

Stem Rust Resistance in *Aegilops tauschii* Germplasm

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ABSTRACT

Aegilops tauschii Coss., the D genome donor of hexaploid wheat, *Triticum aestivum* L., has been used extensively for the transfer of agronomically important traits to wheat, including stem rust resistance genes *Sr33*, *Sr45*, and *Sr46*. To identify potentially new stem rust resistance genes in *A. tauschii* germplasm, we evaluated 456 nonduplicated accessions deposited in the USDA National Small Grains Collection (Aberdeen, ID) and the Wheat Genetic and Genomic Resources Center collection (Kansas State University, Manhattan, KS), with races TTKSK (Ug99), TRTTF, TTTTF, TPMKC, RKQQC, and QTHJC of *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn. Ninety-eight accessions (22%) were identified as resistant to race TTKSK. A broad range of resistant infection types (; to 2+) were found in reaction to race TTKSK. Resistance was significantly associated among most of the races in pairwise comparisons. However, resistance was largely race specific. Only 12 of the accessions resistant to race TTKSK were also resistant to the other five races. Results from this germplasm screening will facilitate further studies on the genetic characterization of accessions with potentially novel sources of resistance to race TTKSK.

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Abbreviations: ARS, Agricultural Research Service; IT, infection type; *Pgt*, *Puccinia graminis* f. sp. *tritici*.

AEGILOPS TAUSCHII Coss. is the donor of the D genome of hexaploid wheat (*Triticum aestivum* L.; Kihara, 1944; McFadden and Sears, 1946). The close relationship between *A. tauschii* and *T. aestivum* has facilitated the rapid introgression of several agronomically important disease traits from *A. tauschii* to *T. aestivum* including resistance to wheat stem rust (caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn.; Kerber and Dyck, 1979; Gill and Raupp, 1987; Marais et al., 1998).

Recent epidemics of stem rust in eastern Africa have raised concern about the resistance of currently grown wheat cultivars to new races of *P. graminis* f. sp. *tritici* (*Pgt*) from Africa. In 1999, isolates of *Pgt* from Uganda, reported under the race name Ug99, were found to possess virulence to the majority of stem rust resistance genes used in agriculture (Pretorius et al., 2000). Isolates of Ug99 as well as those from Kenya were designated as race TTKSK based on the North American stem rust nomenclature (Wanyera et al., 2006; Jin et al., 2008). Race TTKSK and/or variants have spread throughout eastern and southern Africa, Yemen, and Iran (Nazari et al., 2009; Pretorius

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et al., 2010; Singh et al., 2006). Variants of race TTKSK have been identified with additional virulence to resistance genes *Sr24* and *Sr36* (Jin et al., 2008; Jin et al., 2009). These variants (races TTKST and TTTSK, respectively) pose an even greater threat to worldwide wheat production. Screening of currently grown cultivars and breeding germplasm indicated that the majority of the germplasm from Asia, the United States, and Canada are susceptible to TTKSK (Fetch 2007; Jin and Singh, 2006; Singh et al., 2008). Unfortunately, much of the resistance to race TTKSK available in the United States is conferred by *Sr24* and *Sr36* (this resistance is not effective to races TTKST and TTTSK). Of the available sources of resistance to race TTKSK and variants described to date, most of the resistance genes have been introgressed from wild relatives of wheat (Singh et al., 2006; Jin et al., 2007) and have not been utilized extensively in agriculture because of linkage between these genes and deleterious factors (Singh et al., 2008).

Three stem rust resistance genes previously have been transferred from *A. tauschii* to wheat: *Sr33*, *Sr45*, and *Sr46* (Kerber and Dyck, 1979; Marais et al., 1998; E. Lagudah, personal communication, 2010). These genes provide resistance to race TTKSK (Jin et al., 2007; M. Rouse and Y. Jin, unpublished data, 2010). Additional resistance genes may be present in *A. tauschii* germplasm. The identification of new genes will provide breeders with diverse genes for pyramiding to increase the durability of resistance. Our objective was to screen the available accessions of *A. tauschii* for resistance to race TTKSK to facilitate the characterization and introgression of novel resistance.

MATERIALS AND METHODS

Aegilops tauschii accessions were obtained from the USDA-Agricultural Research Service (ARS) National Small Grains Collection (Aberdeen, ID; 118 accessions) and from the Wheat Genetic and Genomic Resources Center (Manhattan, KS; 412 accessions). The accession names and sources were cross checked to eliminate accessions that were redundant among or within the two collections. We identified 456 nonredundant accessions. The geographic origins of these accessions are displayed in Table 1.

Six to ten seedlings of the 456 accessions were inoculated with six races of *Pgt*: TRTTF, TTKSK, TTTTF, QTHJC, RKQQC, and TPMKC (Table 2). Screening with TRTTF, TTKSK, and TTTTF was conducted at the USDA-ARS Cereal Disease Laboratory (Saint Paul, MN). Screening with QTHJC, RKQQC, and TPMKC was conducted at Kansas State University (Manhattan, KS). Accessions that have been used previously to introgress stem rust resistance genes *Sr33* and *Sr45*, RL5288 and RL5289, respectively, were obtained from Colin Heibert (Agriculture and Agri-Food Canada, Winnipeg, MB). The diploid *A. tauschii* source of *Sr46* (AUS 18913) and genetic stocks of *Sr33* and *Sr45* in hexaploid backgrounds, CSID 5404 and CSID 5406, respectively, were obtained from the Commonwealth Scientific and Industrial Research Organization (CSIRO) (Canberra, Australia). These stocks and susceptible 'Chinese Spring'

(CI 14108) were inoculated with the six *Pgt* 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 for 2 to 4 h maintained at 80% relative humidity by a KOH solution (Rowell, 1984). Procedures in inoculation, incubation, and disease assessment were as described previously (Jin et al., 2007). Infection types (ITs) were classified as in Stakman et al. (1962). Infection types with substantial necrosis or chlorosis were designated as "N" or "C," respectively. Low infection frequency was used to indicate notably low density of uredinia for a given leaf area. Infection types 0 to 2++ were considered low ITs indicating host resistance whereas ITs 3= to 4 were considered high ITs indicating host susceptibility. When low and high ITs were present on the same leaf, the plant was considered resistant. Accessions were classified as heterogeneous when both resistant and susceptible plants were present.

Frequencies of resistant, susceptible, and heterogeneous accessions were calculated for each of the six races. For each accession, the reaction to the combined races was determined as susceptible if the IT to any of the six races was high, resistant if the ITs to all six races were low, and heterogeneous if the reaction to one of the races was heterogeneous and the reaction to the five other races was low or heterogeneous. To test for associations of resistance, we calculated χ^2 values based on the assumption of independence of resistance to each race for every pairwise comparison of races. Percent of accessions resistant or heterogeneous for each country of origin were calculated.

To measure the repeatability of visually scoring infection types, a total of 37 randomly selected accessions were planted a second time for screening with *Pgt* races TTTTF, TTKSK, and TRTTF for a second biological replication. This resulted in data available for 100 infection types pairs (poor germination limited the number of infection type pairs). Out of these 100 pairs, seven were inconsistently recorded as resistant (0, 1, or 2) in one replication and susceptible (3 or 4) in the other. The reason for inconsistencies was likely due to heterogeneity in accessions or error in visually scoring infection types. A total of 93 of the infection type pairs were consistent representing a repeatability of classifying resistance and susceptibility of 93%. Similarly, we previously found the repeatability of classifying resistance and susceptibility for the diploid wheat relative *Triticum monococcum* L. to be greater than 95% (Rouse and Jin, 2011).

RESULTS

The seedling ITs of the *A. tauschii* accessions are available as Supplemental Table S1. The frequencies of accessions resistant, susceptible, and heterogeneous to the six races are displayed in Table 3. Ninety-eight accessions (22.2%) were resistant to race TTKSK, but only 12 of these accessions (2.7%) were resistant to the five other races as well. Race TRTTF was the most virulent race within this germplasm (88.2% of the accessions were susceptible) whereas QTHJC was the most avirulent (68.0% of the accessions were susceptible). Relatively few of the accessions were heterogeneous to any of the races (0.5 to 2.1%).

The diploid genetic stocks of *Sr33*, *Sr45*, and *Sr46* (RL5288, RL5289, and AUS 18913, respectively)

Table 1. Geographic origin of *Aegilops tauschii* Coss. accessions and percentage of accessions resistant or heterogeneous to six *Puccinia graminis* f. sp. *tritici* races.

| Country | Accessions | Percent resistant or heterogeneous | | | QTHJC | RKQQC | TPMKC | Combined |
|--------------|------------|------------------------------------|-------|-------|-------|-------|-------|----------|
| | | TRTTF | TTKSK | TTTTF | | | | |
| Afghanistan | 83 | 1 | 6 | 0 | 4 | 17 | 8 | 0 |
| Armenia | 21 | 5 | 24 | 24 | 40 | 30 | 14 | 0 |
| Azerbaijan | 42 | 33 | 48 | 57 | 78 | 41 | 55 | 9 |
| China | 18 | 0 | 0 | 0 | 6 | 18 | 6 | 0 |
| Georgia | 14 | 0 | 14 | 7 | 43 | 29 | 0 | 0 |
| Iran | 64 | 35 | 43 | 20 | 52 | 39 | 36 | 9 |
| Kazakhstan | 8 | 0 | 63 | 38 | 100 | 100 | 100 | 0 |
| Kyrgyzstan | 4 | 0 | 25 | 0 | 0 | 75 | 25 | 0 |
| Pakistan | 10 | 0 | 22 | 0 | 0 | 10 | 0 | 0 |
| Syria | 5 | 0 | 20 | 0 | 20 | 20 | 20 | 0 |
| Tajikistan | 41 | 0 | 12 | 3 | 15 | 13 | 5 | 0 |
| Turkey | 30 | 4 | 14 | 4 | 8 | 4 | 0 | 0 |
| Turkmenistan | 45 | 16 | 18 | 22 | 31 | 48 | 32 | 15 |
| Unknown | 36 | 17 | 34 | 22 | 48 | 23 | 33 | 7 |
| Uzbekistan | 30 | 3 | 27 | 17 | 34 | 37 | 27 | 3 |

Table 2. Races of *Puccinia graminis* f. sp. *tritici* used to screen *Aegilops tauschii* Coss. germplasm.

| Isolate | Race | Origin | Avirulence | Virulence |
|-------------|--------|---------------|-----------------------------|---|
| 04KEN156/04 | TTKSK† | Kenya | 24 36 Tmp | 5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 31 38 McN |
| 06YEM34-1 | TRTTF | Yemen | 8a 24 31 | 5 6 7b 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McN Tmp |
| 01MN84A-1-2 | TTTTF | United States | 24 31 | 5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McN Tmp |
| 75ND717C | QTHJC | United States | 7b 9a 9e 24 30 31 36 38 Tmp | 5 6 8a 9b 9d 9g 10 11 17 21 McN |
| 99KS76A-1 | RKQQC | United States | 9e 10 11 17 24 30 31 38 Tmp | 5 6 7b 8a 9a 9b 9d 9g 21 36 McN |
| 74MN1409 | TPMKC | United States | 6 9a 9b 24 30 31 38 | 5 7b 8a 9d 9e 9g 10 11 17 21 36 Tmp McN |

†Race TTKSK (Ug99) virulence to *Sr21* is uncertain (Jin et al., 2007).

displayed unique infection type patterns to the races used (Table 4). The diploid source of *Sr46* was also included in the germplasm screening (TA 1703, synonymous with AUS 18913). Variation in the *Sr46* lines in reaction to races QTHJC and RKQQC may be attributed to (i) an unstable intermediate reaction to these races and/or (ii) the screening of TA 1703 and AUS 18913 by different individuals in different locations (i.e., E.L. Olson, Manhattan, KS; M.N. Rouse, St. Paul, MN).

Significant positive associations were found for all race pairwise comparisons except for races TTTTTF and RKQQC (Table 5). However, diverse IT patterns were observed indicating the presence of multiple race-specific resistance genes.

Resistance was not equally distributed among countries of origin (Table 1). The 12 accessions resistant to the six *Pgt* races were distributed only among Azerbaijan, Iran, Turkmenistan, and Uzbekistan and of unknown origin. These countries of origin also had higher percentages of accessions resistant to race TTKSK compared to the other countries, with the exception of Kazakhstan where five of eight accessions were resistant to race TTKSK.

DISCUSSION

Previous studies have examined collections of *A. tauschii* or synthetic hexaploid wheats created with *A. tauschii* accessions for resistance to stem rust (Cox et al., 1992; Assefa

Table 3. Number (and frequency) of *Aegilops tauschii* Coss. accessions resistant, susceptible, and heterogeneous to six races of *Puccinia graminis* f. sp. *tritici* and the combined reaction to all races.

| Race | Total | Resistant (%) | Susceptible (%) | Heterogeneous (%) |
|-----------|-------|---------------|-----------------|-------------------|
| TRTTF | 439 | 48 (10.9%) | 387 (88.2%) | 4 (0.91%) |
| TTKSK | 442 | 98 (22.2%) | 338 (76.5%) | 6 (1.36%) |
| TTTTF | 436 | 61 (14.0%) | 366 (83.9%) | 9 (2.06%) |
| QTHJC | 413 | 130 (31.5%) | 281 (68.0%) | 2 (0.48%) |
| RKQQC | 422 | 121 (28.7%) | 299 (70.9%) | 2 (0.47%) |
| TPMKC | 423 | 95 (22.5%) | 326 (77.1%) | 2 (0.47%) |
| All races | 448 | 12 (2.68%) | 432 (96.4%) | 4 (0.89%) |

and Fehrmann, 2004; Friesen et al., 2008; Ogbonnaya et al., 2008). We evaluated a relatively large collection of *A. tauschii* accessions in an attempt to identify resistance to race TTKSK and other races with broad virulence.

Accessions resistant to the six *Pgt* races were confined to five geographic origin classifications. Cox et al. (1992) found that resistance in a subset of these accessions to *Pgt* race TNM was confined to Caspian Iran or Azerbaijan. We confirmed that these countries possess a higher frequency of resistance to multiple races of *Pgt*. The higher number of accessions and wider geographic range of germplasm tested in our study identified Turkmenistan as an additional hotspot for *Pgt* resistance.

Table 4. Infection types of *Aegilops tauschii* Coss. accessions with known stem rust resistance genes and selected lines with unknown genes.

| Accession | Background | Gene | TRTTF | TTKSK | TTTTF | QTHJC | RKQQC | TPMKC |
|----------------|--------------------|-------------|----------------|--------|---------|-------|-------|-------|
| Chinese Spring | <i>T. aestivum</i> | – | 4 [†] | 4 | 4 | 3 | 4 | 4 |
| RL5288 | <i>A. tauschii</i> | <i>Sr33</i> | – | – | 2/2,2+ | 2 | ;;2- | 2 |
| CSID 5405 | <i>T. aestivum</i> | <i>Sr33</i> | – | 2++ | – | 2,2- | 2+ | 2,2+ |
| RL5289 | <i>A. tauschii</i> | <i>Sr45</i> | – | – | 4 | 4 | 4 | 4 |
| CSID 5406 | <i>T. aestivum</i> | <i>Sr45</i> | 4 | 0; | 4 | 3 | 4 | 3+ |
| TA 1703 | <i>A. tauschii</i> | <i>Sr46</i> | 2 | ;;2- | 4 | 2- | 2++ | 1;; |
| AUS 18913 | <i>A. tauschii</i> | <i>Sr46</i> | 2 | ;;1,2- | 3+ | 3 | 3+ | 2- |
| TA 10087 | <i>A. tauschii</i> | – | 1 | ;;2- | ;;1C | ;;1 | 3- | 1 |
| TA 10124 | <i>A. tauschii</i> | – | 1,2 | 1,1+ | 1,2-,3- | ;;1 | 3,2++ | 2,2- |
| TA 10147 | <i>A. tauschii</i> | – | 4 | ;;1N | ;;1N | 1-,2 | ;0 | ;0 |
| TA 10171 | <i>A. tauschii</i> | – | ; | ; | 0; | 0 | 0; | ; |
| TA 10206 | <i>A. tauschii</i> | – | 3+ | ;;1 | 1,3-Z | ;;1 | ;;1 = | ;;1 = |
| Clae 15 | <i>A. tauschii</i> | – | 2+,3 | 1,2-;; | 4 | 3+,4 | 2- | 3 |

[†]Infection types rated on a 0 (immune) to 4 (susceptible) scale where ‘;’ denotes hypersensitive flecking, ‘N’ denotes necrosis, ‘C’ denotes chlorosis, and ‘+’ and ‘-’ signs indicate more or less sporulation, respectively, compared to the standard infection type (Stakman et al., 1962). For accessions heterogeneous for infection types among plants, a ‘/’ was used to separate different infection types corresponding to different plants. Symbol ‘;’ was used to separate different infection types present on the same leaf.

Table 5. Pairwise comparisons of the association between reactions to the six races.

| Association between | | χ^2 | Association type [†] | <i>p</i> value [‡] |
|---------------------|-------|----------|-------------------------------|-----------------------------|
| Race | Race | | | |
| TRTTF | TTKSK | 150.65 | + | 1.91×10^{-32} |
| TRTTF | TTTTF | 59.68 | + | 6.87×10^{-13} |
| TRTTF | QTHJC | 86.72 | + | 1.11×10^{-18} |
| TRTTF | RKQQC | 37.024 | + | 4.55×10^{-08} |
| TRTTF | TPMKC | 114.27 | + | 1.32×10^{-24} |
| TTKSK | TTTTF | 36.77 | + | 5.16×10^{-08} |
| TTKSK | QTHJC | 92.34 | + | 6.89×10^{-20} |
| TTKSK | RKQQC | 63.65 | + | 9.76×10^{-14} |
| TTKSK | TPMKC | 138.93 | + | 6.42×10^{-30} |
| TTTTF | QTHJC | 129.32 | + | 7.59×10^{-28} |
| TTTTF | RKQQC | 6.04 | NS | 0.11 |
| TTTTF | TPMKC | 37.44 | + | 3.72×10^{-08} |
| QTHJC | RKQQC | 51.98 | + | 3.02×10^{-11} |
| QTHJC | TPMKC | 130.32 | + | 4.61×10^{-28} |
| RKQQC | TPMKC | 101.31 | + | 8.13×10^{-22} |

[†]For significant associations, ‘+’ indicates a positive association among resistant accessions and ‘-’ indicates a negative association among resistant accessions. NS, nonsignificant association.

[‡]Analyses performed with Microsoft Excel (Microsoft Corporation, 2007), critical *p* value = 0.05.

In a survey for worldwide virulence in *Pgt* (Huerta-Espino, 1992), isolates with virulence to *Sr33* were not found. Seedling and adult plant resistance of hexaploid monogenic lines carrying *Sr33* to race TTKSK is only moderate (Jin et al., 2007). The dilution of *A. tauschii* resistance when expressed in hexaploids (Kerber and Dyck, 1979) may be one reason why *Sr33* resistance to race TTKSK is moderate. The adult plant resistance to race TTKSK conferred by *Sr45* and *Sr46* is unknown. *Sr45* is ineffective to the predominant races in North America (Table 4; Kerber and Dyck, 1979; Marais et al., 1998). Our data indicate that *Sr46* resistance is race specific (Table 4). If these genes are used to provide resistance to race TTKSK, additional resistance

genes must be used to create gene combinations that will provide resistance to other *Pgt* races.

We interpret the significant positive associations of resistance to various races observed as evidence for genes conferring resistance to multiple races. However, only 12 accessions were found to be resistant to the six races. Diverse IT patterns were observed among the *A. tauschii* accessions. The diversity of IT patterns prevented us from being able to confidently postulate the presence of known genes in the germplasm screened and likely indicate diversity for resistance genes, modifier genes, or genetic background effects. The IT patterns of a subset of accessions with unknown genes are displayed in Table 4. Many IT patterns could not be accounted for by the previously described genes alone or in combination. This suggests that additional stem rust resistance genes are likely present in *A. tauschii* germplasm. As *Sr33* provides resistance to all six races, further studies are needed to test the allelic relationship between resistance in the 12 combined resistant accessions and *Sr33*. Preliminary evidence based on ITs suggest that accessions with resistance to all races screened possess a gene (or genes) independent of *Sr33*. For example, accession TA 10171 exhibited resistance to the six races with ITs much lower than observed on RL5288 (Table 4). Further studies testing the allelic relationship between previously described genes and potentially novel resistance are needed to confirm the presence of novel resistance to race TTKSK specifically. We have initiated crosses to confirm the presence of novel resistance to race TTKSK, to map potentially novel sources of resistance, and to introgress such resistance into adapted wheat backgrounds.

Supplemental Information Available

Supplemental material is available free of charge at <http://www.crops.org/publications/cs>.

The seedling infection types (ITs) of the *Aegilops tauschii* accessions are available as Supplemental Table S1.

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