

Stem Rust Resistance in A-Genome Diploid Relatives of Wheat

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Abstract

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Wheat stem rust, caused by *Puccinia graminis* f. sp. *tritici*, has been effectively controlled through the use of genetic resistance. *P. graminis* f. sp. *tritici* race TTKSK (Ug99) possesses virulence to many resistance genes that have been used in wheat breeding worldwide. One strategy to aid breeders in developing resistant cultivars is to utilize resistance genes transferred from wild relatives to wheat. Stem rust resistance genes have previously been introgressed from *Triticum monococcum* to wheat. In order to identify additional resistance genes, we screened 1,061 accessions of *T. monococcum* and 205 accessions of *T. urartu* against race TTKSK and four additional *P. graminis* f. sp. *tritici* races: TTTTF, TRTTF, QFCSC, and MCCFC. A high frequency

of the accessions (78.7% of *T. monococcum* and 93.0% of *T. urartu*) were resistant to *P. graminis* f. sp. *tritici* race TTKSK, with infection types ranging from 0 to 2+. Among these resistant accessions, 55 *T. monococcum* accessions (6.4% of the total) were also resistant to the other four races. Associations of resistance in *T. monococcum* germplasm to different races indicated the presence of genes conferring resistance to multiple races. Comparing the observed infection type patterns to the expected patterns of known genes indicated that previously uncharacterized genes for resistance to race TTKSK exist in both *T. monococcum* and *T. urartu*.

Puccinia graminis f. sp. *tritici*, the causal agent of wheat stem rust, has caused major yield losses throughout history. Since 1955, severe stem rust epidemics have been effectively controlled in the United States and Canada through the deployment of resistant cultivars. In Uganda in 1999, a race of *P. graminis* f. sp. *tritici* (Ug99) was characterized that is virulent to *Sr31* and many other stem rust resistance genes (15). Ug99 is identified as race TTKSK based on the North American stem rust nomenclature (8). *P. graminis* f. sp. *tritici* race TTKSK has subsequently spread throughout Eastern Africa (20), Yemen, and Iran (14). In 2006, a variant of race TTKSK was found in Kenya that possesses virulence to *Sr24* (race TTKST; 8). In 2007, a variant with virulence to *Sr36*, designated as race TTTSK, was detected (9). The distributions of the variants of race TTKSK are unique and *Sr24* and *Sr36* could be effectively used where virulence is not currently present. However, the rapid detection and emergence of the variants should caution the deployment of *Sr24* or *Sr36* alone.

Preliminary tests conducted in Kenya suggested that nearly all of the current wheat cultivars grown in Asia are susceptible to race TTKSK (19). Jin and Singh (6) evaluated 450 cultivars and advanced breeding lines from the United States and found 84% of the hard red spring wheat, 52% of the hard red winter wheat, and 73% of the soft winter wheat to be susceptible to race TTKSK at the seedling stage. Moreover, many of the resistant lines possessed *Sr24* and *Sr36* (7,9), to which races TTKST and TTTSK are virulent, respectively. Similarly, Fetch (2) found the majority of the Canadian wheat cultivars to be susceptible to race TTKSK. Several genes have been identified to be effective against race TTKSK (7). Most of these effective genes were derived from alien relatives of wheat and many have not been used in breeding due to linkage drag (19).

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*The e-Xtra logo stands for “electronic extra” and indicates that two supplementary tables are available online.

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One of the strategies to develop cultivars resistant to race TTKSK is to identify and introgress additional resistance from the wild relatives of wheat. *Triticum urartu* is the A-genome progenitor of wheat and *T. monococcum* is closely related to *T. urartu*; therefore, introgressions from these species to hexaploid wheat can be made with relative ease (10,23). Accessions of *T. monococcum* were screened with multiple *P. graminis* f. sp. *tritici* races to postulate the presence of resistance genes (23). Three stem rust resistance genes (*Sr21*, *Sr22*, and *Sr35*) have been identified and transferred from *T. monococcum* (3,10,11,22,23). Races of *P. graminis* f. sp. *tritici* with virulence to *Sr21* are common worldwide, except in Australia (5). Virulence to *Sr22* was not identified in a worldwide survey published in 1992 (5) but such races were reported in Israel in 1971 (3). Virulence to *Sr35* was identified in North and South America, Africa, and southern Asia (5). *Sr22* and *Sr35* have been shown to be effective to race TTKSK at both the seedling and adult plant stages (7). The effectiveness of *Sr21* in hexaploid wheat to race TTKSK was considered uncertain (7). The objective of this study was to identify race TTKSK resistance in *T. urartu* and *T. monococcum* germplasm.

Materials and Methods

Accessions (205 of *T. urartu* and 1,062 of *T. monococcum*) were obtained from the United States Department of Agriculture National Small Grains Collection (Aberdeen, ID) in 2007. The *T. monococcum* germplasm was divided into 848 accessions listed as *T. monococcum* subsp. *aegilopoides* (wild einkorn, synonymous *T. aegilopoides*, and *T. boeoticum*) and 214 accessions listed as *T. monococcum* subsp. *monococcum* (cultivated einkorn). One accession classified as *T. monococcum* subsp. *aegilopoides*, PI 306526, is actually *T. dicoccoides* and was not included in the analyses. Accessions were screened with five races of *P. graminis* f. sp. *tritici* (Table 1). Isolate 04KEN156 has previously been identified as race TTKSK (6,7,24) based on the North American differentials for *P. graminis* f. sp. *tritici* (8,16,17). Isolates of races TTTTF and TRTTF were used in this study because of their virulence to genes to which race TTKSK is avirulent (Table 1). Isolates of races QFCSC and MCCFC were selected because of their ability to differentiate among *T. monococcum* resistance genes *Sr21* and *Sr35* when used in combination with the other races.

Urediniospores of stem rust isolates in gelatin capsules stored at -80°C were heat shocked at 45°C for 15 min, and placed in a rehydration chamber maintained at 80% relative humidity by a KOH

solution for 2 to 4 h (18). Procedures for inoculation, incubation, and disease assessment were performed as described previously (7). Susceptible controls ('Chinese Spring' [CI 14108] and 'Rusty' [PI 639869]) were inoculated with each race along with the test entries.

Disease reactions were classified according to Stakman et al. (21). Infection types (ITs) 0, ;, 1, and 2 were considered low ITs characteristic of host resistance and pathogen avirulence. ITs 3 and 4 were considered high and such accessions were classified as susceptible. When low and high ITs were present on the same leaf, the reaction was considered resistant (12). In each assay, 6 to 10 plants were evaluated. When plants segregated for resistance within an accession, the accession was considered heterogeneous. An accession was considered resistant to the five races combined if the reaction to each of the five races was resistant. In total, 107 randomly selected *T. monococcum* accessions (10% of the total) were screened with races TTKSK, TTTTF, and TRTTF a second time to test the repeatability of scoring rust reactions. The frequency of consistent classification of resistance was used as a measure of repeatability.

Frequencies of reactions (resistant, susceptible, and heterogeneous) to each of the five *P. graminis* f. sp. *tritici* races and the combined reaction to all five races were calculated for *T. urartu* and *T. monococcum*. We calculated χ^2 values in order to test the assumption of independence of reaction among the five races. Frequencies of rust reactions within the two *T. monococcum* subspecies were calculated. For *T. urartu*, 91% of the accessions were from either Turkey or Lebanon. Previous studies indicated that *T. urartu* accessions from Turkey formed a distinct phylogenetic clade from accessions collected in Lebanon (4,13). Therefore, we also calculated the frequency of resistant accessions from Turkey and from Lebanon, separately, and χ^2 values were also calculated to test for deviation in percent resistance between the wild and cultivated forms of *T. monococcum* and the Turkey and Lebanon collections of *T. urartu*.

We postulated the presence of *Sr21*, *Sr22*, and *Sr35* in *T. monococcum* accessions based upon known and observed reactions of the *P. graminis* f. sp. *tritici* races on monogenic and digenic lines (11,23). For *Sr21* postulations, we considered race TTKSK ITs of 3- or 3 as indicative of *Sr21* when resistance was also observed to race MCCFC. This deviation from the traditional classification of resistance and susceptibility was made because intermediate ITs

(23-) have been previously reported for avirulent cultures to *Sr21* (12) and the reaction of race TTKSK specifically to *Sr21* was described as not certain (7). For both *T. monococcum* subsp. *aegilopoides* and *T. monococcum* subsp. *monococcum*, we calculated the frequency of accessions postulated to possess known genes.

Results

Screening data are available online. The frequency and number of *T. monococcum* and *T. urartu* accessions resistant, susceptible, and heterogeneous to the five races and the races combined are displayed in Tables 2 and 3, respectively. A high frequency of the *T. monococcum* and *T. urartu* accessions were resistant to race TTKSK. Relatively few *T. monococcum* accessions were resistant to races TRTTF and TTTTF, and no *T. urartu* accessions were resistant to these two races. We found a higher frequency of accessions resistant or heterogeneous to races TRTTF and TTTTF in *T. monococcum* subsp. *monococcum* relative to *T. monococcum* subsp. *aegilopoides* (Tables 2 and 4). In contrast, a higher frequency of *T. monococcum* subsp. *aegilopoides* accessions was resistant to races TTKSK and MCCFC. *T. urartu* accessions collected in Lebanon were more often resistant to races TTKSK and MCCFC than those collected in Turkey (Tables 3 and 4).

Associations of resistance to different races were significant as measured by the pairwise comparisons, except for the TRTTF-MCCFC and TTTTF-MCCFC race comparisons (Table 5). All significant associations of resistance were positive. This means that *T. monococcum* accessions resistant to one race were resistant to other races more often than expected under the assumption that resistance to the five races is independent. For *T. urartu*, associations were not significant (Table 5), indicating that independent race-specific genes likely confer resistance to races TTKSK, MCCFC, and QFCSC.

The ITs of three lines with known *T. monococcum* stem rust resistance genes are given in Table 6. Gene postulations for the tested accessions are listed in Supplementary Table 1. Some accessions displayed IT patterns that could not be explained by the previously characterized resistance genes. The frequency of postulated known genes is displayed in Table 7.

Out of 297 pairwise comparisons of ITs, 14 comparisons were inconsistent, resulting in a repeatability of 95.28%. Of those 14 comparisons, 9 were misclassified for *P. graminis* f. sp. *tritici* TTKSK with a 2+3 IT in one replication and a 3- or 3 IT in the

Table 1. Races of *Puccinia graminis* f. sp. *tritici* used to screen *Triticum monococcum* germplasm

Race	Isolate	Virulence or avirulence formula
TRTTF	06YEM34-1	5,6,7b,9a,9b,9d,9e,9g,10,11,17,21,30,36,38,McN,Tmp/8a,22,24,31,35
TTKSK	04KEN156/04	5,6,7b,8a,9a,9b,9d,9e,9g,10,11,17,30,31,38,McN/22,24,35,36,Tmp ^a
TTTTF	01MN84A-1-2	5,6,7b,8a,9a,9b,9d,9e,9g,10,11,17,21,30,36,McN,Tmp/22,24,31,35,38
QFCSC	03ND76C	5,8a,9a,9d,9g,10,17,21,35,McN/6,7b,9e,9b,11,22,24,30,31,36,38,Tmp
MCCFC	59KS19	5,7b,9g,10,17,35,McN,Tmp/6,8a,9a,9d,9e,9b,11,21,22,24,30,31,36,38

^a *Sr21* is not included in this table for TTKSK.

Table 2. Number (and frequency) of *Triticum monococcum* accessions resistant, susceptible, and heterogeneous to five stem rust races and the combined reaction to the five races

Accessions, race	Total	Number resistant (%)	Number susceptible (%)	Number heterogeneous (%)
<i>T. monococcum</i> subsp. <i>aegilopoides</i>				
TRTTF	804	62 (7.7)	724 (90.0)	18 (2.2)
TTKSK	805	662 (82.2)	109 (13.5)	34 (4.2)
TTTTF	808	55 (6.8)	741 (91.7)	12 (1.5)
QFCSC	702	165 (23.5)	523 (74.5)	14 (2.0)
MCCFC	712	649 (91.1)	42 (5.9)	21 (2.9)
Combined	643	38 (5.9)	594 (92.4)	11 (1.7)
<i>T. monococcum</i> subsp. <i>monococcum</i>				
TRTTF	213	37 (17.4)	161 (75.6)	15 (7.0)
TTKSK	214	140 (65.4)	52 (24.3)	22 (10.3)
TTTTF	213	40 (18.8)	157 (73.7)	16 (7.5)
QFCSC	213	45 (21.1)	162 (76.1)	6 (2.8)
MCCFC	213	182 (85.4)	25 (11.7)	6 (2.8)
Combined	211	17 (8.1)	186 (88.2)	8 (3.8)

other replication. This variability is likely due to *Sr21* and was accounted for in the gene postulations (ITs 3- or 3 to TTKSK were considered as resistant interactions for gene postulation). Excluding this variability, five comparisons were misclassified (98.32% repeatability). For these five misclassified comparisons, the ITs of the replications classified as resistant were 2+3, 23+Z, 2+3/123Z, or ;3+Z, indicating that misclassifications only occurred when the IT of the resistant replication was relatively high. The IT data used for the repeatability test is available online as Supplementary Table 2.

Discussion

Accession PI 428170 (G2919) was used by P. L Dyck to introgress *Sr35* into hexaploid wheat (11). PI 428170 and other accessions postulated to possess *Sr35* displayed a unique pattern of ITs: 0 to TRTTF, 0 to TTKSK, X- LIF (mesothetic with low infection frequency) to TTTTF, 4 to QFCSC, and 4 or ;1 to MCCFC (depending on the presence or absence of *Sr21*). We postulated the presence of *Sr35* in 21 accessions of *T. monococcum* subsp. *monococcum*, and no accessions of *T. monococcum* subsp. *aegilopoides*

(Table 7). The higher frequency of resistance to races TTKSK and MCCFC in *T. monococcum* subsp. *aegilopoides* is likely due to a higher frequency of accessions carrying *Sr21* in this subspecies.

A higher frequency of *T. urartu* accessions from Lebanon were resistant to races TTKSK and MCCFC compared with accessions from Turkey. This difference might be a result of the divergent evolutionary history known in this species from these two countries (4,13). Identification of geographical areas where a higher frequency of collected landraces were resistant to stem rust has been used to prioritize further screening (1). If this strategy is used for identifying stem rust resistance in *T. urartu*, screening of additional accessions from Lebanon, not Turkey, should be prioritized. However, relatively few *T. urartu* accessions were screened in this study and additional screening of accessions could be beneficial, regardless of geographic origin.

Close associations for resistance to different races in *T. monococcum* accessions suggest that resistance is usually effective against multiple races, when it is present. A high frequency of accessions exhibited resistance to races TTKSK and MCCFC. This

Table 3. Number (and frequency) of *Triticum urartu* accessions resistant, susceptible, and heterogeneous to five stem rust races and the combined reaction to the five races

Accessions, race	Total	Number resistant (%)	Number susceptible (%)	Number heterogeneous (%)
<i>Lebanon, T. urartu</i>				
TRTTF	88	0 (0)	88 (100)	0 (0)
TTKSK	87	86 (98.9)	0 (0)	1 (1.1)
TTTTF	92	0 (0)	92 (100)	0 (0)
QFCSC	87	1 (1.1)	86 (98.9)	0 (0)
MCCFC	86	48 (55.8)	37 (43.0)	1 (1.2)
Combined	78	0 (0)	78 (100)	0 (0)
<i>Turkey, T. urartu</i>				
TRTTF	81	0 (0)	81 (100)	0 (0)
TTKSK	81	72 (88.9)	4 (4.9)	5 (6.2)
TTTTF	88	0 (0)	88 (100)	0 (0)
QFCSC	81	2 (2.5)	78 (96.3)	1 (1.2)
MCCFC	79	1 (1.3)	76 (96.2)	2 (2.5)
Combined	71	0 (0)	71 (100)	0 (0)

Table 4. Association of rust reactions between the two subspecies of *Triticum monococcum* and two countries of origin of *T. urartu*

Species	Association between		Race	χ^2	Association type ^a	P value
<i>T. monococcum</i>	Wild	Cultivated	TRTTF	20.38	WS/CR	1.41 E-4
	Wild	Cultivated	TTKSK	19.92	WR/CS	1.76 E-4
	Wild	Cultivated	TTTTF	32.75	WS/CR	3.64 E-7
	Wild	Cultivated	QFCSC	0.45	ns	0.93
	Wild	Cultivated	MCCFC	8.30	WR/CS	0.04
	Wild	Cultivated	Combined	2.30	ns	0.51
<i>T. urartu</i>	Lebanon	Turkey	TTKSK	8.15	LR/TS	0.043
	Lebanon	Turkey	QFCSC	0.80	ns	0.85
	Lebanon	Turkey	MCCFC	62.78	LR/TS	1.50 E-13

^a For significant associations ($P < 0.05$), the association type between classes (W, wild; C, cultivated; L, Lebanon; and T, Turkey) and either resistance (R) or susceptibility (S) are indicated; ns indicates a nonsignificant association.

Table 5. Association of rust reactions among the five races in pairwise comparisons as measured by χ^2 values and probability

Species	Association between races		χ^2	Association type ^a	P value
<i>T. monococcum</i>	TRTTF	TTKSK	15.90	+	0.0012
	TRTTF	TTTTF	554.10	+	8.99 E-120
	TRTTF	QFCSC	163.35	+	3.46 E-35
	TRTTF	MCCFC	1.70	ns	0.64
	TTKSK	TTTTF	17.79	+	4.86 E-4
	TTKSK	QFCSC	15.38	+	0.0015
	TTKSK	MCCFC	149.23	+	3.87 E-32
	TTTTF	QFCSC	131.90	+	2.11 E-28
	TTTTF	MCCFC	1.65	ns	0.65
	QFCSC	MCCFC	15.22	+	0.0016
<i>T. urartu</i>	TTKSK	QFCSC	0.28	ns	0.96
	TTKSK	MCCFC	2.29	ns	0.51
	QFCSC	MCCFC	4.35	ns	0.23

^a For significant associations ($P < 0.05$), + indicates a positive association among resistant accessions, - indicates a negative association among resistant accessions, and ns indicates a nonsignificant association.

Table 6. Infection type patterns of lines containing previously characterized *Triticum monococcum* stem rust resistance genes to stem rust races used in this study

Line	Background	Race					Genes
		TRTTF	TTKSK	TTTTF	QFCSC	MCCFC	
PI 10474	Diploid	3+	;1	3+	3+	;1	<i>Sr21</i>
PI 428170	Diploid	0;	0	X-LIF ^a	4	;1	<i>Sr35</i> + <i>Sr21</i>
PI 660256 ^b	Hexaploid	;2-	2-	2	2-	1	<i>Sr22</i>

^a X indicates a mesothetic infection type with both compatible and incompatible interactions and LIF indicates low infection frequency.

^b Synonymous with Sr22TB, an *Sr22* carrying line previously described as resistant to TTKSK (7).

Table 7. Frequency of postulated stem rust resistance genes in *Triticum monococcum* germplasm

Accessions	Total	Number of accessions (%)					Susceptible	Unknown
		<i>Sr21</i>	<i>Sr22</i>	<i>Sr35</i>	<i>Sr21</i> + <i>Sr35</i>			
<i>T. monococcum</i> subsp. <i>aegilopoides</i>	847	673 (79.5)	52 (6.1)	0 (0)	0 (0)	23 (2.7)	99 (11.7)	
<i>T. monococcum</i> subsp. <i>monococcum</i>	214	128 (59.8)	15 (7.0)	6 (2.8)	15 (7.0)	15 (7.0)	35 (16.4)	
Total <i>T. monococcum</i>	1,061	801 (75.5)	67 (6.3)	6 (0.6)	15 (1.4)	38 (3.6)	134 (12.6)	

resistance may be attributed to *Sr21*. Similarly, The (23) found the majority of *T. monococcum* accessions screened to possess *Sr21*. *P. graminis* f. sp. *tritici* race TTKSK is classified as virulent to *Sr21*; however, experimental evidence is currently inconclusive (7). Though TTKSK is known to produce moderately high ITs (3 or higher) on *Sr21* of some hexaploid wheat lines, a low IT may be observed at the seedling stage in diploids. Several *T. monococcum* accessions displayed IT patterns that could not be explained by *Sr21*, *Sr22*, or *Sr35* alone or in combination.

T. urartu has not been used as a source for the introgression of stem rust resistance genes. Therefore, the stem rust resistance observed is likely due to new genes. Accessions resistant to TTKSK were often susceptible to other races used in this study. Because we did not observe significant associations of resistance between the races, resistance to races TTKSK, QFCSC, and MCCFC is most likely conferred by single race-specific resistance genes.

Major gene resistance introgressed from wild relatives of wheat has been an effective source of genetic resistance to stem rust. Uncharacterized genes resistant to race TTKSK introgressed into adapted germplasm will aid breeders in developing resistant cultivars. Screening the *T. monococcum* and *T. urartu* germplasm in this study resulted in the identification of uncharacterized genes or alleles that provide resistance to race TTKSK. Genetic studies have been initiated to determine the number and allelic relationships of uncharacterized resistance genes, validate our gene postulations, and facilitate the mapping of *Sr21*, *Sr22*, *Sr35*, and uncharacterized genes in diploid backgrounds.

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