSTv-127	551072	1,6,7,9,17,43,44,SP,Exp2	10	7
Mount Vernon, 2016	10	PSTv-75	161062	6,7,8,17,43,44,Exp2	40	8
Mount Vernon, 2016	10	PSTv-131	160062	6,7,8,43,44,Exp2	30	7
Mount Vernon, 2016	10	PSTv-37	171266	6,7,8,9,17,27,43,44,Tr1,Exp2	20	8
Mount Vernon, 2016	10	PSTv-317	531235	1,6,8,9,17,27,44,SP,Tr1,76	10	8
Total	40	11				

^a The octal codes and virulence formulas were based on the 18 *Yr* single-gene differentials: *Yr1*, *Yr5*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr10*, *Yr15*, *Yr17*, *Yr24*, *Yr27*, *Yr32*, *Yr43*, *Yr44*, *YrSP*, *YrTr1*, *YrExp2*, and *Yr76* (Wan and Chen 2014; Wan et al. 2016).

^b IT, infection type.

Yr60 markers, *Xwmc219* amplified a 151-bp amplicon in AvS and a 156-bp amplicon in Eltan; *Xwmc313* amplified a 197-bp amplicon in AvS and a 208-bp amplicon in Eltan, and *Xwmc776* amplified a 196-bp amplicon in AvS but no amplicons in Eltan. All three markers were mapped in the *QYrel.wgp-4AL* region (Fig. 3), but *Xwmc776*, cosegregating with *Yr60*, failed to amplify any amplicon in Eltan. These results may suggest that *QYrel.wgp-4AL* and *Yr60* could be different alleles or closely linked genes. SSR marker *Xgwm234* produced a 239-bp amplicon in Eltan and a 249-bp amplicon in AvS, and the marker locus was mapped 8.6 cM distal of the *QYrel.wgp-5BS* (Fig. 3). Because the SSR marker *Xcfa309* produced a 370-bp amplicon in both Eltan and AvS, the marker locus could not be mapped in the AvS × Eltan population. These results indicated that *QYrel.wgp-5BS* was unlikely to be *Yr47*.

DISCUSSION

Eltan, the most widely grown winter wheat cultivar in the U.S. PNW region, has exhibited a range of resistance levels in the past 30 years. The variation in resistance level can be attributed to the changes of predominant races circumventing ASR and the effects of environmental conditions and disease pressure on HTAP resistance in Eltan. In this study, five QTLs were identified for resistance to stripe rust in Eltan, with two major QTLs and one minor QTL for ASR and two additional QTLs for HTAP resistance detected in the field experiments. Stripe rust samples collected from the RILs in the field experiments of 2015 and 2016 were identified as races virulent on the seedlings of Eltan. Races avirulent to seedlings of Eltan, such as PSTv-4 and PSTv-40 that were predominant in the PNW region

Fig. 3. Linkage groups for quantitative trait loci (QTL) *QYrel.wgp-2BS*, *QYrel.wgp-4AL*, *QYrel.wgp-5BS*, *QYrel.wgp-6AS*, and *QYrel.wgp-7BL* for resistance to stripe rust mapped in the cultivar Avocet S (AvS) × cultivar Eltan recombination inbred population. The map shows the selected portions of the linkage groups containing the QTL; the markers for the entire chromosomes of the five linkages and the remaining 16 chromosomes are not shown.

TABLE 6. Quantitative trait loci (QTLs) for resistance to races PSTv-4 and PSTv-40 of *Puccinia striiformis* f. sp. *tritici* detected in the cultivar Avocet S × cultivar Eltan recombinant inbred line population tested at the seedling stage in the greenhouse under the low-temperature (4 to 20°C) profile^a

QTL and race	Closest marker	Peak position (cM)	LOD	R ^{2b} (%)	AE ^c
<i>QYrel.wgp-2BS</i>					
PSTv-4	<i>IWB26735</i>	57.55	3.42	5.78	-0.35
PSTv-40	<i>IWB32259</i>	54.41	12.72	27.98	-0.41
<i>QYrel.wgp-4AL</i>					
PSTv-4	<i>IWB45728</i>	129.84	17.72	41.98	-0.87
PSTv-40	<i>IWB45728</i>	129.84	8.70	21.02	-0.35
<i>QYrel.wgp-5BS</i>					
PSTv-4	<i>IWB56395</i>	13.35	4.58	9.97	-0.51

^a AE, additive effect; LOD, logarithm (base 10) of odds.

^b R² value was measured as the percentage of the total observed phenotypic variation explained, indicating the effect of the QTL.

^c A negative value indicates that the resistance allele is from Eltan.

from 2000 to 2009 and PSTv-18 that was predominant in the 1990s (Liu et al. 2017; Wan and Chen 2012, 2014), were not detected from the samples collected from the fields for RIL phenotyping. Similarly, the races avirulent to Eltan at seedling stage were detected in very low frequencies in the whole PNW region, but PSTv-37 virulent to seedling Eltan was the predominant race in the region from 2015 to 2018 (A. M. Wan, M. N. Wang, and X. M. Chen, *unpublished data*). Thus, reduction of resistance may have been caused by the appearance and frequency increase of virulent races circumventing ASR. The race-specific ASR QTLs (*QYrel.wgp-2BS*, *QYrel.wgp-4AL*, and *QYrel.wgp-5BS*), which were detected in the greenhouse tests of both seedling and adult plant stages with avirulent race PSTv-4, still showed some residual effects in the fields where virulent races, like PSTv-37, were predominant. In addition, two minor QTLs (*QYrel.wgp-6AS* and *QYrel.wgp-7BL*) conferring nonrace-specific HTAP resistance in Eltan were detected in the fields. The combination of residual race-specific resistance and HTAP resistance has reduced potential yield losses of Eltan by >50% (Chen 2014; Chen et al. 2015, 2016, 2017, 2018).

QYrel.wgp-2BS is an ASR QTL on chromosome 2BS close to the centromere, and it is more effective to race PSTv-40 than to PSTv-4. ASR genes *Yr27* (McDonald et al. 2004) and *Yr41* (Luo et al. 2005) were mapped close to *QYrel.wgp-2BS*. *Yr27* is present in many International Wheat and Maize Improvement Center wheat lines and widely deployed in cultivars in India, Ethiopia, Iran, Pakistan, and Syria. *Yr41* was identified in Chinese wheat AIM6 and is present in other Chinese wheat lines. Based on the pedigree of Eltan, these two genes are not possible in Eltan, making *QYrel.wgp-2BS* likely different from *Yr27* and *Yr41*. Winter wheat Luke is in the pedigree of Eltan, and two QTLs on 2BS *QYrlu.cau-2BS1* and *QYrlu.cau-2BS2* were identified in Luke, with *QYrlu.cau-2BS2* mapped close to the centromere (Guo et al. 2008). It is very likely that *QYrel.wgp-2BS* is the same QTL as *QYrlu.cau-2BS2* in Luke. *Qyrnap.nwafu-2BS* in wheat variety Napo 63 (Wu et al. 2017) was also mapped close to *QYrel.wgp-2BS*. Four KASP markers

developed to detect *Qyrnap.nwafu-2BS* were used to genotype AvS, Eltan, and Luke. Eltan and Luke had the same haplotype of the four KASP markers, confirming that Eltan inherited the haplotype from Luke based on Eltan's pedigree (Peterson et al. 1991). However, our haplotype (C; A; T; T) of Luke and Eltan was different from their haplotype (A; G; T; T) of Luke and Napo 63 (the parent carrying *Qyrnap.nwafu-2BS*) (Wu et al. 2017). The difference might be caused by different Luke plants used in the different experiments. Because Napo 63 was not available in our study, we could not confirm its haplotype, although AvS had the same haplotype in both studies. Because two KASP markers (660K-AN57 and 660K-AN65) were mapped so close to the peak of *QYrel.wgp-2BS* (only 1.3 and 0.4 cM in distance, respectively), it is likely the same as *Qyrnap.nwafu-2BS*. In a 2018 study, *QYr.ucw-2BS* was identified in the region of *QYrel.wgp-2BS* from an Argentinean wheat cultivar (Cobo et al. 2018). RILs carrying only *QYr.ucw-2BS* (IT = 4) were more resistant to PSTv-4 than *QYrel.wgp-2BS* (IT = 6 to 7), and therefore, these two QTL should be different.

QYrel.wgp-4AL was the other major ASR QTL in Eltan mapped to the distal region of 4AL. One minor QTL in the centromeric region of 4AL was also detected in Eltan in one field environment (Pullman 2016). Because the minor QTL did not reach threshold (LOD = 3.02), it was not reported in this study. *QYrel.wak-4A*, mapped to the centromeric region of 4AL, was detected in the Finch × Eltan RIL population in fields (Klarquist et al. 2016). *QYrel.wak-4A* should be the same minor QTL as detected in this study, whereas *QYrel.wgp-4AL* is a major effect ASR QTL, different from *QYrel.wak-4A*. *Yr51* and *Yr60* were also mapped close to *QYrel.wgp-4AL* (Herrera-Foessel et al. 2015; Randhawa et al. 2014). Because Eltan does not have the diagnostic 225-bp marker of *Xsun104* for *Yr51*, *QYrel.wgp-4AL* should be different from *Yr51*. Although *Xwmc219*, *Xwmc313*, and *Xwmc776* for *Yr60* were mapped to the region of *QYrel.wgp-4AL*, *Yr60* cosegregating marker *Xwmc776* failed to amplify any products in Eltan, making *QYrel.wgp-4AL* different from *Yr60*. Therefore, *QYrel.wgp-4AL* is a novel gene for ASR to stripe rust.

TABLE 7. Quantitative trait loci (QTLs) for stripe rust resistance detected in the cultivar Avocet S × cultivar Eltan recombinant inbred line population at the adult plant stage in the fields under natural infection and the greenhouse with race PSTv-4 of *Puccinia striiformis* f. sp. *tritici* at the high-temperature (10 to 30°C) profile^a

QTL and experiment data	Closest marker	Peak position (cM)	LOD	R ^{2b} (%)	AE ^c
<i>QYrel.wgp-2BS</i>					
Pu15-IT	<i>IWB26735</i>	57.55	3.92	11.38	-0.11
Pu16-IT	<i>IWB26735</i>	57.55	6.54	15.84	-0.58
Pu17-IT	<i>IWB32259</i>	54.41	3.21	7.63	-0.29
PSTv-4_HTAP	<i>IWB32259</i>	54.41	3.60	7.21	-0.54
<i>QYrel.wgp-4AL</i>					
Pu16-IT	<i>IWB45728</i>	129.84	4.01	9.52	-0.40
MV16-IT	<i>IWB45728</i>	129.84	4.29	10.85	-0.35
PSTv-4_HTAP	<i>IWB45728</i>	129.84	7.83	17.18	-0.81
<i>QYrel.wgp-5BS</i>					
MV16-IT	<i>IWB56395</i>	12.94	3.84	10.38	-0.36
MV17-IT	<i>IWB56395</i>	12.94	5.21	13.49	-0.65
MV17-rAUDPC	<i>IWB56395</i>	12.94	6.51	14.75	-8.96
Pu18-IT	<i>IWB56395</i>	12.94	4.99	12.01	-0.43
PSTv-4_HTAP	<i>IWB56395</i>	13.35	5.10	10.59	-0.67
<i>QYrel.wgp-6AS</i>					
Pu15-rAUDPC	<i>IWB6565</i>	13.30	5.27	13.54	-8.62
Pu16-rAUDPC	<i>IWB6666</i>	13.76	5.42	11.56	-6.64
Pu18-rAUDPC	<i>IWB7466</i>	11.89	8.45	20.48	-10.50
<i>QYrel.wgp-7BL</i>					
Pu16-rAUDPC	<i>IWB4739</i>	45.15	5.05	10.65	-6.49
MV16-rAUDPC	<i>IWB4739</i>	45.15	4.20	8.62	-6.39
Pu17-rAUDPC	<i>IWB4739</i>	45.15	5.21	13.53	-4.46

^a The environments were field tests in Pullman 2015 (Pu15), Pullman 2016 (Pu16), Mount Vernon 2016 (MV16), Pullman 2017 (Pu17), Mount Vernon 2017 (MV17), and Pullman 2018 (Pu18) under natural infection and greenhouse test at adult plant stage with race PSTv-4 at the high-temperature (10 to 30°C) profile (PSTv-4_high-temperature adult plant [HTAP]). The datasets were infection type (IT) and relative area under the disease progress curve (rAUDPC). AE, additive effect; LOD, logarithm (base 10) of odds.

^b R² value was measured as the percentage of the total observed phenotypic variation explained, indicating the effect of the QTL.

^c A negative value indicates that the resistance allele is from Eltan.

QYrel.wgp-5BS was identified as a minor effect ASR QTL, effective against race PSTv-4 and in some field experiments. Only ASR gene *Yr47* (Bansal et al. 2011; Qureshi et al. 2017) was mapped close to *QYrel.wgp-5BS*. *Yr47* is tightly linked with leaf rust resistance gene *Lr52*, whereas Eltan is susceptible to leaf rust (Peterson et al. 1991). In addition, both *Xgwm234* and *Xcwb309* flanking *Yr47* amplified alleles in Eltan different from those in the *Yr47*-carrying variety. This evidence indicates that *QYrel.wgp-5BS* is different from *Yr47*.

QYrel.wgp-6AS was only detected in some field experiments with the rAUDPC data. On the short arm of 6A, *Yr38* (Marais et al. 2006), *Yr42* (Marais et al. 2009), *QYrex.wgp-6AS* (Lin and Chen 2009), and *QYr.uga-6AS* (Hao et al. 2011) were located closely to *QYrel.wgp-6AS*. *Yr38* and *Yr42* were transferred from wild wheat relatives. *QYrex.wgp-6AS* and *QYr.uga-6AS* are HTAP resistance QTLs detected in spring wheat cultivar Express and winter wheat cultivar Pioneer 26R61, respectively. The relationships of *QYrel.wgp-6AS* with these two HTAP resistance QTLs need additional studies. Similar to *QYrel.wgp-6AS*, *QYrel.wgp-7BL* was also detected only in some field tests with rAUDPC data. A major HTAP resistance gene *Yr39* was mapped in the same region as *QYrel.wgp-7BL* (Lin and Chen 2007). *QYrel.wgp-7BL* might be the same as *Yr39*, but additional studies are needed to determine their relationship.

In summary, two major effect QTLs and one minor effect QTL for ASR and two QTLs for HTAP resistance were identified in Eltan. All QTLs were detected in multiple environments, and the relationships of the QTLs with previously reported genes or QTLs need additional confirmation. Although Eltan has five QTLs that provide a high level of resistance when avirulent races are predominant, the cultivar can have significant yield losses when virulent races are in a higher proportion. However, the partially defeated race-specific ASR can still make some contributions to residual resistance, which together with the low to moderate level of HTAP resistance, has prevented Eltan from becoming completely susceptible. Nevertheless, new cultivars should have a much higher level of resistance than Eltan. Because Eltan is a major elite cultivar in the PNW, it can be used in crosses with other resistant germplasm for developing new cultivars with durable, high-level resistance to stripe rust by combining its QTLs with other genes for effective ASR and HTAP resistance as well as its other desirable agronomic traits. The molecular markers identified in this study should be useful for marker-assisted selection of the stripe rust resistance QTLs from Eltan.

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