Resistance of Sharon Goatgrass (*Aegilops sharonensis*) to Fungal Diseases of Wheat

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ABSTRACT

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Sharon goatgrass (*Aegilops sharonensis*) is a wild relative of wheat that is native to Israel and Lebanon. The importance of *A. sharonensis* as a source of new resistance genes for wheat warrants additional research on the characterization of accessions for economically important genes. Thus, the objectives of this study were to evaluate a collection of *A. sharonensis* accessions for resistance to seven important fungal diseases of wheat and assess the phenotypic diversity of the germplasm for disease reaction. The frequency of resistance in *A. sharonensis* was highest to powdery mildew (79 to 83%) and leaf rust (60 to 77%). Resistance to stem rust also was common, although the percentage of resistant accessions varied markedly depending on the pathogen race—from 13% to race TTTT to 72% to race QCCJ. The frequency of resistance was intermediate to stripe rust (45%) and low to tan spot (15 to 29%) and spot blotch (0 to 34%). None of the *A. sharonensis* accessions was resistant to Fusarium head blight. Many of the accessions tested exhibited heterogeneous reactions (i.e., had both resistant and susceptible plants) to one or more of the diseases, suggesting that heterozygosity may be present at some resistance loci. Substantial variation was observed in the level of diversity to individual diseases because Shannon's Equitability index ranged from 0.116 (for Fusarium head blight) to 0.994 (for tan spot). A high level of diversity was found both between and within collection sites. Moreover, differences in the geographic distribution of resistant accessions were observed. For example, accessions from northern Israel generally were less diverse and less resistant to leaf rust and stripe rust than accessions from more southern locations. Four *A. sharonensis* accessions were highly resistant to most of the diseases evaluated and may provide a source of unique resistance genes for introgression into cultivated wheat.

Additional keywords: disease resistance, wild wheat

Bread wheat (*Triticum aestivum* L.) is one of the most important cereal crops, providing about 20% of the food calories consumed by people worldwide (65). In the United States, wheat is the third most widely grown crop behind corn and soybean and is cultivated on 25 million ha (44). Wheat production can be severely limited by both biotic and abiotic constraints. Disease is the major biotic stress in many regions. More than 200 diseases have been described on wheat, 50 of which are considered economically important (65).

The major fungal diseases of wheat in the United States include Fusarium head blight (FHB) (caused primarily by *Fusarium graminearum* Schwabe, teleomorph: *Gibberella zeae* (Schwein.) Petch), leaf rust (*Puccinia triticina* Erikss.), stem rust (*P. graminis* f. sp. *tritici* Erikss. & Henning), and stripe rust (*P. striiformis* f. sp. *tritici* Erikss.). In the last decade, FHB has become one of most significant plant diseases in the United States, causing losses exceeding $2.5 billion (66). Rusts also can be significant in reducing yield. During the last 20 years in the United States, leaf rust has been prevalent in all wheat-production areas, causing yield losses between 1 and 8% (33). Although stem rust has not been a major problem of wheat in the central and northern Great Plains during the last 40 years, it is still considered the most destructive cereal rust (49). Pathologists and breeders must be vigilant for virulence changes in the stem rust population. For example, in 1999, a new race of *P. graminis* f. sp. *tritici* (race TTKS or isolate Ug99) was discovered in eastern Africa that possesses virulence for many of the wheat cultivars grown in the Great Plains region (48). The introduction of such a race into the United States will have devastating consequences. Stripe rust is another important rust disease of wheat, particularly in the cool and moist regions of the Pacific Northwest. Since 2000, however, this rust disease has become increasingly important in the south-central states and central Great Plains, a region previously considered noncongenial to the pathogen (9). Total yield losses to stripe rust in the United States in 2003 were estimated at 86 million bushels (4.8% of wheat production), making it the most important rust disease of wheat over the past few years (33). Two other diseases that have increased in incidence and severity during the last decade are tan spot (*Pyrenophora tritici-repentis* (Died.) Drechsler, anamorph *Drechslera tritici-repentis* (Died.) Shoemaker) and spot blotch (*Cochliobolus sativus* (S. Ito & Kurib.) Drechsler ex Dastur, anamorph: *Bipolaris sorokiniana* (Sacc.) Shoemaker). The increased severity of these diseases has been favored by the wide adoption of minimum tillage and retention of crop residues on the soil surface (12). Although it is not a serious problem of wheat in the main production regions of the United States, powdery mildew (*Blumeria graminis* (DC.) Speer. f. sp. *tritici* Em. Marchal) has caused significant losses (up to 17%) in winter wheat in the southeastern Atlantic coast states (32).

Although fungicide treatments have become a common practice in cultivated wheat, the increasing environmental concerns regarding their use make the deployment of resistant wheat cultivars an attractive and economically sound alternative for disease control. The use of resistant cultivars to control diseases requires the availability of many sources of resistance to counter the continuing evolution of new virulence types in pathogen populations (21). From the time of first domestication, the genetic diversity of wheat has been seriously eroded. Thus, it is imperative that the wheat gene pool be expanded

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*The *e*-Xtra logo stands for "electronic extra" and indicates that two supplemental tables not included in the print edition are available online. Table 1 contains the complete set of raw infection phenotype data of *Aegilops sharonensis* accessions to seven wheat fungal diseases, and Table 2 gives the numbers of different reactions to seven pathogens in *Aegilops sharonensis* accessions according to collection site.

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by incorporating new genes into breeding programs (21). In this regard, wild wheat relatives offer one of the most diverse sources of unique alleles for wheat improvement (46).

Aegilops is the genus most closely related to *Triticum* (25,26) and comprises 23 species that include diploid, tetraploid, and hexaploid genomes (61). *Aegilops* spp. such as *Aegilops umbellulata, A. speltoides, A. squarrosa, A. longissima*, and *A. comosa* are known to be rich sources of resistance to various pathogens and pests (2,4,5,10,21,37,46,57,64), and many resistance genes have been transferred to wheat. Some of the most important ones include *Lr9*, *Lr21, Lr22, Lr28,* and *Lr35* for leaf rust resistance; *Sr32, Sr34,* and *Sr39* for stem rust resistance; *Yr8* for stripe rust resistance; *Pm13* for powdery mildew resistance; and *Gb5* for greenbug resistance (17,56).

A. sharonensis Eig (Sharon goatgrass) is another potentially rich source of resistance genes for wheat (4,5,21,37,46,64), but has not been exploited to any great extent for wheat improvement. This species is diploid ($2n = 2x = 14$, with a S^l or S^{sh} genome formula) and belongs to the section Sitopsis of the genus *Aegilops* (61). It is, like all members of the section Sitopsis, part of the secondary gene pool of wheat, sharing homoeology with the wheat genome (17,25). *A. sharonensis* originated and appears to be endemic only in the coastal plain of Israel and in a few locations in southern Lebanon (26,29,61), a very limited geographical area that extends for about 210 km north to south and no more than 15 km east from the Mediterranean Sea (43). *A. sharonensis* grows in the most highly populated area of Israel, where agriculture and urbanization are rapidly replacing its natural habitat (29,43). Thus, the genetic diversity present in some *A. sharonensis* populations is at risk (43).

Fig. 1. Map of Israel showing the location of the *Aegilops sharonensis* collection sites.

The importance of *A. sharonensis* as a source of resistance is well documented. Previous investigators have identified in the species sources of resistance to leaf rust (4,5,21,37,46), stem rust (19), powdery mildew (21,46), Karnal bunt (64), Hessian fly (21), and greenbug (21). The results from all studies suggest that a high level of diversity for resistance exists in the species. In spite of the many examples of pathogen and pest resistance in *A. sharonensis*, successful introgression of resistance genes into cultivated wheat has been reported only for leaf rust and stripe rust (38,39).

The importance of *A. sharonensis* as a source of resistance genes for wheat, together with its threatened habitats, warrant additional research on the collection of additional accessions and their characterization for economically important genes. The objectives of this study were to evaluate a collection of *A. sharonensis* accessions for resistance to seven important fungal diseases of wheat and assess the phenotypic diversity of the germplasm for disease reaction.

MATERIALS AND METHODS

Germplasm. In all, 107 accessions of *A. sharonensis* from Israel and Lebanon were evaluated in this study. All but five of these accessions were from Israel. The Israeli accessions were from the Harold and Adele Lieberman Germplasm Bank in the Institute for Cereal Crops Improvement at Tel Aviv University. Four accessions were from Lebanon and provided by Thomas Payne (Centro Internacional de Mejoramiento de Maiz y Trigo [CIMMYT], El Batan, Mexico). One accession provided by Harold Bockelman (United States Department of Agriculture–Agricultural Research Service [USDA-ARS], National Small Grain Collection [NSGC], Aberdeen, ID) originally came from the Aegean Agricultural Research Institute Genebank (Izmir, Turkey), but without any passport information. The Israeli accessions came from 11 collection sites covering most of the known distribution area of the species within the country (43) (from 34.9° to 36.4°N latitude), including the regions of Haifa Bay (3% of the accessions), Central Coastal Plain (40.2% of the accessions), and Southern Coastal Plain (56.8% of the accessions) (Fig. 1; Table 1). These populations reflect the typical habitats of *A. sharonensis* in Israel. The altitude at the collection sites ranged between 0 and 100 m above sea level. Each accession within a collection site in Israel was derived from a single spike gathered at least 5 m apart along a straight transect. No information was available about the collection sites or sampling technique of the accessions provided by CIMMYT or the NSGC. Prior to disease evaluation, all accessions were grown for seed increase in a nethouse and greenhouse.

Pathogen isolates. Information about the fungal pathogens used in the disease phenotyping tests is summarized in Table 2. Three races of *Puccinia triticina* were used. Race BBBB possesses the narrowest virulence spectrum of any culture in the USDA-ARS Cereal Disease Laboratory collection. BBBB was selected because it may have the potential to detect the presence of more resistance genes in the *A. sharonensis* accessions. In contrast, race THBJ has a wider spectrum of virulence and also is one of the most common races found in the Great Plains (28,35). Race THBJ was included because it is virulent for many wheat *Lr* genes and possibly may identify within *A. sharonensis* any genes that are potentially valuable for wheat improvement. Race PNMQ was selected because it has a different virulence spectrum than BBBB and THBJ and, therefore, can identify other genes not selected by these other races. All leaf rust races were verified for their virulence phenotype (34), purified, and then increased on seedlings of the susceptible wheat cv. Thatcher (Cltr 10003).

Table 1. Number and origin of *Aegilops sharonensis* accessions used in this study

Location	Coordinates[z]	Number of accessions
Israel		
Haifa Bay		3
1. En HaMifraz	36.69E/36.42N	3
Central Coastal Plain		41
2. Hefzi Bah	36.68E/35.93N	9
3. Mikhmoret	36.68E/35.88N	2
4. Kefar Ganim	36.67E/35.50N	8
5. Qiryat Ono	36.67E/35.49N	2
6. Palmahim	36.66E/35.34N	13
7. Ben Zakkai	36.64E/35.26N	7
Southern Coastal Plain		58
8. Ashdod	36.65E/35.23N	33
9. HaShikmim Park	36.65E /35.17N	5
10. Nizzanim	36.65E/35.12N	10
11. Ziqim	36.64E/34.98N	10
Lebanon	–/–	4

[z] From Millet et al. (43); – indicates data not available.

Four races of *P. graminis.* f. sp. *tritici* were selected for this study based on their differential virulence phenotype or importance in agriculture. Race TTTT is the most widely virulent race known in the United States and produces high infection types (ITs) on all of the wheat stem rust differential lines (50). Race TTKS originated in eastern Africa and is virulent for *Sr31*, a widely used gene in wheat cultivars worldwide (48). Race TPMK was the predominant race in all areas of the United States during the 1990s (41). Race QCCJ has a markedly different virulence spectrum and, therefore, can identify other genes not distinguished by the other races. All races were verified for their virulence phenotype (50), purified, and then increased on the susceptible wheat cv. McNair 701 (Cltr 15288).

Race PST-78 of *P. striiformis* f. sp. *tritici* was used for the stripe rust evaluation because it is the most predominant race in the United States (9). Urediniospore increases were made on the susceptible wheat cv. Express (PI 573003).

Two isolates (UM05-01 and UM06-01) of *B. graminis* f. sp. *tritici* were used for the powdery mildew evaluations. Both isolates were derived from individual single pustules collected in the greenhouse at the University of Minnesota, verified for their virulence phenotype (23), and then increased on the susceptible wheat cv. Roblin.

Two races of *Pyrenophora tritici-repentis* (race 1 and race 5) were used for the tan spot evaluations. Race 1 is prevalent in the Great Plains region of the United States (3) and produces two host-specific toxins, Ptr ToxA and Ptr ToxC (31). Race 5 produces the host-specific toxin Ptr ToxB (31). Both races induce chlorotic and necrotic reactions on wheat.

Two races of *C. sativus* (race 0 and race 2) were used for the spot blotch evaluations. These races exhibit differential reactions on the spot blotch differential lines of barley (15,60) and also on certain wheat accessions.

Isolate KB-172 of *F. graminearum* was used for the FHB evaluations. This isolate originally was collected from barley in North Dakota in 1994. It is highly virulent on barley and wheat and a reliable producer of deoxynivalenol (DON) (53).

Inoculation protocols and disease assessment. Plants were evaluated to leaf rust and stem rust at both the seedling and adult plant stages; to stripe rust, tan spot, spot blotch, and powdery mildew at the seedling stage only; and to FHB at the adult plant stage only. All experiments were done in a completely randomized design with one replicate and were repeated once. The disease evaluation tests were performed between summer 2003 and winter 2006.

Seedling evaluations. To obtain uniform germination of the *A. sharonensis* accessions, seed was removed from the spikelets and germinated on filter paper moistened with distilled water in 9-cm petri plates (37). Seed were incubated at 4°C for 7 days and then at 22 to 25°C for 1 day. Five seeds of each accession were planted in plastic cones (3.8 cm in diameter by 21 cm in depth) containing soil and Metromix 200 (vermiculite, peat moss, perlite, and sand mix) in a 60:40 ratio. Seedlings were inoculated at the second-leaf stage, 12 to 14 days after planting.

Leaf rust. Seedlings were inoculated with urediniospores suspended in a lightweight mineral oil (approximately 0.014 mg of spores per plant). Following inoculation, plants were transferred to mist chambers and incubated for 16 h in darkness at 18 to 21°C and approximately 100% relative humidity (RH) (37). After the mist period, plants were allowed to slow dry for 4 h before being placed in a growth chamber at 18 to 21°C with a 14-h photoperiod. Twelve days after inoculation, plants were evaluated for their ITs based on the 0-to-4 scale of Long and Kolmer (34). Wheat cv. Thatcher (Cltr 10003) was used as the susceptible control.

Stem rust. The inoculation protocol used for stem rust was the same as described for leaf rust with two exceptions: (i) the spore concentration used was approximately 0.028 mg of spores per plant and (ii) plants were exposed to light during the last 5 h of the misting period, a requirement for the *Puccinia graminis* f. sp. *tritici* infection process (52). Twelve days after inoculation, plants were evaluated for their ITs based on the 0-to-4 scale of Roelfs et al. (51). Wheat cv. McNair 701 (Cltr 15288) was used as the susceptible control.

Stripe rust. The inoculation protocol for stripe rust was the same as described for leaf rust. After inoculation, plants were transferred to a mist chamber at 10°C and approximately 100% RH for 24 h. Then, plants were placed in a growth chamber programmed to change temperature gradually from 4°C at 0200 h to 18°C at 1400 h with a 16-h photoperiod between 0600 and 2200 h (9). ITs were assessed 19 to 22 days after inoculation using the 0-to-4 scale of McIntosh et al. (40). Wheat cv. Express (PI 573003) was used as the susceptible control.

Powdery mildew. Seedlings were inoculated by shaking mildew-infected plants of wheat cv. Roblin (four-leaf stage) over the test entries. Inoculated plants then were kept in the greenhouse at 22 to 28°C. Eight days after inoculation, plants were evaluated for their ITs using the 0-to-4 scale of Mains and Dietz (36). Wheat cv. Roblin was used as the susceptible control.

Tan spot. An inoculum concentration of 3×10^3 conidia/ml (plus one drop of Tween 20 per 0.5 liters of suspension) was used for the tan spot inoculations (2). Inoculum was applied to seedlings at a rate of approximately 0.08 ml/plant using an artist's airbrush (Model H & HS; Paasche

Table 2. Race or isolate designation, virulence phenotype, and source of wheat fungal pathogens used to evaluate resistance in *Aegilops sharonensis*[x]

Pathogen	Race	Isolate	Virulence/avirulence formula[y]	Source[z]
Puccinia triticina	THBJ	99ND588DLL	1, 2a, 2c, 3a, 16, 26, 10, 14a, 18/9, 24, 3ka, 11, 17, 30, B	J. Kolmer, USDA St. Paul
P. triticina	PNMQ	94LA101	1, 2c, 3a, 9, 24, 3ka, 30, B, 10/2a, 16, 26, 11, 17, 14a, 18	J. Kolmer, USDA St. Paul
P. triticina	BBBB	NA	–/1, 2a, 2c, 3a, 9, 16, 24, 26, 3ka, 11, 17, 30, B, 10, 14a, 18	J. Kolmer, USDA St. Paul
P. graminis f. sp. *tritici*	TTTT	02MN84A-1-2	5, 21, 9e, 7b, 11, 6, 8a, 9g, 36, 9b, 30, 17, 9, 9d, 10, Tmp/–	Y. Jin, USDA St. Paul
P. graminis f. sp. *tritici*	TTKS	99UGA	5, 21, 9e, 7b, 11, 6, 8a, 9g, 9b, 30, 17, 9a, 9d, 10/36, Tmp	Y. Jin, USDA St. Paul
P. graminis f. sp. *tritici*	TPMK	95NE115-A	5, 21, 9e, 7b, 11, 8a, 9g, 36, 17, 9d, 10, Tmp/6, 9b, 30, 9a	J. Kolmer, USDA St. Paul
P. graminis f. sp. *tritici*	QCCJ	01TX27C	5, 21, 9g, 17, 9d, 10/9e, 7b, 11, 6, 8a, 36, 9b, 30, 9a, Tmp	J. Kolmer, USDA St. Paul
P. striiformis f. sp. *tritici*	PST-78	NA	1, 3, 11, 12, 16, 17, 18, 19, 20/2, 4, 5, 6, 7, 8, 9, 10, 13, 14, 15	X. Chen, USDA Pullman
Blumeria graminis f. sp. *tritici*	NA	UM05-01	1a, 2a, 3a, 3c, 3e, 3f, 5a, 6, 7, 8/3b, 4a, 4b, 9, 17, 25	P. Olivera, Univ. of MN
B. graminis f. sp. *tritici*	NA	UM06-01	1a, 2a, 3b, 3c, 3e, 5a, 6, 7, 8, 9/3a, 3f, 4a, 4b, 17, 25	P. Olivera, Univ. of MN
Fusarium graminearum	NA	KB172	NA	B. Steffenson, Univ. of MN
Pyrenophora tritici-repentis	1	Asc1	…	L. Lamari, Univ. of Mba.
P. tritici-repentis	5	Alg3-24	…	L. Lamari, Univ. of Mba.
Cochliobolus sativus	0	ND93-1	…	B. Steffenson, Univ. of MN
C. sativus	2	ND 90Pr	…	B. Steffenson, Univ. of MN

[x] NA = not applicable or not available.

[y] – Indicates no differential in the virulence or avirulence category, and … = resistance genes for all of the differential genotypes have not been characterized.

[z] USDA = United States Department of Agriculture–Agricultural Research Service; St. Paul = Cereal Disease Laboratory. St. Paul, MN; Pullman = Wheat Genetics, Physiology, Quality, and Disease Research Unit, and Department of Plant Pathology, Washington State University, Pullman; Univ. = University; MN = Minnesota; and Mba. = Manitoba, Canada.

Airbrush Company, Chicago) pressurized by a CO_2 tank at 138 kPa. After inoculation, plants were placed in a mist chamber for 16 h at 18 to 22°C and approximately 100% RH (30). Following the mist period, inoculated plants were allowed to dry for 4 h and then placed in a growth chamber at 20 to 23°C with a 14-h photoperiod. Plants were evaluated for their IT 8 days after inoculation using the scale of Lamari and Bernier (30). Wheat differential lines 6B635, Katepwa, Erik (PI 476849), Coulter (Cltr 17757), 6B662, Salamouni (PI 182673), Glenlea (Cltr 17272), and 4B1149 were used as the controls (31).

Spot blotch. The inoculum concentration used for the spot blotch inoculations was 6 to 8×10^3 conidia/ml (60) (plus one drop of Tween 20 per 0.5 liters of suspension). Inoculum was applied at a rate of approximately 0.08 ml/plant with an artist's airbrush as described above. After inoculation, plants were placed in a mist chamber for 16 to 18 h in the dark at 18 to 22°C and approximately 100% RH. Following the mist period, plants were allowed to slow dry before being placed into a growth chamber at 21 to 23°C with a 16-h photoperiod. Seedlings were assessed for their ITs 6 and 8 days after inoculation. A 0-to-5 scale adapted from Adlakha et al. (1) was used for assessing the ITs, where 0 = no visible sign of infection, 1 = pinpoint lesions, 2 = small lesions, 3 = medium lesions, 4 = large lesions, and 5 = very large lesions showing coalescence. Barley cv. Bowman (PI 483237) and barley lines ND5883 and ND B112 (CIho 11531) were used as controls (60).

For the rusts and powdery mildew, ITs from 0 to 1 were considered indicative of resistance, 2 of an intermediate reaction, and 3 to 4 of susceptibility. For tan spot and spot blotch, infection responses from 0 to 2 were considered indicative of resistance, 3 of an intermediate reaction, and 4 to 5 of susceptibility. Accessions were classified as heterogeneous if they clearly contained both resistant and susceptible plants, resistant and intermediate plants, or susceptible and intermediate plants.

Adult plant evaluations. In all, 5 germinated seeds per accession were planted in peat pots (1 seed per pot) filled with soil and Metromix 200 at a 70:30 ratio. When the plants reached the three-leaf stage, they were transferred to a vernalization chamber (4°C and 6-h photoperiod) for 6 weeks. Following vernalization, plants were transplanted into plastic pots (10 by 10 cm) filled with soil and Metromix 200 (70:30 ratio) and grown in a greenhouse at 18 to 25°C with a 14-h photoperiod until they were inoculated.

Leaf rust and stem rust. For the leaf rust evaluation, fully expanded flag, flag-1 and flag-2 leaves were inoculated at the heading stage with urediniospores suspended in mineral oil (4.0 mg per 0.7 ml of oil) at a rate of approximately 0.4 mg of spores/plant. The incubation protocols were the same as described for the seedling tests. Plants were evaluated for their leaf rust response using the modified Cobb scale (47). For stem rust, inoculations were made at the heading stage on the upper two internodes of each plant with a urediniospore suspension (8.0 mg per 0.7 ml of oil) at a rate of approximately 0.8 mg/plant. Again, the infection period protocols were the same as described for the seedling tests. At 12 to 14 days after inoculation, plants were evaluated for their infection response using the scale of Roelfs et al. (51).

FHB. For FHB evaluations, the spray and needle injection inoculation techniques were applied to identify resistance to initial infection (i.e., type I) and resistance to spread (i.e., type II), respectively (11). Both inoculations were done when plants were at 30 to 50% anthesis using a concentration of 4×10^5 macroconidia/ml (11). For the single floret inoculation, a metered hypodermic syringe (Model PB600; Hamilton Company, Reno, NV) was used to inject 5 µl of inoculum into each of the two central spikelets of the spike. For spray inoculation, approximately 0.7 ml of inoculum/spike was delivered using an artist's airbrush as described previously. After inoculation, plants were transferred to a mist chamber at 18 to 21°C and approximately 100% RH for 40 h. Following the mist period, inoculated plants were placed in a greenhouse at 17 to 28°C with a 14-h photoperiod. FHB assessments were made 14 and 21 days post inoculation by counting the number of infected spikelets. FHB severity then was calculated by dividing the number of infected spikelets by the total number of spikelets in the spike. Wheat cvs. Sumai 3 (PI 481542) and Wheaton (PI 469271) were the resistant and susceptible controls, respectively.

For leaf rust and stem rust, IT R was considered indicative of resistance, MR and MS of an intermediate reaction, and S of susceptibility. For FHB, 0 to 25% infection was considered indicative of resistance, 25 to 50% as an intermediate reaction, and 50 to 100% of susceptibility. Accessions were classified as heterogeneous if they clearly contained both resistant and susceptible plants.

Data analysis. The percentage of accessions giving resistant, intermediate, susceptible, and heterogeneous reactions to each pathogen at the seedling stage was calculated. In addition, χ^2 values were calculated from contingency tables to assess the relationship of the reactions of *A. sharonensis* to races within a pathogen (e.g., *P. triticina* races BBBB versus THBJ). Phenotypic diversity for disease reaction in *A. sharonensis* was estimated using the Shannon diversity index (h_s), where $h_s = -\Sigma p_i \ln(p_i)$, with a maximum $h_s = 1.099$ (16). Values of Shannon's equitability (E_h) ($E_h = h_s/h_{max}$) higher than 0.85 were considered indicative of high diversity, 0.85 to 0.50 of intermediate diversity, and <0.50 of low diversity. Both analyses were performed using the three general reaction classes of resistant, intermediate, and susceptible.

RESULTS

Infection phenotypes of the differential host lines used to assign pathotypes of each pathogen were consistent with previously published results (*data not shown*). The same was true for the controls included in each experiment. Overall, the infection phenotypes of the *A. sharonensis* accessions to each of the respective pathogen races or isolates were similar between the two replicates of each experiment.

Among all the pathogens evaluated, the highest percentage of resistance found in *A. sharonensis* was to *B. graminis* f. sp. *tritici* (79.4 and 83.2% for isolates UM05-01 and UM06-01, respectively; Table 3). Most (87 and 94%) of these resistant accessions exhibited very low ITs of 0 and 0; indicating a very high level of resistance. Only 2 (1.9%) and 3 (2.8%) accessions were heterogeneous in their IT to the respective isolates, suggesting a very low level of heterozygosity at the resistance loci. The percentage of resistance to *P. triticina* was similarly high at the adult plant stage to races THBJ (76.6%) and PNMQ (77.4%) (Table 3). Again, most (73 and 69%) of these resistant accessions were highly resistant, giving ITs of 0;. At the seedling stage, the percentage of accessions resistant to *P. triticina* was lower: 59.8% to race BBBB and 62.6% for race THBJ. Heterogeneous leaf rust reactions were found in 12.3 to 22.4% of the accessions, the highest frequency being to race BBBB. This suggests a fairly high level of heterozygosity for leaf rust resistance loci. Although a higher frequency of leaf rust-resistant accessions was observed at the adult plant stage compared with the seedling stage, the χ^2 value obtained from the contingency table for race THBJ (seedling versus adult plant stage) indicated a strong association in the reactions (Table 4). In addition, strong associations were found for the reactions elicited by all leaf rust races in pairwise comparisons.

Resistance to *P. graminis* f. sp. *tritici* also was common in *A. sharonensis*, although the percentage of resistant accessions varied markedly depending on the pathogen race. The highest percentage of resistance found was in response to races QCCJ (72.0%) and TTKS (69.2%) and the lowest to races TPMK (32.7%) and TTTT (13.1%) in seedling plants (Table 3). The percentage of highly resistant accessions (IT of 0; and 1) to stem rust in seedling plants also was lower than for leaf rust and varied depending on the pathogen race (28% for TTTT and QCCJ, 42% for TTKS, and 57% for TPMK). The percentage of resistance to race TTTT was more than three times higher at the adult stage

(41.7%) than at the seedling stage (13.1%); however, the χ^2 value obtained from the contingency table indicated a significant association in the reaction to race TTTT at the two growth stages (Table 4). The same was true for pairwise comparisons of reactions to races TTKS, TPMK, and QCCJ at the seedling stage (Table 4). Accessions with heterogeneous stem rust reactions were observed, but at an overall lower frequency (1.2 to 12.1%) than found with leaf rust.

Nearly 45% of the accessions were resistant to *P. striiformis* f. sp. *tritici* (Table 3). Of these resistant accessions, 89% were highly resistant, giving low ITs of 0; to 1. In all, 13.1% of accessions were heterogeneous in their reactions to stripe rust, a level comparable with that observed with the other two rust pathogens at the seedling stage.

Although the frequency of resistant plus intermediate accessions was similar (approximately 60%) to both races of *Pyrenophora tritici-repentis*, the frequency of resistant accessions to race 5 (29.0%) was almost twice that found to race 1 (15.0%) (Table 3). In general, the level of resistance exhibited in response to *P. tritici-repentis* was not as high as that observed in response to powdery mildew and the rusts, because only two accessions exhibited low ITs to the two races. The frequency of accessions with heterogeneous tan spot reactions was low (2.8 to 3.7%), suggesting a low level of heterozygosity at the resistance loci. The χ^2 value obtained from the contingency table indicated no association between the reactions elicited by race 1 and race 5 of *P. tritici-repentis* (Table 4).

Marked differences were observed in response to the two races of *C. sativus*; the frequency of resistance ranged from 0% with race 0 to 33.6% with race 2. The number of accessions exhibiting heterogeneous spot blotch reactions ranged from 3.7 to 9.3%, indicating a low to moderate level of heterozygosity for the resistance loci. The χ^2 value obtained from the contingency table indicated no association between the reactions to race 0 and race 2 of *C. sativus* (Table 4). None of the accessions was highly resistant to race 2, because the lowest IT observed was 12.

Accessions with resistance to *F. graminearum* were not identified in *A. sharonensis*, and only 2.8% of the accessions exhibited an intermediate reaction (Table 3). Heterogeneous reactions were not observed for any accession in response to this pathogen.

The *A. sharonensis* accessions 2172, 2173, 591, and 1644 exhibited the broadest spectrum of resistance to the various pathogen races or isolates that were used in this study. Accessions 2172 and 2173 were similar in their reactions, being susceptible only to FHB, stripe rust, and race 0 of *C. sativus*. Both accessions exhibited an intermediate reaction to *Puccinia graminis* f. sp. *tritici* race TTTT at seedling stage. Accession 591 also exhibited resistant reactions to most of the pathogen isolates, but was intermediate to race 0 of *C. sativus*, race TTKS of *P. graminis* f. sp. *tritici*, and race 5 of *Pyrenophora tritici-repentis*, and was susceptible only to FHB. Accession 1644 was susceptible only to FHB and spot blotch, and was intermediate in its reaction to race 1 of *P. tritici-repentis*.

Table 4. Probability and χ^2 values from contingency tables for associations of the reactions of *Aegilops sharonensis* accessions to various pathogens, pathogen races, and ontogenetic stages

	Association between			
Fungal pathogen	**Race**	**Race**	**χ^2 value**	***P* value[x]**
Puccinia triticina	THBJ[y]	PNMQ[y]	59.76	3.26 E-12
P. triticina	THBJ[y]	THBJ[z]	52.10	1.31 E-10
P. triticina	THBJ[y]	BBBB[z]	30.38	4.09 E-06
P. triticina	PNMQ[y]	THBJ[z]	39.01	6.93 E-08
P. triticina	PNMQ[y]	BBBB[z]	31.24	2.74 E-06
P. triticina	THBJ[z]	BBBB[z]	62.32	9.4 E-13
P. graminis f. sp. *tritici*	TTTT[y]	TTTT[z]	24.99	0.0002
P. graminis f. sp. *tritici*	TTTT[y]	TTKS[z]	8.82	0.066
P. graminis f. sp. *tritici*	TTTT[y]	TPMK[z]	8.50	0.075
P. graminis f. sp. *tritici*	TTTT[y]	QCCJ[z]	2.18	0.70
P. graminis f. sp. *tritici*	TTTT[z]	TTKS[z]	2.46	0.65
P. graminis f. sp. *tritici*	TTTT[z]	TPMK[z]	7.34	0.12
P. graminis f. sp. *tritici*	TTTT[z]	QCCJ[z]	2.11	0.71
P. graminis f. sp. *tritici*	TTKS[z]	TPMK[z]	18.07	0.0012
P. graminis f. sp. *tritici*	TTKS[z]	QCCJ[z]	5.15	0.272
P. graminis f. sp. *tritici*	TPMK[z]	QCCJ[z]	14.44	0.006
Pyrenophora tritici-repentis	1	5	3.76	0.440
Cochliobolus sativus	0	2	6.01	0.198
Blumeria graminis	UM01-05	UM01-06	8.85	0.065

[x] *P* value at significance level = 0.01.
[y] Adult plant evaluation.
[z] Seedling evaluation.

Table 3. Number and percentage of *Aegilops sharonensis* accessions exhibiting resistant, intermediate, susceptible, or heterogeneous reactions to seven different fungal pathogens of wheat and corresponding values for Shannon's diversity and equitability indices[w]

Pathogen	**Resistant**	**Intermediate**	**Susceptible**	**Heterogeneous**	**Total**	**h_s[x]**	**h_s/h_{max}**
Puccinia triticina race THBJ[y]	82 (76.6)	2 (1.9)	9 (8.4)	14 (13.1)	107 (100)	0.487	0.443
P. triticina race PNMQ[y]	82 (77.4)	3 (2.8)	8 (7.5)	13 (12.3)	106 (100)	0.495	0.450
P. triticina race THBJ[z]	67 (62.6)	7 (6.5)	15 (14.0)	18 (16.8)	107 (100)	0.747	0.680
P. triticina race BBBB[z]	64 (59.8)	2 (1.9)	17 (15.9)	24 (22.4)	107 (100)	0.674	0.613
P. graminis f. sp. *tritici* race TTTT[y]	43 (41.7)	10 (9.7)	40 (38.8)	10 (9.7)	103 (100)	0.958	0.872
P. graminis f. sp. *tritici* race TTTT[z]	14 (13.1)	5 (4.7)	75 (70.1)	13 (12.1)	107 (100)	0.658	0.599
P. graminis f. sp. *tritici* race TTKS[z]	74 (69.2)	12 (11.2)	14 (13.1)	7 (6.5)	107 (100)	0.767	0.697
P. graminis f. sp. *tritici* race TPMK[z]	35 (32.7)	20 (18.7)	45 (42.1)	7 (6.5)	107 (100)	1.043	0.949
P. graminis f. sp. *tritici* race QCCJ[z]	59 (72.0)	13 (15.9)	9 (11.0)	1 (1.2)	82 (100)	0.771	0.702
P. striiformis f. sp. *tritici* race PST-78[z]	48 (44.9)	6 (5.6)	39 (36.4)	14 (13.1)	107 (100)	0.889	0.809
Blumeria graminis f. sp. *tritici* isol. UM05-01[z]	85 (79.4)	6 (5.6)	14 (13.1)	2 (1.9)	107 (100)	0.611	0.556
B. graminis f. sp. *tritici* isol. UM06-01[z]	89 (83.2)	5 (4.7)	10 (9.3)	3 (2.8)	107 (100)	0.518	0.471
Fusarium graminearum isolate KB172[y]	0 (0.0)	3 (2.8)	104 (97.2)	0 (0.0)	107 (100)	0.128	0.116
Pyrenophora tritici-repentis race 1[z]	16 (15.0)	48 (44.9)	39 (36.5)	4 (3.7)	107 (100)	1.012	0.920
P. tritici-repentis race 5[z]	31 (29.0)	35 (32.7)	38 (35.5)	3 (2.8)	107 (100)	1.092	0.994
Cochliobolus sativus race 0[z]	0 (0.0)	7 (6.5)	96 (87.9)	4 (3.7)	107 (100)	0.276	0.251
C. sativus race 2[z]	36 (33.6)	12 (11.2)	49 (45.8)	10 (9.3)	107 (100)	0.970	0.882

[w] Number given in parentheses is the percentage of that class out of the total number of accessions tested.
[x] Shannon's diversity index, where $h_s = -\Sigma p_i \ln(p_i)$ with a maximum $h_s = 1.099$.
[y] Adult plant evaluation.
[z] Seedling evaluation.

The level of diversity in *A. sharonensis* to the seven fungal pathogens varied considerably; the Shannon equitability (h_s/h_{max}) values ranged from 0.116 to 0.994 (Table 3). A high level of diversity was found in response to *P. tritici-repentis* races 1 (0.920) and 5 (0.994), *C. sativus* race 2 (0.882), and *Puccinia graminis* f. sp. *tritici* races TPMK (seedling stage) (0.949) and TTTT (0.872 for adult). An intermediate level of diversity was observed in response to *P. striiformis* f. sp. *tritici* (0.809), THBJ (0.680 for seedling), and BBBB (0.613); *P. graminis* f. sp. *tritici* races TTTT (0.599 for seedling), TTKS (0.697), and QCCJ (0.702); and *B. graminis* f. sp. *tritici* isolate UM05-01 (0.556). Low levels of diversity were found in response to *P. triticina* races THBJ and PNMQ (0.443 and 0.450 for adult stage) and *B. graminis* f. sp. *tritici* isolate UM06-01 (0.471), due to a high percentage of resistant accessions. A very low level of diversity was found for reaction to *C. sativus* race 0 (0.251) and *F. graminearum* (0.116) because most of the accessions exhibited a susceptible response.

Although the number of accessions tested from some collection sites and regions was low, some distinct differences were observed in the frequency distribution of resistant accessions within Israel for some of the pathogens evaluated at the seedling stage. To leaf rust, the percentage of resistant accessions was very low in northern Israel. None of the accessions from the northernmost collection sites of En HaMifraz (Haifa Bay) and Hefzi Bah (Central Coastal Plain) were resistant to the two races of *P. triticina* (Fig. 1). In contrast, the percentage of leaf rust resistance for sites south of Hefzi Bah was high, often 100% but in nearly every case over 40%. With stem rust, the percentage and distribution of resistant accessions varied according to the pathogen race. A high percentage of resistance to races TTKS and QCCJ was found at all Israeli collection sites and was often 100% but always higher than 44%. In contrast, resistance to race TTTT was relatively rare; the highest percentage of resistant accessions (>50%) was found only in the northernmost collection site of the Central Coastal Plain (Hefzi Bah) and in Lebanon. With race TPMK, a high percentage of resistance (>57%) was observed only in collections from the Central Coastal Plain (Mikhmoret, Qiryat Ono, Palmahim, and Ben Zakkai). With stripe rust, the highest percentage of resistance was found at sites in the Southern Coastal Plain (Nizzanim, 90%; HaShikmim Park, 60%; and Ashdod, 58%) and at one site in the southern half of the Central Coastal Plain (Palmahim, 61%) (Fig. 1), although some sites in these regions had a low frequency of resistance (i.e., Ben Zakkai, 14%, and Ziqim, 20%). In contrast, no resistant accessions were found in the Haifa Bay region (En HaMifraz) or the northern part of the Central Coastal Plain (Mikhmoret and Qiryat Ono). No notable geographic trends were observed for the frequency of resistance to powdery mildew, spot blotch, or tan spot (Fig. 1).

DISCUSSION

The results of this study clearly demonstrate that *A. sharonensis* is a rich and diverse source of disease resistance to some of the most important pathogens of wheat. Many of the accessions exhibited a broad spectrum of resistance to the pathogens evaluated and were highly diverse in their disease reactions (Table 3). This result confirms previous studies documenting the diversity for reaction to different fungal diseases (e.g., leaf rust, stripe rust, and stem rust) in this species (4–6,19,58) and also in closely related *Aegilops* spp. (*A. speltoides, A. longissima, A. bicornis*, and *A. searsii*) native to Israel (4,5,19). A high level of diversity in *A. sharonensis* also was reported for water-soluble leaf proteins (42), isoenzymatic characters (7), mitochondrial DNA (8), and genomic DNA (13,22).

Despite having a very restricted geographic distribution with relatively uniform climate and soil type, *A. sharonensis* possesses a high level of diversity for disease resistance that is comparable with other species that have a much wider geographic range and more widely variable environments. Thus, it appears that *A. sharonensis* populations are capable of maintaining sufficient genetic variability for long-term evolution. Geographical differences in the frequency of resistance were observed in *A. sharonensis* despite the narrow habitat range of the species and also the relatively small sample size from some regions. Although represented with fewer accessions than other regions, the Haifa Bay region appeared to be less diverse than the Central and Southern Coastal Plain regions because no variation was observed for disease reaction to *B. graminis* f. sp. *tritici, P. striiformis* f. sp. *tritici,* and *P. triticina*. Similar results for *P. triticina* were obtained by Anikster et al. (5), who suggested that stand density of *Aegilops* populations, rather than differences in environmental parameters between regions, might be a more critical determinant in the development of resistance and level of diversity. The fact that fewer and smaller *A. sharonensis* populations are present in the north around Haifa Bay compared with the Central and Southern Coastal Plains (43) may be a reason for the lower diversity in the species. A low level of diversity also was found for the Lebanese accessions; however, no inferences can be made about population diversity because details on the exact origin of these accessions are not known. Additional studies that include more accessions from En HaMifraz and other populations from the Haifa Bay region and Lebanon should be conducted to assess the amount of diversity at the regional and population levels.

Marked differences in diversity both within and between *A. sharonensis* populations were observed in the Central and Southern Coastal Plain regions. Resistant and susceptible accessions were observed at most of the collection sites in these regions and for most of the diseases. Moreover, the frequency of resistant accessions varied greatly between populations located in close proximity to each other (e.g., Ashdod and HaShikmim Park or Ben Zakkai and Palmahim). A high level of interpopulation variability in *A. sharonensis* also was described by Asins and Carbonell (7) based on the study of three enzymatic characters. These authors concluded that *A. sharonensis* is a self-pollinated species with local adaptation over short distances. Diversity at the collection site level also was reported in wild barley (*Hordeum vulgare* subsp. *spontaneum*) at its center of origin (16,24).

All of the Israeli accessions of *A. sharonensis* used in this study were derived from a single spike. Nevertheless, we detected heterogeneous reactions (i.e., presence of resistant and susceptible plants within the same accession) to nearly all of the diseases evaluated. This result suggests that the resistance loci are still heterozygous even though this species is considered self-pollinated (26). This phenomenon has been reported previously in *A. sharonensis* (4,5,21,37) and in other wild wheat (5,37,46) and barley (16) species, suggesting that it is a common feature of wild grasses. The presence of heterozygosity for restriction fragment length polymorphism loci in *A. sharonensis* also was reported by Dvorak et al. (13), who suggested that this species may have a mixed mating system combining self- and cross-pollination. It should be mentioned that, during the seed increase of accessions for this study, the plants were grown in close proximity to each other within a nethouse and greenhouse. Thus, it is possible that some cross-pollination might have occurred, thereby contributing to heterozygosity at some resistance loci. Regardless of the reason, the basis for heterozygosity in these accessions should be investigated further.

A. sharonensis exhibited a high percentage and high level (IT of 0; and 1) of resistance to all *P. triticina* races evaluated in this study (Table 3). These results are consistent with previous studies made at both the seedling and adult plant stages (4,5,37,46,58). The strong association found for the reactions elicited by all leaf rust races in pairwise comparisons suggests that the same gene or genes condition resistance to the different races (Table 4). In our study, the selected races of THBJ and PNMQ together possess virulence for

13 of the 16 *Lr* genes included in the leaf rust differential set, including *Lr9* (from *A. umbellulata*) and *Lr24* (from *T. ponticum*) (17). Thus, *A. sharonensis* accessions resistant to these races are potentially valuable sources of novel *Lr* genes for wheat improvement.

Leaf rust resistance in many *A. sharonensis* accessions was effective at both the seedling and adult plant stages. With respect to race THBJ, the frequency of resistance was higher at the adult plant stage than at the seedling stage. These results agree with previous reports (6,37,58), where relatively fewer accessions exhibited resistance to leaf rust at the seedling stage compared with the adult plant stage. Although the contingency table test (Table 4) suggested that no additional leaf rust resistance genes were acting at the adult stage, we cannot discount the possibility of such genes acting in some *A. sharonensis* accessions because adult plant *Lr* genes have been documented in the close relative *A. speltoides* (27). Genetic studies on the ontogenetic expression of leaf rust resistance are needed to clarify this question. The fact that high levels of resistance to leaf rust are expressed at the adult stage makes *A. sharonensis* a possible alternative source of resistance genes for wheat breeding in the northern Great Plains, where rust infections occur later in the growing season (mid-June to July). Seedling resistance also may be valuable in wheat lines of the Southern Great Plains, where early infections can occur when *P. triticina* survives the winter. However, the use of alien genes for wheat improvement is no guarantee of greater durability because the effectiveness of many resistance genes derived from diploid wild species has been short-lived (27). Although adult plant leaf rust resistance genes are preferred due to their greater durability, seedling resistance genes bred in combination with adult plant resistance can confer high levels of resistance in cultivated wheat (27) that may be long lived.

Although only three accessions from the Haifa Bay region were included in this investigation, another study that included 13 and 19 additional accessions from the Haifa Bay (Kishon and Na'aman) and northern Central Coastal Plain regions (Nasholim, HaBonim, and Newe Yam), respectively, was made, and only 1 accession was found to be resistant to leaf rust (P. Olivera and B. Steffenson, *unpublished*). This result is in agreement with Anikster et al. (5) and confirms the low frequency of leaf rust resistance in northern Israeli collection sites of *A. sharonensis*. However, the Lebanese accessions exhibited a percentage of resistance that was similar to that obtained for collections in the Central and Southern Coastal Plain regions, indicating that sources of resistance also may be present in the northernmost *A. sharonensis* populations.

The percentage of accessions with resistance to stem rust was lower than for leaf rust. Moreover, marked differences were observed in the percentage of accessions resistant to the different stem rust races (Table 3). The lack of association between the response to *P. graminis* f. sp. *tritici* races in pairwise comparisons at the seedling stage (Table 4) suggests the presence of more than one stem rust resistance gene in *A. sharonensis*. Other investigators have reported resistance to stem rust in *A. sharonensis* (19) and other *Aegilops* spp. (*A. speltoides, A. longissima, A. bicornis,* and *A. searsii*) belonging to the section Sitopsis (5,19). The presence of a variety of stem rust resistance genes appears to be a common feature in *Aegilops* spp. belonging to Sitopsis because several have been identified in *A. speltoides* (e.g., *Sr32* and *Sr39*) and transferred into cultivated wheat (17,55,56). Moreover, Gerechter-Amitai and Loegering (19) used 20 cultures of *P. graminis* f. sp. *tritici* and postulated 12 to 13 different *Sr* genes in 44 selected accessions of *A. sharonensis* and *A. longissima*. Although the percentage of resistance to race TTTT was higher at the adult stage than at the seedling stage, the χ^2 value obtained from the contingency table indicated a significant association in the reaction to this race at the two growth stages (Table 4). This indicates that the same gene or genes are acting at both growth stages. However, as discussed for leaf rust, we cannot discount the presence of adult plant resistance genes acting in some *A. sharonensis* accessions.

The percentage and level of resistance to *B. graminis* f. sp. *tritici* was the highest among all the diseases evaluated (Table 3). Similar results were reported by other investigators (21,46), albeit with a smaller collection of samples. Resistant accessions appear to be widely distributed in Israel. Although the percentage of accessions resistant to the two isolates was very similar, the χ^2 value (0.065) from the contingency table (Table 4) suggested that resistance to the isolates is conferred by different genes. This is not surprising given that the two pathogen isolates differed in their reaction for the resistance genes *Pm3a*, *Pm3b*, *Pm3f*, and *Pm9* of the powdery mildew differential set.

A lower frequency and level of resistance to *Pyrenophora tritici-repentis* was found in *A. sharonensis*, and different results were obtained with the two races evaluated (Table 3). Although no previous results have been reported regarding the resistance of *A. sharonensis* to tan spot, Zhang et al. (67) found resistance (IT < 2) only in *A. speltoides* and not in other species of the section Sitopsis, such as *A. longissima, A. bicornis*, and *A. searsii.* The differences in the ITs observed to the two races evaluated, along with the presence of both chlorotic and necrotic symptoms, suggest that *A. sharonensis* may carry genes for sensitivity to Ptr toxin A (race 1) and Ptr toxin B (race 5). The identification of new races of *P. tritici-repentis* (31) highlights the need to continue research in identifying additional sources of tan spot resistance for wheat, and *A. sharonensis* may be an important source of such resistance.

As was the case for *P. tritici-repentis*, marked differences were observed in *A. sharonensis* for the percentage of resistant accessions to races of *C. sativus*. Races 0 and 2 appear to exhibit differential virulence on wheat and barley based on preliminary studies (B. Steffenson, *unpublished*). Race 0 is avirulent on most barleys, but is virulent on some wheats. In contrast, race 2 is highly virulent on some two-rowed barley lines but is mostly avirulent on wheat. The *A. sharonensis* accessions tested in this study followed the same general pattern as wheat. Aldakha et al. (1) studied the inheritance of spot blotch resistance in wheat and found that resistance was controlled by one or two genes. Given the marked differences observed in the frequency of resistance and the ITs to the two races of *C. sativus*, resistance in *A. sharonensis* also may be conferred by a few genes with major effects.

Although resistance to *F. graminearum* has been reported in other *Aegilops* spp. (14,18), none of the accessions of *A. sharonensis* screened in this study were resistant to this pathogen. Only two accessions exhibited slower and restricted disease development (intermediate reaction), but these may not be of high value for introgression into cultivated wheat. In a preliminary study (45), five accessions exhibited a high level of type I and type II resistance during an initial screening test; however, repeat screening of progeny derived from these plants revealed that all individuals were susceptible. These results underscore the difficulties in screening germplasm for FHB resistance, and the need to reevaluate accessions before reaching conclusive results about the presence of resistance.

The highest percentage of highly resistant *A. sharonensis* accessions (ITs of 0; and 1) was found to the biotrophic pathogens of powdery mildew and the rusts. *A. sharonensis*, like other wild grasses, has coevolved in association with the cereal rusts and powdery mildew, being exposed to reciprocal selection pressure (62,63). This long-term process occurring in the center of diversity (i.e., the coastal plains of Israel) has resulted in the selection of host genotypes with different levels of resistance and pathogen isolates with a broad spectrum of virulence (54). *P. tritici-repentis* also is present in the Fertile Crescent region (59) and may have co-evolved with *A. sharonensis* in the coastal plains of Israel, resulting in the selection of genotypes with diverse resistance. Resistance to pathotype 0 of *C. sativus* and *F. graminea-*

rum was lacking in *A. sharonensis*. These two pathogens have not been reported on wheat or on any wild grass in Israel. Thus, one reason for the low percentage and level of resistance found may be due to a lack of co-evolution with the pathogens. It is interesting to note that although *A. sharonensis* has a similar geographic distribution to *A. longissima* (26) and shares some of the same population sites, the former species possesses at least some resistance to tan spot and spot blotch, whereas the latter species does not (57). However, resistance to both diseases was reported in *A. speltoides* (57), a species that is more widely distributed in the Middle East region, including northern Israel.

A. sharonensis, like other wild relatives, is a potential source of novel and unique genes for disease resistance in wheat. The transfer of such genes into wheat is not routine, but is possible. Cytogenetic methods such as wheat-alien amphiploid production (6) and development of wheat-alien addition, substitution and translocation lines may result in the successful introgression of resistance genes (17,20, 25,55). Antonov and Marais (6) and Marais et al. (39) introgressed into *T. aestivum* cv. Chinese Spring two genes for leaf rust and stripe rust resistance through direct hybridization and embryo rescue. These resistance genes are fully expressed in the hexaploid background and exhibited preferential transmission in the Chinese Spring background, perhaps due to the presence of a gametocidal gene (38,39). Gene introgression from *A. sharonensis* is a long and laborious process; therefore, it would be more efficient to use an accession that carries multiple disease resistance so that more than one useful resistance gene could be transferred to wheat. One of our objectives was to identify *A. sharonensis* accessions that carry a high level of resistance to all or most of the pathogens evaluated in this study. Four *A. sharonensis* accessions (591, 2172, 2173, and 1644) exhibited highly resistant reactions to most of the diseases evaluated in this study and would be ideal candidates for an introgression project with wheat. These multiple-resistant accessions were collected from three sites (Qiryat Ono, Palmahim, and Ashdod) located within an approximately 15-km radius, and were from two neighboring populations. Anikster et al. (5) suggested the use of geographically separated accessions to reduce the chances of transferring the same genes into wheat. Considering that these four accessions were collected from closely located sites, it certainly is possible that they may carry some of the same resistance genes. To determine whether any of these selected accessions carry the same gene or combination of genes, additional evaluations should be made with pathogen races that have different virulence spectra. With this additional information, one or two accessions could be selected for a gene introgression project. Selection of accessions for a wide crossing program involving *A. sharonensis* also should consider specific new and emerging disease threats to wheatlike stem rust race TTKS (48). The frequency of resistance to this race was high in *A. sharonensis*; thus, several accessions with potentially different resistance alleles could be used to enhance the diversity for race TTKS resistance in wheat.

In conjunction with the gene introgression effort with wheat, it also is important to elucidate the genetics of resistance within the diploid species itself. Investigations on the genetics of disease resistance in *A. sharonensis* are in progress. We have made crosses between *A. sharonensis* accessions resistant and susceptible to leaf rust, stem rust, and powdery mildew to determine the inheritance of resistance and to map the genes within this diploid species (P. Olivera and B. Steffenson, *unpublished*). The information generated from this study will be useful in gene introgression programs and for comparative mapping in the Triticeae.

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