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Special Issue: Rust Diseases of Field Crops and Forest Trees

High density genetic mapping of stripe rust resistance in a ‘Strongfield’ / ‘Blackbird’ durum wheat population

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Abstract: Resistance breeding is an effective strategy against wheat stripe (yellow) rust caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*). To identify and map quantitative trait loci (QTL) associated with stripe rust resistance, a durum wheat doubled haploid population ($n = 87$) derived from ‘Strongfield/Blackbird’ was evaluated for disease severity near Toluca, Mexico (2017–2019) and Lethbridge, Canada (2016–2019). The population was genotyped with the wheat 90 K Illumina iSelect single nucleotide polymorphism (SNP) array and simple sequence repeat (SSR) markers, and QTL analysis was performed with MapQTL 6. We identified stripe rust-resistance QTL contributed by ‘Blackbird’ on chromosomes 3A (2 loci, designated *QYr.spa-3A.1*, *QYr.spa-3A.2*) and 5B (*QYr.spa-5B*), and ‘Strongfield’ on 2B (*QYr.spa-2B*). All seem to represent QTL not reported previously. The *QYr.spa-3A.2* was most consistently effective against *Pst* races across the Lethbridge and Toluca nurseries. With a LOD value of 4.9, *QYr.spa-3A.2* explained a maximum phenotypic variation of 22.7% observed at the Toluca 2019 nursery. The *QYr.spa-2B* from ‘Strongfield’ and *QYr.spa-3A.1* from ‘Blackbird’ expressed in multiple years at Toluca but were not detected at Lethbridge. *QYr.spa-5B* was identified in the Lethbridge 2016 environment. The identified QTL should be valuable in diversifying resistance genes used in breeding durum wheat cultivars with stripe rust resistance. ‘Blackbird’ was particularly useful for introducing the new QTL *QYr.spa-3A.2* resistance that is effective in Canada and Mexico into traditional durum wheat germplasm. SNP markers associated with QTL will have application in marker-assisted breeding of resistance to *Pst* in durum wheat.

Keywords: durum wheat, QTL mapping, resistance, SNP markers, stripe rust

Résumé: La sélection pour la résistance est une stratégie efficace contre la rouille (jaune) causée par *Puccinia striiformis* f. sp. *tritici* (*Pst*). Pour identifier et cartographier les locus à caractère quantitatif (QTL) associés à la résistance à la rouille, une population dihaploïde de blé dur ($n = 87$) dérivée de ‘Strongfield/Blackbird’ a été évaluée pour la gravité de la maladie près de Toluca, au Mexique (2017 à 2019), et de Lethbridge, au Canada (2016 à 2019). La population a été génotypée avec la puce Illumina iSelect 90K de polymorphisme à nucléotide simple (SNP) et des marqueurs à séquences répétitives simples (SSR), puis on a procédé à l’analyse QTL avec MapQTL 6. Nous avons identifié le QTL de résistance à la rouille fourni par ‘Blackbird’ sur les chromosomes 3A (2 locus, désignés *QYr.spa-3A.1*, *QYr.spa-3A.2*) et 5B (*QYr.spa-5B*), et par ‘Strongfield’ sur 2B (*QYr.spa-2B*). Tous semblent représenter des QTL jamais rapportés auparavant. Le locus *QYr.spa-3A.2* était le plus constamment efficace contre les races de *Pst* dans les pépinières de Lethbridge et de Toluca. Avec un LOD score de 4,9, *QYr.spa-3A.2* expliquait un maximum de 22,7% de variations génotypiques à la pépinière de Toluca en 2019. Le locus *QYr.spa-2B* de

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‘Strongfield’ et le *QYr.spa-3A.1* de ‘Blackbird’ se sont exprimés depuis plusieurs années à Toluca, mais n’ont pas été détectés à Lethbridge. *QYr.spa-5B* a été identifié dans l’environnement de Lethbridge de 2016. Le QTL identifié devrait être utile pour diversifier les gènes de résistance utilisés pour sélectionner les cultivars de blé dur résistants à la rouille. ‘Blackbird’ a été particulièrement utile pour introduire la nouvelle résistance basée sur le QTL *QYr.spa-3A.2* qui est efficace au Canada et au Mexique dans les germoplasmes de blés durs traditionnels. Les marqueurs SNP associés au QTL serviront à la sélection assistée par marqueurs pour la résistance à *Pst* chez le blé dur.

Mots clés: Blé dur, cartographie des QTL, résistance, marqueurs SNP, rouille jaune

Introduction

Canada is a major durum (*Triticum turgidum* spp. *durum* (*Desf*) Husn.) wheat-producing country with about three times the combined production of the United States and Mexico (Sopiwnyk 2018). For the period 2016–2020 inclusive, Canada produced an average of 6.4 MMT (Statistics Canada 2021). Global durum production for the same period is about 40 million metric tons (International Grains Council [IGC] 2020). Stripe (yellow) rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Eriks. (*Pst*) is a fungal pathogen that threatens production of durum wheat and bread wheat (*Triticum aestivum* L.) globally (Line 2002; Milus et al. 2009; Lyon and Broders 2017). Stripe rust was first reported in North America in 1915 (Carleton 1915; Line 2002). Until 2000, *Pst* was confined to the Pacific Northwest (PNW) regions in the USA, British Columbia, and southern Alberta (Aboukhaddour et al. 2020). Severe epidemics occurred in the 1960s followed by the most widespread epidemic in 2000, and thereafter (Chen et al. 2002; Line 2002; Chen 2007).

Pst is adapted to cool environmental conditions and may survive under mild winter conditions by reproducing asexually (Lin et al. 2018). However, epidemics that have occurred since 2000 in North America, Australia and Europe were mainly due to change in adaptation by the fungus allowing the incursions of more aggressive *Pst* lineages from cooler and wetter areas to the warmer and drier regions where it was previously infrequent or absent (Wellings 2007; Hovmöller et al. 2008, 2011; Milus et al. 2009; Chen et al. 2014; Beddow et al. 2015; Ali et al. 2017; Lyon and Broders 2017). The newer, more aggressive *Pst* pathogen genotypes can also infect previously resistant wheat cultivars, leading to rapid pathogen migration across and between continents (Hovmöller et al. 2008; Schwessinger 2017). For example, the two dominant *Pst* strains *PstS1* and *PstS2* have become adapted to high temperatures (Hovmöller et al. 2008; Brar et al. 2018; De Vallavieille-pope et al. 2018). *PstS1* was predominant in North America, *PstS2* in West Asia and North Africa, and both *PstS1* and *PstS2* in East Africa (Ali et al. 2017; Brar et al. 2018). *PstS1* and *PstS1*-related races are dominant in

western Canada (Brar et al. 2019). Similarly, the geographic range of *Pst* has expanded in the United States, and the old population of races was replaced by a new population (Milus et al. 2006; Markell and Milus 2008). The new races are better adapted and, thus, more aggressive at warmer temperatures than the old isolates (Milus et al. 2006; Brar et al. 2019) posing severe threats to current wheat production.

In Canada, stripe rust was mainly a problem in the western provinces of British Columbia and southern Alberta before 2000, but it later expanded to Saskatchewan, and the eastern provinces of Manitoba and Ontario (Chen 2005; Fetch et al. 2011; Brar et al. 2019). Up to about 2000, stripe rust infections were occasionally observed after mid-August in spring planted winter wheat cultivars ‘Norstar’ (Grant 1980) and ‘CDC Kestrel’ (Fowler 1997) in irrigated disease nurseries near Swift Current, SK. About the year 2002, stripe rust symptoms were observed in juvenile wheat plants on both irrigated and dryland by mid-July. In 2005, stripe rust symptoms observed in late June on dryland wheat in the semiarid region was really startling. The source of these infections in Canada was unknown, but it is possible to be from the ‘Puccinia pathway’ along the Pacific coast starting from north-western Mexico or the great central plains pathway starting from north central Mexico or from overwintering on winter wheat or foxtail barley (*Hordeum jubatum* L.) (Brar et al. 2019).

Eighty-three *Yr* genes have been formally documented to date (McIntosh et al. 2018a; Li et al. 2020; McIntosh et al. 2020). The majority of the genes belong to all-stage (seedling) resistance (ASR) and a few to adult-plant resistance (APR) (Chen 2007; Schwessinger 2017; Jamil et al. 2020). ASR genes are characterized by a strong to moderate immune response that fully curtails fungal infection and sporulation at all developmental stages (Schwessinger 2017). Unlike ASR, APR genes express at the adult plant stage and provide more durable resistance (Chen et al. 2014; Rinaldo et al. 2017; Schwessinger 2017). APR *Yr* genes are generally effective against multiple races of *Pst*. *Yr* genes such as *Yr7* (Zhang et al. 2009), *Yr15* (Klymiuk et al. 2018), *Yr24/Yr26* (McIntosh et al. 2018b), *Yr30/Sr2* (Randhawa et al. 2018) and *Yr36* (Uauy et al. 2005) originate from

tetraploid wheat. *Yr36* is known to confer high-temperature adult-plant (HTAP) resistance (Uauy et al. 2005). Furthermore, QTL conferring stripe rust resistance in durum wheat have been reported (Singh et al. 2013; Lin et al. 2018).

Control of *Pst* can be achieved with fungicides and/or genetic resistance. Genetic resistance is the most economically and environmentally sustainable strategy for controlling wheat stripe rust. The stripe rust pathogen has a rather high mutation rate from avirulence to virulence (Hovmöller and Justesen 2007), and variation can arise through asexual and sexual recombination (Jin et al. 2010; Ali et al. 2014); therefore, there is a need for prophylactic measures.

The 'Strongfield' was the most widely grown durum cultivar from 2007 to 2015 due to its combination of high grain yield, protein concentration, low cadmium uptake, and improved semolina and pasta quality. Consequently, 'Strongfield' became a major parent of modern cultivars of Canada Western Amber Durum (CWAD) market-class. However, Canadian durum wheat production was threatened when reports that 'Strongfield' and the majority of Canadian durum germplasm were susceptible to stripe rust in the seedling stage (Lin et al. 2018). The tetraploid *T. carthlicum* Nevski wheat accession, 'Blackbird', had been observed to express resistance to stripe rust in spontaneous epidemic conditions in field nurseries near Swift Current, Saskatchewan. Determining if the 'Blackbird' resistance was different from that of 'Strongfield' would potentially reveal additional resistance that could be characterized and exploited in breeding. The present study sought to determine how similar genetically the resistance was between the durum wheat genotypes, 'Strongfield' and 'Blackbird'. If different, the intention was to determine the genomic regions controlling stripe rust response and to identify molecular markers associated with the resistance genes.

Materials and methods

Plant materials

A doubled haploid (DH) population comprising 87 lines was developed from the cross 'Strongfield'/'Blackbird' following the maize pollen method described by Humphreys and Knox (2015). 'Strongfield' has high yield, high grain protein concentration, low grain cadmium concentration, and is adapted to the durum production area of the southern Canadian prairies (Clarke et al. 2005). 'Blackbird' is a *T. carthlicum* (Nevski)

accession with genome AABB, black awns, and glumes (Somers et al. 2006).

Stripe rust disease assessment

The parents and DH lines were evaluated in response to stripe rust under field conditions at nurseries near Toluca, Mexico, from 2017 to 2019, and Lethbridge, Ab, Canada from 2016 to 2019. Both at Toluca and Lethbridge, parents and DH lines were grown in unreplicated single row plots. Being a biparental population, each allele at each locus under study is replicated in about half of the 87 lines. Therefore, the precision gained from additional experimental replication was considered not worth the cost. In Lethbridge, nurseries were artificially inoculated using *Pst* spores collected during the previous growing season. At Toluca, nurseries were planted as single rows of 1.5 m. Susceptible spreader plants included in the nurseries were inoculated with a *Pst* isolate MX16.04, which is virulent on lines carrying *Yr24/Yr26*. Isolate MEX16.04 belongs to the aggressive race group first identified in North America in 2000 and which became predominant in the subsequent year (Huerta-Espino and Singh 2017). The rationale behind using two different approaches for disease pressure on DH population that involved a natural mix of races at Lethbridge and a specific race at Toluca was to take advantage of the collaborating institution systems in place for evaluating germplasm. Disease severity was recorded as per cent of leaf area infected by stripe rust using the modified Cobb Scale (Peterson et al. 1948) except in 2018 and 2019 at Lethbridge when a 0 to 9 disease scale was used. The Lethbridge 2018 and 2019 data were converted to percentage for QTL analysis. In order to convert the 0 to 9 scale into a percentage, we divided each datapoint by 9 and then multiplied it by 100 as $[(0-9 \text{ scale datapoint})/9]/100$. Readings were done thrice every 7 days at Toluca and once at Lethbridge. Pearson correlation coefficients between locations and seasons were calculated to determine the consistency of disease severity across the environments.

Genotyping, linkage mapping and QTL analysis

The genotyping and linkage mapping of the 'Strongfield'/'Blackbird' population were described by Pei (2019). Briefly, the DH lines and their parents-were genotyped with a combination of simple sequence repeat (SSR) and single nucleotide polymorphism (SNP) markers. The SNP markers were genotyped in

the population using the Illumina 90 K iSelect Infinium array and scored in GenomeStudio software (Illumina Inc., San Diego, CA). After discarding severely distorted loci, a total of 12 014 markers composed of 11 681 SNPs and 333 SSRs were mapped by linkage analysis resulting in 16 linkage groups corresponding to the 14 chromosomes of tetraploid wheat. The linkage map was 2782 cM in length with 1068 linkage bins. The average marker density was 4.3 loci/cM or 0.23 cM/locus.

QTL associated with stripe rust resistance were detected by carrying out QTL analysis to stripe rust reaction and genotypic data within MapQTL.6® (Van Ooijen 2009). A permutation test option of 1000 within MapQTL was used to determine the significance threshold for the logarithm of odds (LOD). Chromosome-wide threshold levels were used to declare significant QTL at the 5% level of significance. Automatic co-factor detection based on backward elimination to identify the cofactor markers as well as manual cofactor selection was performed for Multiple QTL Mapping (MQM) in MapQTL. MapChart v. 2.2 (Voorrips 2002) was used as a tool for visual presentation of the chromosomal locations of QTL. The detected QTL were assigned chromosomal arms based on the position of QTL associated SNP markers on the hexaploid wheat high-density consensus map by Wang et al. (2014). To investigate the combined QTL effects on disease severity, an analysis of variance was carried out by SAS (SAS institute, Cary, NC). The analysis was conducted on disease severity data from environments at which the main effects of QTL were detected. For the analysis, lines of the ‘Strongfield’/‘Blackbird’ population were classified based on marker haplotypes at each locus.

Results

The *T. carthlicum* accession ‘Blackbird’ was relatively more resistant to stripe rust than the durum cultivar ‘Strongfield’ at Lethbridge except in 2016 (Table 1). In contrast, ‘Strongfield’ was relatively more resistant than ‘Blackbird’ at Toluca. The frequency distribution of disease severity of the DH lines was continuous with pronounced skewness towards susceptible reactions with some degree of variation in distribution among environments (Fig. 1). Significant correlations were observed between phenotypic data across environments with some exceptions (Table 2). Lethbridge 2019 did not correlate with any Toluca environments nor with Lethbridge 2017 and 2018 environments. The correlation between Lethbridge nurseries was generally weak or non-significant compared to among Toluca nurseries. Toluca 2018 and 2019 showed reasonably strong correlations with Lethbridge 2016 and 2018.

Four QTL associated with resistance to *Pst* were identified on chromosomes 2B, 3A (2 loci) and 5B designated as *QYr.spa-2B*, *QYr.spa-3A.1*, *QYr.spa-3A.2* and *QYr.spa-5B*, respectively. Table 3 depicts the QTL identified in the ‘Strongfield’/‘Blackbird’ population with associated markers, LOD value, parent allele mean value, additive value and phenotypic variation explained (PVE). Fig. 2 shows a partial linkage map and position of the QTL identified. Derived from ‘Strongfield’, the *QYr.spa-2B* was detected in all 3 years at Toluca, but was not detected at Lethbridge. With peak SNP marker *wsnp_Ra_c4321_7860456* and flanked by markers *RAC875_c87052_193* and *Ku_c55088_455*, *QYr.spa-2B* spanned 9.4 cM in the genetic map of the ‘Strongfield’/‘Blackbird’ population (Fig. 2). SNP markers associated with the QTL were mapped on chromosome arm 2BS in a high-density consensus map by Wang et al. (2014). Among the environments in which *QYr.spa-2B* expressed its highest peak LOD value of 3.5 and PVE of 17% was observed at Toluca in 2018.

Table 1. Mean of parents and mean, standard deviation, and range of stripe rust severity for the ‘Strongfield’/‘Blackbird’ durum wheat population tested in different environments near Lethbridge, Canada and Toluca, Mexico.

Environment / Stripe rust severity (%) ^a	‘Strongfield’/‘Blackbird’ population				
	Range	Mean	StdDev ^b	‘Blackbird’	‘Strongfield’
Lethbridge 2016	1–100	20.7	28.1	7.6	3.0
Lethbridge 2017	1–85	18.2	28.3	9.8	17.4
Lethbridge 2018	0–100	54.3	30.0	15.6	64.4
Lethbridge 2019	11–88.9	26.3	22.2	11.1	40.7
Toluca 2017	5–70	29.6	13.3	24	8.0
Toluca 2018	0–90	30.3	24.2	14	4.0
Toluca 2019	0–90	37.7	26.5	26	13

^aFor the Lethbridge 2018 and 2019 nurseries, disease severity scale was recorded on 0 to 9 and converted to 100%.

^bStdDev; standard deviation.

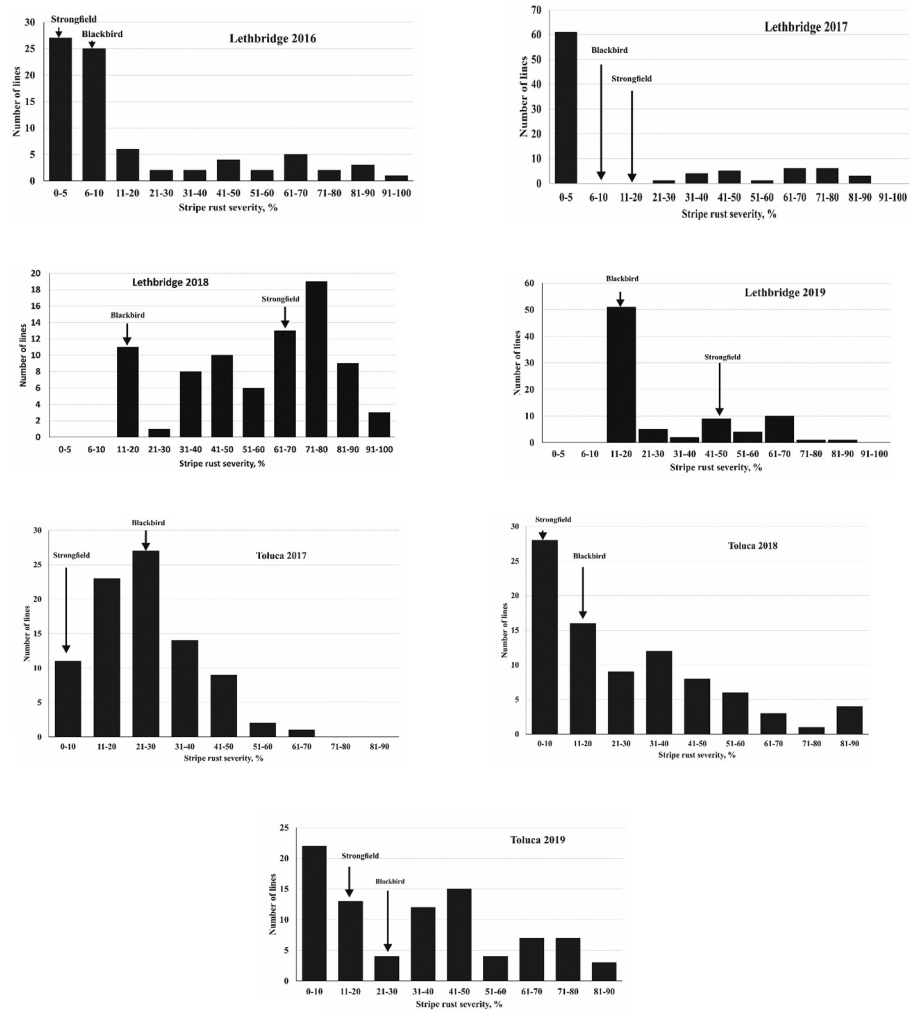


Fig. 1 Frequency distribution of stripe rust severities of the ‘Strongfield’/‘Blackbird’ population evaluated in the field nurseries near Toluca, Mexico from 2017–2019 and Lethbridge, Canada from 2016–2019. Mean stripe rust severities of ‘Blackbird’ and ‘Strongfield’ are indicated with dark arrows.

Table 2. Pearson correlation between stripe rust severity (%) of ‘Strongfield’/‘Blackbird’ durum wheat population tested in different environments near Lethbridge, Canada and Toluca, Mexico.

Environment	Lethbridge 2017	Lethbridge 2018	Lethbridge 2019	Toluca 2017	Toluca 2018	Toluca 2019
Lethbridge 2016	0.30**	0.27*	0.30**	0.22ns	0.43***	0.39***
Lethbridge 2017	-	0.32**	0.17ns	0.20ns	0.29**	0.30**
Lethbridge 2018		-	0.11ns	0.34**	0.45***	0.58***
Lethbridge 2019			-	0.19ns	0.19ns	0.15ns
Toluca 2017				-	0.56***	0.62***
Toluca 2018					-	0.80***

Contributed by ‘Blackbird’, *QYr.spa-3A.1* was identified in all 3 years at Toluca (Table 3). This QTL was also not detected at Lethbridge. Based on the SNP markers associated with the QTL, *QYr.spa-3A.1* is located in the centromeric region of chromosome 3A. *QYr.spa-3A.1*'s

highest LOD was associated with marker *JD_c1187_1398* in 2018 and 2019, and with marker *BS00021981_51* in 2017 with the latter LOD from year 2017 of 3.1 being the highest of the three Toluca environments. The highest LOD corresponds to a maximum

Table 3. Associated chromosome, position on the chromosome, marker associated with the peak LOD value, LOD value, mean severity associated with each parental allele, percent phenotypic variation explained, additive effects, and favourable allele source for stripe rust resistance QTL identified in the ‘Strongfield’/‘Blackbird’ population evaluated at Toluca, Mexico from 2017 to 2019 and Lethbridge, AB, Canada from 2016 to 2019.

Environment	QTL designation	Position	Peak marker	Location of peak marker ^a	IWGSC RefSeq V2.0 ^b	LOD value ^c	‘Blackbird’	‘Strongfield’	R ² (%) ^d	Additive ^e
Toluca 2017	QYr.spa-2B	11.5	wspn_Ra_c4321_7860456	2BS	27890231-27890083	3.0	35.5	25.0	14.6	5.3
Toluca 2018	QYr.spa-2B	11.5	wspn_Ra_c4321_7860456	2BS	27890231-27890083	3.5	41.8	21.3	17.0	10.3
Toluca 2019	QYr.spa-2B	11.5	wspn_Ra_c4321_7860456	2BS	27890231-27890083	2.2	47.9	29.6	11.1	9.2
Toluca 2017	QYr.spa-3A.1	75.5	BS00021981_51	3AS	61734723-61734623	3.1	24.9	35.0	13.8	-5.0
Toluca 2018	QYr.spa-3A.1	92.8	JD_c1187_1398	3AL	491564020-491563920	3.0	21.1	38.5	11.6	-8.7
Toluca 2019	QYr.spa-3A.1	92.8	JD_c1187_1398	3AL	491564020-491563920	2.3	29.1	45.9	9.0	-8.4
Lethbridge 2016	QYr.spa-3A.2	156.7	Tdurum_contig51339_447	3AL	683109041-683108941	2.9	9.5	32.2	15.6	-11.4
Lethbridge 2017	QYr.spa-3A.2	156.7	Tdurum_contig51339_447	3AL	683109041-683108941	2.1	10.1	28.1	10.0	-9.0
Lethbridge 2018	QYr.spa-3A.2	156.7	Tdurum_contig51339_447	3AL	683109041-683108941	3.3	42.5	66.5	16.1	-12
Toluca 2017	QYr.spa-3A.2	156.7	Tdurum_contig51339_447	3AL	683109041-683108941	1.9	25.9	34.1	9.4	-4.1
Toluca 2018	QYr.spa-3A.2	156.7	Tdurum_contig51339_447	3AL	683109041-683108941	4.2	20.6	42.2	19.9	-10.8
Toluca 2019	QYr.spa-3A.2	156.7	Tdurum_contig51339_447	3AL	683109041-683108941	4.9	26.3	51.7	22.7	-12.7
Lethbridge 2016	QYr.spa-5B	150.4	BS00062762_51	5BL	580378587-580378505	2.9	7.2	30.6	15.9	-11.7
Lethbridge 2017	QYr.spa-5B	150.4	BS00062762_51	5BL	580378587-580378505	1.5	8.5	23.9	7.0	-7.7

^aChromosomal location of QTL peak marker as determined by their positions in the high-density SNP map by Wang et al. (2014).

^bPhysical position in the IWGSC wheat RefSeq V2.0 of the SNP markers associated with the QTL detected.

^cMaximum likelihood LOD score for the QTL. LOD values greater than 2.1 are significant at 5% probability level based on 1000 permutations. Non-significant QTL were included to add further evidences for the QTL being real.

^dPhenotypic variation explained by the QTL.

^ePositive additive values indicate that ‘Strongfield’ was the source of resistance allele, whereas negative additive values indicate ‘Blackbird’ was the source of resistance allele.

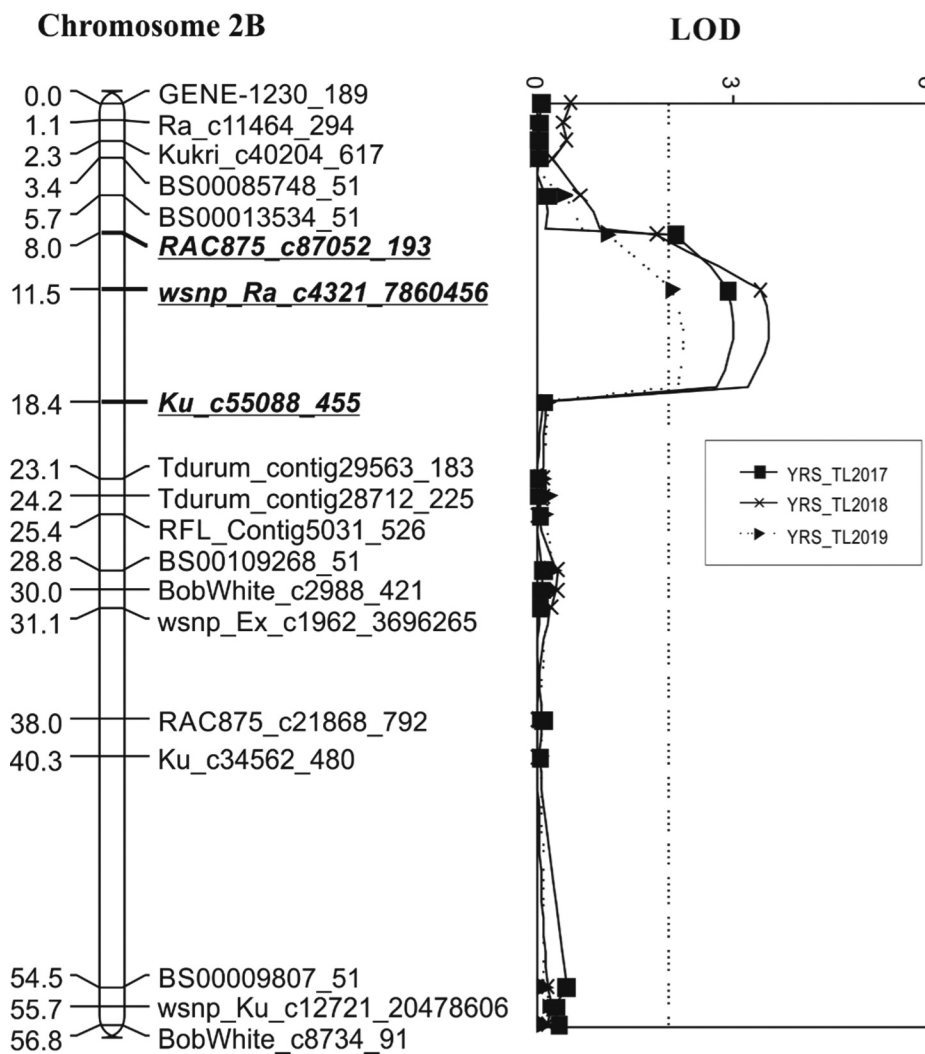


Fig. 2 Linkage map of chromosomes 2B, 3A, and 5B showing positions of stripe rust resistance QTL identified in the ‘Strongfield’/‘Blackbird’ population. ‘Strongfield’ contributed the QTL on chromosome 2B detected in Canada. ‘Blackbird’ contributed the QTL on chromosome 3A, 3A.1 (*QYr.spa-3A.1*) detected in Mexico and 3A.2 (*QYr.spa-3A.2*) detected in Canada and Mexico, and 5B detected in Mexico. Numbers on the left side of the graphs represent map position given in cM values.

PVE of 13.8%. The *QYr.spa-3A.1* stripe rust severity PVE was slightly lower than *QYr.spa-2B*, although both QTL had similar LOD values. Flanked by *BS00021981_51* and *JD_s1187_1398*, *QYr.spa-3A.1* spanned about 17.3 cM (Fig. 2).

As with *QYr.spa-3A.1*, the desirable allele for the second QTL on chromosome 3A, *QYr.spa-3A.2* was derived from ‘Blackbird’. This QTL was the most stable QTL identified in the present study expressing in three out of 4 years at Lethbridge and two out of 3 years at Toluca. Located between *BS00023337_51* and *RAC875_c52805_182* on chromosome arm 3AL (Wang et al. 2014), *QYr.spa-3A.2*

spanned about 8.2 cM of the 3A genome on the genetic map of the ‘Strongfield’/‘Blackbird’ population. With a peak marker, *Tdurum_contig51339_447*, *QYr.spa-3A.2* was associated with LOD values that ranged from 2.1 to 4.0 at Lethbridge, and 4.2 to 4.9 at Toluca. The maximum explained variation for stripe rust severity across environments was 16.1% (LOD, 3.3) at Lethbridge and 22.7% (LOD, 4.2) at Toluca.

A QTL on chromosome 5B, *QYr.spa-5B*, was detected at Lethbridge in a 2016 test environment. With the desirable allele contributed by ‘Blackbird’, this QTL was the only QTL specific to Canada unlike the two QTL *QYr.spa-2B*

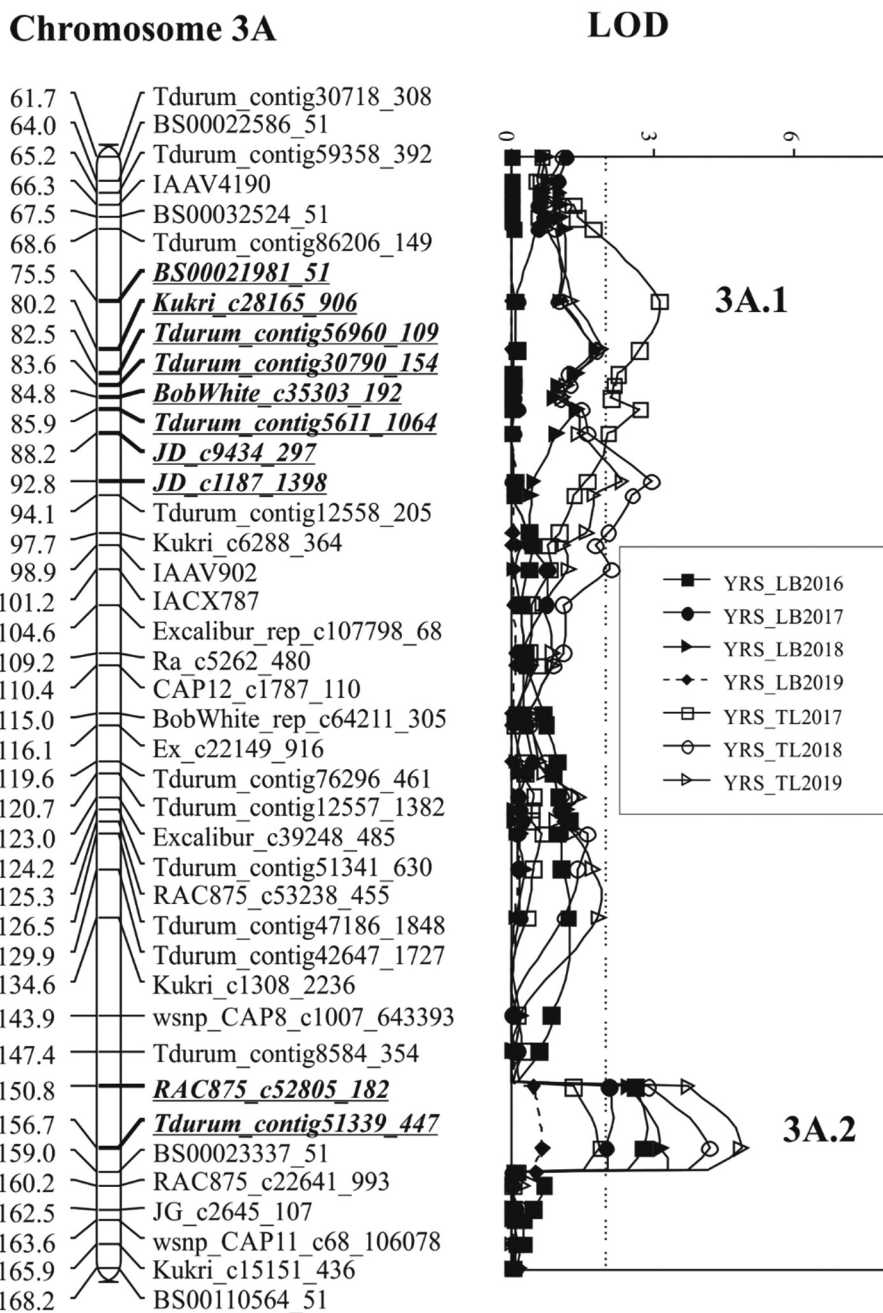


Fig. 2 (Continued).

and *QYr.spa-3A.1*, the expression of which was confined to Mexico. *QYr.spa-3A.2* expressed in both countries. The marker associated with the peak of *QYr.spa-5B* was *BS00062762_51* which mapped on chromosome arm 5BL (Wang et al. 2014). Associated with a LOD of 2.9, *QYr.spa-5B* explained 15% PVE of the stripe rust severity in the Lethbridge 2016 environment.

The statistical analysis of gene combinations indicated that there were significant additive effects between the main effect QTL identified in this study (Fig. 3). A combination of *QYr.spa-2B* with *QYr.spa-3A.1*, *QYr.spa-2B* with *QYr.spa-3A.2* and *QYr.spa-3A.2* with *QYr.spa-5B* resulted in elevated disease resistance compared with individual QTL effects over environments.

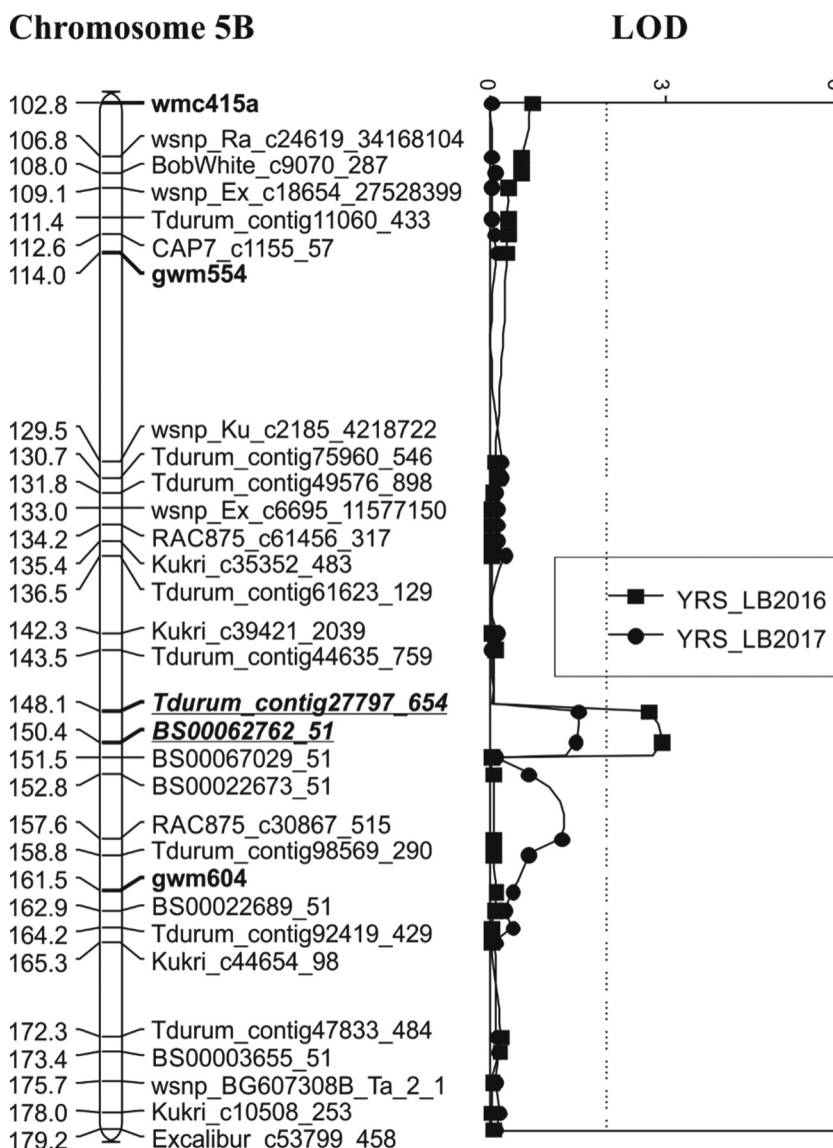


Fig. 2 (Continued).

Discussion

The variation observed among the phenotypic distributions of the DH lines across environments indicates that environmental conditions produce a differential effect on the expression of resistance. Temperature is known to affect the expression of some *Pst*-resistance genes, such as the high-temperature adult plant gene *Yr36* (Uauy et al. 2005), *Yr8* (Chen and Zhao 2007), *Yr17* (Milus et al. 2015), and *Yr28* (Zheng et al. 2020). The shape of the distribution of DH lines to stripe rust in Toluca is rather similar each year, with most lines being resistant

to moderately resistant. The more varied distributions might also be caused by differences in *Pst* race virulence and/or aggressiveness. This variation in phenotypic distributions of the lines across environments is in line with the low to moderate correlations observed among years at Lethbridge and Toluca and Lethbridge not being correlated in 3 of 4 years. The skewness of the frequency distribution of the DH lines for stripe rust severity towards resistance indicates the additive effect of the minor to moderate effect resistance identified in either parent of the population. The effectiveness of *QYr.spa-*

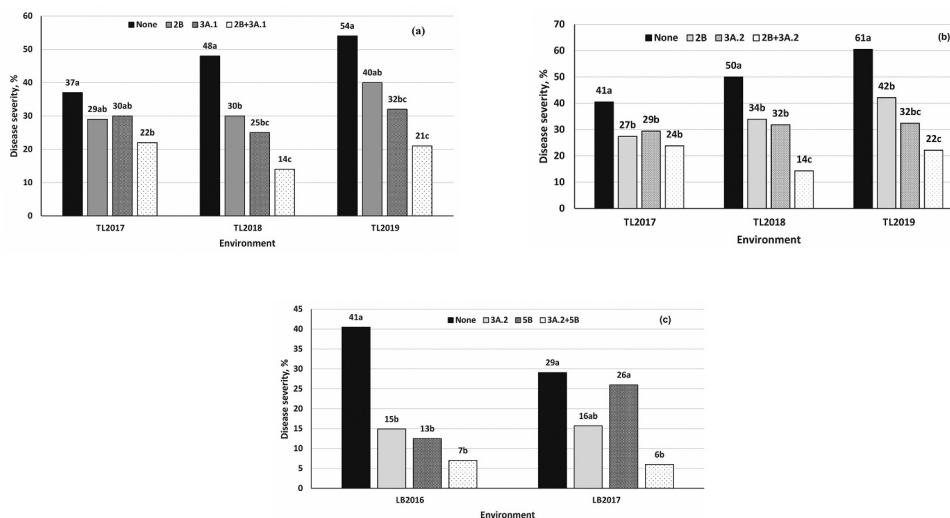


Fig. 3 The difference in the effect of QTL combination compared with individual QTL on stripe rust severity in the ‘Strongfield’/‘Blackbird’ population evaluated near Toluca, Mexico and Lethbridge, Canada. Additive effects of (a) 2B and 3A.1 at Toluca 2017–2019, (b) 2B and 3A.2 at Toluca 2017–2019, and (c) 3A.2 and 5B at Lethbridge 2016 and 2017. QTL descriptions: 2B stands for *QYr.spa-2B*, 3A.1 for *QYr.spa-3A.1*, 3A.2 for *QYr.spa-3A.2*, and 5B for *QYr.spa-5B*. Bars with the same letter within each test environment are not significantly different according to the Duncan’s Multiple Range test at $P = 0.05$.

2B and *QYr.spa-3A.1* at Toluca, and their absence at Lethbridge indicates the presence of virulent *Pst* races unique to Canada. Furthermore, the detection of *QYr.spa-5B* at Lethbridge and its absence at Toluca indicates the ineffectiveness of this QTL against the MX16.04 *Pst* race. Considering the fact that natural infections were also present as the main sources of an inoculum in the field tests, the simultaneous detection of *QYr.spa-3A.2* in Canada and Mexico suggests that this QTL is effective against *Pst* races prevalent in both countries.

‘Strongfield’ contributed *QYr.spa-2B* associated with markers located on chromosome arm 2BS, the expression of which was consistent across years at Toluca. The absence of this QTL in Canada might be due to the presence of virulent *Pst* races specific to Canada or an environment not favourable to expression. Three *Yr* genes *Yr27*, *Yr31* and *Yr41* have been reported to reside on chromosome 2BS (Luo et al. 2009; McIntosh et al. 2014; Maccaferri et al. 2015; Wu et al. 2017). *QYr.spa-2B* is unlikely to be controlled by *Yr27* because a marker for the gene, *Xgwm55* (McDonald et al. 2004), was located 96.6 cM from *QYr.spa-2B* marker *RAC875_c87052_193*. Moreover, *Yr27* is susceptible to *Pst* populations common in Mexico (McDonald et al. 2004). The effectiveness of *Yr31* has been lost due to a virulent race MX16.04 that was detected at Toluca in 2009 (Rosewarne et al. 2012; Yang et al. 2013) suggesting it is also different from *QYr.spa-2BS*. *Yr41* is an all-stage resistance gene and associated

with *Xgwm410* (Jiang et al. 2020). *Xgwm410* is located 107 cM from the *QYr.spa-2B* associated marker *RAC875_c87052_193* on the consensus map by Wen et al. (2017) suggesting the factor controlling *QYr.spa-2B* is distinct from *Yr41*. *QYr.spa-2B* from ‘Strongfield’ was not detected by Singh et al. (2013) in the ‘Sachem’/‘Strongfield’ mapping population tested for stripe rust in Toluca, Mexico, in 2009 and 2011, and Njoro, Kenya, in 2010. In contrast, they reported a different QTL contributed by Sachem on chromosome 2B associated with DArT marker *wPt-3632* at Toluca in 2011. The *QYr.spa-2B* would not be detected if both ‘Sachem’ and ‘Strongfield’ have the QTL.

In another study, Lan et al. (2014) reported a seedling resistance gene *QYr.cim-2BS* (designated *YrF*) in wheat line ‘Francolin#1’ that conferred intermediate seedling reaction and resistance at the adult plant stage in Mexican and Chinese environments. However, a marker for *YrF*, *Xwmc474*, was 85.59 cM from *RAC875_c87052_193* on the Bokore et al. (2020) consensus map, suggesting distinct factors. In the Canadian spring wheat population ‘Carberry’/‘AC Cadillac’, Singh et al. (2014) reported two stripe rust-resistance QTL on chromosome 2B. The first, from ‘Carberry’, was associated with *Xwmc25*, which was located at 16.7 cM from a peak marker for *QYr.spa-2B* on the consensus map by Bokore et al. (2020). The second, from ‘AC Cadillac’, was associated with *Xwmc770* and was located at 22.6 cM from the closest marker for the *QYr.*

spa-2B in ‘Strongfield’ on the map by Bokore et al. (2020). Despite their proximity to the chromosome, the similarity of ‘AC Cadillac’ or ‘Carberry’ QTL with that of ‘Strongfield’ requires further investigation. Perez-Lara et al. (2017) identified a QTL, *QYrlo.wpg-2BS*, associated with HTAP stripe rust resistance in an American spring wheat cultivar ‘Louise’ on chromosome 2BS within a region flanked by *Xwmc474* and *Xgwm148*. *QYrlo.wpg-2BS* should be different from *QYr.spa-2B* as *Xwmc474* is 85.59 cM from *QYr.spa-2B* (Bokore et al. 2020). The most closely associated *QYr.spa-2B* marker, *wsnp_Ra_c4321_7860456*, has been reported to be associated with resistance to tan spot caused by *Pyrenophora tritici-repentis* in Canadian spring wheat cultivars (Perez-Lara et al. 2017) which suggests the usefulness of this chromosomal region. Such close association of the two traits may be a benefit or a challenge depending on whether or not the leaf spot and stripe rust resistance are in coupling or repulsion. Overall, the *QYr.spa-2B* may represent a new QTL not reported before in durum wheat.

The Blackbird has two stripe rust resistance QTL on chromosome 3A located at a physical distance of about 191 Mbp on the IWGSC refseq. V. 2.0 based on the most closely associated markers *JD_c1187_1398* for *QYr.spa-3A.1* and *Tdurum_contig51339_447* for *QYr.spa-3A.2*. No named *Yr* gene is found on the chromosome where the two *Yr* QTL, *QYr.spa-3A.1* and *QYr.spa-3A.2* from ‘Blackbird’ are found (Rosewarne et al. 2013; McIntosh et al. 2014; Maccaferri et al. 2015; McIntosh et al. 2018a). However, a few studies report QTL conferring resistance against *Pst* on the chromosome (Christopher et al. 2013; Singh et al. 2014; Ma et al. 2016). For example, Christopher et al. (2013) report a QTL in a US American winter wheat-line Neuse. Singh et al. (2014) similarly found a *Yr* QTL on chromosome 3A expressed in a single environment in Canada derived from the spring wheat cultivar ‘AC Cadillac’. Both Christopher et al. (2013) and Singh et al. (2014) used DArT markers in their studies making a comparison of their QTL with those in our study difficult. Lillemo et al. (2008) report a major QTL for stripe rust resistance on chromosome 3A in the wheat line ‘Saar’, but it resides on the short arm of the chromosome as opposed to the markers for the two QTL in ‘Blackbird’ – the *QYr.spa-3A.1* that is located in the centromeric region of chromosome 3A and the *QYr.spa-3A.2* that is located on 3AL. To our understanding, there is no *Yr* gene previously reported on chromosome 3AL of durum wheat. Therefore, *QYr.spa-3A.1* and *QYr.spa-3A.2* are most likely novel.

The sporadic ‘Blackbird’ derived QTL, *QYr.spa-5B*, conditioned resistance against *Pst* races specific to

Canada. This QTL generated a significant LOD value at Lethbridge in 2016 and a lower stripe rust severity in the ‘Blackbird’ haplotype at Lethbridge in 2017 (Table 3) but not significant at the 5% level. *Yr47* maps to the short arm of chromosome 5B, which disqualifies it as the source of *QYr.spa-5B* which associated with markers located on the long arm of 5B and there has been no *Yr* gene reported the 5BL thus far (Maccaferri et al. 2015; Qureshi et al. 2017; McIntosh et al. 2018a). Singh et al. (2014) reported a stripe rust QTL on chromosome 5B associated with *Xbarc59* in the spring wheat cultivar ‘AC Cadillac’. *Xbarc59* is located 76.7 cM from the peak marker associated with *QYr.spa-5B* from ‘Blackbird’ on the hexaploid wheat SNP consensus map of Bokore et al. (2020) suggesting the Singh et al. (2014) QTL is different from *QYr.spa-5B*. Hou et al. (2015) reported all an stage stripe rust HTAP-resistance QTL on 5BL associated with *wsnp_JD_rep_c50403_34392266* in a soft white winter wheat cultivar ‘Druchamp’ (PI 174622) introduced to the US Pacific Northwest for production in 1949 from France. This QTL may be controlled by the same factor as *QYr.spa-5B* mapping within 49 cM of *QYr.spa-5B* on the consensus map by Bokore et al. (2020). Using the same consensus map, a peak marker *BS00062762_51* for the *QYr.spa-5B* in ‘Blackbird’ was located 43.21 cM from *wsnp_Ku_c4427_8029592*, a marker associated with *QYr.usw-5B* in durum wheat-line W9262-260D3 (Lin et al. 2018). Another QTL was reported by Yang et al. (2013) in hexaploid wheat that was effective in China, but not effective in Mexico, where *QYr.spa-5B* was similarly ineffective. The relatedness of these genes with the *QYr.spa-5B* requires further resolution.

In addition to the present study, the ‘Strongfield’/‘Blackbird’ population has previously been used in different trait mapping studies including leaf rust resistance and Fusarium head blight resistance (Sari et al. 2018). ‘Blackbird’ is susceptible to leaf rust, while ‘Strongfield’ is resistant (Pei 2019). None of the leaf rust QTL identified by Pei (2019) using this population corresponded with or located near the stripe resistance QTL we discovered in the present study. Sari et al. (2018) determined several FHB resistance QTL segregating in the ‘Strongfield’/‘Blackbird’ population of which a QTL on chromosome 3A of ‘Blackbird’ was associated with the same SNP marker, *BS00021981_51*, as the ‘Blackbird’ derived *QYr.spa-3A.1*. Knowledge of such gene relationships is helpful in stacking of genes governing different traits in new varieties.

The identification of the *QYr.spa-2B* in ‘Strongfield’ is an addition to the stripe rust QTL Singh et al. (2013) detected on chromosome 7B of this cultivar in the ‘Sachem’/‘Strongfield’ population in Toluca, Mexico,

in 2011. The absence of segregation among DH lines of the ‘Blackbird’/‘Strongfield’ population could be due to the QTL being common in both parents but could also be the result of a race change in Mexico.

It is challenging finding consistent and durable resistance genes with the constant evolution of new rust strains and their adaptation to higher temperatures (Bryant et al. 2014). For example, despite their effectiveness in Toluca, where one of the aggressive *Pst* races MEX16.04 was present, the two ‘Blackbird’ derived QTL, *QYr.spa-2B* and *QYr.spa-3A.1*, were not effective at Lethbridge, Canada.

The major route for the migration of *Pst* into southern Alberta (Lethbridge) is the Pacific Northwest of United States (Oregon, Washington, and northern Idaho) (Line 2002; Xi et al. 2015; Aboukhaddour et al. 2020). Alternatively, movement to Canada occurs through the Central Great Plains ‘*Puccinia* pathway’ from inoculum that primarily overwinters in southern Texas, northern Mexico and along the Gulf Coast in Louisiana and Mississippi. Deployments of QTL, such as *QYr.spa-3A.2*, that are effective against different *Pst* populations in multiple regions, and countries should be helpful in controlling the disease, regardless of the source of the pathogen.

In summary, we mapped a stripe rust resistance QTL contributed by the durum wheat cultivar ‘Strongfield’ on chromosome arm 2B (*QYr.spa-2B*) and three QTL contributed by the *T. carthlicum* accession ‘Blackbird’ on chromosomes 3A (2 loci, *QYr.spa-3A.1*, *QYr.spa-3A.2*) and 5B (*QYr.spa-5B*). As this study was based on adult plant response, seedling test studies are needed to investigate the nature of these QTL. The *QYr.spa-3A.2* QTL was effective in Canada and Mexico, *QYr.spa-2B* and *QYr.spa-3A.1* in Mexico, and *QYr.spa-5B* was effective in Canada indicating the difference in the *Pst* populations between these two countries, or the effect of environment on expression. To our knowledge, none of these QTL corresponds with the previously reported *Yr* genes or QTL in durum wheat suggesting they are new genetic factors. The identification of the *QYr.spa-3A.2* in ‘Blackbird’ is of particular interest because it represents a stable QTL that is effective in two countries over multiple years. The SNP markers associated with the QTL identified will be useful in marker assisted breeding of resistance to *Pst* in durum wheat.

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