Resistance to Stripe Rust and Eyespot Diseases of Wheat in *Triticum tauschii*

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ABSTRACT

Yildirim, A., Jones, S. S., Murray, T. D., Cox, T. S., and Line, R. F. 1995. Resistance to stripe rust and eyespot diseases of wheat in *Triticum tauschii*. Plant Dis. 79:1230-1236.

A collection of 279 *Triticum tauschii* (syn. *Aegilops squarrosa*) accessions was evaluated for resistance to stripe rust (*Puccinia striiformis*) and eyespot (*Pseudocercosporella herpotrichoides*) diseases. Seedlings were inoculated with four different races of *P. striiformis* that represent all known virulences in the Pacific Northwest, and a genetically modified strain of *P. herpotrichoides* expressing β-glucuronidase. Seventeen percent (44) of the *T. tauschii* accessions were resistant to all Pacific Northwest races of stripe rust, and 45% (115) were resistant to eyespot. Thirty-nine of the 279 accessions were resistant to the stripe rust races and the eyespot pathogen. Accessions resistant to stripe rust were mainly from the Caspian Sea region of Iran and Azerbaijan, with the majority belonging to *T. tauschii* subsp. *strangulata* and *T. t.* subsp. *meyeri*. There was no clear association between resistance to eyespot and geographical origin or taxonomic subgroup.

Additional keywords: *Triticum aestivum,* wild wheat

Triticum tauschii (Coss.) Schmal. (syn. *Aegilops squarrosa,* 2n = 2x = 14, DD), a wild diploid, is the D-genome donor of hexaploid wheat (*Triticum aestivum* L.) (2n = 6x = 42, AABBDD) (18,26). Its close evolutionary relationship and the relative ease of hybridization with other *Triticum* spp. have made *T. tauschii* a subject of interest for the genetic improvement of hexaploid wheat (3,20). Accessions of *T. tauschii* are resistant to leaf rust (caused by *Puccinia recondita* Roberge ex Desmasz. f. sp. *tritici*), eyespot (caused by *Pseudocercosporella herpotrichoides* (Fron.) Deighton), powdery mildew (caused by *Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici* Em. Marchal), tan spot (caused by *Pyrenophora tritici-repentis* (Died.) Drechs.), greenbug (*Schizaphis graminum* (Rondani)), Hessian fly (*Mayetiola destructor* (Say)), Karnal bunt (*Tilletia indica* Mitra), and wheat curl mite (*Eriophyes tulipae* Keifer) (3,11,17,28,-35,39), and possess genes that improve agronomic and end-use quality traits of wheat (16,32,38).

Stripe rust, caused by *Puccinia striiformis* Westend., is an important yield-limiting foliar disease in the U.S. Pacific Northwest as well as in several other wheat growing areas worldwide. This disease occurs on many grasses and cereal crops, including wheat, barley, Triticale, and rye (31). Cultivars with nonspecific and/or race-specific resistance are used to control stripe rust. Although race-specific resistance may become ineffective, usually within a few years of general use, resistant cultivars with this type of resistance have been effective in controlling the disease.

Eyespot, caused by *Pseudocercosporella herpotrichoides* (teleomorph = *Tapesia yallundae* Wallwork & Spooner), is another economically important disease of winter wheat in the Pacific Northwest and other temperate areas of the world (5,15,30,36). The disease has been effectively controlled with chemicals, but the discovery of isolates of the pathogen resistant to fungicides (29) has prompted plant breeders to focus on genetic control. Breeding programs have improved resistance in commercial cultivars (7,19,27), but progress is slow because only two resistance genes have been described for eyespot in wheat (25,37), and one on chromosome 4V in *Dasypyrum villosum* (L) (29), and these genes have not been combined in the same cultivar. Sprague (35) evaluated several wheat relatives, including *T. tauschii,* for eyespot resistance and suggested the use of wheat relatives in general, and *Aegilops ventricosa* in particular, as sources of resistance genes in breeding for resistance. Simonet (33) transferred resistance to eyespot from *A. ventricosa* (genomes DDM^vM^v) into the hexaploid wheat cultivar Marne. Maia (25) then selected the line VPM-1 from this material based on its high degree of resistance to eyespot. VPM-1 has since become a widely used source of resistance in breeding programs. Identifying new sources of resistance is critical to maintaining a high level of resistance and to preventing the pathogen from circumventing resistance genes (12).

Cox et al. (3) and others (9,10,20,35) found that *T. tauschii* is a valuable source of genes for resistance to wheat pathogens. The objective of this study was to evaluate *T. tauschii* accessions for resistance to stripe rust and eyespot.

MATERIALS AND METHODS

Genetic stocks. Accessions of *T. tauschii* were obtained from the Wheat Genetic Resource Center, Kansas State University. Most of these accessions have been described previously (3,18,24). The following lines were used as controls for eyespot reaction: VPM-1, highly resistant; Cappelle-Desprez and Cerco, resistant; and Chinese Spring and Selection 101, susceptible.

Stripe rust reaction. Four races of *P. striiformis* representing the virulence of all Pacific Northwest (PNW) races (Table 1) were used for inoculation (23). Verified pure inoculum was increased on race-specific differential cultivars in isolation booths to prevent contamination. Freshly collected urediospores were used as inoculum for all tests. The seedlings were grown in a rust-free growth chamber with a diurnal temperature cycle of 10 to 25°C. Ten to 15 seedlings of each accession were uniformly inoculated with urediospores at the two-leaf stage, incubated in a dew chamber at 10°C for 18 to 24 h, and then placed in a growth chamber with a diurnal temperature cycle that gradually changed between 4 and 20°C. Day length was adjusted to 16 h with metal halide lights. Control cultivars and differential cultivars were planted in each experiment to determine viability of inoculum and purity of the races.

Stripe rust infection type was recorded 15 to 18 days and 21 to 23 days after inoculation to reduce variability attributable to time (23). Infection types were recorded as 2, 5, and 8, representing resistant, intermediate, and susceptible, respectively, using the concept of the basic and expanded scales (23). Resistant accessions were retested to confirm their resistance.

Eyespot reaction. A genetically modified strain of *P. herpotrichoides* (P84-8) expressing β-glucuronidase (GUS) was

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Accepted for publication 19 September 1995.

used to evaluate resistance (6,14). Two seeds per accession were sown in peat pots in a commercial potting mixture (55% peat:35% pumice:10% sand, wt/wt/wt) and covered with 2 cm of vermiculite. Fifty pots were then placed randomly in plastic flats (54 × 27 × 6 cm). Following germination, the flats were placed in a growth chamber at 12°C with 12 h light and 95 to 100% relative humidity. Two-week-old seedlings were inoculated, and disease progress was evaluated with a GUS assay 6 weeks after inoculation as described previously (6). Visual ratings of disease severity were modified from de la Peña and Murray (6) as follows: 1 = a lesion on the first leaf sheath only; 2 = a lesion on the first leaf sheath and a small lesion or speck on the second leaf sheath; 3 = a lesion on the first and up to half of the second leaf sheath; and 4 = a lesion covering the entire first and second leaf sheaths. Relative resistance was determined by comparing accessions with the reactions of known control genotypes or cultivars. All resistant accessions were reevaluated in a second experiment to confirm their resistance reactions.

Experimental design and statistical analysis. Accessions were arranged in a randomized complete block design with three replicates. Analysis of variance was conducted with SAS statistical analysis software (SAS Institute, Cary, NC). GUS data were transformed by a logarithmic transformation before analysis because means and variances were not independent. Means were differentiated by Fisher's least significant difference ($P = 0.01$). Accessions with mean GUS values that exceeded the mean of the sum of the VPM value plus the LSD value were considered susceptible.

RESULTS

Seventeen percent of the *T. tauschii* accessions were resistant to all PNW races of *P. striiformis*, and an additional 21% exhibited resistance to specific races (Table 2). *T. tauschii* subsp. *typica* had the fewest accessions that were resistant to stripe rust (33%), whereas *T. t.* subsp. *strangulata* and *T. t.* subsp. *meyeri* had the most resistant accessions (59 and 66% resistant to all races, respectively). Eighteen percent of the accessions had an intermediate reaction to one or more CDL races. Some of the accessions had poor germination or few seeds and therefore were not tested for all races or both diseases. Most of the stripe rust resistant accessions originated from Iran and Azerbaijan near the Caspian Sea. No resistant accessions were found among the collections from Turkey, Afghanistan, Pakistan, or China.

Forty-five percent of the accessions were resistant to eyespot. Differences among accessions were highly significant ($P = 0.01$). All subspecies had some resistant accessions. Two of the resistant accessions in the first experiment were determined to be susceptible in the second experiment (Table 2). The resistance of all other accessions was confirmed. *T. t.* subsp. *strangulata* and *T. t.* subsp. *meyeri* had the most resistant accessions, with 77 and 100% resistance to eyespot, respectively.

Thirty nine accessions from Turkmenistan, Iran, and Azerbaijan were resistant to both diseases, whereas most of the accessions from Afghanistan, Pakistan, and China were susceptible. Although all accessions from Turkey were highly susceptible to stripe rust, many were resistant to eyespot. Susceptibility was common in *T. tauschii* subsp. *anathera* and *T. t.* subsp. *typica,* whereas all accessions of *T. t.* subsp. *strangulata* and *T. t.* subsp. *meyeri* exhibited multiple resistance. The Caspian seacoast of Azerbaijan and Iran appeared to hold the main concentration of resistant accessions for both diseases.

DISCUSSION

Several accessions had resistance to all races of *P. striiformis* and to *P. herpotrichoides*. Resistance to both pathogens was most common in *T. t.* subsp. *strangulata* and *T. t.* subsp. *meyeri*. Cox et al. (3) found 13 of these same lines to be resistant to leaf rust, stem rust, powdery mildew, and tan spot. The occurrence of lines with multiple resistance should allow for the transfer of several beneficial genes from single crosses. Although we have not attempted to study the allelic relationships of already characterized stripe rust resistance genes in the D-genome, *Yr8, Yr16, Yr18* (31,34), it is possible that some genes in *T. tauschii* lines will be different than genes already characterized. We also identified 32 spring-habit *T. tauschii* accessions among *T. t.* subsp. *typica*, mainly from Afghanistan. Generation time in the greenhouse can be greatly reduced because these lines have no vernalization requirement.

Another interesting result was the diversity among accessions in relation to their geographic origin. Resistance to eyespot was more dispersed geographically than that of stripe rust. *T. t.* subsp. *strangulata* from Iran had the highest frequency of resistance to stripe rust, eyespot, and other diseases studied by Cox et al. (3). *T. t.* subsp. *strangulata* is also easy to cross with wheat because it has larger heads and greater pollen shed than the other subspecies.

Accessions TA 2450 and TA 2460, which are resistant to both diseases, and accessions TA 2542 and TA 2547, which are susceptible to both diseases, have produced hexaploid progenies with soft endosperm (4). The only known soft-endosperm gene in hexaploid wheat is located on the short arm of chromosome 5D (22) and probably was transferred from the original *T. tauschii* parents of hexaploid wheat. The existence of a soft endosperm gene in *T. tauschii* offers an opportunity to improve the disease resistance of the Pacific Northwest soft white wheat cultivars while simultaneously manipulating kernel softness, an important end-use quality characteristic.

When Sprague screened wild relatives of wheat in 1936 (35), he reported that *Aegilops squarrosa* L. var. *typica* was moderately resistant, but *Aegilops tauschii* Coss. was mostly susceptible. Although he used a different classification for his accessions, they are now considered to be different subspecies of *T. tauschii.* We also found that 45% of *T. t.* subsp. *typica* accessions were moderately resistant to eyespot, whereas *T. t.* subsp. *strangulata* and *T. t.* subsp. *meyeri* were highly resistant. There have been no further reports on the use of *T. tauschii* for eyespot resistance since the initial report of Sprague.

There was a positive correlation observed between visual scores and GUS activity ($r = 0.86$), although a few exceptions were observed, for example accessions TA 1618 and 1649 from Iran. In both cases, high visual disease scores were associated with low GUS activity. In this situation, the hypersensitive reaction may result in a phenotypic appearance similar to that of a susceptible plant but limited disease development due to rapid death of infected epidermal cells. Similar responses

Table 1. Virulence of Cereal Disease Laboratory (CDL) races of *Puccinia striiformis* on North American differential cultivars

	Differential wheat cultivar[a]														
CDL race	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
17	V	V	V	A	A	A	A	A	V	A	V	A	A	A	A
37	V	A	V	A	A	V	A	V	V	V	V	V	A	A	A
43	V	A	V	V	V	A	A	A	A	A	A	V	A	V	A
45	V	A	V	A	A	A	A	A	A	A	A	V	V	A	V

[a] 1: Lemhi; 2: Chinese 166; 3: Heines VII; 4: Moro; 5: Paha; 6: Druchamp; 7: Riebesel 47-51; 8: Produra; 9: Yamhill; 10: Stephens; 11: Lee; 12: Fielder; 13: Tyee; 14: Tres; 15: Hyak. V: Virulent, A: Avirulent

Table 2. Reactions of *Triticum tauschii* accessions to *Pseudocercosporella herpotrichoides* and North American races of *Puccinia striiformis*

WGRC[a] acc. no.	Region	Subspecies	Reaction to CDL race[b] 17	37	43	45	Eyespot[c]	Visual score	GUS activity	Growth habit
1604	Afghanistan	*typica*	ND[d]	ND	ND	ND	S	4.0	3.8	Winter
1620	Afghanistan	Unknown	S	S	S	S	ND	ND	ND	Winter
1629	Afghanistan	*typica*	S	S	S	S	ND	ND	ND	Winter
1632	Afghanistan	*typica*	S	S	S	S	S	3.2	2.4	Spring
1637	Afghanistan	Unknown	S	S	S	S	S	4.0	2.6	Winter
1638	Afghanistan	*typica*	S	S	S	S	R	1.5	1.7	Spring
1655	Afghanistan	*typica*	S	S	S	S	R	1.8	1.9	Spring
1703	Afghanistan	Unknown	S	S	S	S	S	3.4	2.5	Spring
1705	Afghanistan	*typica*	S	S	S	S	ND	ND	ND	Winter
2387	Afghanistan	*typica*	S	S	S	S	S	3.6	2.3	Winter
2389	Afghanistan	*typica*	S	S	S	S	S	3.0	2.4	Winter
2390	Afghanistan	*typica*	S	S	S	S	S	3.8	2.4	Winter
2391	Afghanistan	*typica*	S	S	ND	I	S	4.0	2.6	Spring
2394	Afghanistan	*typica*	S	S	S	S	S	4.0	2.6	Winter
2395	Afghanistan	*typica*	S	S	S	I	R	2.5	1.9	Winter
2396	Afghanistan	*typica*	S	S	S	S	S	3.5	2.3	Winter
2397	Afghanistan	*typica*	S	S	S	S	R	2.4	2.1	Winter
2398	Afghanistan	*typica*	S	S	S	S	R	2.3	1.7	Winter
2399	Afghanistan	*typica*	S	S	S	S	R	1.0	1.4	Winter
2400	Afghanistan	*typica*	ND	ND	ND	ND	R	1.0	1.4	Winter
2401	Afghanistan	*typica*	S	S	S	S	R	1.0	1.3	Winter
2402	Afghanistan	*typica*	S	S	S	S	S	4.0	2.6	Winter
2403	Afghanistan	*typica*	S	I	ND	I	S	4.0	2.8	Spring
2405	Afghanistan	*anathera*	S	S	S	S	S	3.8	2.6	Winter
2406	Afghanistan	*typica*	S	S	ND	S	S	4.0	2.5	Spring
2407	Afghanistan	*anathera*	S	S	S	S	S	3.0	2.8	Winter
2408	Afghanistan	*typica*	S	S	S	S	ND	ND	ND	Winter
2409	Afghanistan	*typica*	S	S	S	S	S	2.3	2.3	Spring
2410	Afghanistan	*typica*	ND	ND	ND	ND	R	1.2	1.2	Winter
2412	Afghanistan	*typica*	ND	ND	ND	ND	R	2.6	1.9	Winter
2415	Afghanistan	*typica*	S	S	S	S	R	2.6	1.9	Winter
2416	Afghanistan	*typica*	S	S	S	S	S	3.0	2.2	Winter
2417	Afghanistan	*anathera*	S	S	S	S	S[e]	2.2	2.6	Winter
2418	Afghanistan	*typica*	S	S	S	S	S	4.0	2.3	Winter
2419	Afghanistan	*typica*	S	S	ND	S	ND	ND	ND	Spring
2420	Afghanistan	*typica*	S	S	ND	S	S	3.0	2.3	Spring
2421	Afghanistan	*typica*	S	S	S	S	S	4.0	2.8	Spring
2422	Afghanistan	*typica*	S	S	S	S	S	3.1	2.5	Winter
2423	Afghanistan	*typica*	S	S	ND	S	R	2.0	1.3	Spring
2424	Afghanistan	*typica*	S	S	ND	S	R	1.5	1.5	Spring
2426	Afghanistan	*typica*	S	S	ND	S	S	4.0	3.3	Spring
2427	Afghanistan	*typica*	S	S	ND	S	S	4.0	2.6	Spring
2428	Afghanistan	*typica*	S	S	ND	S	S	4.0	2.9	Spring
2430	Afghanistan	*typica*	S	S	S	S	S	4.0	3.1	Winter
2432	Afghanistan	*typica*	S	S	S	S	S	4.0	2.8	Winter
2433	Afghanistan	*typica*	S	S	S	S	S	3.6	2.8	Winter
2434	Afghanistan	*typica*	S	S	S	S	S	3.5	2.5	Winter
2435	Afghanistan	*typica*	S	S	I	I	S	3.5	2.5	Winter
2437	Afghanistan	*typica*	S	S	ND	S	S	4.0	2.7	Spring
2438	Afghanistan	*typica*	S	S	ND	S	S	4.0	2.9	Spring
2439	Afghanistan	*typica*	S	S	S	S	S	3.6	2.8	Winter
2440	Afghanistan	*typica*	S	S	S	S	S	4.0	3.0	Winter
2442	Afghanistan	*typica*	S	S	ND	S	S	4.0	2.6	Spring
2443	Afghanistan	*typica*	S	S	ND	S	S	3.7	2.8	Spring
2444	Afghanistan	*typica*	S	S	S	S	S	3.5	2.6	Winter
2532	Afghanistan	*typica*	S	S	S	S	S	4.0	2.7	Winter
2533	Afghanistan	*typica*	ND	ND	ND	ND	S	3.1	2.6	Winter
2535	Afghanistan	*typica*	ND	ND	ND	ND	S	4.0	3.0	Winter
2536	Afghanistan	*typica*	S	S	S	S	S	4.0	3.0	Winter
2537	Afghanistan	*typica*	S	S	S	S	S	4.0	2.8	Winter
2538	Afghanistan	*typica*	ND	ND	ND	ND	S	4.0	2.9	Winter
2539	Afghanistan	*typica*	S	S	S	S	S	4.0	3.0	Winter
2540	Afghanistan	*typica*	S	S	S	S	S	2.4	2.4	Winter
2541	Afghanistan	*typica*	S	S	S	S	S	4.0	2.9	Winter
2542	Afghanistan	*typica*	S	S	S	S	S	4.0	2.7	Winter
2543	Afghanistan	*typica*	S	S	S	S	S	4.0	3.0	Winter
2544	Afghanistan	*typica*	S	S	S	S	S	4.0	2.7	Winter

(*continued on next page*)

[a] WGRC: Wheat Genetics Resource Center, Manhattan, Kansas.
[b] Infection types were recorded as 2, 5, 8, representing resistant (R), intermediate (I) and susceptible (S), respectively, using basic and expanded scales.
[c] Disease progress was evaluated visually and with a GUS assay 6 wk after inoculation.
[d] ND: Not determined.
[e] Determined to be susceptible in the second experiment.

Table 2. (*continued from preceding page*)

WGRC[a] acc. no.	Region	Subspecies	Reaction to CDL race[b] 17	37	43	45	Eyespot[c]	Visual score	GUS activity	Growth habit
2545	Afghanistan	*typica*	I	I	I	I	S	4.0	3.0	Winter
2546	Afghanistan	*typica*	S	S	S	S	S	4.0	2.7	Winter
2547	Afghanistan	*typica*	S	S	S	S	ND	ND	ND	Winter
2548	Afghanistan	*typica*	S	S	S	S	S	4.0	2.5	Winter
2549	Afghanistan	*typica*	S	S	S	S	S	3.2	2.7	Winter
2550	Afghanistan	*typica*	S	S	S	S	S	4.0	2.8	Winter
2553	Afghanistan	*typica*	S	S	S	S	S	4.0	3.1	Winter
2555	Afghanistan	*typica*	S	S	S	S	S	4.0	2.8	Winter
2558	Afghanistan	*typica*	S	S	S	S	S	4.0	2.6	Winter
2559	Afghanistan	*typica*	S	S	S	S	R	1.0	1.1	Spring
2587	Afghanistan	*typica*	S	S	S	S	S	4.0	2.4	Winter
1640	Armenia	Unknown	S	S	S	S	ND	ND	ND	Winter
1700	Armenia	Unknown	S	S	S	S	S	2.8	4.5	Winter
2566	Armenia	*anathera*	S	S	S	I	S	3.0	2.4	Winter
2567	Armenia	*typica*	S	S	S	S	R	2.7	2.0	Winter
2568	Armenia	*typica*	R	R	R	R	ND	ND	ND	Winter
2569	Armenia	*typica*	S	S	S	S	S	4.0	2.9	Winter
2570	Armenia	*typica*	S	S	S	S	ND	ND	ND	Winter
2571	Armenia	*typica*	I	S	S	S	R	2.5	1.9	Winter
2574	Armenia	*typica*	S	S	S	S	S	4.0	2.6	Winter
2575	Armenia	*typica*	S	S	S	S	ND	ND	ND	Winter
1622	Azerbaijan	Unknown	S	S	S	S	R	1.8	0.7	Winter
1624	Azerbaijan	Unknown	R	R	R	R	R	1.6	0.7	Winter
1656	Azerbaijan	*typica*	I	R	R	R	R	2.0	1.8	Winter
1657	Azerbaijan	*typica*	I	R	R	R	R	1.5	1.6	Winter
1658	Azerbaijan	*typica*	ND	ND	ND	ND	S	4.0	2.6	Winter
1659	Azerbaijan	*strangulata*	R	R	R	R	R	1.5	1.7	Winter
1660	Azerbaijan	Unknown	I	S	S	S	S	3.6	2.6	Winter
1662	Azerbaijan	*typica*	I	R	R	R	S	3.0	2.5	Winter
1664	Azerbaijan	Unknown	S	I	I	I	R	1.3	1.6	Winter
1665	Azerbaijan	Unknown	R	R	R	R	R	1.0	1.3	Winter
1666	Azerbaijan	Unknown	ND	ND	ND	ND	R	1.3	1.5	Winter
1667	Azerbaijan	*typica*	ND	ND	ND	ND	R	1.5	1.4	Winter
1668	Azerbaijan	*typica*	R	R	R	R	R	1.0	1.3	Winter
1669	Azerbaijan	Unknown	S	S	S	S	R	2.0	1.4	Winter
1670	Azerbaijan	*typica*	I	R	R	R	R	2.9	2.0	Winter
1671	Azerbaijan	*typica*	R	R	R	R	S	2.5	2.2	Winter
1672	Azerbaijan	Unknown	I	S	I	S	R	1.5	1.3	Winter
1674	Azerbaijan	*typica*	S	I	I	S	S	3.0	2.5	Winter
1675	Azerbaijan	*typica*	I	R	R	R	R	1.0	1.2	Winter
1676	Azerbaijan	Unknown	S	S	S	S	S	3.1	2.4	Winter
1677	Azerbaijan	Unknown	R	R	R	R	R	3.0	2.2	Winter
1678	Azerbaijan	*typica*	S	R	R	R	R	1.0	1.1	Winter
1680	Azerbaijan	*typica*	S	S	I	R	R	1.5	1.8	Winter
1681	Azerbaijan	Unknown	S	R	I	I	R	1.0	1.1	Winter
1682	Azerbaijan	*typica*	R	R	R	R	R	1.5	1.6	Winter
1684	Azerbaijan	Unknown	I	R	R	R	R	2.0	1.6	Winter
1685	Azerbaijan	Unknown	ND	ND	ND	ND	R	1.5	1.4	Winter
1686	Azerbaijan	*typica*	R	R	R	R	R	1.5	1.5	Winter
1687	Azerbaijan	*typica*	ND	ND	ND	ND	R	1.8	1.7	Winter
2560	Azerbaijan	*typica*	R	R	R	R	ND	ND	ND	Winter
2562	Azerbaijan	*typica*	R	R	R	R	ND	ND	ND	Winter
1601	China	*typica*	S	S	S	S	S	3.3	2.8	Winter
1602	China	Unknown	S	S	S	S	S	2.9	2.7	Winter
1603	China	Unknown	S	S	S	S	S	3.5	3.0	Winter
1698	Dagestan	Unknown	S	S	I	S	R	3.0	2.1	Winter
1699	Dagestan	*typica*	S	S	S	S	S	4.0	3.0	Winter
2369	Dagestan	*typica*	S	S	S	I	ND	ND	ND	Winter
2577	Georgia	*typica*	I	S	S	S	ND	ND	ND	Winter
2578	Georgia	*typica*	S	S	S	S	ND	ND	ND	Winter
2579	Georgia	*typica*	R	R	I	R	S	4.0	2.7	Winter
2580	Georgia	*typica*	ND	ND	S	S	S	4.0	3.0	Winter
2581	Georgia	*typica*	S	S	S	S	S	3.8	2.5	Winter
2585	Georgia	*typica*	I	S	S	ND	ND	ND	ND	Winter
2586	Georgia	*typica*	S	S	S	S	S	4.0	2.8	Winter
1599	Iran	*meyeri*	S	S	S	S	R	1.3	1.4	Winter
1600	Iran	Unknown	S	I	I	I	R	1.2	1.5	Winter
1618	Iran	Unknown	S	I	I	I	R	3.3	1.7	Winter
1619	Iran	*meyeri*	S	I	R	R	ND	ND	ND	Winter
1641	Iran	*strangulata*	I	R	R	I	R	1.5	1.2	Winter
1642	Iran	*strangulata*	R	R	R	R	R	1.5	1.6	Winter
1643	Iran	*typica*	R	I	R	R	R	1.2	1.3	Winter
1644	Iran	*typica*	R	R	R	R	R	2.0	1.7	Winter

(*continued on next page*)

Table 2. (*continued from preceding page*)

WGRC[a] acc. no.	Region	Subspecies	Reaction to CDL race[b] 17	37	43	45	Eyespot[c]	Visual score	GUS activity	Growth habit
1645	Iran	Unknown	I	I	R	R	S	2.8	2.3	Winter
1649	Iran	*meyeri*	R	R	R	R	R	3.2	2.0	Winter
1706	Iran	*strangulata*	R	R	R	R	R	2.4	2.0	Winter
1715	Iran	*typica*	R	R	R	R	S	2.2	2.2	Winter
1717	Iran	Unknown	S	S	S	R	S	4.0	2.8	Winter
1718	Iran	Unknown	R	R	R	R	S	3.5	2.6	Winter
2377	Iran	*strangulata*	R	R	R	R	R	1.6	1.7	Winter
2377.1	Iran	*strangulata*	R	R	R	R	R	1.0	1.5	Winter
2445	Iran	*typica*	R	I	R	R	ND	ND	ND	Winter
2446	Iran	*typica*	R	I	S	R	R	1.0	1.4	Winter
2447	Iran	*typica*	I	I	I	R	S	2.7	2.2	Winter
2448	Iran	*typica*	S	I	ND	R	S	4.0	2.6	Winter
2449	Iran	*strangulata*	R	R	R	R	R	1.0	1.4	Winter
2450	Iran	*strangulata*	R	R	R	R	R	1.0	1.5	Winter
2452	Iran	*strangulata*	R	R	R	R	S	3.7	2.4	Winter
2452.1	Iran	*strangulata*	R	I	R	I	R	1.7	1.9	Winter
2453	Iran	*strangulata*	R	R	R	R	R	2.5	2.0	Winter
2454	Iran	*strangulata*	R	I	R	I	S	3.9	2.2	Winter
2455	Iran	*strangulata*	R	S	I	S	S	3.6	2.4	Winter
2457	Iran	*typica*	R	R	R	R	R	1.1	1.2	Winter
2458	Iran	*typica*	S	S	I	S	ND	ND	ND	Winter
2459	Iran	*typica*	R	R	R	I	R	1.0	1.3	Winter
2460	Iran	*typica*	R	R	ND	R	R	1.1	1.6	Winter
2463	Iran	*strangulata*	S	S	S	I	R	1.5	1.5	Winter
2464	Iran	*strangulata*	S	S	I	S	S	2.8	2.3	Winter
2465	Iran	*strangulata*	I	S	I	I	R	2.0	1.8	Winter
2466	Iran	*strangulata*	I	I	I	I	ND	ND	ND	Winter
2467	Iran	*strangulata*	R	R	R	R	ND	ND	ND	Winter
2468	Iran	*strangulata*	R	I	R	I	R	2.6	1.9	Winter
2469	Iran	*strangulata*	R	R	R	R	S	4.0	2.4	Winter
2470	Iran	*strangulata*	R	R	ND	R	R	1.7	1.9	Winter
2471	Iran	*typica*	R	I	I	R	R	2.5	2.0	Winter
2472	Iran	*typica*	R	R	R	R	R	2.1	1.9	Winter
2473	Iran	*meyeri*	R	R	ND	R	R	2.1	1.3	Winter
2474	Iran	*typica*	R	R	I	R	S	4.0	3.0	Winter
2475	Iran	*typica*	R	R	I	R	S	3.5	2.3	Winter
2476	Iran	*typica*	R	R	I	R	R	3.0	2.0	Winter
2477	Iran	*typica*	I	I	I	I	R	2.5	2.0	Winter
2478	Iran	*typica*	I	R	I	I	R	2.0	1.6	Winter
2479	Iran	*typica*	S	S	S	S	S	3.5	2.3	Winter
2480	Iran	*typica*	R	R	R	R	R	1.0	1.0	Winter
2481	Iran	*meyeri*	R	R	R	R	R	3.5	2.1	Winter
2483	Iran	*typica*	R	R	R	R	R	1.5	1.5	Winter
2485	Iran	*typica*	R	R	R	R	S	4.0	2.6	Winter
2486	Iran	*typica*	S	S	S	S	S	3.2	2.7	Winter
2487	Iran	*typica*	S	S	S	S	S	3.6	2.6	Winter
2488	Iran	*typica*	R	R	I	R	S	4.0	3.0	Winter
2489	Iran	*typica*	S	S	S	S	S	4.0	3.0	Winter
2490	Iran	*typica*	R	R	R	R	R	1.0	1.2	Winter
2492	Iran	*typica*	S	S	S	S	R	1.1	1.5	Winter
2493	Iran	*typica*	S	S	S	S	R	1.6	1.5	Winter
2494	Iran	*typica*	S	ND	ND	S	R	1.0	1.3	Winter
2495	Iran	*typica*	R	R	R	R	R	1.5	1.4	Winter
2496	Iran	*typica*	ND	ND	ND	ND	R	1.0	1.2	Winter
2497	Iran	*typica*	ND	ND	ND	ND	R	1.6	1.3	Winter
2498	Iran	*typica*	ND	ND	ND	ND	R	1.7	1.4	Winter
2499	Iran	*typica*	ND	ND	ND	ND	R	1.2	1.3	Winter
2511	Iran	*typica*	R	S	R	S	R	1.0	1.2	Winter
2512	Iran	*typica*	S	S	R	S	R	1.0	1.3	Winter
2513	Iran	*typica*	S	S	S	S	S	3.2	2.4	Winter
2515	Iran	*typica*	S	S	S	S	S	2.5	2.4	Winter
2517	Iran	*typica*	S	S	S	S	ND	ND	ND	Winter
2519	Iran	*typica*	S	S	S	S	S	4.0	2.8	Winter
2520	Iran	*typica*	S	S	S	S	S	3.7	2.4	Winter
2521	Iran	*typica*	ND	ND	ND	ND	S	3.9	2.4	Winter
2523	Iran	*typica*	ND	ND	ND	ND	S	3.6	2.9	Winter
2524	Iran	*typica*	R	R	R	R	R	1.0	1.2	Winter
2525	Iran	*typica*	R	R	R	R	R	1.0	1.4	Winter
2527	Iran	*meyeri*	S	S	S	I	R	1.1	1.3	Winter
2528	Iran	*typica*	R	R	R	R	R	1.0	1.3	Winter
2529	Iran	*meyeri*	R	R	R	R	R	1.7	1.3	Winter
2530	Iran	*meyeri*	R	R	R	R	R	1.9	1.5	Winter
2374	Pakistan	*anathera*	S	S	S	I	S	4.0	2.5	Spring

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Table 2. (*continued from preceding page*)

WGRC[a] acc. no.	Region	Subspecies	Reaction to CDL race[b] 17	37	43	45	Eyespot[c]	Visual score	GUS activity	Growth habit
2379	Pakistan	*typica*	S	S	S	S	S[e]	2.7	2.2	Winter
2380	Pakistan	*typica*	S	S	S	S	S	2.7	2.3	Winter
2381	Pakistan	*anathera*	S	S	S	S	S	4.0	2.9	Winter
2382	Pakistan	*anathera*	S	ND	ND	ND	S	3.5	2.6	Spring
2383	Pakistan	*typica*	S	S	S	S	R	1.7	1.2	Spring
2384	Pakistan	Unknown	S	S	ND	S	S	2.8	2.5	Spring
2385	Pakistan	*typica*	S	S	ND	S	ND	ND	ND	Spring
2386	Pakistan	*anathera*	S	S	ND	I	ND	ND	ND	Spring
1652	Tadshikistan	Unknown	I	S	S	S	ND	ND	ND	Winter
1653	Tadshikistan	*typica*	S	S	S	S	S	3.8	2.5	Winter
1704	Tadshikistan	Unknown	S	S	S	S	R	2.7	1.9	Winter
1582	Turkey	Unknown	S	S	S	S	S	2.5	2.7	Winter
1584	Turkey	*typica*	S	S	S	S	S	3.6	2.9	Winter
1586	Turkey	Unknown	S	S	S	S	S	1.6	2.2	Winter
1587	Turkey	Unknown	S	S	S	S	S	4.0	3.2	Winter
1588	Turkey	Unknown	S	S	S	S	S	2.2	2.2	Winter
1589	Turkey	Unknown	S	S	S	S	R	1.0	1.8	Winter
1590	Turkey	Unknown	S	S	S	S	S	2.8	2.3	Winter
1591	Turkey	Unknown	S	S	S	S	R	2.0	2.0	Winter
1593	Turkey	Unknown	S	S	S	S	S	2.2	2.9	Winter
1594	Turkey	Unknown	S	S	S	S	R	1.0	1.5	Winter
1595	Turkey	Unknown	S	S	S	S	S	3.9	3.6	Winter
1596	Turkey	Unknown	S	S	S	S	S	3.2	2.4	Winter
1634	Turkey	Unknown	S	S	S	S	S	4.0	2.9	Winter
2500	Turkey	*typica*	ND	ND	ND	ND	S	2.4	2.9	Winter
2503	Turkey	*typica*	ND	ND	ND	ND	R	1.7	2.0	Winter
2504	Turkey	*typica*	ND	ND	ND	ND	R	1.0	1.8	Winter
2505	Turkey	*typica*	ND	ND	ND	ND	R	1.0	1.6	Winter
2507	Turkey	*typica*	S	S	S	S	S	3.7	2.3	Winter
2508	Turkey	*typica*	S	S	S	S	R	1.0	1.3	Winter
2509	Turkey	*typica*	S	S	S	S	S	3.0	2.5	Winter
2510	Turkey	*typica*	S	S	S	S	R	1.0	1.5	Winter
1614	Turkmenistan	*typica*	R	R	R	R	R	1.7	1.8	Winter
1615	Turkmenistan	*typica*	R	R	R	R	R	1.2	1.8	Winter
1616	Turkmenistan	*typica*	S	S	S	S	R	1.5	1.6	Winter
1617	Turkmenistan	Unknown	S	S	S	S	R	2.0	1.5	Winter
1623	Turkmenistan	Unknown	S	I	I	I	R	1.7	1.3	Winter
1626	Turkmenistan	Unknown	R	S	I	R	R	1.8	1.3	Winter
1692	Turkmenistan	Unknown	S	I	I	I	S	3.7	2.8	Winter
1693	Turkmenistan	Unknown	S	R	R	R	R	1.0	1.6	Winter
1598	USSR	Unknown	S	S	S	S	R	2.1	1.7	Winter
1625	USSR	Unknown	S	S	S	S	S	3.6	2.6	Winter
1577	Unknown	Unknown	S	S	S	S	S	3.8	3.4	Winter
1578	Unknown	Unknown	S	S	S	S	S	3.0	3.3	Winter
1579	Unknown	Unknown	S	S	S	S	S	3.6	3.6	Winter
1580	Unknown	Unknown	S	S	S	S	S	3.7	3.7	Winter
1581	Unknown	Unknown	S	S	S	S	S	4.0	3.1	Spring
1597	Unknown	Unknown	S	S	S	S	S	3.8	3.5	Winter
1605	Unknown	*strangulata*	I	R	R	R	R	1.5	2.0	Winter
1621	Unknown	Unknown	S	S	S	S	S	3.5	2.4	Winter
1635	Unknown	*strangulata*	I	S	I	I	R	2.0	1.7	Winter
1651	Unknown	Unknown	R	R	R	R	R	2.2	1.1	Winter
1688	Unknown	*typica*	S	S	S	S	ND	ND	ND	Spring
1689	Unknown	*typica*	S	S	S	S	S	3.5	2.8	Spring
1691	Unknown	*meyeri*	R	R	R	R	R	1.8	1.8	Winter
1695	Unknown	*strangulata*	R	R	R	R	R	1.8	1.8	Winter
1696	Unknown	*meyeri*	R	R	R	R	R	3.3	2.0	Winter
1697	Unknown	*anathera*	S	S	S	S	S	4.0	2.9	Winter
1707	Unknown	Unknown	R	R	R	R	R	2.5	2.2	Winter
1708	Unknown	Unknown	S	S	I	S	S	4.0	2.7	Winter
1709	Unknown	Unknown	S	S	I	S	S	3.8	2.5	Winter
1712	Unknown	Unknown	S	S	S	S	S	3.4	2.5	Winter
2118	Unknown	*anathera*	S	S	S	S	S	4.0	2.6	Spring
2370	Unknown	*typica*	S	S	I	I	S	4.0	2.9	Winter
2370.1	Unknown	*typica*	S	S	R	S	S	4.0	3.0	Winter
2373	Unknown	*typica*	S	S	S	I	R	2.1	1.8	Spring
	Percent resistance:		*23*	24	24	26	45			
VPM-1							R	1.0	1.5	Winter
Cappelle-Desprez							R	2.0	1.7	Winter
Cerco							R	2.3	1.7	Winter
Selection 101							S	3.7	2.4	Winter
Chinese Spring							S	4.0	2.7	Spring
	LSD ($P = 0.01$)							0.7	0.7	

were identified by Strausbaugh and Murray (36).

The French cultivar Cappelle-Desprez was the first wheat cultivar reported to be resistant to eyespot (37). Although the gene conferring the resistance is located on chromosome 7A (21), the source of this gene is unknown. After VPM-1 was selected (25), it was used extensively to transfer resistance into wheat cultivars because its resistance is more effective than the resistance of Cappelle-Desprez. Genetic analysis of VPM-1 revealed that the resistance gene was located on chromosome 7D (8,13). Allan et al. (1,2) used VPM-1 to produce Madsen and Hyak, which were the first eyespot-resistant cultivars in the United States. The only cultivar thought to contain both the 7A and 7D resistance genes is Rendezvous (12); however, this genotype still sustains yield loss when disease is severe (12).

It is not clear at this point whether the new eyespot resistance genes in *T. tauschii* are allelic to, or separate genes from, those in commercial use. However, based on the GUS assay, accessions TA 1622 and TA 1624 from Azerbaijan were significantly ($P = 0.01$) more resistant to eyespot than VPM-1. These two accessions warrant further study.

Wheat breeding programs utilize both race-specific and nonspecific resistances to stripe rust; therefore it is important to continue the characterization of new genes even if they may be circumvented. There is concern that the eyespot pathogen may circumvent existing resistance genes and render them ineffective in the future. It is clear from the variation in these accessions that *T. tauschii* offers a diverse source of resistance for stripe rust and eyespot.

LITERATURE CITED

1. Allan, R. E., Peterson, C. J., Jr., Rubenthaler, G. L., Line, R. F., and Roberts, D. E. 1989. Registration of 'Madsen' wheat. Crop Sci. 29:1575-1576.
2. Allan, R. E., Peterson, C. J., Jr., Rubenthaler, G. L., Line, R. F., and Roberts, D. E. 1989. Registration of 'Hyak' wheat. Crop Sci. 30:234.
3. Cox, T. S., Raupp, W. J., Wilson, D. L., Gill, B. S., Leath, S., Bockus, W. W., and Browder, L. E. 1992. Resistance to foliar diseases in a collection of *Triticum tauschii* germ plasm. Plant Dis. 76:1061-1064.
4. Cox, T. S., Sears, R. G., and Bequette, R. K. 1995. Winter wheat X *Triticum tauschii* backcross populations: I. Germplasm evaluation. Theor. Appl. Genet. 90:571-577.
5. Cu, R. M., and Line, R. F. 1994. An expert advisory system for wheat disease Management. Plant Dis. 78:209-215.
6. de la Peña, R., and Murray, T. D. 1994. Identifying wheat genotypes resistant to eyespot disease with a β-glucuronidase-transformed strain of *Pseudocercosporella herpotrichoides*. Phytopathology 84:972-977.
7. Dosba, F., and Dossinault, G. 1973. Resistance to eyespot (*Cercosporella herpotrichoides*) introduced to bread wheat from *Aegilops ventricosa*. Pages 409-413 in: Proc. Int. Wheat Genet. Symp., 4th.
8. Doussinault, G., Dosba, F., and Jahier, J. 1983. New results on the improvement of the level of resistance to eyespot in wheat. Pages 193-198 in: Proc. Int. Wheat Genet. Symp., 6th.
9. Dyck, P. L. 1979. Identification of the gene for adult-plant leaf rust resistance in Thatcher. Can. J. Plant Sci. 59:449-501.
10. Gill, B. S., Raupp, W. J., Browder, L. E., and Cox, T. S. 1988. Registration of KS86WGRC02 leaf rust resistant hard red winter wheat germplasm. Crop Sci. 28:207.
11. Gill, B. S., Raupp, W. J., Sharma, H. C., Browder, L. E., Hatchett, J. H., Harvey, T. L., Moseman, J. G., and Waines, J. G. 1986. Resistance in *Aegilops squarrosa* to wheat leaf rust, wheat powdery mildew, greenbug, and Hessian fly. Plant Dis. 70:553-556.
12. Hollins, T. W., Lockley, K. D., Blackman, J. A., Scott, P. R., and Bingham, J. 1988. Field performance of Rendezvous, a wheat cultivar with resistance to eyespot (*Pseudocercosporella herpotrichoides*) derived from *Aegilops ventricosa*. Plant Pathol. 37:251-260.
13. Jahier, J., Doussinault, G., Dosba, F., and Bourgeois, F. 1978. Monosomic analysis of resistance to eyespot in the variety 'Roazon'. Pages 437-440 in: Proc. Int. Wheat Genet. Symp., 5th.
14. Jefferson, R. A., Kavanagh, T. A., and Bevan, M. W. 1987. GUS fusions: β-glucuronidase as a sensitive and versatile gene fusion marker in higher plants. EMBO J. 6:3901-3907.
15. Johnson, R. 1992. Reflections of a plant pathologist on breeding for disease resistance, with emphasis on yellow rust and eyespot of wheat. Plant Pathol. 41:239-254.
16. Johnson, R. C., Kebede, H., Mornhinweg, D. W., Carver, B. F., Lane Rayburn, A., and Nguyen, H. T. 1987. Photosynthetic difference among *Triticum* accessions at tillering. Crop Sci. 27:1046-1050.
17. Kerber, E. R., and Dyck, P. L. 1969. Inheritance in hexaploid wheat of leaf rust resistance and other characters derived from *Aegilops squarrosa*. Can. J. Genet. Cytol. 11:639-647.
18. Kihara, H., Yamashita, K., and Tanaka, M. 1965. Morphological, physiological, genetical, and cytological studies in *Aegilops* and *Triticum* collected in Pakistan, Afghanistan, and Iran. Results Kyoto Univ. Sci. Exped. Karakoram Hindukush, 1955. 1:1-118.
19. Kimber, G. 1967. The incorporation of the resistance of *Aegilops ventricosa* to *Cercosporella herpotrichoides* into *Triticum aestivum*. J. Agric. Sci. Camb. 68:373-376.
20. Lange, W., and Jochemsen, G. 1992. Use of the gene pools of *Triticum turgidum* ssp. *dicoccoides* and *Aegilops squarrosa* for the breeding of common wheat (*T. aestivum*), through chromosome-doubled hybrids. I. Two strategies for the production of the amphiploids. Euphytica 59:197-212.
21. Law, C. N., Scott, P. R., Worland, A. J., and Hollins, T. W. 1976. The inheritance of resistance to eyespot (*Cercosporella herpotrichoides*) in wheat. Genet. Res. Camb. 25:73-79.
22. Law, C. N., Young, C. F., Brown, J. W. S., Snape, J. W., and Worland A. J. 1978. The study of grain protein control in wheat using whole chromosome substitution lines. Page 438 in: Seed Protein Improvement by Nuclear Techniques. Int. At. Energy Agency, Vienna.
23. Line, R. F., and Qayoum, A. 1991. Virulence, aggressiveness, evolution, and distribution of races of *Puccinia striiformis* (the cause of stripe rust of wheat) in North America, 1968-87. U.S. Dep. Agric. Tech. Bull. 1788.
24. Lubbers, E. L., Gill, K. S., Cox, T. S., and Gill, B. S. 1991. Variation of molecular markers among geographically diverse accessions of *Triticum tauschii*. Genome 34:354-361.
25. Maia, N. 1967. Obtention de blés tendres résistants au piétinverse par croisements interspécifiques blés x *Aegilops*. C. R. Acad. Agric. France 53:149-154.
26. McFadden, E. S., and Sears, E. R. 1946. The origin of *Triticum spelta* and its free threshing hexaploid relatives. J. Hered. 37:81-89.
27. McMillin, D. E., Allan, R. E., and Roberts, D. E. 1986. Association of an isozyme locus and strawbreaker foot rot resistance derived from *Aegilops ventricosa* in wheat. Theor. Appl. Genet. 72:743-747.
28. Multani, D. S., Dhaliwal, H. G., Singh, P., and Gill, K. S. 1988. Synthetic amphiploids of wheat as a resistance source to Karnal bunt (*Neovossia indica*). Plant Breed. 10:122-125.
29. Murray, T. D., de la Pena, R., Yildirim, A., and Jones, S. S. 1994. A new source of resistance to *Pseudocercosporella herpotrichoides*, cause of eyespot disease of wheat, located on chromosome 4V of *Dasypyrum villosum*. Plant Breed. 113:281-286.
30. Oldenstadt, D. L., Allan, R. E., Bruehl, G. W., Dillman, D. A., Michalson, E. L., Papendick, R. I., and Rydrych, D. J. 1982. Solutions to environmental and economic problems (STEEP). Science 217:904-909.
31. Roelfs, A. P., Singh, R. P., and Saari, E. E. 1992. Rust diseases of wheat: Concepts and methods of disease management. CIMMYT, Mexico, D.F.
32. Shah, S. H., Gorham, J., Forster, B. P., and Wyn Jones, R. G. 1987. Salt tolerance in the *Triticeae*: The contribution of the D genome to cation selectivity in hexaploid wheat. J. Exp. Bot. 38:254-269.
33. Simonet, M. 1957. Hybrides interspécifiques et intergénériques. Ann. Amelior. Plant. 4:395-411.
34. Singh, R. P., and Rajaram, S. 1994. Genetics of adult plant resistance to stripe rust in ten bread wheats. Euphytica 72:1-7.
35. Sprague, R. 1936. Relative susceptibility of certain species of gramineae to *Cercosporella herpotrichoides*. J. Agric. Res. 53:659-670.
36. Strausbaugh, C. A., and Murray, T. D. 1989. Inheritance of resistance to foot rot (*Pseudocercosporella herpotrichoides*) in three cultivars of winter wheat. Phytopathology 79:1048-1053.
37. Vincent, A., Ponchet, J., and Koller, J. 1952. Recherche de variete de bles tendres peu sensibles au pietin-verse: resultats preliminaires. Ann. Amelior. Plant. 2:459-472.
38. Waines, J. G., Ehdaie, B., and Barnhart, D. 1987. Variability in *Triticum* and *Aegilops* species for seed characteristics. Genome 29:41-46.
39. Whelan, E. D. P., and Thomas, J. B. 1989. Chromosomal location in common wheat of a gene (*Cnc 1*) from *Aegilops squarrosa* that conditions resistance to colonization by the wheat curl mite. Genome 32:1033-1036.