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Resistance to Leaf Rust, Stripe Rust, and Stem Rust in *Aegilops* spp. in Israel

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ABSTRACT

Anikster, Y., Manisterski, J., Long, D. L., and Leonard, K. J. 2005. Resistance to leaf rust, stripe rust, and stem rust in *Aegilops* spp. in Israel. *Plant Dis.* 89:303-308.

In all, 1,323 single plant accessions of *Aegilops bicornis*, *A. kotschyi*, *A. longissima*, *A. ovata*, *A. searsii*, *A. sharonensis*, *A. speltoides*, and *A. variabilis* collected from 18 regions in Israel and 2 adjacent regions in Lebanon and Egypt were evaluated for leaf rust (*Puccinia triticina*) and stripe rust (*P. striiformis*) resistance in field plots and for seedling resistance to leaf rust and stem rust (*P. graminis* f. sp. *tritici*) in greenhouse tests. Nearly all accessions of *A. speltoides* were highly resistant to leaf rust, stripe rust, and stem rust. *A. longissima* and *A. ovata* were highly resistant to stripe rust, whereas *A. bicornis* and *A. kotschyi* were highly susceptible. *A. searsii* was highly susceptible to stem rust, but 24 to 51% of accessions of *A. bicornis*, *A. longissima*, *A. ovata*, and *A. variabilis* were resistant to stem rust. Except for *A. ovata* and *A. speltoides*, more than 95% of the *Aegilops* accessions were susceptible to leaf rust caused by *P. recondita* alternating on *Anchusa* spp. Only *Aegilops ovata* was susceptible to *P. recondita* from *Echium* spp. *A. bicornis*, *A. kotschyi*, and *A. searsii* were highly susceptible as seedlings to common wheat leaf rust caused by *P. triticina*. Most accessions of *A. variabilis* and about half of the accessions of *A. longissima* had good seedling resistance to *P. triticina*. Few accessions of *A. ovata* showed seedling resistance to the *P. triticina* population in Israel, but 30% were resistant to U.S. isolates. In field tests, *A. bicornis* showed high susceptibility to common wheat leaf rust, but more than 90% of the accessions of the other *Aegilops* spp. developed little or no leaf rust on adult plants. The *Aegilops* spp. in Israel and adjoining countries provide a rich and varied source of rust resistance for wheat breeding.

Additional keywords: wild wheat

Rusts are among the most important diseases of common bread wheat (*Triticum aestivum*) throughout most of the world's wheat-producing regions (24). The three widely distributed wheat rust fungi are *Puccinia graminis* f. sp. *tritici* (stem rust), *P. striiformis* (stripe rust), and *P. triticina* (leaf rust). In addition, a form of *P. recondita* found in Morocco and the Iberian Peninsula causes another leaf rust disease of durum wheat (*T. turgidum*). Other forms of *P. recondita* cause leaf rust on wild relatives of wheat in the genus *Aegilops* (2). Most rust resistance in wheat and other small grains is race specific and its effectiveness has been short-lived when used in predominant cultivars. The supply of rust resistance genes in known wheat cultivars and land races has been largely exhausted, but wild relatives of wheat are a rich and

relatively little-used source of additional resistance genes (7,14,22).

The use of wild relatives of crops as sources of disease resistance may be limited by low fertility in intercrossing with crop species and by difficulties in breaking unfavorable linkages between resistance genes and agronomically undesirable traits. Among species of *Aegilops*, those with S or D genomes are regarded as the most readily available sources for resistance to diseases and insects for transfer to wheat (7,12). Common bread wheat, a hexaploid, has three genomes, A, B, and D. The B genome is closely related to the S

genome of the *Sitopsis* group of *Aegilops* spp., which are considered an important part of the secondary gene pool for wheat (10,27). Interspecific hybrids within the *Sitopsis* group show full or nearly full chromosome pairing and are either fertile or semifertile (28).

The *Sitopsis* group of *Aegilops* spp. includes five diploid species: *A. speltoides*, which is thought to be the donor for the B genome in wheat, *A. bicornis*, *A. longissima*, *A. sharonensis*, and *A. searsii*. Wild populations of all five species occur naturally in Israel. Two closely related tetraploid species, *A. kotschyi* and *A. variabilis*, which also are found in Israel, contain the S and U genomes. Another tetraploid species in Israel, *A. ovata*, has the U and M genomes and has been found to hybridize occasionally with *A. variabilis* in nature (15). The objectives of this research were to sample wild populations of these eight species of *Aegilops* in Israel and to test the accessions as potential sources of new genes for resistance to leaf rust, stem rust, and stripe rust.

MATERIALS AND METHODS

Seed were collected from 1,323 single plants representing eight *Aegilops* spp. from natural populations at 83 sites in 18 regions of Israel as well as 1 region in southern Lebanon and 1 region in Egypt adjacent to Israel (Tables 1 and 2). Seed of single plant accessions were increased through two to five generations in screen houses and nurseries at Tel Aviv. All accessions are deposited in the Lieberman Germplasm Bank, Institute for Cereal Crops Improvement, Tel Aviv University. Accessions of *Aegilops* spp. were grown in a field nursery at Tel Aviv where they were

Table 1. Numbers of accessions (Acc.) of *Aegilops* spp. tested for rust resistance and source regions of collections in Israel and adjacent regions of Egypt and Lebanon

<i>Aegilops</i> sp. (genome) ^a	Greenhouse, Israel		Field, Israel		Greenhouse, Minnesota	
	Acc.	Regions	Acc.	Regions	Acc.	Regions
<i>A. bicornis</i> (S)	19	2	21	2	11	2
<i>A. kotschyi</i> (SU)	29	5	37	5	0	0
<i>A. longissima</i> (S)	476	5	502	5	379	5
<i>A. ovata</i> (UM)	125	8	98	8	91	7
<i>A. searsii</i> (S)	88	2	91	2	59	2
<i>A. sharonensis</i> (S)	257	3	230	3	0	0
<i>A. speltoides</i> (S)	194	5	200	5	181	4
<i>A. variabilis</i> (SU)	128	11	144	11	137	10

^a Species designated S are diploids in the *Sitopsis* group within the genus *Aegilops*; species with SU or UM genomes are tetraploid. The S genome is closely related to the B genome of cultivated wheat.

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inoculated with bulk collections of *P. striiformis* and *P. triticina* obtained from wild and cultivated wheat lines in Israel. Most accessions also were tested for seedling resistance to leaf rust or stem rust in greenhouses at Tel Aviv and at the United States Department of Agriculture–Agricultural Research Service, Cereal Disease Laboratory in St. Paul, MN.

Tel Aviv tests. Accessions of *Aegilops* spp. were planted in November in single 1-m rows in a field nursery at Tel Aviv. Spreader rows of a leaf rust-susceptible wheat cultivar were inoculated by spraying with a suspension of urediniospores of *P. triticina* and *P. striiformis* in light mineral oil (Soltrol 170) in February. Leaf rust inoculum consisted of a bulk uredinial population of *P. triticina* derived from aeciospores from leaves of *Thalictrum speciosissimum*. The basidiospores that infected the *T. speciosissimum* plants were produced by incubating the plants with germinating teliospores from collections of telia obtained from naturally infected cultivated and wild wheat plants at multiple locations throughout Israel. Stripe rust inoculum consisted of a bulk uredinial population of *P. striiformis* collected from cultivated and wild wheat plants at multiple locations in Israel. The accessions of *Aegilops* spp. in the nursery were evaluated twice for leaf rust and stripe rust severity and reaction type in late April and early May. General reaction types (i.e., S = susceptible, R = resistant, MR = moderately resistant, and so on) also were recorded for each accession.

In the greenhouse at Tel Aviv, 1,316 accessions of *Aegilops* spp. also were tested for seedling resistance to *P. triticina* and two forms of *P. recondita*. Inocula for these three forms of leaf rust consisted of uredinial populations of: (i) *P. triticina*

derived from aeciospores from *T. speciosissimum*, the alternate host for wheat leaf rust; (ii) the *A. longissima* form of *P. recondita* derived from aeciospores from *Anchusa aggregata*, the alternate host for leaf rust of *Aegilops longissima*; and (iii) the *A. ovata* form of *P. recondita* derived from aeciospores from *Echium glomeratum*, the alternate host for leaf rust of *A. ovata*. For each of the three leaf rusts, the aecial populations were obtained by exposing the alternate host to a collection of leaves of the appropriate host with abundant telia that had been pretreated to induce germination of the teliospores (1). Telial collections of *P. triticina* on cultivated wheat and telial collections of *P. recondita* on wild populations of *Aegilops* spp. were obtained from multiple locations throughout Israel. Thus, each aecial population was a representative sample of the virulence diversity within Israel.

For seedling tests with each form of leaf rust, four accessions were planted per pot with four seed per accession and grown in a temperature-controlled greenhouse at 20 ± 2°C. At 7 to 10 days after planting, the seedlings were inoculated with urediniospores of *P. triticina* or *P. recondita*. Seedlings were sprayed with a suspension of urediniospores in light mineral oil (Soltrol 170), the oil was allowed to evaporate, and the inoculated plants were incubated overnight in a dew chamber before being returned to the greenhouse. At 12 to 14 days after inoculation, the plants were scored for infection type (IT) on a standard 0-to-4 scale (17). ITs of 0 to 2 were considered resistant, ITs of 3 to 4 were considered susceptible, and ITs scored as 2,3 or 3,2 (i.e., with mixtures of IT2 and IT3 uredinia) were considered less than fully susceptible.

St. Paul tests. In St. Paul, 858 accessions of six of the eight *Aegilops* spp. were

tested for seedling resistance to leaf rust in three tests and for resistance to stem rust in two tests (Table 1). In the first two seedling tests for leaf rust resistance, plants were inoculated with single isolates of race TBBL and race SBDB of *P. triticina*, which were common in the United States. In the third leaf rust test, the seedlings were inoculated with a composite of 12 races (BBGL, CBGB, DBBG, KDBL, MFBL, MGBL, PBRG, PLMQ, PQRS, SBDJ, TBBL, and TLGG), all of which had been isolated from wheat fields in the United States. Virulence formulas for these races are derived as described in Long et al. (18). In the first seedling test for stem rust resistance, plants were inoculated with a single isolate of race TPMK of *P. graminis* f. sp. *tritici*, which had been the most common wheat stem rust race in the United States for many years. In the second stem rust test, the seedlings were inoculated with a composite of four common races: QCCJ, QFCS, RCRS, and TPMK.

In each test, seed of the accessions to be inoculated were grown in vermiculite in 8-cm² plastic pots with three to five seed each of four accessions planted in the corners of each pot. Glumes were removed from the seed before planting. The pots were arranged in trays holding six pots each, and the plants were grown in a rust-free greenhouse for 7 days before inoculation. The seedlings were fertilized at 5 and 8 days after planting with a water-soluble fertilizer (23-19-17, NPK) at 2.5 g/tray. On the seventh day after planting, the seedlings were inoculated by spraying them with a suspension of urediniospores in light mineral oil. The oil was allowed to evaporate for 30 min, and the inoculated seedlings were placed in a dew chamber overnight at 18°C. For stem rust, the dew chamber was programmed for fluorescent

Table 2. Regions from which accessions of *Aegilops* spp. were collected

Region	No. of sites with indicated <i>Aegilops</i> sp. ^a							
	bic	kot	lon	ova	sea	sha	spe	var
Southern Lebanon	2
Haifa Bay	1
Mt. Carmel	4	2	1
Upper Galilee	7	2
Eastern Upper Galilee	1	2
Golan Heights	1
Mt. Hermon	2
Plateau of Menashe	1
Valley of Esdraelon	1	...
Samaria	1	1	1
Coast of Carmel	12	2
Central Coastal Plain	13	1	...	9	...	7
Southern Coastal Plain	1	3	2	3
Southern Coastal Plain (Egypt)	3
Judean Desert	...	1	1
Judean Foothills	1
Judean Mts.	...	3	...	1	3	1
Negev Mts.	...	5	1
Northern Negev	7	1	2
Western Negev	...	5	2

^a *Aegilops* spp.: bic = *A. bicornis*, kot = *A. katschyi*, lon = *A. longissima*, ova = *A. ovata*, sea = *A. searsii*, sha = *A. sharonensis*, spe = *A. speltoides*, and var = *A. variabilis*.

lights to turn on for 3 to 4 h before the dew chamber was opened to allow the seedlings to dry slowly for 2 h while the temperature rose gradually to 25°C. When dry, the plants were returned to the greenhouse, where temperatures varied between 18 and 28°C daily. At 12 to 14 days after inoculation, the plants were scored for IT as described for greenhouse tests at Tel Aviv.

RESULTS

Accessions of *Aegilops* spp. were obtained from 18 different regions of Israel and from adjacent regions of Egypt and southern Lebanon. The most widely collected species was *A. variabilis* from 11 regions, and the most restricted species were *A. searsii* and *A. sharonensis* from 2 and 3 regions, respectively, and *A. bicornis* from the Southern Coastal Plain and Northern Negev of Israel and the adjacent region of Egypt (Table 2).

Field tests. In field trials, all accessions of *A. ovata* and *A. speltoides* remained largely free of stripe rust: no accessions of these species had greater than 5% severity of stripe rust (Table 3). Most accessions of *A. longissima* and *A. variabilis* had only 1 or 2% stripe rust severity, although a few accessions of each species had severities of as much as 30% or more. All accessions of *A. bicornis* and all but one accession of *A. kotschyi* had stripe rust severities of 20% or more. Accessions of *A. searsii* and *A. sharonensis* ranged from highly resistant to highly susceptible to stripe rust, with mean severity values in the intermediate range for the *Aegilops* spp. tested. Mean severities of leaf rust in field plots were low for all eight species, but only *A. kotschyi* had no susceptible accessions (Table 3). Of the 200 accessions of *A. speltoides*, 2 had leaf rust severity of 20 and 30%; the other 198 had only 1% severity. There was essentially no correlation between stripe rust and leaf rust severities on accessions of any of the *Aegilops* spp. tested in the field (Table 3).

For *A. bicornis*, *A. longissima*, *A. ovata*, *A. searsii*, *A. sharonensis*, and *A. spel-*

toides, accessions collected from different regions did not differ appreciably in mean stripe rust severity in the field tests. Accessions of *A. kotschyi* from four regions had mean stripe rust severity values from 40 to 58%, but the four accessions from the Judean Desert averaged 75% severity. Due to the small numbers of accessions of *A. kotschyi*, these differences were not statistically significant. Accessions of *A. variabilis* from Samaria and Upper Galilee averaged 1.0 and 1.1% severity, respectively, whereas mean stripe rust severity values for the other five regions ranged from 5 to 12%. Mean stripe rust severities for accessions from Samaria and Upper Galilee were significantly lower ($P < 0.05$, *t* test) than severities for accessions from the Central Coastal Plain, Golan Heights, or the Southern Coastal Plain.

Mean leaf rust severity values in field tests were similar among regions for accessions of *A. bicornis*, *A. kotschyi*, *A. searsii*, and *A. speltoides*. Accessions of *A. longissima* from the Central Coastal Plain were most resistant to leaf rust, with mean severity of 3.8%. Accessions from the Negev Mountains with mean severity of 23.4% were significantly ($P < 0.05$, *t* test) more susceptible than accessions from the other four regions. Severity values for the Northern Negev, Western Negev, and Southern Coastal Plain ranged from 6 to 12%. Accessions of *A. ovata* from all but two regions had low mean leaf rust severities (<7%). There was only one *A. ovata* accession each from the Central Coastal Plain and Samaria and each was susceptible, with severity values of 40 and 20%, respectively. The 6 accessions of *A. sharonensis* from the Haifa Bay region averaged 25.7% leaf rust severity, whereas the 183 accessions from the Central Coastal Plain averaged 2.3% and the 41 accessions from the Southern Coastal Plain averaged 2.1% leaf rust severity. Because there were only six accessions from the Haifa Bay region and because their severities ranged from 1 to 80%, the differences between

regions for *A. sharonensis* were not statistically significant. The five accessions of *A. variabilis* from the Plateau of Menashe averaged 16% leaf rust severity, which was significantly greater ($P < 0.05$, *t* test) than the mean severities for accessions from the six other regions. The 15 accessions from Upper Galilee averaged only 1.2%, which was significantly ($P < 0.05$, *t* test) less than the mean severities for accessions of *A. variabilis* from any other region. Four accessions of *A. variabilis* from Mt. Carmel, Eastern Upper Galilee, and the Judean Mountains also were all highly resistant (<2% severity). Accessions from the Central Coastal Plain, Golan Heights, Judean Foothills, Samaria, and Southern Coastal Plain averaged from 2.4 to 5.7% leaf rust severity.

Greenhouse seedling tests, Tel Aviv.

The population of *P. recondita* derived from *E. glomeratum* in Israel was virulent to 95% of the accessions of *A. ovata* but avirulent on all accessions of the other seven *Aegilops* spp. except for *A. variabilis*, in which 98% of the accessions were resistant and 2% had mixed susceptible and resistant reactions to the *Echium* population of *P. recondita* (Table 4). All or nearly all of the accessions of *A. bicornis*, *A. kotschyi*, *A. longissima*, *A. searsii*, *A. sharonensis*, and *A. variabilis* were susceptible to the population of *P. recondita* derived from *Anchusa aggregata*, which is not virulent to common wheat. All of the accessions of *Aegilops speltoides* and most accessions from *A. ovata* were resistant to *P. recondita* from *Anchusa* spp. (Table 4).

All eight *Aegilops* spp. had some accessions that were susceptible to the population of *P. triticina* derived from *T. speciosissimum* in Israel (Table 4). *Aegilops speltoides* was the most resistant, with only 1% of the accessions susceptible to *P. triticina*. *A. longissima*, *A. sharonensis*, and *A. variabilis* had good resistance with 25% or less the accessions showing full susceptibility as seedlings. *A. bicornis*, *A. kotschyi*, *A. ovata*, and *A. searsii* were

Table 3. Response of accessions (acc.) of *Aegilops* spp. to *Puccinia striiformis* and *P. triticina* in field plots at Tel Aviv^a

Species	No. of acc.	<i>P. striiformis</i>			<i>P. triticina</i>			Corr. ^d
		Res (%) ^b	Severity (%)		Res (%) ^b	Severity (%)		
			Mean ^c	Range		Mean ^c	Range	
<i>A. bicornis</i>	19	0	41.6 ± 4.2	20–80	0	4.3 ± 2.1	2–20	–0.055
<i>A. kotschyi</i>	37	3	48.2 ± 4.8	2–90	91	1.3 ± 0.7	0–2	nd
<i>A. longissima</i>	512	91	3.6 ± 2.5	1–30	97	7.1 ± 3.3	1–60	–0.053
<i>A. ovata</i>	142	99	1.1 ± 0.7	1–5	82	4.4 ± 2.6	1–40	nd
<i>A. searsii</i>	91	18	23.8 ± 3.5	1–40	91	5.7 ± 3.4	1–80	0.146
<i>A. sharonensis</i>	239	57	15.0 ± 4.2	1–80	96	2.9 ± 3.1	0–80	0.035
<i>A. speltoides</i>	200	100	1.0 ± 0.3	1–2	99	1.2 ± 1.6	1–30	nd
<i>A. variabilis</i>	144	77	6.3 ± 3.1	1–60	96	4.9 ± 2.3	1–20	–0.003

^a Field plots were inoculated with bulks of isolates of *P. striiformis* and *P. triticina* from cultivated and wild wheat plants collected throughout Israel.

^b Percentage of accessions with resistance ratings of very resistant, resistant, or moderately resistant based on size and appearance of uredinia. For *A. kotschyi*, 16 accessions were so severely infected by *P. striiformis* that no readings could be obtained for *P. triticina*; all but 2 of the remaining 21 accessions were rated resistant or moderately resistant to *P. triticina*.

^c Mean severity ± standard error.

^d Coefficients of correlation between severity ratings for *P. striiformis* and *P. triticina* on each accession; nd indicates that no correlation was calculated due to limited variation in severity ratings for one or both rusts.

mostly susceptible; fewer than 10% of the accessions of those species showed resistant or mixed reactions (Table 4).

In most cases, the proportions of accessions resistant or susceptible to *P. triticina* in the seedling stage did not differ greatly among regions from which the accessions were collected. With *A. longissima*, *A. sharonensis*, and *A. variabilis*, however, some regional differences were found. In *A. longissima*, greatest percentage of resistant accessions, $78 \pm 7\%$ (95% confidence interval), was found in the Negev Mountains and the least resistance, $14 \pm 19\%$, was found in the Southern Coastal Plain. Percentages of resistant accessions from other regions were Central Coastal Plain, $50 \pm 4\%$; Northern Negev, $58 \pm 9\%$; and Western Negev, $60 \pm 19\%$. With *A. sharonensis*, $67 \pm 5\%$ of the accessions from the Central Coastal Plain, $54 \pm 10\%$ from the Southern Coastal Plain, and $33 \pm 27\%$ from the Haifa Bay region were resistant. With *A. variabilis*, high levels of resistance were found in Upper Galilee (100%), the Judean Foothills ($86 \pm 19\%$), the Plateau of Menashe ($75 \pm 30\%$), and the Central Coastal Plain ($61 \pm 8\%$), whereas only $22 \pm 19\%$ of the accessions from the Golan Heights were resistant to *P. triticina*.

Greenhouse seedling tests, St. Paul. All of the accessions of *A. speltoides* tested as seedlings in St. Paul were resistant to races SBDB and TBBL and the composite inoculum of *P. triticina*, but all of the accessions of *A. bicornis* were susceptible (Table 5). Most accessions of *A. variabilis*

(74 to 88%) and some of the accessions of *A. longissima* (37 to 39%) and *A. ovata* (30 to 33%) also were resistant as seedlings to the U.S. isolates of *P. triticina*. Few accessions of *A. searsii* (5 to 6%) were resistant to race SBDB or the composite inoculum of *P. triticina*, but 18% were resistant to race TBBL (Table 5).

In *A. longissima*, the greatest resistance occurred in accessions from the Negev Mountains ($81 \pm 10\%$), whereas none of the accessions from the Southern Coastal Plain was resistant to either race or the composite inoculum. With *A. variabilis*, most of the accessions from Upper Galilee ($79 \pm 15\%$), the Judean Foothills ($75 \pm 30\%$), the Plateau of Menashe (100%), and the Central Coastal Plain ($83 \pm 6\%$) were resistant to the composite inoculum. Less

resistance occurred among accessions from the Golan Heights ($43 \pm 26\%$) and the Southern Coastal Plains ($65 \pm 15\%$). There were too few accessions from other regions for reliable comparisons. Proportions of accessions of *A. variabilis* resistant to races SBDB and TBBL generally were similar to those resistant to the composite inoculum, although a small percentage of accessions showed different reactions to the three inocula. Accessions of *A. kotschy* and *A. sharonensis* were not tested in St. Paul.

All of the accessions of *A. speltoides* were resistant to *P. graminis* f. sp. *tritici* as seedlings in greenhouse tests in St. Paul (Table 6). On the other hand, 95 to 96% of *A. searsii* accessions were susceptible. Accessions of *A. bicornis*, *A. longissima*,

Table 6. Seedling reactions of accessions of *Aegilops* spp. from Israel to North American isolates of *Puccinia graminis* f. sp. *tritici*^a

Host species	Race TPMK			Composite ^b		
	Res (%)	Mixed (%)	Susc (%)	Res (%)	Mixed (%)	Susc (%)
<i>A. bicornis</i>	50 ± 22	5	45	24 ± 18	24	52
<i>A. longissima</i>	34 ± 5	15	51	32 ± 5	21	48
<i>A. ovata</i>	44 ± 11	20	36	36 ± 19	12	52
<i>A. searsii</i>	5 ± 6	0	95	4 ± 5	0	96
<i>A. speltoides</i>	100	0	0	100	0	0
<i>A. variabilis</i>	51 ± 8	3	46	44 ± 15	40	16

^a Results of greenhouse tests in St. Paul, MN; 95% confidence intervals for percent resistant accessions were calculated by the normal approximation method (26); for values of 0 or 100%, no confidence interval can be determined. Res = resistant, Mixed = resistant and susceptible combined, Susc = susceptible.

^b Composite of four races of *P. graminis* f. sp. *tritici* collected in field surveys in the United States: QCCJ, QFCS, RCRS, and TPMK.

Table 4. Seedling reactions of accessions of *Aegilops* spp. from Israel to leaf rust fungi from three aecial hosts^a

Host species	<i>Thalictrum</i> ^b			<i>Anchusa</i> ^c			<i>Echium</i> ^c		
	Res (%)	Mixed (%)	Susc (%)	Res (%)	Mixed (%)	Susc (%)	Res (%)	Mixed (%)	Susc (%)
<i>A. bicornis</i>	5 ± 10	0	95	0	0	100	100	0	0
<i>A. kotschy</i>	7 ± 9	0	93	0	0	100	100	0	0
<i>A. longissima</i>	55 ± 4	29	16	1 ± 1	0	99	100	0	0
<i>A. ovata</i>	5 ± 4	3	92	82 ± 7	5	13	5 ± 4	0	95
<i>A. searsii</i>	2 ± 3	0	98	0	1	99	99 ± 2	1	0
<i>A. sharonensis</i>	64 ± 6	11	25	1 ± 1	2	97	100	0	0
<i>A. speltoides</i>	96 ± 3	3	1	100	0	0	100	0	0
<i>A. variabilis</i>	59 ± 8	20	20	0	0	100	98 ± 3	2	0

^a Results of greenhouse tests at Tel Aviv; 95% confidence intervals for percent resistant accessions were calculated by the normal approximation method (26); for values of 0 or 100%, no confidence interval can be determined. Res = resistant, Mixed = resistant and susceptible combined, Susc = susceptible.

^b Leaf rust caused by *Puccinia triticina*.

^c Leaf rust caused by *Puccinia recondita*.

Table 5. Seedling reactions of accessions of *Aegilops* spp. from Israel to North American isolates of *Puccinia triticina*^a

Host species	Race SBDB			Race TBBL			Composite ^b		
	Res (%)	Mixed (%)	Susc (%)	Res (%)	Mixed (%)	Susc (%)	Res (%)	Mixed (%)	Susc (%)
<i>A. bicornis</i>	0	0	100	0	0	100	0	0	100
<i>A. longissima</i>	39 ± 6	21	40	39 ± 5	18	43	37 ± 5	29	34
<i>A. ovata</i>	32 ± 10	7	61	33 ± 10	10	57	30 ± 10	25	45
<i>A. searsii</i>	5 ± 7	26	68	18 ± 10	11	71	6 ± 6	8	87
<i>A. speltoides</i>	100	0	0	100	0	0	100	0	0
<i>A. variabilis</i>	88 ± 6	2	10	79 ± 7	7	14	74 ± 7	5	21

^a Results of greenhouse tests in St. Paul, MN; 95% confidence intervals for percent resistant accessions were calculated by the normal approximation method (26); for values of 0 or 100%, no confidence interval can be determined. Res = resistant, Mixed = resistant and susceptible combined, Susc = susceptible.

^b Composite of 12 races of *P. triticina* collected in field surveys in the United States: BBGL, CBGB, DBBG, KDBL, MFBL, MGBL, PBRG, PLMQ, PQRS, SDBJ, TBBL, and TLGG.

A. ovata, and *A. variabilis* were nearly equally divided between resistant and susceptible, although many accessions exhibited mixed ITs to race TPMK or the composite inoculum of *P. graminis* f. sp. *tritici* (Table 6). Accessions of *A. kotschyi* and *A. sharonensis* were not tested for stem rust resistance. No clear regional differences in proportions of accessions resistant to stem rust were seen for *A. biornis*, *A. ovata*, *A. searsii*, or *A. speltooides*. With *A. longissima*, no resistant accession was found from the Negev Mountains, Northern Negev, Western Negev, or the Southern Coastal Plain, but $51 \pm 5\%$ of the accessions from the Central Coastal Plain were resistant to race TPMK and $49 \pm 4\%$ were resistant to the composite inoculum of *P. graminis* f. sp. *tritici*. With *A. variabilis*, $74 \pm 14\%$ of the accessions from the Southern Coastal Plain, $50 \pm 8\%$ from the Central Coastal Plain, and $13 \pm 16\%$ from the Golan Heights were resistant to race TPMK of *P. graminis* f. sp. *tritici*. Accessions from regions other than the Central Coastal Plain were not tested against the composite inoculum; $44 \pm 10\%$ of the accessions from the Central Coastal Plain were resistant to the composite.

DISCUSSION

The *Aegilops* spp. evaluated in this research compose a rich and varied source of potential new genes for rust resistance genes for wheat breeding (16). Hundreds of accessions were identified with resistance to leaf rust, stripe rust, or stem rust. Collection information and rust reaction data for all of the accessions are available on request from the Lieberman Germplasm Bank at the Institute for Cereal Crops Improvement, Tel Aviv University. Seed of selected accessions also may be obtained from the Lieberman Germplasm Bank.

Among the five *Aegilops* spp. in the *Sitopsis* group, which have the S genome, there was a wide range of susceptibility to the rust diseases. Nearly all accessions of *A. speltooides* were resistant to leaf rust and stripe rust in field tests and to leaf rust and stem rust in seedling tests in the greenhouse. *A. longissima* and *A. sharonensis* also appear to be good sources of rust resistance, although *A. sharonensis* was not tested for stem rust resistance. In contrast, nearly all accessions of *A. bicornis* were susceptible to leaf rust and stripe rust, and nearly all accessions of *A. searsii* were susceptible to leaf rust and stem rust in seedling tests. Most accessions of *A. searsii*, however, appeared to have good adult plant resistance to leaf rust and stripe rust, but *A. bicornis* accessions were susceptible to both rusts. All of the *Aegilops* spp. tested except *A. searsii* had moderate to high proportions of accessions that were resistant to stem rust in seedling tests. These results are consistent with earlier, less extensive studies in Israel (11,19,23) and generally also are consistent with stud-

ies of the same *Aegilops* spp. from other countries (4,6,12,22,25). One exception was the apparent high level of resistance in *A. bicornis* accessions to leaf rust in field tests in India (4). Also, Salazar and Branas (25) reported that the *A. bicornis* accessions that they tested were resistant to stem rust in Portugal.

The high level of resistance of *A. speltooides* to leaf rusts in Israel is especially interesting. *Anchusa* and *Echium* spp., the alternate hosts for *P. recondita*, are native to Israel; therefore, it is logical to assume a long history of coevolution between *P. recondita* and *Aegilops bicornis*, *A. longissima*, *A. searsii*, and *A. sharonensis*, all of which have limited distributions centered in Israel or, in the case of *A. bicornis*, extending from the Israeli Negev west along the coastal sandy steppe of North Africa. The distribution of *A. speltooides*, on the other hand, includes much of the Near East and Anatolia with its southernmost populations in Israel, where *A. speltooides* is relatively rare and found mainly on the alluvial soils of the coastal belt and Mt. Carmel (28). *Thalictrum* spp., the alternate host of *P. triticea*, do not occur in Israel. It may be a result of this that relatively few accessions of *A. longissima* or *A. sharonensis* and almost none of *A. speltooides* were susceptible to isolates of *P. triticea* from wheat. It seems odd, however, that a rare forma specialis of *P. triticea* that is virulent to *A. speltooides* but avirulent to cultivated wheat was discovered in Israel and is unknown elsewhere (3).

Among the three tetraploid species evaluated, *A. kotschyi* appeared to have good adult plant resistance but little seedling resistance to leaf rust. Most accessions of *A. variabilis* were resistant to leaf rust and stripe rust, and about half were resistant to stem rust. *A. ovata*, which is more distantly related to common wheat than the other *Aegilops* spp. tested, also may be a good source of resistance to stripe rust, stem rust and, perhaps, to U.S. races of leaf rust.

It is interesting that *A. longissima*, *A. sharonensis*, and *A. variabilis*, which had high proportions of accessions with seedling resistance to leaf rust caused by *P. triticea*, showed little or no resistance to the endemic leaf rust caused by *P. recondita* (aecial host *Anchusa* spp.) in Israel. *Aegilops ovata* was largely resistant to *P. recondita* from *Anchusa* spp. but susceptible to its leaf rust caused by *P. recondita* (aecial host *Echium* spp.) as well as to *P. triticea*. Apparently, natural selection in Israel has resulted in an accumulation of virulence genes in *P. recondita* (aecial host *Anchusa* spp.) to match the resistance genes in *A. longissima*, *A. sharonensis*, and *A. variabilis*, whereas natural selection in *P. recondita* (aecial host *Echium* spp.) resulted in accumulation of virulence genes to match the resistance genes in *A. ovata* but not those in other *Aegilops* spp.

Nearly all accessions of *A. speltooides* were resistant to both forms of *P. recondita* as well as to races of *P. triticea* commonly found on wheat.

Even though nearly all accessions of *A. speltooides* were highly resistant to *P. triticea*, *A. speltooides* has an underlying compatibility to wheat leaf rust, as shown by the one accession with full susceptibility in seedling tests at Tel Aviv and the two accessions that developed severe leaf rust infection as adult plants in field tests. This underlying compatibility also is evidenced by the discovery of a new form of *P. triticea* in Israel that is virulent on most accessions of *A. speltooides*, *A. bicornis*, *A. longissima*, *A. searsii*, and *A. sharonensis* but avirulent to bread wheat cultivars (3). Apparently, the high level of resistance to wheat leaf rust in *A. speltooides* is due to a variety of major genes for hypersensitive, race-specific resistance for which the corresponding virulence alleles are largely absent in populations of *P. triticea* on common wheat in Israel and the United States. Five known leaf rust resistance genes, *Lr28*, *Lr35*, *Lr36*, *Lr47*, and *Lr51*, have been transferred to bread wheat from *A. speltooides* (9,14,20,21). In addition, uncharacterized leaf rust resistance genes have been transferred to wheat from four other accessions of *A. speltooides* (8,20). Thus, it appears likely that numerous additional genes for leaf rust resistance for use in wheat breeding could be found in accessions of *A. speltooides* described in this research.

In transferring genes for rust resistance from wild species to cultivated species, the goal is to maximize the chances that the new resistance genes will be unique as well as highly effective against known rust races. With no known rust races with specific virulence to distinguish between new resistance genes, laborious genetic tests will be necessary to confirm that the new resistance genes really are different from previously isolated resistance genes that are also effective against all known rust races. To reduce the chances of repeatedly transferring the same genes from *Aegilops* spp. to common wheat, it will be useful to choose donor accessions from several different *Aegilops* spp. as well as from geographically separated collections within species. Our results provide some guidance for selection of sites and *Aegilops* spp. from which to select accessions for crosses for gene transfer to wheat.

There were no obvious associations between elevation and yearly rainfall for individual collection sites and the proportion of resistant accessions of *Aegilops* spp. obtained per site. Accessions of *A. kotschyi* from the Judean Desert were more susceptible to stripe rust than accessions from other regions of Israel, including those from the Negev, which has even less rainfall than the Judean Desert. The proportion of accessions of *A. longissima*

from the Negev Mountains with seedling resistance to leaf rust in both the Tel Aviv and St. Paul greenhouse tests was greater than that from other regions with greater rainfall, but accessions from the Negev Mountains developed more severe leaf rust than accessions from any other region as adult plants in field plots. Conversely, accessions of *A. variabilis* from the Menashe Plateau (with greater rainfall) were more susceptible to leaf rust as adult plants in field tests than accessions from the Southern Coastal Plain (with less rainfall), but accessions from the Menashe Plateau were less susceptible to leaf rust as seedlings in the greenhouse. Accessions of *A. sharonensis* from the Haifa Bay region were more susceptible to leaf rust than accessions from the Central or Southern Coastal Plain, as both seedlings in the greenhouse and adult plants in field tests. The average annual rainfall of sites in the Southern Coastal Plain was less than that in the Haifa Bay site, but annual rainfall in the Central Coastal Plain sites was nearly the same as at Haifa Bay. There were few interregional differences in proportions of accessions of *Aegilops* spp. resistant to stem rust, but accessions of *A. variabilis* from the Golan Heights (greatest annual rainfall) were considerably more susceptible than accessions from other regions of Israel. It seems likely that long-term stand density of *Aegilops* populations may be a more critical determinant of local epidemic development of rust diseases than differences in temperature or rainfall from region to region in Israel. This could lead to evolution of greater rust resistance in sites where each species of *Aegilops* is best adapted and where their populations have been allowed to reach their greatest density.

Each of the *Aegilops* spp. evaluated in this study can serve as a donor for rust resistance genes for wheat breeding. For example, leaf rust and stripe rust resistance have been transferred to common wheat, *Triticum aestivum*, from *A. ovata*, a species that does not share a common genome with common wheat (5). Ittu et al. (13) reported the transfer of a gene for leaf rust resistance from the tetraploid species *A. variabilis* to common winter wheat. Among the five species in the *Sitopsis* group, only *A. speltoides* has been used as a source of leaf rust and stem rust resistance in current wheat cultivars (20). However, the powdery mildew resistance gene *Pm13* was transferred to common wheat

from *A. longissima* (10). Our results suggest that *A. longissima* and *A. sharonensis* also could be rich sources of genes for resistance to leaf rust and stripe rust. Zhang et al. (27) showed that there is a high degree of conserved colinearity in chromosomes of the S genomes of *A. longissima* and *A. sharonensis* and the D genome of common wheat. Thus, transfer of resistance from these species should not be much more difficult than transferring resistance genes from *A. speltoides* to common wheat.

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