Resistance to *Erysiphe graminis* f. sp. *tritici, Puccinia recondita* f. sp. *tritici,* and *Septoria nodorum* in Wild *Triticum* Species

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ABSTRACT

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Seventy-nine accessions encompassing 23 *Triticum* species were inoculated with cultures or culture composites of *Erysiphe graminis* f. sp. *tritici, Puccinia recondita* f. sp. *tritici*, or *Septoria nodorum*. The cultures of *E. graminis* and *P. recondita* were chosen so that most of the virulence genes found in the eastern United States were represented. Powdery mildew and leaf rust ratings were bimodally distributed, with high ratings outnumbering low ratings by as much as 1.8 to 1. Ratings of leaf symptoms caused by *S. nodorum* were skewed toward resistance and susceptibility outnumbered resistance by as much as 4.1 to 1. Reaction to *S. nodorum* was correlated with reaction to *E. graminis. Triticum carthlicum* may be a source of resistance to *E. graminis, T. monococcum* may provide resistance to *E. graminis* and *P. recondita*, and resistance to *E. graminis, P. recondita*, and *S. nodorum* may be found in the *T. timopheevi* population. Nine accessions had resistance to all three pathogens. Seven of these were highly pubescent. The association of resistance to leaf pubescence may affect the expression of any resistance transferred to *T. aestivum*.

Leaf rust, powdery mildew, and glume blotch diseases decrease yields of wheat (*Triticum aestivum* L. em Thell) worldwide (1). Losses attributed to leaf rust, caused by *Puccinia recondita* f. sp. *tritici* Rob. ex Desm., seldom exceed 5%, and rarely approach 30% in wheat-growing areas of the United States (17). The most widely used method for controlling leaf rust has been with genetic resistance. Although the phenomenon of slow-rusting is receiving attention (8,21,22), resistance has generally been conferred by specific genes. Of the 35 genes listed by Browder (2), four originated in *Triticum* species other than *aestivum* (former genus *Aegilops*), three in *Agropyron elongatum* (Host) Beauv., and two in rye (*Secale cereale* L.).

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Powdery mildew of wheat has been observed to reduce grain yield by 34% in plots in Maryland (7). Although several new fungicides control powdery mildew on wheat (16), disease resistance is the most practicable control method over large geographical areas and in developing countries. Six of the eight loci that have been identified as conditioning resistance to *E. graminis* f. sp. *tritici* originated in species other than *T. aestivum* (13).

Septoria nodorum (Berk.) Berk., the cause of glume blotch, and *S. tritici* Rob. ex Desm., the cause of leaf blotch, could cause yield losses of 30–50% under ideal conditions for disease development (5). Yield losses attributed to glume blotch have been correlated with short-statured, early-maturing cultivars (20) and with conservation tillage practices (3). Resistance to *S. nodorum* has been reported to be simply inherited (6); however, resistance to *S. nodorum* is more commonly reported to be quantitatively inherited (12,14,15,19).

Resistance to *P. recondita* has been estimated to remain effective for about 5.6 yr (9). Resistance to *E. graminis* has been less ephemeral although fewer genes for resistance to *E. graminis* have been identified than for resistance to *P. recondita*. Resistance to *S. nodorum* is not common. This study was conducted to determine the presence of resistance to *P. recondita, E. graminis,* and *S. nodorum* in a sample of *Triticum* species.

MATERIALS AND METHODS

Accessions of the collection of *Triticum* species maintained at the University of Missouri were ranked according to ease of crossing with *T. aestivum*. A total of 79 accessions, including nine accessions of *T. aestivum*, were selected for testing. The accessions tested are among those most easily crossable with *T. aestivum*.

P. recondita f. sp. *tritici* culture 6 (PR6, culture 6PRTUS of L. E. Browder, ATCC PR76) was chosen because its avirulence/virulence formula of 2A,9,16,18,19,24/1,2C,2D,3,10,11,17 makes it virulent on most of the resistance genes found in cultivars grown in the eastern United States (L. E. Browder, *personal communication*). Four cultures of *E. graminis* were used. A composite (QMO10) was composed of culture Q, virulent on *Pm*2, *Pm*3a, *Pm*3c, *Pm*4, and the Michigan Amber gene (collected near Quincy, FL, in 1980) and culture MO10, virulent on *Pm*2, *Pm*3a, *Pm*3c, and the Michigan Amber gene (collected in Michigan in 1980). A second composite (ABK127) was composed of culture ABK, virulent on *Pm*1 and *Pm*2, and culture 127, virulent on *Pm*3b and *Pm*3c. Between them, the two composites possessed most of the virulence genes found in the United States (J. G. Moseman, *unpublished*). Two *S. nodorum* cultures were combined in a composite (SN68). Culture SN6 was collected near Tifton, GA, in 1982 and culture SN8 was provided by A. L. Scharen (his culture 79-69). A third culture, SN11, collected near Quincy, FL, in 1982 was used singly.

Five plantings of the *Triticum* accessions were made in sterilized potting soil. A shortage of seed precluded replication in some tests. The multiple-inoculation technique of Kilpatrick et al (10) was modified for testing with PR6, QMO10, and ABK127. Two plantings were inoculated at the first-leaf stage with PR6. Seven days after inoculation with PR6, one planting each was inoculated with QMO10 and ABK127.

The *S. nodorum* cultures were started as single-pycnidium or mass-transfer isolations. After 2 days in the dark, the cultures were grown on Czapek-Dox V-8 juice agar under continuous near-ultraviolet light. Composite SN68 was composed of culture SN6 (7.4×10^5 conidia per milliliter) and SN8 (3.4×10^6 conidia per milliliter), having a final concentration of 2.3×10^6 conidia per milliter. Culture SN11 had a concentration of 2.9×10^6 conidia per milliliter. All cultures were 2 wk old when inoculated.

Three plantings of the *Triticum* accessions were sprayed with light oil before inoculation. One planting was inoculated with composite SN68 and two plantings were inoculated with culture SN11. About 100 ml of inoculum amended with one drop of Tween 20 was sprayed onto each planting. After inoculation, plants were placed in a moist chamber at 21 C for 72 hr, after which they were placed in a growth room at 21 C equipped with a cool mist humidifier, which maintained the relative humidity between 80 and 100%. Plants were subjected to a 12-hr photoperiod in the moist chamber and growth room.

Leaf rust ratings were made 11 and 13 days after inoculation, mildew ratings were made 15 and 17 days after inoculation with *P. recondita* (8 and 10 days after inoculation with *E. graminis*), and *Septoria* ratings were made 9 and 12 days after inoculation. The second set of readings was used to confirm the first set. Ratings for all diseases were on a 0–9 scale:

For leaf rust: 0 = immune, no visible sign of infection; 1–3 = resistant, increasing from no necrosis to large necrotic areas or halos around the pustules, increasing from no urediospores to few urediospores; 4–6 = moderately resistant, necrotic areas or halos around pustules changing to chlorotic areas, increasing production of urediospores; and 7–9 = susceptible, decreasing from chlorotic areas to no chlorosis, increasing size and number of pustules and production of urediospores to complete susceptibility.

For powdery mildew: 0 = immune, no visible sign of infection; 1–3 = resistant, increasing from no necrosis to large necrotic areas, increasing from no mycelium to little mycelium; 4–6 = moderately resistant, necrotic areas changing to chlorotic areas, increasing in amount of mycelium and conidiospores production; and 7–9 = susceptible, decreasing from chlorotic areas to no chlorosis, increasing in amount of mycelium and conidiospore production to complete susceptibility.

For *S. nodorum*: 0 = immune, no visible sign of infection; 1–3 = resistant, decreasing from small, isolated necrotic flecks to small, isolated chlorotic flecks; 4–6 = moderately resistant, increasing from small isolated chlorotic flecks to chlorotic lesions with some coalescence of lesions; and 7–9 = susceptible, increasing from coalescing lesions to large areas of leaf chlorosis and necrosis.

Disease ratings were grouped into three classes. Class 1 (resistant) included ratings of 0–3, class 2 (moderately resistant) included ratings of 4–6, and class 3 (susceptible) included ratings of 7–9.

RESULTS

A frequency distribution of the rating class for each composite or culture is given in Figure 1. Distributions for culture PR6 and composites QMO10 and ABK127 are bimodal, with most of the accessions in class 3. Reactions to SN68 were essentially normally distributed and reactions to SN11 were skewed toward resistance. Susceptiblity (class 3) outnumbers resistance (class 1) to PR6 by 1.7 to 1, to QMO10 by 1.8 to 1, to ABK127 by 1.7 to 1, to SN68 by 1.7 to 1, and to SN11 by 4.1 to 1.

Simple correlations of disease ratings between composites and cultures are presented in Table 1. Although all correlation coefficient values are significant at least at the 0.01 level, values less than 0.50 probably are not meaningful. Disease ratings between composite SN68 and culture SN11 are moderately well correlated and disease ratings between the two *E. graminis* composites are very well correlated. Ratings of composites QMO10 and ABK127 were moderately well correlated with ratings to composite SN68 and ratings of composite QMO10 were moderately well correlated with ratings to culture SN11.

Reactions of *Triticum* species represented by at least three accessions are given in Table 2. Although sample sizes were small, it appears that *T. monococcum* and *T. timopheevi* may be the best sources of resistance to *P. recondita*. Resistance to *E. graminis* may be available in *T. carthlicum, T. monococcum*, and *T. timopheevi. T. timopheevi* may be the best source of resistance to *S. nodorum*. Although only *T. timopheevi*

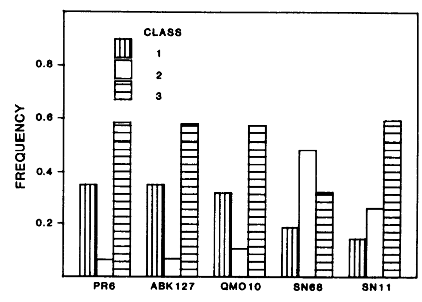

Fig. 1. Frequency distributions of disease rating classes according to reactions of a *Triticum* species population to several fungal pathogens. PR6 is a culture of *Puccinia recondita* f. sp. *tritici*, QMO10 and ABK127 are both composites of two cultures of *Erysiphe graminis* f. sp. *tritici*, SN68 is a composite of two *Septoria nodorum* cultures, and SN11 is a single *S. nodorum* culture. Disease ratings were on a 0–9 scale, where 0 = immunity and 9 = full susceptibility. Class 1 includes ratings of 0–3, class 2 includes ratings of 4–6, and class 3 includes ratings of 7–9. The frequency distribution for each pathogen group is composed of 71–79 *Triticum* accessions.

Table 1. Correlation of disease ratings of several cultures and culture composites of three fungal pathogens in *Triticum* species

	PR6[a]	QMO10	ABK127	SN68	SN11
PR6	···	0.31*[b] (75)[c]	0.35* (74)	0.41* (73)	0.32* (74)
QMO10	···	···	0.96** (72)	0.55** (73)	0.52** (73)
ABK127	···	···	···	0.59** (71)	0.42** (71)
SN68	···	···	···	···	0.64** (72)

[a] PR6 is a culture of *Puccinia recondita* f. sp. *tritici*, QMO10 and ABK127 are each composites of *Erysiphe graminis* f. sp. *tritici*, SN68 is a composite of two *Septoria nodorum* cultures, and SN11 is a single culture of *S. nodorum*.
[b] * = Correlation significant at $P \leqslant 0.01$ and ** = correlation significant at $P \leqslant 0.001$.
[c] Number in parentheses is number of observations in the computation. This value is less than 79 because of missing seedlings in some plantings.

consistently possesses resistance to *S. nodorum*, the standard error is small. Resistance was also found in several other species with only one or two accessions in our sample.

Resistance to all three diseases in one host is highly desirable. Nine accessions with an average disease rating of 3 or less are presented in Table 3. Seventy-eight percent of the accessions with multiple resistance had pubescent leaves.

DISCUSSION

Wild relatives of wheat have provided resistance to leaf rust and powdery mildew in the past (2,11). Control of both of these diseases has been primarily through major gene resistance. Distributions shown in Figure 1 indicate that resistance to *P. recondita* and *E. graminis* is common in the *Triticum* population and that intermediate reactions occur less frequently than either resistant or susceptible reactions. A completely different pattern was observed with *S. nodorum* (Fig. 1). In our study, most accessions had intermediate reactions to composite SN68 and intermediate and susceptible reactions to culture SN11. The difference in the distributions probably reflects differences in aggressiveness among the cultures, a situation frequently observed with *S. nodorum* (18).

Although resistance to *S. nodorum* may be less common than resistance to *P. recondita* or *E. graminis*, the wild *Triticum* species may be a source of resistance to all three pathogens (11,13,19). For all three diseases, susceptible accessions outnumbered resistant accessions; however, the proportion of resistant accessions ranged from about 13% for *S. nodorum* to 35% for *E. graminis* and *P. recondita*, with most resistance found in *T. diccocoides, T. monococcum*, and *T. timopheevi*. We suggest that the resistance in the wild *Triticum* population is a source of disease resistance worth exploiting. The presence in individual accessions of multiple resistance indicates that it may be possible to transfer resistance to more than one pathogen at one time. Even if linkage between resistance genes is low, the presence of multiple resistance in an accession should simplify the crossing and progeny testing when attempting to transfer resistance to cultivated wheats.

The observation that most of the accessions possessing multiple resistance had pubescent leaves is of particular concern. It may be that the resistance observed in these lines, particularly in *T. timopheevi*, may have resulted from mechanical exclusion of the pathogen from the leaf surface, although trichome infection has been observed with *S. nodorum* (23). Leaf pubescence may be linked with other factors, either favorable or unfavorable, which may affect resistance, crossability, or agronomic desirability. Additional research is needed to determine if the association of pubescence with resistance in these accessions will affect the expression of resistance transferred to *T. aestivum*.

The wild relatives of wheat have provided genes for resistance to *P. recondita* and *E. graminis* (2,11,13). *Triticum* species have also been proposed as sources of resistance to *S. nodorum* (4,19). Our preliminary survey of a collection of *Triticum* species indicates that the *Triticum* population continues to be a valuable genetic resource for germ plasm enhancement.

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Table 2. Reaction of *Triticum* species to several cultures and culture composites of three fungal pathogens

	PR6[a]			QMO10			ABK127			SN68			SN11		
Species	Mean	N[b]	Std[c]	Mean	N	Std	Mean	N	Std	Mean	N	Std	Mean	N	Std
T. aestivum	6.2[d]	9	1.0	7.8	9	0.2	7.3	9	0.4	5.3	9	0.4	7.3	9	0.3
T. carthlicum	4.7	3	1.7	1.7	3	0.3	1.7	3	0.3	7.3	3	0.3	7.0	3	0.6
T. diccocoides	6.8	14	0.6	3.5	12	0.6	3.8	13	0.8	4.3	13	0.6	4.9	12	0.6
T. dicoccum	6.8	6	0.6	5.7	6	1.5	5.7	6	1.5	6.5	6	0.2	8.2	6	0.3
T. durum	7.0	3	1.0	6.3	3	0.0	6.3	3	0.0	5.3	3	1.5	8.3	3	0.0
T. monococcum	1.8	6	0.3	4.0	6	1.2	3.0	6	1.0	3.8	5	0.7	6.2	6	0.8
T. sphaerococcum	7.7	3	0.3	7.7	3	0.7	7.3	3	0.3	7.7	3	0.9	9.0	3	0.0
T. timopheevi	3.0	5	1.3	2.6	5	1.4	2.4	5	1.4	2.4	5	0.7	3.6	5	0.6

[a] PR6 is a culture of *Puccinia recondita* f. sp. *tritici*, QMO10 and ABK127 are each composites of two cultures of *Erysiphe graminis* f. sp. *tritici*, SN68 is a composite of two cultures of *Septoria nodorum*, and SN11 is a single culture of *S. nodorum*.
[b] Number of accessions in the mean.
[c] Standard error of the mean.
[d] Mean is average disease rating for N accessions. Disease ratings were on a 0–9 scale, where 0 = immunity, 1–3 = resistance, 4–6 = moderate resistance, and 7–9 = susceptibility.

Table 3. *Triticum* species showing resistance to several cultures and culture composites of three fungal pathogens

Accession[a]	Species	PR6[b]	QMO10	ABK127	SN68	SN11	Average	Leaf character
76TM34-11	*T. aegilopoides*	2[c]	1	1	4	2	2.0	Hairy
75TT01-1	*T. diccocoides*	2	2	1	2	4	2.2	Hairy
77TT04-5	*T. diccocoides*	2	5	3	1	2	2.4	Hairy
78TT07-2	*T. diccocoides*	7	1	1	3	2	2.8	Smooth
79TM21-1	*T. monococcum*	1	1	1	2	3	1.6	Smooth
TG01	*T. timopheevi*	2	1	1	2	3	1.8	Hairy
TG02	*T. timopheevi*	2	1	1	2	3	1.8	Hairy
TG03	*T. timopheevi*	2	1	1	2	2	1.6	Hairy
TG06	*T. timopheevi*	1	2	1	1	5	2.0	Hairy

[a] University of Missouri accession number.
[b] PR6 is a culture of *Puccinia recondita* f. sp. *tritici*, QMO10 and ABK127 are each composites of two cultures of *Erysiphe graminis* f. sp. *tritici*, SN68 is a composite of two cultures of *Septoria nodorum*, and SN11 is a single culture of *S. nodorum*.
[c] Value is disease rating on a scale of 0–9, where 0 = immunity, 1–3 = resistance, 4–6 = moderate resistance, and 7–9 = susceptibility.

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