Resistance to Foliar Diseases in a Collection of *Triticum tauschii* Germ Plasm

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ABSTRACT

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The wild diploid wheat *Triticum tauschii* (syn. *Aegilops squarrosa*) is a valuable genetic resource for improvement of pest resistance in hexaploid wheat (*T. aestivum*). A collection of 219 *T. tauschii* accessions, obtained from Kyoto University, Japan, and representing most of the species' geographic range, was screened for reaction to four diseases: leaf rust (caused by *Puccinia recondita* f. sp. *tritici*), stem rust (caused by *P. graminis* f. sp. *tritici*), powdery mildew (caused by *Blumeria graminis* f. sp. *tritici* [syn. *Erysiphe graminis* f. sp. *tritici*]), and tan spot (caused by *Pyrenophora tritici-repentis*). Accessions were classified by region of origin, by botanical group, and by genetic group. Genetic groups were assigned based on previously determined molecular-marker genotypes. Resistance to rusts was concentrated in accessions collected near the Caspian Sea and in those classified as subspecies *strangulata*. Most such accessions belonged to genetic group A. Resistance to powdery mildew and tan spot was more dispersed but more common in accessions collected from regions ranging from the Caspian Sea eastward to Pakistan. Over 30% of 108 accessions that were screened for all diseases were classified as resistant to two or more, and 12% were resistant to three or more. Because disease resistance genes can readily be transferred from *T. tauschii* to *T. aestivum*, this collection is proving very useful for wheat improvement.

Additional keywords: breeding, conservation, interspecific hybridization, RFLP

Deployment of resistance genes in crop cultivars generally places selection pressure on populations of pathogens and insects, leading to loss of effective protection for the crop. Strategies designed to enhance the durability of genetic resistance usually require an ample and diverse supply of resistance genes available for deployment in the host population.

Genetic resistance is widely used to protect common wheat (*Triticum aestivum* L.) against a large array of pathogens and insects. Wheat can be hybridized with many related species, and several resistance genes commonly found in wheat cultivars were transferred from other species or genera. One species rich in genes for disease and insect resistance is the diploid *T. tauschii* (Coss.) Schmal. (syn. *Aegilops squarrosa* L.) (10,20, 21,24).

T. tauschii is a valuable source of genes for diversifying pest resistance in wheat. The chromosomes of *T. tauschii* are homologous to those of hexaploid wheat's D genome, and the two species can be hybridized directly (3,7). Several genes for resistance to leaf rust (caused by *Puccinia recondita* Roberge ex Desmasz. f. sp. *tritici*) (4,8,9,14,22) and Hessian fly (*Mayetiola destructor* Say) (6,11,12) have been transferred to and expressed in common wheat germ plasm lines.

Gill et al (10) reported on reaction to leaf rust, powdery mildew (caused by *Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici* Em. Marchal [syn. *Erysiphe graminis* DC. f. sp. *tritici* Em. Marchal]), greenbug (*Schizaphis graminum* Rondani), and Hessian fly in 60 accessions of *T. tauschii* held by the Wheat Genetics Resource Center (WGRC) in Manhattan, Kansas. Since obtaining 219 new accessions of *T. tauschii* (15) from Kyoto University, Japan, in 1985, the WGRC, with its cooperators at other institutions, has been evaluating accessions for their reactions to a wide range of pathogens and insects. This collection of *T. tauschii* is especially valuable, being the only one that covers most of the species' geographical range and carries detailed collection data (15). It also has been the subject of a detailed study of variation of molecular-marker loci (19) and is being used widely for wheat improvement. Therefore, to facilitate use of this collection, we are reporting herein results of screening for resistance to four foliar diseases of major economic importance: leaf rust, stem rust (caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn.), powdery mildew, and tan spot (caused by *Pyrenophora tritici-repentis* (Died.) Drechs).

MATERIALS AND METHODS

Seeds of the *T. tauschii* accessions described by Kihara et al (15) were obtained from Kyoto University, Japan, and are maintained by the WGRC, Dept. of Plant Pathology, Kansas State University, Manhattan. Accessions were screened for reaction to the powdery mildew pathogen at the USDA-ARS/North Carolina State University facilities at Raleigh. Screening for other diseases was done at WGRC facilities.

For leaf and stem rust screening, eight to 10 seedlings each were inoculated with culture PRTUS6 of *P. r. tritici* (avirulence/virulence formula *Lr2a, Lr9, Lr16, Lr18, Lr19, Lr24/Lr1, Lr2c, Lr2d, Lr3a, Lr10, Lr11, Lr17*) and culture TNM of *P. g. tritici* (avirulence/virulence formula *Sr8a, Sr9, Sr17, Sr30/Sr5, Sr6, Sr7b, Sr9e, Sr9g, Sr11, Sr21, Sr36*), respectively, using the urediniospore oil suspension inoculation and plant-growth methods of Browder (1). Leaf rust infection types were coded according to the system of Browder and Young (2), in which the first digit indicates relative uredinia number, and the second indicates relative uredinia size, both on a scale of 0 to 9. The letter following the digits describes the nature of tissue damage. Letter codes found in this study include P (pale green tissue), C (chlorosis), and X (mixed). Stem rust reaction was scored on a scale of 1 to 9, with 1 the lowest infection type.

Powdery mildew evaluations were completed in 46 × 36 × 7 cm (L × W × D) flats with 13 entries and a row of the susceptible wheat cultivar Chancellor in each flat. Flats were filled with a commercial potting medium, and four seeds per line were planted for evaluation. Inoculations were made 7 days after planting, at the two-leaf stage, and powdery mildew was scored 7 and 9 days after inoculation. Inoculation was with either culture nos. 2 or 7-12, which have avirulence/virulence formulas of *Pm3a, Pm3b, Pm3c, Pm6/Pm1, Pm2, Pm4a, Pm4b, Pm5, Pm7, Pm8, MA* and *Pm1, Pm2, Pm3b, Pm4b, Pm6, Pm8/Pm3a, Pm3c, Pm4a, Pm5, Pm7, MA*, respectively. Inoculum was maintained and increased on live plants

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as described by Leath and Heun (18), and virulence phenotypes of cultures were evaluated and confirmed on detached leaves. Inoculations of *T. tauschii* accessions were completed by gently shaking an infected plant directly over the flat. Plants were scored for reaction on a scale of 1 to 9 (18). The entire experiment was run twice.

Reaction to the toxin (*Ptr* toxin) produced by the tan spot fungus was evaluated by the method of Tomás and Bockus (23). After anthesis, three flag leaves of each accession were infiltrated with nonconcentrated culture filtrates of the fungus. Reactions were scored on a scale of 1 to 5, with 1 indicating no visible injury and 5 indicating necrosis throughout and beyond the infiltration site (23).

For each disease, accessions were classified as resistant if their reaction fell below a threshold known from experience to be of practical significance in breeding. Accessions also were grouped by three other classification methods: geographic, botanical, and genetic. The geographic classification included the eight regions used by Lubbers et al (19) for subdividing this collection (Fig. 1). Kihara et al (15) originally assigned the accessions to the botanical categories commonly used at the time to subdivide the species *A. squarrosa* (*T. tauschii*). These included three varieties of *T. tauschii* ssp. *eusquarrosa*—*typica, anathera,* and *meyeri*—and one variety of *T. t.* ssp. *strangulata*. Although *T. tauschii* is now considered to comprise only the two varieties *eusquarrosa* and *strangulata* (16), we retained the original classification of the collection for purposes of this study. The genetic classification included two divergent groups based on analysis of 20 molecular-marker loci in 101 of the accessions (19). Genetic groups A and B, comprising 29 and 72 accessions, respectively, were determined by the primary branch of the dendrogram in the cluster analysis based on molecular markers (19).

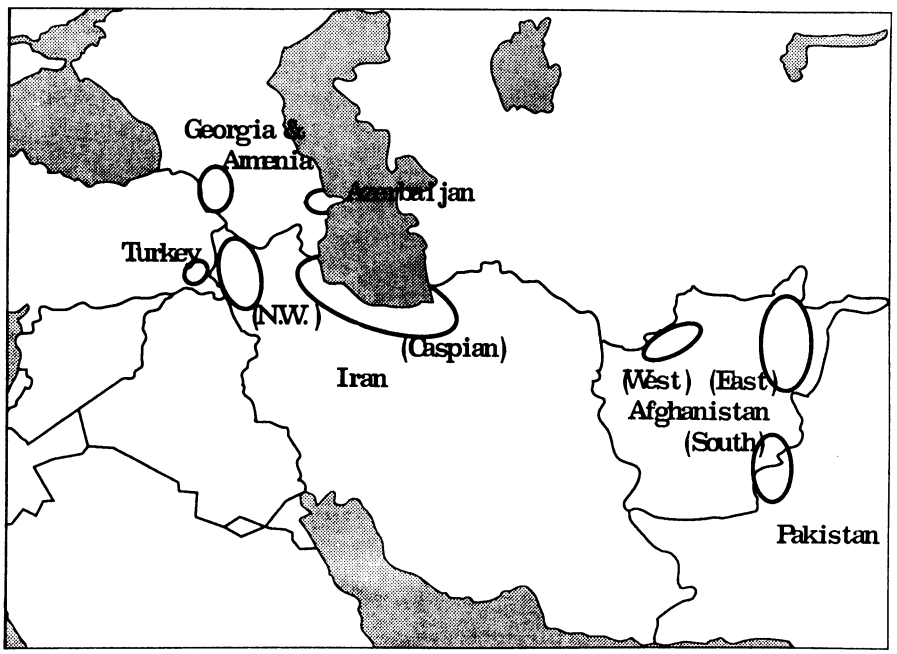

Fig. 1. Regions in which *Triticum tauschii* accessions evaluated herein were collected. Map shows national boundaries, with collection regions bounded by ovals.

RESULTS

Reactions to each pathogen varied widely among *T. tauschii* accessions, and resistant and susceptible *T. aestivum* checks had consistent reactions. A complete list of accessions—including their geographic, botanical, and genetic classifications—and their reactions to the four pathogens is available from the WGRC. Some accessions were not evaluated for

Table 1. Percentages of *Triticum tauschii* accessions falling below resistance thresholds for four diseases

Geographic origin	Taxonomic group[a]	No. of accessions	Leaf rust < 78X[b]	Stem rust < 5	Powdery mildew[c] 2 < 4	Powdery mildew[c] 7-12 < 4	Tan spot < 2
Pakistan + S. Afghanistan	*anathera*	5	0	0	100	100	100
	typica	10	0	0	16	16	89
E. Afghanistan	*anathera*	5	0	0	0	0	67
	typica	53	0	0	18	9	50
W. Afghanistan	*anathera*	1	0	0	0	0	...
	typica	24	0	0	18	14	20
Caspian Iran	*typica*	31	23	11	3	6	68
	strangulata	17	47	29	21	14	88
	meyeri	7	57	20	0	20	60
N.W. Iran	*typica*	24	4	0	5	5	67
Azerbaijan	*typica*	6	50	40	0	0	80
Georgia + Armenia	*anathera*	1	0	0	0	0	0
	typica	21	0	0	16	47	50
Turkey	*typica*	12	0	0	0	0	18
Unknown	*typica*	2	0	0	0	0	100
All accessions		219	11	6	12	14	61
No. tested		...	219	193	177	177	188
Genetic classification[d]							
Group A		29	38	29	5	5	78
Group B		72	4	0	8	11	46

[a] *T. t.* ssp. *eusquarrosa* varieties *anathera*, *meyeri*, and *typica*; *T. t.* ssp. *strangulata* var. *strangulata*.
[b] X = mixed damage.
[c] Powdery mildew isolates.
[d] Determined by restriction fragment length polymorphism.

certain diseases because of poor emergence. To identify patterns of variation, we computed percentages of low reaction types (Table 1) for each classification and disease.

Leaf and stem rust resistances were concentrated in accessions of ssp. *strangulata* and var. *meyeri* from areas of Iran near the Caspian Sea and nearby Azerbaijan (Table 1). Resistance to rusts was much more common in genetic group A than in group B.

Accessions resistant to powdery mildew were more varied in their geographical origins than those resistant to the rusts (Table 1), occurring in all regions except Azerbaijan and Turkey. The percentage of accessions resistant to mildew was slightly higher in group B than A. Reactions to the two *B. g. tritici* isolates were highly correlated ($r = 0.73$).

A very high percentage of all accessions had no damage from infiltration with tan spot toxin (Table 1). Accessions from the three westernmost regions (N.W. Iran, Armenia, and Turkey) were more susceptible on average; however, resistant accessions were found in all groups. As with the rusts, resistant accessions occurred more often in genetic group A.

Overall, 30% of the 108 accessions screened for all diseases were classified as resistant to two or more diseases each, and 12% were resistant to three or more. Examples of accessions with high levels of resistance to one or more diseases are shown in Table 2. Multiple resistance was common among accessions from Afghanistan and Pakistan (resistance to powdery mildew and tan spot, but not to leaf or stem rust) as well as among those from the Caspian seacoasts of Azerbaijan and Iran (where resistance to all four diseases was common). One accession, TA 2456 from Caspian Iran, was resistant to all four diseases. All accessions from Turkey were susceptible to all diseases, except for a small percentage resistant to the tan spot toxin.

DISCUSSION

We transferred four genes for leaf rust resistance from *T. tauschii* to hexaploid winter wheat lines that were released as germ plasms (4,8,9, and *unpublished*). They include genes derived from two *T. tauschii* accessions listed herein: TA 2450 (an unnamed gene transferred to KS91WGRC11) and TA 2460 (*Lr41*, transferred to KS91WGRC10).

We obtained backcross lines segregating for resistance genes derived from 10 of the 18 remaining accessions that have some level of leaf rust resistance as seedlings. Genetic studies of leaf rust resistance from *T. tauschii* in both diploid and hexaploid backgrounds are underway.

Table 2. Reactions to leaf and stem rust, powdery mildew, and tan spot of 33 *Triticum tauschii* accessions along with four *T. aestivum* checks

Accession no.				Genetic	Leaf	Stem	Powdery mildew[g]		
KU[a]	WGRC[b]	Region[c]	Taxon. group[d]	group[e]	rust[f]	rust[g]	2	7-12	Tan spot[h]
20-9	TA 2377	C. Iran	*strangulata*	A	78X	3	5.7	6.0	1
20-10	TA 2378	C. Iran	*meyeri*	A	02C	3	6.5	5.5	1
2004	TA 2382	Pakistan	*anathera*	...	88P	8	3.2	2.7	...
2009	TA 2386	Pakistan	*anathera*	...	88P	...	2.5	1.7	1
2014	TA 2391	Pakistan	*typica*	...	88P	9	3.0	3.5	1
2025	TA 2402	E. Afghanistan	*typica*	B	88P	8	2.2	4.0	2
2027	TA 2404	E. Afghanistan	*typica*	B	88P	9	2.7	1.5	1
2033	TA 2410	E. Afghanistan	*typica*	...	88P	9	3.0	2.0	1
2048	TA 2425	W. Afghanistan	*typica*	...	88P	8	2.5	3.2	1
2065	TA 2442	W. Afghanistan	*typica*	...	88P	7	2.5	3.0	1
2074	TA 2450	C. Iran	*strangulata*	A	15X	7	...	...	2
2080	TA 2456	C. Iran	*strangulata*	...	15X	3	3.2	2.7	1
2082	TA 2458	C. Iran	*typica*	B	03C	8	5.2	5.5	2
2084	TA 2460	C. Iran	*typica*	A	03C	7	...	...	1
2087	TA 2462	C. Iran	*typica*	A	02C	7	6.0	5.7	3
2088	TA 2463	C. Iran	*strangulata*	...	88P	3	5.5	5.7	1
2090	TA 2464	C. Iran	*strangulata*	A	88P	2	5.5	5.2	1
2091	TA 2465	C. Iran	*strangulata*	...	88P	7	1.2	0.7	1
2092	TA 2466	C. Iran	*strangulata*	A	88P	2	3.0	5.5	1
2094	TA 2468	C. Iran	*strangulata*	...	03C	5	5.0	4.2	1
2096	TA 2470	C. Iran	*strangulata*	A	02C	5	5.0	4.5	1
2098	TA 2472	C. Iran	*typica*	A	03C	5	4.7	4.5	1
2106	TA 2479	C. Iran	*typica*	...	88P	7	3.0	2.7	1
2110	TA 2483	C. Iran	*typica*	...	15X	2	6.7	6.7	1
2122	TA 2495	N.W. Iran	*typica*	B	04C	5	6.5	5.0	1
2156	TA 2525	C. Iran	*typica*	A	88P	3	4.2	2.5	2
2158	TA 2527	C. Iran	*meyeri*	A	04C	...	...	...	...
2159	TA 2528	C. Iran	*typica*	...	04C	5	4.5	5.0	4
2160	TA 2529	C. Iran	*meyeri*	A	02C	5	6.2	6.2	1
2161	TA 2530	C. Iran	*meyeri*	A	04C	7	5.0	5.7	...
2627	TA 2547	E. Afghanistan	*typica*	B	88P	9	2.2	3.0	3
2825	TA 2576	Georgia	*typica*	...	88P	5	3.0	3.0	5
2832	TA 2582	Georgia	*typica*	...	88P	8	2.7	3.2	4
T. aestivum checks									
TAM 107					88P	...	...	...	5
Wichita					88P	9	...	...	...
Chancellor					...	...	8.2	7.6	...
Karl					...	...	...	...	1

[a] Kyoto University.
[b] Wheat Genetics Resource Center, Manhattan, Kansas.
[c] C = central, E = eastern, W = western, NW = northwestern.
[d] *T. t.* ssp. *eusquarrosa* varieties *anathera*, *meyeri*, and *typica*; *T.t.* ssp. *strangulata* var. *strangulata*.
[e] As determined by restriction fragment length polymorphism.
[f] Percent affected. C = chlorosis, P = pale green tissue, X = mixed damage.
[g] Rated on a scale of 1 to 9, where 1 = lowest infection.
[h] Rated on a scale of 1 to 5, where 1 = no injury and 5 = necrosis throughout and beyond the infection site.

Wheat workers in the WGRC and USDA-ARS/North Carolina State University are transferring genes for resistance to the other three diseases as well. Preliminary screening of backcross progeny indicates that these resistance genes are also expressed at the hexaploid level.

Within the collection, reaction to all pathogens—but in particular to the rusts—was related to the geographic origins of the accessions. All accessions with seedling resistance to leaf or stem rust were from the regions surrounding the Caspian Sea. These regions are the most humid parts of *T. tauschii*'s range and may have provided more selection pressure to increase the frequency of rust resistance alleles. However, resistance to the powdery mildew fungus (which also is adapted to humid conditions) and/or the tan spot toxin was common among accessions from both the Caspian seacoast and the relatively drier areas farther east. We screened only for reaction to the tan spot toxin and not for the ability of accessions to resist colonization by *P. tritici-repentis*; however, toxin reaction is highly correlated with field reaction to tan spot (23). Of named genes for resistance to powdery mildew, only *Pm2* is known to be located in the D genome. Since isolate no. 2 was virulent to *Pm2*, resistance in these accessions is conditioned by previously undescribed gene(s).

Multiple disease resistance was most common in ssp. *strangulata* and var. *meyeri*, which are very similar to each other at the DNA level and very dissimilar to the other two botanical groups (19). They also are found exclusively in the Caspian Sea region, and ssp. *strangulata* is considered the most likely donor of the D genome of modern bread wheats (13,17). All accessions of ssp. *strangulata* evaluated for restriction fragment length polymorphism patterns by Lubbers et al (19), and all but one of var. *meyeri*, fell into genetic group A. Patterns of resistance in group A, therefore, were similar to those of ssp. *strangulata*, var. *meyeri*, and regions bordering the Caspian Sea (Tables 1 and 2).

Evaluating resistance only by seedling inoculation and toxin infiltration may underestimate the potential of this collection for wheat improvement. For example, the adult-plant leaf rust resistance gene *Lr22a* was transferred from *T. tauschii* (5), and we released a winter wheat germ plasm line with adult-plant resistance to leaf rust, KS91WGRC12. Resistance in the latter is derived from *T. tauschii* accession TA 2541, which was collected in eastern Afghanistan. Like all accessions from that region, TA 2541 was highly susceptible to leaf rust at the seedling stage.

The Kyoto collection and other collections of *T. tauschii* are proving to be crucial resources for improvement and diversification of wheat. Their continuing preservation, evaluation, and utilization should be of the highest priority. Furthermore, the species should be monitored in its Asian habitat and collected and/or protected where it is threatened by overgrazing, urbanization, intensive agriculture, or other activities.

Seed requests. Wheat workers interested in utilizing the Kyoto collection for improvement of foliar disease resistance in wheat may obtain complete screening data and/or small quantities of seed of individual accessions from the WGRC (at the first author's address) upon request. Requests from workers in countries requiring a seed import permit should include one.

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