Genetics of Resistance to Wheat Leaf Rust, Stem Rust, and Powdery Mildew in *Aegilops sharonensis*

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ABSTRACT

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Aegilops sharonensis (Sharon goatgrass) is a wild relative of wheat and a rich source of genetic diversity for disease resistance. The objectives of this study were to determine the genetic basis of leaf rust, stem rust, and powdery mildew resistance in *A. sharonensis* and also the allelic relationships between genes controlling resistance to each disease. Progeny from crosses between resistant and susceptible accessions were evaluated for their disease reaction at the seedling and/or adult plant stage to determine the number and action of genes conferring resistance. Two different genes conferring resistance to leaf rust races THBJ and BBBB were identified in accessions 1644 and 603. For stem rust, the same single gene was found to confer resistance to race TTTT in accessions 1644 and 2229. Resistance to stem rust race TPMK was conferred by two genes in accessions 1644 and 603. A contingency test revealed no association between genes conferring resistance to leaf rust race THBJ and stem rust race TTTT or between genes conferring resistance to stem rust race TTTT and powdery mildew isolate UM06-01, indicating that the respective resistance genes are not linked. Three accessions (1644, 2229, and 1193) were found to carry a single gene for resistance to powdery mildew. Allelism tests revealed that the resistance gene in accession 1644 is different from the respective single genes present in either 2229 or 1193. The simple inheritance of leaf rust, stem rust, and powdery mildew resistance in *A. sharonensis* should simplify the transfer of resistance to wheat in wide crosses.

Additional keywords: germplasm resources, wild wheat.

Aegilops sharonensis Eig (common name: Sharon goatgrass) is a wild relative of wheat, endemic to the coastal plain of Israel and southern Lebanon (28). The species belongs to the secondary gene pool of wheat and possesses the S^l genome, which is homeologous to the B genome of wheat (4). Increasing urbanization and agricultural development threaten many *A. sharonensis* populations across its native range (19); thus, renewed efforts to collect and characterize additional accessions have been initiated (19,21). *A. sharonensis* is a rich source of genes for disease and insect resistance. Previous investigators have identified accessions with resistance to leaf rust (caused by *Puccinia triticina* Eriks.), stem rust (caused by *P. graminis* Pers.: Pers f. sp. *tritici* Eriks. & E. Henn), stripe rust (caused by *P. striiformis* Westend. f. sp. *tritici* Eriks.), powdery mildew (caused by *Blumeria graminis* [DC] E.O. Speer. f. sp. *tritici* Em. Marchal), Karnal bunt (caused by *Tilletia indica* Mitra [*Neovossia indica* Mitra] Mundkur), tan spot (caused by *Pyrenophora tritici-repentis* [Died.] Drechs., anamorph *Drechslera tritici-repentis* [Died.] Shoem.), spot blotch (caused *Cochliobolus sativus* [Ito & Kurib.] Drechs. ex Dastur, anamorph: *Bipolaris sorokiniana* [Sacc.] Shoem.) (1,5,6,14,21,27, 29), Hessian fly (caused by *Mayetiola destructor* [Say]), and greenbug (caused by *Schizaphis graminum* [Rondani]) (6). In spite of several genetic constraints for gene transfer from *A. sharonensis* into cultivated wheat (18), successful introgression of leaf rust and stripe rust resistance genes has been achieved (15). The potential for increasing the diversity of disease resistance in wheat with genes from *A. sharonensis* is great as Olivera et al. (21) recently identified many accessions with resistance to the important wheat diseases of leaf rust, stem rust, stripe rust, powdery mildew, spot blotch, and tan spot.

The most effective and environmentally sound means of combating wheat diseases is through the use of host resistance. Novel resistance alleles carried in wild wheats are an important source of genetic diversity for countering virulence shifts in pathogen populations. To develop an efficient wide-crossing program using wheat relatives such as *A. sharonensis*, it is important to obtain information on the number and mode of action of genes controlling traits of interest. For some species, these genetic studies are best done within the wild species itself before any attempt at wide crossing is made. The objectives of this study were to determine the genetic basis of leaf rust, stem rust, and powdery mildew resistance in *A. sharonensis* and also the allelic relationships between genes controlling resistance to each disease. Leaf rust, stem rust, and powdery mildew were targeted in this study because they are important on wheat in many production areas (9,11,22,24).

MATERIALS AND METHODS

Plant materials. Four *A. sharonensis* accessions from Israel (Table 1) were selected for this study based on their differential reaction to wheat leaf rust, stem rust, and powdery mildew (21). Accession 2229 was collected from En HaMifraz in the Northern Coastal (Akko) Plain, 1193 from Hefzi Bah in the Central Coastal Plain, 603 from Palmahim in the Southern Coastal Plain, and 1644 from Ashdod in the Southern Coastal Plain. In total, seven crosses were developed to investigate the number of genes controlling resistance or to determine the relationship between resistance genes in allelism tests. F_1 plants were grown and selfed to produce F_2 populations. One to three different seed lots from

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each F_2 population were used for the disease evaluations (Table 2). Individual F_2 plants were then selfed to produce $F_{2:3}$ families. Each F_2 seed lot was evaluated for reaction to a single pathogen, with the exception of seed lot number 1-A from 1644/1193 and lot number 2-A from 1193/1644. Seed lot number 1-A from 1644/1193 was evaluated to leaf rust race THBJ and then stem rust race TTTT at the seedling stage in sequential inoculations conducted 14 days apart, whereas seed lot number 2-A from the reciprocal cross 1193/1644 was evaluated to stem rust race TTTT and then leaf rust race THBJ in sequential inoculations of the same interval. At the adult plant stage, these same F_2 plants were inoculated with leaf rust race THBJ (on the flag and flag-1 leaves) and stem rust race TTTT (on the upper two internodes) on the same day. Care was taken to not overspray the respective pathogens onto the other plant tissues. All the spikes of F_1 and F_2 plants were bagged before anthesis to prevent any chance of cross-pollination.

Pathogen isolates. The pathogen races/isolates used in this study were selected based on their differential virulence pattern and/or importance in agriculture (21). Race THBJ of *P. triticina* has a wide spectrum of virulence and is a common race in the Great Plains (13). Race BBBB possesses the narrowest virulence spectrum of any leaf rust pathogen culture in the USDA-ARS Cereal Disease Laboratory collection. It was selected because it may have the potential to detect the presence of additional resistance genes in the *A. sharonensis* accessions. Both races were purified by single uredinium isolation, verified for their virulence phenotype, and then increased on seedlings of the susceptible wheat cultivar Thatcher (Cltr 10003). Race TTTT of *P. graminis* f. sp. *tritici* is the most widely virulent race known in the United States and produces high infection types (IT) on all of the wheat stem rust differential lines (23). Race TPMK was the predominant stem rust race in all regions of the United States during the 1990s (17). Because this race possesses a narrower virulence spectrum than race TTTT, it may detect the presence of additional stem rust resistance genes in *A. sharonensis*. Both races were purified by single uredinium isolation, verified for their virulence phenotype, and then increased on the susceptible wheat cultivar McNair 701 (Cltr 15288). Isolate UM06-01 of *B. graminis* f. sp. *tritici* was derived from a single pustule collected in the greenhouse at the University of Minnesota St. Paul campus. The isolate was characterized for its virulence phenotype (8) and then increased on the wheat cv. Thatcher (Cltr 10003).

Plant growth conditions, inoculation protocols, and disease assessment. The sowing, maintenance, inoculation, and disease assessment protocols for plant materials were done as described by Olivera et al. (21). A summary of the disease evaluations of *A. sharonensis* crosses and seed lots including pathogen races used,

TABLE 1. Accession number, origin, and disease reaction to leaf rust, stem rust and powdery mildew in selected *Aegilops sharonensis* accessions used in genetic studies conducted in the greenhouse at St. Paul, MN, in 2004 and 2006

		Disease reaction				
		Leaf rust pathogen races		Stem rust pathogen races		Powdery mildew pathogen isolate
Accession number	Origin	THBJ	BBBB	TTTT	TPMK	UM06-01
2229	En HaMifraz	33–[a]	3+4	1–1	0;1	0;–
1193	Hefzi Bah	3	3+	3	33–	1–1
603	Palmahim	1	0;	3	1	33+
1644	Ashdod	0;1–	0;	10;	0;1–	0;–

[a] Infection types were based on a 0 to 4 scale where 0, 0;, 1, and 2 are considered indicative of host resistance and 3 and 4 of host susceptibility (21). "–"and "+" indicate lower (–) or higher (+) sporulation for infection types than described in the original scale.

TABLE 2. Disease reaction of F_1 plants and segregation of F_2 populations of various crosses and seedlots of *Aegilops sharonensis* to leaf rust, stem rust, and powdery mildew conducted in the greenhouse at St. Paul, MN, in 2006 and 2007

					F_1		F_2				
Cross[a]	Seed lot no.[b]	Pathogen	Race/isolate	Growth stage	No. plants tested	IT[c]	Resistant	Susceptible	Ratio tested	χ^2	*P* value
1644 (R) / 1193 (S)	1-A	LR	THBJ	Seedling	3	1–0;	88	33	3:1	0.33	0.56
1644 (R) / 1193 (S)	1-A	LR	THBJ	Adult	3	1–1	92	20	3:1	3.05	0.08
1193 (S) / 1644 (R)	2-A	LR	THBJ	Seedling	4	10;1+	100	29	3:1	0.44	0.51
1193 (S) / 1644 (R)	2-A	LR	THBJ	Adult	4	10;	105	27	3:1	1.46	0.23
603 (R) / 1193 (S)	4-A	LR	THBJ	Seedling	2	1–0;	117	28	3:1	2.50	0.11
603 (R) / 1193 (S)	4-A	LR	THBJ	Adult	2	0;1-	102	26	3:1	1.50	0.22
1644 (R) / 603 (R)	3-A	LR	THBJ	Seedling	1	0;1–	273	24	15:1	1.67	0.19
1644 (R) / 1193 (S)	1-A	SR	TTTT	Seedling	3	1–10;	84	42	3:1	4.67	0.03
1644 (R) / 1193 (S)	1-A	SR	TTTT	Adult	3	11–	90	23	3:1	1.30	0.25
1193 (S) / 1644 (R)	2-A	SR	TTTT	Seedling	4	11–1+	94	39	3:1	1.33	0.25
1193 (S) / 1644 (R)	2-A	SR	TTTT	Adult	4	1	90	42	3:1	3.27	0.07
1193 (S) / 2229 (R)	6-A	SR	TTTT	Seedling	1	1	112	30	3:1	1.14	0.29
1644 (R) / 2229 (R)	5-A	SR	TTTT	Seedling	2	1–0;	160	0	15:1	10.67	0.001
1644 (R) / 1193 (S)	1-B	SR	TPMK	Seedling	—	—	114	11	15:1	1.39	0.24
603 (R) / 1193 (S)	4-B	SR	TPMK	Seedling	—	—	143	13	15:1	1.16	0.28
1644 (R) / 2229 (R)	5-B	SR	TPMK	Seedling	—	—	258	0	15:1	17.20	$3.36E^{-5}$
1644 (R) / 603 (S)	3-B	PM	UM06-01	Seedling	1	0;	99	38	3:1	0.55	0.46
603 (S) / 1193 (R)	4-C	PM	UM06-01	Seedling	2	1–0;	127	40	3:1	0.10	0.75
2229 (R) / 603 (S)	7-A	PM	UM06-01	Seedling	1	0;1–	99	40	3:1	0.26	0.30
1644 (R) / 1193 (R)	1-C	PM	UM06-01	Seedling	2	1–0;	284	25	15:1	1.79	0.18
1644 (R) / 2229 (R)	5-C	PM	UM06-01	Seedling	1	0;	150	8	15:1	0.38	0.54

[a] Female parent/male parent; (R) and (S) indicate the resistant and susceptible parent, respectively.
[b] Seed lot refers to a subsample derived from the same F_2 population.
[c] Infection types were based on a 0 to 4 scale where 0, 0;, 1, and 2 are considered indicative of host resistance and 3 and 4 of host susceptibility (21). "–" and "+" indicate lower (–) or higher (+) sporulation for infection types than described in the original scale.

plant growth stage, and filial generation, is given in Tables 2 and 3. F_2 seedlings from the populations 1644/1193 and 1193/1644 were inoculated at the three to four leaf stage instead of the two leaf stage with stem rust race TTTT and leaf rust race THBJ, respectively. When $F_{2:3}$ families were evaluated against different pathogens or races, independent evaluations were made using different subsamples of the same $F_{2:3}$ family. For the summary of data, plants exhibiting IT from zero to two were classified as resistant, whereas those exhibiting IT from three to four were classified as susceptible (12,23).

Inheritance and allelism studies. To determine the genetic control of resistance to the three diseases, crosses between resistant and susceptible *A. sharonensis* accessions (Tables 1 and 2) were evaluated. F_1 plants were evaluated to assess gene action. F_2 populations (120 to 170 plants) and $F_{2:3}$ families were then evaluated to determine the inheritance of resistance based on phenotypic ratios. Twenty plants from each $F_{2:3}$ family were screened in these tests. According to Hanson (7), this $F_{2:3}$ family size has a 99% probability of distinguishing between segregating and nonsegregating families for monogenic inheritance. The allelism tests involved testing F_2 populations (160 to 320 plants) derived from crosses between two *A. sharonensis* accessions resistant to the respective diseases of leaf rust, stem rust, and powdery mildew (Tables 1 and 2).

Data analysis. The chi-square (χ^2) test was applied to determine the goodness of fit for expected genetic ratios in the F_2 and $F_{2:3}$ generations. Additionally, chi-square values also were calculated from a contingency table to assess the relationship of the reactions of *A. sharonensis* to different fungal pathogens (e.g., *P. triticina* versus *P. graminis* f. sp. *tritici*), races within a pathogen (e.g., *P. triticina* races BBBB versus THBJ), or growth stages (e.g., seedling versus adult plant).

RESULTS AND DISCUSSION

Inheritance of leaf rust resistance. F_1 plants from all the evaluated crosses between resistant and susceptible accessions exhibited IT (range of 0; to 1+; Table 2) that were similar to the resistant parent (Table 1) to race THBJ of *P. triticina* at the seedling and adult plant stage. Moreover, all of the F_2 populations from crosses between resistant and susceptible accessions segregated in their response to leaf rust. The number of resistant/susceptible plants conformed to a 3:1 ratio at both the seedling and adult plant stages (Table 2). This indicates that resistance to race THBJ in accessions 1644 and 603 is controlled by a single dominant gene. In the $F_{2:3}$ generation, the populations segregated in a 1:2:1 ratio for homozygous resistant/segregating/homozygous susceptible families, confirming that a single dominant gene is involved in conferring resistance to race THBJ (Table 3).

The chi-square value from the contingency table indicated a strong association in the reaction to race THBJ at the seedling and adult plant stages (Table 4), suggesting that the same gene conditions resistance at both growth stages. This result is in contrast to the work of Snyman et al. (26) who documented adult plant leaf rust resistance in *A. sharonensis* accessions that were susceptible at the seedling stage. Moreover, *Lr35*, a gene transferred from the close relative *A. speltoides* (10), also confers adult plant resistance to leaf rust. In this study, we selected accessions that exhibited a resistant reaction at both seedling and adult plant stages (21); thus, we cannot discount the possibility that some *A. sharonensis* accessions may possess adult plant resistance only.

In the allelism test, the F_2 population derived from the cross between the two resistant accessions (1644 and 603 from the nearby sites of Ashdod and Palmahim, respectively) segregated in an approximate 15:1 ratio for resistant and susceptible plants to

TABLE 3. Segregation of $F_{2:3}$ populations of various crosses and seed lots of *Aegilops sharonensis* to leaf rust, stem rust and powdery mildew conducted at St. Paul, MN, in 2006 and 2007

Cross[a]	Seed lot no.[b]	Pathogen	Race/isolate	$F_{2:3}$ families			Ratio tested	χ^2	*P* value
				Resistant	Segregating	Susceptible			
1644 (R) / 1193 (S)	1-A	LR	THBJ	33	54	34	1:2:1	1.41	0.49
1193 (S) / 1644 (R)	2-A	LR	THBJ	29	65	39	1:2:1	1.57	0.46
603 (R) / 1193 (S)	4-A	LR	THBJ	28	62	35	1:2:1	0.79	0.67
1644 (R) / 1193 (S)	1-A	LR	BBBB	30	58	34	1:2:1	0.56	0.76
603 (R) / 1193 (S)	4-A	LR	BBBB	29	67	32	1:2:1	0.42	0.81
1644 (R) / 1193 (S)	1-A	SR	TTTT	32	56	34	1:2:1	0.89	0.64
1193 (S) / 1644 (R)	2-A	SR	TTTT	41	60	34	1:2:1	2.39	0.30
1644 (R) / 603 (S)	3-B	SR	TTTT	29	66	25	1:2:1	1.47	0.48
1644 (R) / 603 (S)	3-B	PM	UM06-01	31	35	55	1:2:1	1.26	0.53
603 (S) / 1193 (R)	4-C	PM	UM06-01	46	68	38	1:2:1	2.53	0.28
2229 (R) / 603 (S)	7-A	PM	UM06-01	33	74	28	1:2:1	1.62	0.44

[a] Female parent/male parent; (R) and (S) indicate the resistant and susceptible parent, respectively.
[b] Seed lot refers to a subsample derived from the same F_2 population.

TABLE 4. Chi-square and *P* values from contingency tables showing the association in the reaction of *Aegilops sharonensis* to different fungal pathogens, races within a pathogen, or growth stages

Fungal pathogen and races	Cross[a]	Seed lot	Generation	χ^2	*P* value
P. triticina race THBJ[b] vs. *P. graminis* f. sp. *tritici* race TTTT[b]	1644 / 1193	1-A	$F_{2:3}$	2.37	0.67
P. triticina race THBJ[b] vs. *P. graminis* f. sp. *tritici* race TTTT[b]	1193 / 1644	2-A	$F_{2:3}$	2.22	0.69
P. graminis f. sp. *tritici* race TTTT[b] vs. *B. graminis* f. sp. *tritici* isol. UM06-01[b]	1644 / 603	3-B	$F_{2:3}$	1.79	0.77
P. triticina race THBJ[b] vs. *P. triticina* race BBBB[b]	1644 / 1193	1-A	$F_{2:3}$	160.8	$9.75\ E^{-34}$
P. triticina race THBJ[b] vs. *P. triticina* race BBBB[b]	603 / 1193	4-A	$F_{2:3}$	170.7	$7.23\ E^{-36}$
P. triticina race THBJ[c] vs. *P. triticina* race THBJ[b]	1644 / 1193	1-A	F_2	69.9	$7.32\ E^{-17}$
P. triticina race THBJ[c] vs. *P. triticina* race THBJ[b]	1193 / 1644	2-A	F_2	105.3	$1.04\ E^{-21}$
P. triticina race THBJ[c] vs. *P. triticina* race THBJ[b]	603 / 1193	4-A	F_2	54.8	$1.31E^{-13}$
P. graminis f. sp. *tritici* race TTTT[c] vs. *P. graminis* f. sp. *tritici* race TTTT[b]	1644 / 1193	1-A	F_2	47.8	$4.85\ E^{-12}$
P. graminis f. sp. *tritici* race TTTT[c] vs. *P. graminis* f. sp. *tritici* race TTTT[b]	1193 / 1644	1-A	F_2	90.1	$2.54\ E^{-21}$

[a] Female parent/male parent.
[b] Seedling evaluation.
[c] Adult plant evaluation.

race THBJ (Table 2). This indicates that the accessions carry different independently segregating dominant resistance genes. The diversity for leaf rust resistance genes found between accessions from different collection sites is not surprising given that Olivera et al. (21) found a high degree of variation in the frequency of resistant accessions between populations located in close proximity to each other, including the locations of Ashdod and Palmahim.

To identify additional leaf rust resistance genes in *A. sharonensis*, we evaluated $F_{2:3}$ families from the crosses 1644/1193 and 603/1193 for their reaction to race BBBB of *P. triticina.* Both crosses segregated in a 1:2:1 ratio for homozygous resistant/segregating/homozygous susceptible families, indicating that a single dominant gene confers resistance to race BBBB (Table 3). The general reaction of the $F_{2:3}$ families to race BBBB was the same as that found for race THBJ in nearly every case. Moreover, the chi-square value from the contingency table for $F_{2:3}$ families confirmed a strong association between the reactions to races THBJ and BBBB (Table 4). This suggests that accessions 1644 and 603 each carry a single dominant unique resistance gene that is effective against both pathogen races. Olivera et al. (21) found a high correspondence in the reactions of 107 accessions from Israel and Lebanon to *P. triticina* races THBJ, BBBB, and PNMQ, suggesting that the same dominant resistance gene might be acting in *A. sharonensis*. Our results agree with these findings as accessions 1644 and 603 were resistant not only to races THBJ and BBBB, but also race PNMQ (21). Races THBJ and PNMQ together possess virulence for 13 out of the 16 *Lr* genes included in the leaf rust differential set (12), including *Lr9* (from *A. umbellulata*) and *Lr24* (from *T. ponticum*) (4). Thus, these selected *A. sharonensis* accessions are potentially valuable sources of novel *Lr* genes for wheat improvement. The single leaf rust resistance gene introgressed into wheat from *A. sharonensis* by Marais et al. (16) also was effective to a wide range of *P. triticina* races.

Inheritance of stem rust resistance. F_1 seedling and adult plants from all of the crosses between resistant and susceptible accessions exhibited IT (range of 0; to 1+; Table 2) that were similar to the resistant parent (Table 1) to race TTTT of *P. graminis* f. sp. *tritici*, indicating that resistance is controlled by a completely dominant gene(s). All but one (seed lot no. 1-A from 1644/1193 with $P = 0.03$) of the F_2 populations segregated in an approximate 3:1 ratio (at $P > 0.05$) for the number of resistant/susceptible plants (Table 2). This indicates that resistance to race TTTT in accessions 1644 and 2229 is controlled by a single dominant gene. The deviation from the expected ratio in seed lot number 1-A from cross 1644/1193 could be due to the sequential inoculation, in which the initial leaf rust infection may have interfered with the subsequent stem rust infection (i.e., induced resistance) or possibly the misclassification of plants. However, at the adult plant stage, the segregation ratio in response to stem rust in this seed lot fit a 3:1 ratio (Table 2), confirming single gene control to this pathogen. All of the $F_{2:3}$ populations segregated in an approximate 1:2:1 ratio for homozygous resistant/segregating/homozygous susceptible families, confirming the results found in the F_2 generation (Table 3).

The chi-square value from the contingency table showed a strong association between the seedling reaction and adult plant reaction to race TTTT (Table 4). This indicates that the same gene conditions resistance at both growth stages, and that no additional genes are effective at the adult plant stage.

F_2 plants from crosses 1644/1193 and 603/1193 were evaluated for their reaction to race TPMK of *P. graminis* f. sp. *tritici* with the objective of identifying additional stem rust resistance genes in *A. sharonensis*. The F_2 populations of both crosses segregated in an approximate 15:1 ratio for resistant and susceptible plants, indicating the presence of two independently segregating dominant genes conferring resistance to race TPMK (Table 2). Accession 1644 carries at least two different stem rust resistance genes, one effective against races TTTT and TPMK, and the second only to race TPMK. In accession 603, two resistance genes effective against race TPMK also were identified, but neither of them was effective against race TTTT (Table 1). This work highlights the importance of using multiple races with different virulence spectra to identify different resistance genes in *A. sharonensis*. The identification of multiple stem rust resistance genes in *A. sharonensis* is in agreement with Gerechter-Amitai and Loegering (5), who postulated 12 or 15 different genes for resistance in 44 selected accessions of *A. sharonensis* and *A. longissima* using 20 cultures of *P. graminis* f. sp. *tritici.* The presence of different stem rust resistance genes in *A. sharonensis* also was suggested by Olivera et al. (21), who reported a high level of variation in the frequency of resistance in 107 *A. sharonensis* accessions to four different stem rust races and the absence of significant associations in the reactions elicited by them. The existence of a number of stem rust resistance genes appears to be a common feature of *Aegilops* species belonging to the section Sitopsis as two have been identified in *A. speltoides* (e.g., *Sr32* and *Sr39*) and transferred into cultivated wheat (4).

In the allelism test, the F_2 population derived from the cross between two resistant accessions (1644 and 2229) produced only resistant progeny to race TTTT (Table 2). This suggests that both accessions carry resistance alleles at the same locus or different genes that are tightly linked with each other. As observed in the allelism test with race TTTT, the F_2 population derived from the cross between resistant accessions 1644 and 2229 produced only resistant progeny to race TPMK (Table 2), confirming the presence of the same or tightly linked resistance genes in the accessions.

Overall, these experiments suggest a more complex genetic system for stem rust resistance than leaf rust resistance in *A. sharonensis*. This is based on the fact that we identified accessions that carry multiple and different stem rust resistance genes.

Inheritance of powdery mildew resistance. F_1 plants from crosses between resistant and susceptible accessions exhibited IT (range of 0; to 1–; Table 2) similar to those of the resistant parent (Table 1) to isolate UM06-01 of *B. graminis* f. sp. *tritici*, indicating that resistance is controlled by a completely dominant gene(s) (Table 2). The derived F_2 populations all segregated in an approximate 3:1 ratio for resistant and susceptible plants (Table 2), indicating that resistance is controlled by a single dominant gene in accessions 1644, 1193, and 2229. All of the $F_{2:3}$ populations segregated in an approximate 1:2:1 ratio for homozygous resistant/segregating/homozygous susceptible families, corroborating the results found in the F_2 generation (Table 3).

In the allelism tests, the F_2 populations made between the pairs of resistant accessions (i.e., 1644/2229 and 1644/1193) segregated for resistance and susceptibility to isolate UM06-01. In both crosses, the number of resistant/susceptible plants conformed to a 15:1 ratio as given by the chi-square test (Table 2). This result indicates that the resistance gene in accession 1644 (southern Coastal Plain) is different from the respective single genes present in either 2229 (northern Coastal Plain) or 1193 (central Coastal Plain). The relationship between the single genes present in accessions 2229 and 1193 cannot be resolved until the proper allelism test is made. From the evaluation of 107 *A. sharonensis* accessions for reaction to two isolates of *B. graminis* f. sp. *tritici* with different virulence spectra, Olivera et al. (21) postulated the presence of different resistance genes effective to each of the isolates tested. This result indicates that additional powdery mildew resistance genes may be identified in *A. sharonensis* using isolates with different virulence spectra. Multiple powdery mildew resistance genes have been identified in *A. speltoides* (*Pm12*, *Pm29*, and *Pm32*) (8) and *A. tauschii* (*Pm2*, *Pm34*) (8,20), indicating that the presence of multiple resistance genes to powdery mildew is a common feature in *Aegilops* species.

Maternal effects. Reciprocal crosses were made to assess whether any maternal effects were involved in resistance. The reaction of F_1 plants and the segregation of F_2 and $F_{2:3}$ populations from the reciprocal crosses of 1644/1193 and 1193/1644 indicated that no maternal effects were involved in the inheritance of leaf rust and stem rust resistance (Tables 2 and 3). A similar result was reported by Ecker et al. (2,3) in their study on the genetics of Septoria glume blotch resistance in the closely related species of *A. speltoides* and *A. longissima.* In contrast, marked differences were detected in the F_2 segregation ratio of reciprocal crosses between leaf rust resistant and susceptible *A. speltoides* accessions (E. Millet, *unpublished data*). These contrasting results suggest that the influence of maternal factors in *A. sharonensis* may depend on the interaction of both the host and pathogen evaluated.

Relationship between genes controlling resistance to different pathogens. *A. sharonensis*, like other wild relatives, is a potential source of novel genes for disease resistance in wheat. Since gene introgression from *A. sharonensis* is a long and laborious process, it would be more efficient to utilize an accession that carries multiple and linked resistance genes so that more than one of them could be transferred to wheat. One of our objectives was to identify possible associations between genes for resistance to the three diseases. $F_{2:3}$ families from the same seed lot of the reciprocal crosses 1644/1193 (no. 1-A) and 1193/1644 (no. 2-A), and from the cross 1644/603 (no. 3-C) were evaluated for their reaction to race THBJ of *P. triticina* and race TTTT of *P. graminis* f. sp. *tritici*, and to isolate UM06-01 of *B. graminis* f. sp. *tritici* and race TTTT of *P. graminis* f. sp. *tritici*, respectively, to study the possible association between genes conferring resistance to the respective pathogens. For the reciprocal crosses 1644/1193 and 1193/1644, the chi-square value from the contingency table revealed that the response to leaf rust is independent of the response to stem rust (Table 4). A lack of association also was observed in the response to powdery mildew and stem rust in the cross 1644/603 (Table 4). The lack of association revealed by the contingency test indicates that different genes confer resistance to the respective pathogens and that the respective resistance genes are located at unlinked chromosomal positions. The presence of independently segregating leaf rust and stem rust resistance genes in *A. sharonensis* also was reported by Marais et al. (15). The lack of association between leaf rust and stem rust resistance genes will make the simultaneous introgression of resistance to both pathogens into hexaploid wheat a more difficult task.

This study was the first to characterize the genetics of disease resistance in *A. sharonensis*, and one of the few completed in any of the species of the section Sitopsis (2,3). Our results clearly demonstrated that resistance to wheat leaf rust, stem rust, and powdery mildew in *A. sharonensis* is controlled by dominant genes with major effect. Similar findings were reported in several closely related *Aegilops* species of section Sitopsis to these same wheat pathogens. In fact, a number of these major resistance genes have been successfully introgressed into wheat; *Lr28*, *Lr35*, *Lr36*, *Lr47*, *Lr51*, *Sr32*, *Sr39*, *Pm12*, *Pm29*, and *Pm32* from *A. speltoides* and *Pm13* from *A. longissima* (4,8,10,25). Prior knowledge regarding the inheritance of resistance in wild wheat relatives is important in selecting a transfer approach in alien gene introgression programs. The simple inheritance found in *A. sharonensis* indicates that the introgression of resistance genes to leaf rust, stem rust, and powdery mildew into wheat will be relatively straightforward, not withstanding the inherent genetic constraints of the wide cross (19).

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