Diversity and Sources of Multiple Disease Resistance in *Hordeum spontaneum*

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ABSTRACT

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Hordeum spontaneum, the progenitor of cultivated barley, is known to be a rich source of disease resistance genes. The objective of this study was to assess the diversity of *H. spontaneum* accessions from Israel and Jordan for their reaction to six fungal pathogens of importance to cultivated barley in the United States and Canada. Overall, a high level of macro-scale (across collection sites) and micro-scale (within a collection site) diversity for disease reaction was found in the 116 accessions of *H. spontaneum* evaluated at the seedling stage. Additionally, genetic heterozygosity for resistance loci was common in *H. spontaneum*. The frequency of resistance in accessions from Jordan and Israel was high for Septoria speckled leaf blotch (77 and 98%, respectively), leaf rust (70 and 90%), net blotch (72 and 68%), and powdery mildew (58 and 70%); intermediate for spot blotch (53 and 46%); and low for stem rust (2 and 26%). The level of disease resistance in *H. spontaneum* was not strongly correlated with any of the weather variables (temperature, precipitation, and humidity) monitored near the collection sites. However, in general, resistance was more often found in germ plasm from mesic (e.g., Mediterranean coast) than in xeric (e.g., Negev Desert) areas. Two *H. spontaneum* accessions (Shechem 12-32 and Damon 11-11) were resistant to all six pathogens and may be useful parents in programs breeding barley for multiple disease resistance. The high level of diversity and heterozygosity for disease reaction found in this study indicates that *H. spontaneum* is an extraordinarily rich and largely untapped source of unique disease resistance alleles for cultivated barley improvement.

Additional keywords: *Hordeum vulgare*, wild barley

The Upper Midwest region of the United States and the central provinces of Canada comprise one of the largest barley (*Hordeum vulgare* L.) growing regions in North America. Diseases that commonly impact barley production in this region include stem rust (caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn.), net blotch (caused by *Pyrenophora teres* Drechs. f. *teres* Smedeg. [anamorph: *Drechslera teres* f. *teres* (Sacc.) Shoem.]), spot blotch (caused by *Cochliobolus sativus* (Ito & Kurib.) Drechs. ex Dastur [anamorph: *Bipolaris sorokiniana* (Sacc.) Shoem.]), Septoria speckled leaf blotch (SSLB) (caused by *Septoria passerinii* Sacc.), and to a lesser degree leaf rust (caused by *Puccinia hordei* G. Oth.) and powdery mildew (caused by *Blumeria* [=*Erysiphe*] *graminis* (DC.) E.O. Speer f.

sp. *hordei* Ém. Marchal) (39,41). The deployment of host resistance is often the preferred method of control for these diseases because it is an effective, economical, and environmentally sound strategy.

Although sources of resistance to these diseases have been identified in *H. vulgare*, they do not represent the greatest potential diversity available for breeding purposes. An alternative and rich source of genetic diversity for disease resistance is the wild barley species *H. spontaneum* (syn. *H. vulgare* L. subsp. *spontaneum* (C. Koch) Thell.). *H. spontaneum* is native to the Fertile Crescent (32,50), a large region extending from Israel and western Jordan to southeastern Turkey and arcing down through eastern Iraq and western Iran (12). In this region, the host and its pathogens have co-evolved over thousands of years (3), resulting in a high degree of diversity for both resistance in the host and virulence in the pathogen. Indeed, previous investigators have identified numerous sources of resistance in *H. spontaneum* to powdery mildew (11,15,31), leaf rust (17,27), net blotch (14,22,38), SSLB (22,28,45), and leaf scald (1).

The center of origin for wild progenitor species is often the place where the greatest genetic diversity may be found. With respect to *H. spontaneum*, the region of the Fertile Crescent bounded by Israel and

Jordan may contain the greatest genetic diversity for the species (4,32). Disease resistance is common in *H. spontaneum*; thus, it may be possible to identify individual accessions with resistance to all of the important diseases in the Upper Midwest region of the United States and central provinces of Canada. These accessions could then be crossed with advanced barley breeding lines to simultaneously transfer genes for multiple disease resistance and also increase allelic diversity. Thus, the objective of this study was to assess the diversity of *H. spontaneum* accessions from Israel (including Palestinian authority lands of the West Bank and the Gaza Strip) and Jordan for their reaction to six fungal pathogens and to identify sources of multiple disease resistance. A preliminary report of this research has been published (10).

MATERIALS AND METHODS

Plant materials. One hundred and sixteen *H. spontaneum* accessions from the Institute of Evolution, University of Haifa, Israel, were evaluated for resistance to six foliar pathogens in the greenhouse. Each accession was derived from a single plant and was arbitrarily selected from 57 collection sites in Israel and Jordan (Fig. 1). The accessions at each site were collected no closer than 1 m apart along a transect of 25 to 200 m. Collection sites were ecogeographically diverse and varied greatly with respect to humidity (34 to 65% mean annual relative humidity (RH) at 1400 hours), precipitation (71 to 1,600 mm annually), temperature (1 to 16°C and 20 to 33°C mean annual temperature for January and August, respectively), and elevation (–350 to 1,530 m below/above sea level) (Tables 1 and 2). Standard susceptible and resistant checks and differential host lines (if available) also were included in the experiments to verify the infection type (IT)/infection response (IR) and virulence pattern, respectively, to each pathogen (8,18,21,40,45,52).

Pathogen isolates. Information on the isolate designation, source, and pathotype (if known) of each fungal pathogen used is given in Table 3. All pathogen isolates were collected from infected barley plants in the field with the exception of the *B. graminis* f. sp. *hordei* isolate, which was taken from an infected plant in the greenhouse. Pathogens were stored as dried urediniospores at –80°C (rusts) or as conidiospores using a silica gel method (9), with the exception of the *B. graminis* f. sp.

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Fig. 1. Geographic location of sampling sites of *Hordeum spontaneum* in Israel and Jordan.

hordei isolate, which was from fresh plants. The pathogen isolates used represent common virulence spectra found in the Upper Midwest region of the United States. Two pathotypes of the stem rust pathogen were used in this study to more fully characterize the resistance spectra present in *H. spontaneum*. Pathotype QCCJ possesses virulence for the barley stem rust resistance gene *Rpg1* and avirulence for *rpg4*, while pathotype MCCF possesses avirulence for both *Rpg1* and *rpg4* (18).

Inoculation protocols. For each disease evaluation, five seeds of each *H. spontaneum* accession were planted either in plastic pots (10 cm square) or in cones (3.8 cm diameter and 21 cm depth) filled with a peat moss:perlite (3:1 ratio) potting mixture. Fertilizer was applied at planting with water-soluble (15-0-15, N-P-K) and controlled release (14-14-14, N-P-K) formulations. Plants were grown in a greenhouse at $22 \pm 3^\circ\text{C}$ with a 13-h photoperiod provided by sunlight and metal halide bulbs (530 to $710 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). For leaf and stem rust evaluations, 7-day-old seedlings (primary leaf fully expanded) were inoculated with heat-shocked urediniospores suspended in a lightweight mineral oil (4 mg of spores in 0.7 ml of oil per 100 plants). Plants were then placed in mist (generated by ultrasonic humidifiers) chambers and incubated

Table 1. Ecogeographical data for collection sites of *Hordeum spontaneum* from Israel^a

Location	Longitude	Latitude	Altitude ^c	Mean temperature ^b		Annual rainfall ^d	Mean humidity ^e
				Jan.	Aug.		
1. Mt. Hermon	35.45	33.17	1,530	1	20	1,600	52
3. Afik	35.42	32.47	325	11	27	450	41
4. Tel Hay	35.33	33.14	400	8	25	769	50
5. Rosh Pinna	35.31	32.57	700	9	25	697	48
6. Gadot	35.37	33.01	100	11	28	500	45
7. Tabigha	35.32	32.52	0	15	32	436	45
8. Zefat	35.30	32.56	800	8	24	718	48
9. Mt. Meron	35.24	33.00	1,150	6	22	1,010	49
10. Maalot	35.16	33.00	500	8	23	785	50
11. Damon	35.00	32.44	425	11	24	686	59
12. Shechem	35.14	32.14	400	9	24	618	46
13. Bar Giyyora	35.05	31.43	760	10	26	537	49
14. Talpiyyot	35.14	31.45	800	9	24	486	50
15. Eyzariya	35.16	31.46	600	10	26	380	48
16. Tel Shoket	34.55	31.19	375	11	26	280	45
17. Bor Mashash	34.50	31.04	350	10	27	150	38
18. Revivum	34.45	31.01	320	10	27	130	38
19. Yeroham	34.54	30.59	490	10	26	130	35
20. Sede Boqer	34.47	30.52	450	9	26	91	36
21. Bet Shean	35.30	32.30	-120	13	30	300	40
22. Mehola	35.29	32.24	-150	13	30	270	34
23. Wadi Qilt	35.23	31.50	50	14	30	170	40
24. Akhziv	35.06	33.03	10	12	26	620	60
25. Atlit	34.57	32.42	50	13	26	500	65
26. Caesarea	34.54	32.30	10	13	26	539	65
27. Herzliyya	34.48	32.10	25	13	26	530	65
28. Ashqelon	34.36	31.38	50	14	27	424	64
31. Machtesh Gadol	34.58	30.58	600	9	26	170	35
32. Ein Zukim	35.26	31.44	-200	15	31	210	35
33. Avedat	34.46	30.49	525	9	25	168	36

^a Meteorological data provided is from Nevo et al. 1984 (34).

^b Mean temperature is the average temperature ($^\circ\text{C}$) for January and August.

^c Altitude is in meters above or below mean sea level.

^d Annual rainfall is in mm of precipitation.

^e Mean humidity is the average relative humidity at 1400 h on an annual basis.

at 20°C for 16 h in the dark at near 100% RH. After the mist period, leaf rust inoculated plants were allowed to slowly dry for at least 3 h before being placed in a growth chamber at 19 to 20°C. Stem rust inoculated plants were exposed to light (120 to 160 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a temperature ramp increasing from 20 to 24°C) after the mist period and allowed to slowly dry for at least 3 h before being placed into one of two growth chamber environments (19 to 20°C or 27 to 28°C). The two incubation environments were used because some stem rust resistance genes are known to be temperature sensitive (18). For net and spot blotch evaluations, inoculum was produced on agar plates seeded with silica gel crystals containing adsorbed conidia. Seedlings were inoculated (5 to 6×10^4 conidia per ml of H_2O , 1.7×10^{-1} ml per plant) when the third leaf was fully expanded. Plants were placed in mist chambers overnight at 20°C and then incubated in a greenhouse at $22 \pm 3^\circ\text{C}$. For powdery mildew evalua-

tions, seedlings were inoculated at the primary leaf stage by shaking mildew-infected plants (previously infected with a single pustule isolate) over the *H. spontaneum* accessions and then incubating at ambient greenhouse temperature ($23 \pm 2^\circ\text{C}$) (41). For SSLB evaluations, accessions were inoculated (5×10^5 pycnidiospores per ml of H_2O , 5.0×10^{-1} ml per plant) when the second leaf was fully expanded and then subjected to a 72-h mist period at 21°C/dark and 25°C/light (45). The first 40 h were in darkness, followed by a photoperiod of 5 h for the remainder of the mist period. Plants were then incubated in a greenhouse at $22 \pm 3^\circ\text{C}$. All experiments were repeated once.

Disease assessment. Disease reactions were assessed after specific incubation periods using published assessment guides for each respective pathogen. Leaf and stem rust reactions were rated 10 to 13 days postinoculation using scales modified from Levine and Cherewick (24) and

Miller and Lambert (29), respectively. Powdery mildew was rated 9 to 10 days postinoculation using the 0 to 4 scale of Torp et al. (44). Net and spot blotch reactions were rated 10 to 12 days postinoculation using the 1 to 9 scales of Tekauz (43) and Fetch and Steffenson (9), respectively. SSLB was rated 17 to 18 days postinoculation using a 0 to 5 scale (45). For the rusts, powdery mildew, and SSLB, ITs/IRs of 0 or 1 were considered indicative of resistance, 2 of intermediate resistance, and 3 or higher of susceptibility. For net and spot blotch, IRs of 1 to 3 were considered indicative of resistance, 4 to 5 of intermediate resistance, and 6 to 9 of susceptibility.

Statistical analyses. Phenotypic diversity for disease reaction in *H. spontaneum* was estimated using the Shannon information index, where $h_{sj} = -\sum p_i \ln(p_i)$, with maximum $h_{sj} = 1.099$ (16). For this analysis, the ITs/IRs for each disease were separated into the general reaction classes of resistant, intermediate, and susceptible as

Table 2. Ecogeographical data for collection sites of *Hordeum spontaneum* from Jordan^a

	Location	Longitude	Latitude	Altitude ^c	Mean temperature ^b		Annual rainfall ^d	Mean humidity ^e
					Jan.	Aug.		
1.	Shūna, N.	35.37	32.38	-200	13	29	300	52
2.	Irbid	35.51	32.33	425	9	25	300	53
3.	Irbid, E.	35.59	32.32	340	9	25	250	53
4.	Mafrāq, W.	36.09	32.24	625	8	24	100	56
5.	Mafrāq	36.11	32.14	745	7	24	100	56
6.	Zarqa	36.22	32.03	511	9	26	142	52
7.	Amman	35.57	31.57	750	8	25	300	49
8.	Madaba	35.48	31.43	785	8	24	358	55
9.	Mt. Nebo	35.44	31.45	755	8	24	350	55
10.	Wadi Wala	35.47	31.33	450	10	26	200	51
11.	Wadi Mūjib	35.48	31.27	138	10	26	266	52
12.	Talal	35.49	31.26	145	10	24	145	60
13.	Karak	35.42	31.11	1,000	8	24	258	53
14.	Wadi Hasa	35.44	30.58	900	7	23	250	51
15.	Laban	35.58	30.55	825	8	25	250	51
16.	Tafila	35.36	30.50	1,000	7	23	250	49
17.	Danā	35.36	30.39	1,273	7	24	300	49
18.	Wadi Mūsā	35.29	30.19	1,100	4	20	229	54
19.	Safī	35.27	31.03	-350	16	33	71	47
20.	Shūna, S.	35.38	31.54	-230	15	32	<100	49
21.	‘Ira	35.40	32.00	650	8	25	400	54
22.	Salt	35.43	32.02	850	6	22	500	57
23.	Jarash	35.54	32.16	585	6	22	500	60
24.	Sakib	35.47	32.16	1,000	6	23	500	58
25.	Ajlun	35.45	32.20	1,150	6	23	600	61
26.	Irbid, S.	35.51	32.27	785	9	25	400	58
27.	El Hamma	35.41	32.42	-75	13	30	377	60

^a Meteorological data provided courtesy of Faisal Nimer.

^b Mean temperature is the average temperature ($^\circ\text{C}$) for January and August.

^c Altitude is in meters above or below mean sea level.

^d Annual rainfall is in mm of precipitation.

^e Mean humidity is the average relative humidity at 1400 h on an annual basis.

Table 3. Isolate designation, source, and pathotype of fungal pathogens used to evaluate resistance in *Hordeum spontaneum*

Pathogen	Isolate	Source	Pathotype	Citation for pathotype name
<i>Puccinia graminis</i> f. sp. <i>tritici</i>	A-1	J. Miller	MCCF	Roelfs and Martens, 1988 (37)
<i>Puccinia graminis</i> f. sp. <i>tritici</i>	QCC-2	J. Miller	QCCJ	Roelfs and Martens, 1988 (37)
<i>Pyrenophora teres</i> f. <i>teres</i>	ND89-19	B. Steffenson	1-2-6-7-10-13-16-18-25	Steffenson and Webster, 1992 (42); Wu et al., 2003 (52)
<i>Cochliobolus sativus</i>	ND85F	B. Steffenson	1	Valjavec and Steffenson, 1997 (47)
<i>Septoria passerinii</i>	ND97-15	B. Steffenson	Not established	Not established
<i>Blumeria graminis</i> f. sp. <i>hordei</i>	ND99-1	B. Steffenson	2.0.0.0.5.5.0.6	Limpert and Muller, 1994 (25)
<i>Puccinia hordei</i>	ND8702	Y. Jin	MCJ	Long et al., 1995 (26)

previously described. Shannon's information index (h_{sj}) was determined based on the frequency (p_i) of each class. Chi-square values were calculated using contingency tables (2×3) to estimate the homogeneity between populations derived from Israel and Jordan for each disease. Pearson correlation coefficients (PROC CORR, SAS version 8, SAS Institute, Cary, NC) were used to assess the relationship between the average infection response (IR/IT) of each accession and the environmental parameters (i.e., those most likely to affect disease pressure) at each *H. spontaneum* collection site. For net and spot blotch, the actual IR was used for correlation, while for the other diseases the IR/IT was adjusted from a 0 to 4 scale to a 1 to 5 scale (by adding 1) for statistical purposes.

RESULTS

The reactions of control and differential lines were consistent with previously published results (8,18,21,40,45,52). Accessions of *H. spontaneum* exhibited similar, but not identical ITs/IRs in the two experiments. The most common ITs/IRs observed on *H. spontaneum* across the two experiments are presented in Tables 4 and 5.

The highest frequency of disease resistance found in *H. spontaneum* was to *S. passerinii*. Over 98% of accessions from Israel (Table 4; all but Eyzariya 15-29) and 77% of accessions from Jordan (Table 5) exhibited IRs of 0 to 2 to *S. passerinii*. Most accessions (83% from Israel and 57% from Jordan) exhibited an IR of 0, indicating a very high level of resistance. Resistant and susceptible accessions were found within individual collection sites in both Israel (Eyzariya) and Jordan (N. Shūna, Wadi Mūjib, Talal, Karak, Laban, Tafila, S. Shūna, and Jarash). This indicates that micro-scale diversity exists for *S. passerinii* reaction at some locations.

Accessions of *H. spontaneum* with resistance (ITs of 0 to 2) to powdery mildew and leaf rust also were very common in both Israel (Table 4; 70 and 90%, respectively) and Jordan (Table 5; 58 and 70%, respectively). Highly resistant (IR of 0 or IT of 0; accessions comprised 41 and 44% of the total from Israel and 36 and 13% of the total from Jordan for the two respective diseases. Resistant and susceptible accessions were found at a number of collection sites in both Israel (Gadot, Shechem, Bar Giyyora, Eyzariya, Tel Shoket, Bor Mashash, Yeroham, Wadi Qilt, Ein-Zukim, and Avedat) and Jordan (Irbid, East Irbid, West Mafraq, Amman, Madaba, Mt. Nebo, Wadi Mūjib, Talal, Laban, Tafila, Wadi Mūsa, Safi, South Shūna, Salt, Sakib, and S. Irbid), indicating micro-scale diversity for reaction to the two diseases. Plants resistant and susceptible to powdery mildew were found within several accessions from Israel (Gadot 6-35, Eyzariya 15-29, and Ein-zukim 32-05). The same was true

for leaf rust with accessions Yeroham 19-32, Sede Boqer 20-22, and Machtesh 31-13. This result suggests heterozygosity for powdery mildew and leaf rust resistance loci in these single plant-derived accessions.

Resistance to net blotch also was frequent in *H. spontaneum*, as about 70% of accessions from both Israel (Table 4) and Jordan (Table 5) exhibited IRs of 1 to 5. Approximately one-third of the accessions from both countries were highly resistant (IRs of 1 to 2). Resistant and susceptible accessions were found at 11 of the 30 collection sites in Israel and 15 of the 27 collection sites in Jordan. This indicates that micro-scale diversity for net blotch reaction exists across a number of locations in both countries, especially Jordan. Resistant and susceptible plants were detected within three accessions (Laban 15-09, Danā 17-48, and Ajlun 25-35) from Jordan, suggesting heterozygosity at net blotch resistance loci.

Resistance to spot blotch was less common in *H. spontaneum*, as only 46 and 53% of accessions from Israel (Table 4) and Jordan (Table 5), respectively, exhibited IRs of 1 to 5. Only six highly resistant (IRs of 1 to 2) accessions were found from the two countries. Resistant and susceptible accessions were found at 14 of the 30 collection sites in Israel and 10 of the 27 collection sites in Jordan, again indicating micro-scale diversity for spot blotch reaction across a number of locations. Resistant and susceptible plants also were detected within two accessions (Tabigha 7-12 and Eyzariya 15-29) from Israel, suggesting heterozygosity at spot blotch resistance loci.

The lowest frequency of disease resistance in *H. spontaneum* was to stem rust. Only 26 and 11% of the accessions from Israel exhibited ITs of 0; to 2⁺ to pathotypes MCCF and QCCJ, respectively, at the low incubation temperature (Table 4). The resistance in most of these accessions was temperature sensitive, as only 4 of 16 and 1 of 7 accessions remained resistant to pathotypes MCCF and QCCJ, respectively, at the high incubation temperature. Shechem 12-37 was the only highly resistant (IT = 0; accession identified (pathotype MCCF at low temperature). Accessions Mt. Hermon 1-46, Gadot 6-35, Zefat 8-05, Damon 11-11, Shechem 12-32, Tel Shoket 16-46, and Revivim 18-04 exhibited some resistance to both pathotypes at the low incubation temperature. Resistance to stem rust was rare in *H. spontaneum* accessions from Jordan, as only three accessions (Zarqa 6-21, Madaba 8-32, Wadi Wala 10-05) exhibited ITs of 2⁻ to 2⁺ to pathotype MCCF or QCCJ under either of the two incubation environments (Table 5). Zarqa 6-21 was the only accession that was resistant to both pathotypes (low incubation temperature only). Resistant and susceptible accessions to at least one of the patho-

types were found at 12 of the 30 collection sites in Israel and three of the 27 collection sites in Jordan. Resistant and susceptible plants also were detected within five accessions (Rosh Pinna 5-23, Shechem 12-37, Tel Shoket 16-46, Revivim 18-04, and Yeroham 19-32) from Israel to at least one of the two pathotypes, suggesting heterozygosity at stem rust resistance loci.

A high level of diversity ($h_{sj} = 0.993$ to 1.025) for reaction to powdery mildew, leaf rust, net blotch, and spot blotch was found in the combined analysis for accessions from both Israel and Jordan (Table 6). The lowest level of diversity found was for reaction to SSLB and stem rust (pathotype MCCF) ($h_{sj} = 0.615$ and 0.519, respectively). Chi-square analysis using 2×3 contingency tables revealed that the frequency of general disease reactions was similar between accessions from Israel and Jordan for powdery mildew ($\chi^2 = 1.64$, $P = 0.45$, NS), net blotch ($\chi^2 = 0.84$, $P > 0.95$, NS), and spot blotch ($\chi^2 = 1.67$, $P = 0.45$, NS). However, significant differences in class frequencies were found between accessions from the two countries for SSLB ($\chi^2 = 13.04$, $P < 0.005$) and leaf rust ($\chi^2 = 9.87$, $P < 0.01$). These differences were attributed to a lower than expected frequency of susceptible responses for accessions from Israel and a higher than expected frequency of susceptible responses for accessions from Jordan for both SSLB and leaf rust. Since there were no values in the resistant class for stem rust reaction among the accessions from Jordan, a 2×2 contingency table was used. Significant differences in class frequencies were detected between accessions from Israel and Jordan for stem rust (MCCF, low temperature regime) ($\chi^2 = 5.61$, $P < 0.025$). These differences were mainly attributed to a higher than expected frequency of intermediate responses for accessions from Israel and a lower than expected frequency of intermediate responses for accessions from Jordan.

The relationship between environmental parameters near the collection sites and the general disease response of *H. spontaneum* accessions is presented in Table 7. In general, no consistent and statistically significant relationships were detected between the environmental parameters of altitude, temperature, rainfall, or humidity and the disease response of *H. spontaneum*. A low but significant correlation was found between the level of resistance to *Puccinia hordei* and the amount of rainfall and level of humidity in both Israel and Jordan. In Israel, resistance to *B. graminis* f. sp. *hordei* was associated with high humidity and cooler daytime temperatures in August.

DISCUSSION

Overall, a high level of macro-scale diversity (i.e., across collection sites) for disease reaction was found in the 116 accessions of *H. spontaneum* evaluated. This

Table 4. Disease reactions of *Hordeum spontaneum* accessions from Israel to *Septoria passerinii*, *Blumeria graminis* f. sp. *hordei*, *Puccinia hordei*, *Pyrenophora teres* f. *teres*, *Cochliobolus sativus*, and *Puccinia graminis* f. sp. *tritici*

Line	<i>Septoria passerinii</i> ^a		<i>B. g. f. sp. hordei</i> ^b		<i>Puccinia hordei</i> ^c		<i>Pyrenophora teres</i> f. <i>teres</i> ^d		<i>Cochliobolus sativus</i> ^d		<i>Puccinia graminis</i> f. sp. <i>tritici</i>							
	IR	IP ^e	IR	IP	IT	IP	IR	IP	IR	IP	MCCF lo ^c		MCCF hi ^c		QCCJ lo ^c		QCCJ hi ^c	
Mt. Hermon 1-13	0	R	2	I	1n	R	3	R	6	S	3 ⁻	S	3 ⁻	S	3	S	3 ⁺	S
Mt. Hermon 1-46	1	R	0	R	1N	R	8	S	7	S	1 ⁺	R	3 ⁻	S	2 ⁻	I	3	S
Afiq 3-11	0	R	3	S	0;n	R	8	S	5	I	3	S	3	S	3	S	3	S
Afiq 3-23	0	R	3	S	0;n	R	8	S	6	S	3	S	3	S	3	S	3 ⁻	S
Tel Hay 4-13	0	R	0	R	2cn	I	6	S	5	I	3c	S	3	S	3	S	3C	S
Tel Hay 4-19	1	R	1	R	2 ⁺ c	I	4	I	6	S	3	S	3	S	3	S	3C	S
Tel Hay 4-43	0	R	0	R	1cn	R	3	R	4	I	3c	S	3	S	3	S	3C	S
Rosh Pinna 5-23	1	R	0	R	0;c	R	8	S	5	I	3 ⁻ c	S	3 ⁺	S	3c	S	3 ⁺ /2 ⁺	S/I
Rosh Pinna 5-58	0	R	0	R	0;cn	R	8	S	6	S	3 ⁻ c	S	3 ⁺	S	3	S	3	S
Gadot 6-35	0	R	2/3	I/S	2cn	I	7	S	2	R	1 ⁺	R	2 ⁺	I	1 ⁺	R	3 ⁻	S
Gadot 6-45	0	R	4	S	0;c	R	3	R	7	S	3 ⁻	S	3	S	3	S	3 ⁻	S
Tabigha 7-06	0	R	2	I	2C	I	3	R	5	I	3 ⁻	S	3 ⁺	S	3	S	3	S
Tabigha 7-12	0	R	2	I	2 ⁻ c	I	7	S	3/6	R/S	3 ⁻ c	S	3	S	3	S	3	S
Zefat 8-05	0	R	0	R	0;N	R	6	S	6	S	2 ⁻	I	3	S	2 ⁺	I	3 ⁻	S
Zefat 8-11	0	R	0	R	1n	R	1	R	7	S	3	S	3 ⁻	S	3	S	3	S
Zefat 8-58	2	I	2	I	1N	R	2	R	4	I	3 ⁻ c	S	3 ⁻	S	3 ⁻ c	S	3 ⁻	S
Mt. Meron 9-09	0	R	0	R	2c	I	3	R	6	S	3	S	3 ⁻	S	3 ⁻	S	3	S
Mt. Meron 9-53	0	R	0	R	2c	I	3	R	6	S	2 ⁺	I	3 ⁻	S	3 ⁻	S	3	S
Maalot 10-24	0	R	3	S	0;n	R	7	S	6	S	3 ⁻	S	3	S	3 ⁻	S	3	S
Maalot 10-36	0	R	3	S	0;n	R	8	S	6	S	3 ⁻	S	3	S	3 ⁻	S	3	S
Damon 11-02	0	R	0	R	0;c	R	2	R	5	I	1 ⁺	R	3 ⁻	S	3 ⁻	S	3	S
Damon 11-11	0	R	0	R	0;cn	R	4	I	5	I	1	R	2 ⁻	I	2 ⁺	I	3 ⁻	S
Shechem 12-32	0	R	2	I	1 ⁺ cn	R	1	R	3	R	1 ⁺	R	3 ⁻	S	1 ⁺	R	3	S
Shechem 12-37	0	R	3	S	0;Nc	R	1	R	5	I	0/3 ⁻	R/S	1 ⁺	R	3	S	3 ⁻	S
Bar Giyyora 13-29	0	R	3	S	0;N	R	2	R	5	I	3 ⁻	S	3	S	3	S	3	S
Bar Giyyora 13-56	0	R	2	I	0;nc	R	4	I	6	S	3 ⁻	S	3	S	3 ⁻	S	3 ⁻	S
Talpiyyot 14-13	0	R	1	R	0;N	R	6	S	5	I	3	S	3	S	3 ⁺	S	3	S
Talpiyyot 14-20	0	R	0/2	R/I	0;N	R	5	I	5	I	3	S	3	S	3	S	3	S
Eyzariya 15-29	5	S	0/3	R/S	2c	I	5	I	3/6	R/S	3	S	3	S	3	S	3	S
Eyzariya 15-46	0	R	1	R	3 ⁻ c	S	7	S	4	I	3 ⁻	S	3 ⁺	S	3 ⁻	S	3	S
Tel Shoket 16-05	0	R	2	I	1 ⁺ nc	R	2	R	6	S	3 ⁻	S	3 ⁻	S	3 ⁻	S	3 ⁺	S
Tel Shoket 16-46	0	R	3	S	0;n	R	2	R	7	S	1 ⁺	R	3	S	2 ⁺ /3	I/S	3	S
Bor Mashash 17-05	1	R	3	S	2c	I	2	R	5	I	3	S	3	S	3	S	3	S
Bor Mashash 17-11	0	R	3	S	3 ⁻ C	S	3	R	6	S	3	S	3	S	3	S	3	S
Revivim 18-04	2	I	0	R	0;nc	R	8	S	6	S	2 ⁺ c	I	2	I	2 ⁻ c	I	3 ⁻ c/2 ⁺	S/I
Revivim 18-26	0	R	0	R	0;nc	R	7	S	7	S	2c	I	3 ⁻	S	3 ⁻ c	S	3 ⁻ C	S
Yeroham 19-03	0	R	3	S	3 ⁻ C	S	4	I	3	R	3	S	3	S	3	S	3	S
Yeroham 19-32	0	R	2	I	3/1n	S/R	2	R	5	I	2 ⁻ /3	I/S	3 ⁻	S	3	S	3	S
Sede Boqer 20-22	0	R	3	S	1n/3	R/S	2	R	6	S	2 ⁻	I	3 ⁻	S	3 ⁻	S	3	S
Sede Boqer 20-45	0	R	3	S	0;n	R	7	S	6	S	3 ⁻	S	3	S	3	S	3 ⁺	S
Bet Shean 21-15	0	R	1	R	0;nc	R	4	I	7	S	3	S	3 ⁻	S	3	S	3	S
Bet Shean 21-46	0	R	2	I	0;n	R	1	R	2	R	3 ⁻	S	3	S	3	S	3	S
Mehola 22-16	2	I	3	S	0;n/2 ⁻ c	R/I	7	S	6	S	3	S	3	S	3	S	3	S
Mehola 22-42	0	R	3	S	1 ⁺ cn	R	3	R	2	R	3	S	3	S	3	S	3	S
Wadi Qilt 23-67	0	R	0	R	2 ⁺ c	I	2	R	6	S	3	S	3	S	3c	S	3	S
Wadi Qilt 23-72	0	R	0	R	3 ⁻ c	S	2	R	5	I	3 ⁻	S	3 ⁻	S	3 ⁻	S	3	S
Akhziv 24-39	0	R	4	S	0;n	R	2	R	3	R	3 ⁻ c	S	3	S	3c	S	3	S
Akhziv 24-57	0	R	4	S	0;nc	R	2	R	3	R	3 ⁻	S	3	S	3	S	3	S
Atlit 25-08	0	R	0	R	1N	R	7	S	6	S	3	S	3 ⁻	S	3	S	3	S
Atlit 25-20	0	R	0	R	1N	R	8	S	6	S	2	I	3 ⁻	S	3	S	3	S
Atlit 25-36	1	R	0	R	0;n	R	2	R	6	S	3	S	3 ⁻	S	3 ⁻	S	3	S
Caesarea 26-22	0	R	0	R	1N	R	5	I	5	I	3 ⁻	S	3 ⁻	S	3	S	3	S
Caesarea 26-47	0	R	0	R	1N	R	5	I	6	S	3 ⁻	S	3	S	3c	S	3	S
Herzliya 27-55	0	R	1	R	2c	I	2	R	6	S	3	S	3	S	3	S	3	S
Herzliya 27-59	0	R	1	R	1 ⁺ cn	R	1	R	6	S	3	S	3	S	3	S	3	S
Ashqelon 28-03	0	R	2	I	0;n	R	3	R	7	S	3 ⁻	S	3	S	3	S	3	S
Ashqelon 28-37	0	R	2	I	2c	I	2	R	3	R	3	S	3	S	3	S	3	S
Machtesh 31-13	2	I	0	R	2 ⁻ /3	I/S	2	R	5	I	3 ⁻	S	3	S	3 ⁻	S	3	S
Machtesh 31-22	0	R	0	R	2 ⁻ c	I	3	R	6	S	2 ⁺ c	I	3	S	3 ⁻	S	3	S
Ein Zukim 32-05	2	I	0/3	R/S	0;	R	3	R	6	S	3 ⁻	S	3	S	3	S	3	S
Ein Zukim 32-11	0	R	3	S	0;	R	6	S	6	S	3 ⁻	S	3	S	3 ⁻	S	3 ⁻	S
Avedat 33-28	0	R	3	S	2 ⁺ c	I	3	R	2	R	1 ⁺	R	3	S	3 ⁻	S	3	S
Avedat 33-54	0	R	0	R	3 ⁻	S	5	I	7	S	3 ⁻	S	3 ⁻	S	3 ⁻	S	3	S
Number/percent of:	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Low IR/IT	57	90	32	51	42	67	33	52	11	17	8	13	1	2	2	3	0	0
Intermediate IR/IT	5	8	12	19	15	23	10	16	18	29	8	13	3	5	5	8	0	0
High IR/IT	1	2	19	30	6	10	20	32	34	54	47	74	59	93	56	89	63	100

^a Accessions exhibiting infection responses of 0 to 1, 2, and 3 to 5 were considered resistant, intermediate, and susceptible, respectively, to *S. passerinii* (Toubia-Rahme and Steffenson, 1999 [45]).

^b Accessions exhibiting infection types of 0 to 1, 2, and 3 to 4 were considered resistant, intermediate, and susceptible, respectively, to *B. graminis* f. sp. *hordei* (Torp et al., 1978 [44]).

^c Accessions exhibiting infection types of 0 to 1, 2, and 3 to 4 were considered resistant, intermediate, and susceptible, respectively, to *Puccinia hordei* (Levine and Cherewick, 1952 [24]) and *P. graminis* f. sp. *tritici* (Miller and Lambert, 1955 [29]).

^d Accessions exhibiting infection responses of 1 to 3, 4 to 5, and 6 to 9 were considered resistant, intermediate, and susceptible, respectively, to *Pyrenophora teres* f. *teres* (Tekauz 1985 [43]) and *Cochliobolus sativus* (Fetch and Steffenson, 1999 [9]).

^e IP = infection phenotypes, where R = resistant, I = intermediate resistant, and S = susceptible.

Table 5. Disease reactions of *Hordeum spontaneum* accessions sampled from Jordan to *Septoria passerinii*, *Blumeria graminis* f. sp. *hordei*, *Puccinia hordei*, *Pyrenophora teres* f. *teres*, *Cochliobolus sativus*, and *Puccinia graminis* f. sp. *tritici*

Line	<i>Septoria passerinii</i> ^a		<i>B. g. f. sp. hordei</i> ^b		<i>Puccinia hordei</i> ^c		<i>Pyrenophora teres</i> f. <i>teres</i> ^d		<i>Cochliobolus sativus</i> ^d		<i>Puccinia graminis</i> f. sp. <i>tritici</i>							
											MCCF lo ^c		MCCF hi ^c		QCCJ lo ^c		QCCJ hi ^c	
	IR	IP ^e	IR	IP	IT	IP	IR	IP	IR	IP	IT	IP	IT	IP	IT	IP	IT	IP
Shūna, N. 1-32	0	R	0	R	1 ⁺ c	R	2	R	5	I	3	S	3 ⁺	S	3	S	3	S
Shūna, N. 1-43	4	S	0	R	1 ⁺ cn	R	2	R	2	R	3	S	3	S	3	S	3	S
Irbid 2-14	0	R	3	S	0;n	R	3	R	2	R	3	S	3 ⁻	S	3	S	3	S
Irbid 2-34	1	R	1	R	3	S	7	S	3	R	3	S	3 ⁻	S	3	S	3	S
Irbid, E. 3-31	0	R	3	S	1 ⁺ N	R	4	I	6	S	3 ⁻	S	3 ⁻	S	3 ⁻	S	3 ⁺	S
Irbid, E. 3-36	0	R	3	S	3	S	2	R	6	S	3 ⁻	S	3 ⁺	S	3 ⁻ c	S	3	S
Mafrag, W. 4-07	0	R	2	I	3 ⁻	S	2	R	5	I	3	S	3 ⁻	S	3	S	3	S
Mafrag, W. 4-11	0	R	3	S	3cn	S	5	I	5	I	3 ⁻	S	3	S	3 ⁻	S	3C	S
Mafrag 5-34	0	R	3	S	3	S	4	I	6	S	3	S	3 ⁻	S	3	S	3	S
Zarqa 6-21	1	R	2	I	1 ⁺ c	R	2	R	5	I	2 ⁻	I	3	S	2c	I	3 ⁻ c	S
Zarqa 6-38	2	I	1	R	2 ⁺	I	3	R	8	S	3	S	3	S	3	S	3	S
Amman 7-06	0	R	0	R	2c	I	4	I	3	R	3 ⁻	S	3	S	3	S	3 ⁻	S
Amman 7-48	1	R	0	R	3c	S	6	S	4	I	3 ⁻	S	3	S	3 ⁺	S	3C	S
Madaba 8-08	0	R	0	R	1 ⁺ c	R	7	S	3	R	3 ⁻	S	3 ⁻	S	2 ⁻	I	3 ⁻	S
Madaba 8-32	1	R	4	S	1n	R	3	R	3	R	3 ⁻	S	3 ⁻	S	2 ⁻	I	3 ⁻	S
Mt. Nebo 9-25	1	R	0	R	2C	I	7	S	8	S	3	S	3 ⁻	S	3 ⁻	S	3 ⁻	S
Mt. Nebo 9-39	0	R	3	S	3 ⁻	S	3	R	6	S	3 ⁻	S	3 ⁻	S	3 ⁻	S	3 ⁻	S
Wadi Wala 10-05	0	R	0	R	2 ⁻ c	I	2	R	6	S	3 ⁻	S	3	S	2 ⁺ c	I	3 ⁻	S
Wadi Wala 10-38	0	R	2	I	2c	I	3	R	4	I	3	S	3	S	3	S	3	S
Wadi Mūjib 11-09	4	S	3	S	3 ⁻ C	S	5	I	6	S	3	S	3	S	3	S	3C	S
Wadi Mūjib 11-17	1	R	3	S	2 ⁺ c	I	3	R	6	S	3	S	3	S	3	S	3	S
Talal 12-13	5	S	0	R	3	S	7	S	6	S	3 ⁻	S	3 ⁻	S	3 ⁻	S	3C	S
Talal 12-21	2	I	4	S	2c	I	2	R	4	I	3	S	3 ⁻	S	3	S	3C	S
Karak 13-10	3	S	3	S	0;N	R	7	S	4	I	3	S	3 ⁻	S	3	S	3	S
Karak 13-43	0	R	3	S	1n	R	2	R	4	I	3	S	3	S	3	S	3	S
Wadi Hasa 14-02	0	R	2	I	0;n	R	4	I	6	S	3	S	3 ⁻	S	3 ⁻	S	3	S
Wadi Hasa 14-27	0	R	1	R	1nc	R	2	R	6	S	3	S	3	S	3 ⁻ c	S	3C	S
Laban 15-09	5	S	1	R	0;N	R	3/6	R/S	6	S	3 ⁻	S	3 ⁻	S	3 ⁻	S	3	S
Laban 15-39	0	R	0	R	3 ⁻ c	S	8	S	7	S	3 ⁻	S	3 ⁻	S	3 ⁺	S	3	S
Tafila 16-04	3	S	0	R	3 ⁻	S	7	S	7	S	3	S	3	S	3	S	3	S
Tafila 16-33	2	I	2	I	2c	I	3	R	5	I	3	S	3	S	3	S	3	S
Danā 17-43	5	S	3	S	3 ⁻ c	S	7	S	3	R	3	S	3	S	3 ⁺	S	3	S
Danā 17-48	5	S	3	S	3	S	5/7	I/S	5	I	3	S	3	S	3	S	3	S
Wadi Mūsā 18-08	5	S	4	S	2 ⁺ c	I	4	I	7	S	3	S	3	S	3 ⁺	S	3	S
Wadi Mūsā 18-42	5	S	3	S	3 ⁻ c	S	6	S	5	I	3 ⁻	S	3	S	3	S	3	S
Safi 19-23	0	R	3	S	3 ⁻	S	7	S	5	I	3 ⁺	S	3	S	3	S	3	S
Safi 19-29	0	R	2	I	2c	I	2	R	6	S	3	S	3	S	3	S	3	S
Shūna S. 20-04	5	S	0	R	3 ⁻ c	S	7	S	6	S	3	S	3	S	3 ⁻	S	3	S
Shūna S. 20-14	0	R	0	R	2C	I	2	R	4	I	3	S	3	S	3 ⁺	S	3	S
'Ira 21-21	0	R	3	S	1 ⁺ C	R	3	R	4	I	3	S	3	S	3 ⁺	S	3	S
'Ira 21-33	0	R	3	S	2C	I	2	R	4	I	3	S	3 ⁺	S	3 ⁺	S	3	S
Salt 22-07	0	R	2	I	0;c	R	2	R	5	I	3 ⁻ c	S	3 ⁻	S	3 ⁻	S	3	S
Salt 22-15	0	R	3	S	2C	I	6	S	6	S	3	S	3	S	3 ⁻ c	S	3	S
Jarash 23-06	0	R	0	R	0;N	R	4	I	5	I	3	S	3	S	3	S	3 ⁻	S
Jarash 23-44	4	S	0	R	1 ⁺ c	R	2	R	4	I	3	S	3	S	3 ⁺	S	3	S
Sakib 24-25	0	R	0	R	2c	I	6	S	6	S	3	S	3	S	3 ⁻	S	3	S
Sakib 24-32	0	R	3	S	1cn	R	3	R	6	S	3	S	3 ⁻	S	3	S	3	S
Ajlun 25-29	0	R	0	R	1nc	R	5	I	7	S	3 ⁻	S	3 ⁻	S	3	S	3	S
Ajlun 25-35	0	R	0	R	0;n	R	5/7	I/S	7	S	3 ⁻	S	3 ⁻	S	3	S	3	S
Irbid, S. 26-09	2	I	0	R	1N	R	2	R	4	I	3	S	3 ⁺	S	3	S	3	S
Irbid, S. 26-26	0	R	3	S	2cn	I	2	R	7	S	3	S	3 ⁺	S	3	S	3	S
El Hamma 27-01	0	R	2	I	1 ⁺ c	R	5	I	6	S	3	S	3 ⁻	S	3	S	3	S
El Hamma 27-28	1	R	0	R	1 ⁺ c	R	7	S	5	I	3	S	3 ⁺	S	3 ⁺	S	3	S
Number/percent of:	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Low IR/ITs	37	70	23	43	22	42	26	49	7	13	0	0	0	0	0	0	0	0
Intermediate IR/ITs	4	7	8	15	15	28	12	23	21	40	1	2	0	0	3	6	0	0
High IR/ITs	12	23	22	42	16	30	15	28	25	47	52	98	53	100	50	94	53	100

^a Accessions exhibiting infection responses of 0 to 1, 2, and 3 to 5 were considered resistant, intermediate, and susceptible, respectively, to *S. passerinii* (Toubia-Rahme and Steffenson, 1999 [45]).

^b Accessions exhibiting infection types of 0 to 1, 2, and 3 to 4 were considered resistant, intermediate, and susceptible, respectively, to *B. graminis* f. sp. *hordei* (Torp et al., 1978 [44]).

^c Accessions exhibiting infection types of 0 to 1, 2, and 3 to 4 were considered resistant, intermediate, and susceptible, respectively, to *Puccinia hordei* (Levine and Cherewick, 1952 [24]) and *P. graminis* f. sp. *tritici* (Miller and Lambert, 1955 [29]).

^d Accessions exhibiting infection responses of 1 to 3, 4 to 5, and 6 to 9 were considered resistant, intermediate, and susceptible, respectively, to *Pyrenophora teres* f. *teres* (Tekauz 1985 [43]) and *Cochliobolus sativus* (Fetch and Steffenson, 1999 [9]).

^e IP = infection phenotypes, where R = resistant, I = intermediate resistant, and S = susceptible.

result confirms previous studies documenting diversity for reaction to different diseases (e.g., powdery mildew, leaf rust, and leaf scald) in this wild species (1,15,30). Other studies reporting a high level of macro-scale diversity in *H. spontaneum* have included assays of DNA polymorphism (5,6,46), allozymic variation in proteins (33,35), growth physiology (48), and agronomic traits (34). The level of macro-scale diversity to individual pathogens varied greatly in this study as measured by Shannon's information index. In the combined analysis from both Israel and Jordan, the highest level of diversity was observed for reaction to *B. graminis* f. sp. *hordei* (1.025) and *Pyrenophora teres* f. *teres* (1.021), and the lowest to *S. passerinii* (0.615) and *Puccinia graminis* f. sp. *tritici* (0.519). The low level of diversity found for reaction to *S. passerinii* and *Puccinia graminis* f. sp. *tritici* was due to a high frequency of resistance and susceptibility, respectively. In addition to macro-scale diversity, we also detected micro-scale diversity within individual collection sites where accessions were gathered no closer than 1 m apart along transects of 25 to 200

m. Micro-scale diversity within individual collection sites also was found for powdery mildew and leaf rust reaction by Jana and Nevo (15), who studied accessions of *H. spontaneum* from Iran, Syria, and Turkey. Resistant and susceptible plants were identified within individual accessions (originally derived from single plants) to all diseases except SSLB, indicating that genetic heterozygosity exists for many resistance loci. This phenomenon appears to be a common feature of gramineous species at their center of origin (53). The disease evaluations in this investigation were all done on seedling plants to just one or two pathotypes of each pathogen. As such, these evaluations assess the effects of seedling resistance genes with major effects and therefore represent only a small fraction of the potential diversity for disease resistance that may be important in agriculture. A wide spectrum of diversity for adult plant resistance (both qualitative and quantitative) also exists in *H. spontaneum* (3), but was not considered in this investigation. With the high level of macro- and micro-scale diversity for disease reaction, extensive genetic heterozygosity for resis-

tance loci, and largely uncharacterized mechanisms of adult plant resistance, *H. spontaneum* is an incredibly rich and largely untapped source of unique disease resistance alleles for cultivated barley improvement.

The environment can be a key component contributing to the range of genetic diversity found in various organisms (49). Patterns of genetic variation in *H. spontaneum*, including disease resistance, are influenced by environmental factors such as temperature and humidity and are not random (33,36). Environmental conditions that favor high disease pressure should increase selection for disease resistance. This implies that possible locations of resistance sources can be predicted using environmental and ecological information. However, in this study, there generally was not a relationship between environment and disease resistance. Low but significant correlations were found between the level of resistance to *Puccinia hordei* and the amount of rainfall and level of humidity at collection sites in both Israel and Jordan. Higher levels of leaf rust resistance were associated with higher rainfall and humid-

Table 6. Frequency and diversity index of *Hordeum spontaneum* accessions from Israel and Jordan exhibiting resistant, intermediate, and susceptible reactions to *Septoria passerinii*, *Blumeria graminis* f. sp. *hordei*, *Puccinia hordei*, *Pyrenophora teres* f. *teres*, *Cochliobolus sativus*, and *Puccinia graminis* f. sp. *tritici*

Pathogen	Israel (n = 63)				Jordan (n = 53)				Combined (n = 116)			
	R ^a	I ^a	S ^a	h _s ^b	R ^a	I ^a	S ^a	h _s ^b	R ^a	I ^a	S ^a	h _s ^b
<i>S. passerinii</i>	0.905	0.079	0.016	0.357	0.698	0.075	0.226	0.781	0.810	0.078	0.112	0.615
<i>B. graminis</i> f. sp. <i>hordei</i>	0.508	0.190	0.302	1.021	0.434	0.151	0.415	1.012	0.474	0.172	0.353	1.025
<i>Puccinia hordei</i>	0.667	0.238	0.095	0.836	0.415	0.283	0.302	1.084	0.552	0.259	0.190	0.993
<i>Pyrenophora teres</i> f. <i>teres</i>	0.524	0.159	0.317	0.995	0.491	0.226	0.283	1.042	0.509	0.190	0.302	1.021
<i>C. sativus</i>	0.175	0.286	0.539	0.996	0.132	0.396	0.472	0.988	0.155	0.336	0.509	0.999
<i>Puccinia graminis</i> f. sp. <i>tritici</i> ^c	0.127	0.127	0.746	0.743	0	0.019	0.981	0.094	0.069	0.078	0.853	0.519

^a Frequency of accessions exhibiting resistant (R), intermediate (I), or susceptible (S) reactions.

^b Shannon's diversity index where $h_s = -\sum p_i \ln(p_i)$, with maximum $h_s = 1.099$.

^c Diversity based on reaction to pathotype MCCF (incubated at low temperature) only.

Table 7. Pearson correlation coefficients between environmental parameters and infection response to *Septoria passerinii*, *Blumeria graminis* f. sp. *hordei*, *Puccinia hordei*, *Pyrenophora teres* f. *teres*, *Cochliobolus sativus*, and *Puccinia graminis* f. sp. *tritici*

Pathogen	Environmental variables ^a				
	Altitude	TJan	TAug	Rain	Humidity
Israel					
<i>S. passerinii</i>	0.041	-0.036	0.052	-0.071	-0.109
<i>B. hordei</i> f. sp. <i>hordei</i>	-0.252* ^b	0.162	0.267*	-0.223	-0.282*
<i>Puccinia hordei</i>	0.022	0.001	0.100	-0.261*	-0.253*
<i>Pyrenophora teres</i> f. <i>teres</i>	0.153	-0.183	-0.063	0.103	-0.122
<i>C. sativus</i>	0.207	-0.164	-0.169	0.133	0.031
<i>Puccinia graminis</i> f. sp. <i>tritici</i>	-0.163	0.206	0.265*	-0.057	0.058
Jordan					
<i>S. passerinii</i>	0.104	-0.087	-0.121	-0.183	-0.149
<i>B. hordei</i> f. sp. <i>hordei</i>	0.129	-0.163	-0.189	-0.186	-0.054
<i>Puccinia hordei</i>	-0.114	0.107	0.097	-0.481**	-0.301*
<i>Pyrenophora teres</i> f. <i>teres</i>	0.108	-0.002	0.035	-0.051	-0.065
<i>C. sativus</i>	0.116	-0.122	-0.100	-0.027	0.119
<i>Puccinia graminis</i> f. sp. <i>tritici</i> ^c	NA	NA	NA	NA	NA

^a Environmental variables where Alt = altitude, TJan = mean January temperature, TAUG = mean August temperature, Rain = mean annual precipitation, and Hum = mean humidity at 1400 h.

^b All coefficients were nonsignificant except where denoted by * = significant at 0.05 and ** = significant at 0.01.

^c Since all accessions in Jordan were susceptible to stem rust, no correlation was necessary.

ity. These significant correlations are not surprising given that *Puccinia hordei* requires moist conditions for infection and that high rainfall and humidity will increase disease pressure. However, *S. passerinii*, *Pyrenophora teres* f. *teres*, *C. sativus*, and *Puccinia graminis* f. sp. *tritici* also require moisture for infection, but no significant correlations were found to environmental parameters for these pathogens. There are several possible reasons for this result. For *S. passerinii* and *Puccinia graminis* f. sp. *tritici*, the lack of correlation between resistance and environmental parameters is likely related to the low degree of diversity found in the accessions for reaction to the two pathogens. Another possibility is that the general environmental data taken from weather stations near the collection sites may not be indicative of the micro-scale environment where *H. spontaneum* is subject to pathogen infection (e.g., in valleys or other water courses where moisture accumulates). It is also likely that the critical periods for pathogen infection and spread occur within short and specific time intervals, and that the environmental conditions that favor infection during these periods are not reflected in the values (e.g., average annual rainfall or humidity at 1400 hours, January temperature) that were used in this analysis. Environmental parameters such as leaf wetness duration, relative humidity, and temperature measured at the time of year that corresponds to critical plant growth stages (tillering to heading) may give a better indication of environmental influence on disease pressure, which is more likely to correlate to evolution of disease resistance. Due to the overall lack of correlation between resistance and environmental parameters assessed in this study, it would be difficult to reliably identify specific sites where possible sources of resistance to specific diseases might be found. However, this may be possible at a regional level. The frequency of resistance in *H. spontaneum* was generally higher in areas of greater precipitation. Thus, one may be more likely to find resistant *H. spontaneum* accessions in environments that are mesic (e.g., along the Mediterranean coast and Jordan River) than in those that are xeric (e.g., Negev Desert).

The frequency (77 to 98%) and level (most with IR of 0) of resistance to SSLB in *H. spontaneum* was the highest among all diseases examined in this study. This was especially true for accessions from Israel. Resistance to SSLB appears to be very common in *H. spontaneum*, as many resistant accessions have been reported from other countries such as Iraq, Lebanon, Syria, and Turkey (22,28,45). *S. passerinii* has been reported on cultivated barley in Israel (19), but its role in the co-evolution of *H. spontaneum* resistance is not known. It is possible that a higher level of variation for reaction to SSLB exists in

H. spontaneum but was simply not detected by the isolate of *S. passerinii* used in this study. Additional studies using isolates of *S. passerinii* from the Middle East and other regions should be conducted to obtain a more comprehensive assessment of the diversity in *H. spontaneum* to SSLB. It was interesting to note that accessions with SSLB resistance were found at several collection sites (e.g., Bor Mashash, Revivim, Yeroham, and Sede Boqer) in the Negev Desert, where precipitation is less than 200 mm per year. This result was unexpected given that *S. passerinii* is a splash-dispersed pathogen and requires moist weather conditions for infection and spread.

Several previous studies have found *H. spontaneum* to be a rich source of powdery mildew resistance (7,15). Our data confirmed these findings, as 58 and 70% of accessions from Jordan and Israel, respectively, exhibited resistant infection responses. In this study, resistance was more common in mesic environments, although several highly resistant accessions were also identified in the xeric environments of Revivim and Machtesh-Gadol in the Negev Desert of Israel. This result is in contrast to previous research where powdery mildew resistance was absent at sites near the Negev Desert (31). The contrasting results found between this and the other two studies may be due to the different pathogen cultures used or perhaps a limited host sample size. Nevertheless, this indicates that sources of powdery mildew resistance can be found in areas where the environment might be considered unfavorable for the development of the disease. Fischbeck and Jahoor (11) studied the genetics of powdery mildew resistance in *H. spontaneum* accessions obtained from Israel and found that the resistance response was quantitative when challenged by local isolates of *B. graminis* f. sp. *hordei*, but qualitative (hypersensitive reactions) when challenged by European pathogen isolates. This finding has important implications regarding the choice of pathogen isolates used in disease screening tests. Future evaluations of this germ plasm should be made to local pathotypes isolated at or near sites where the *H. spontaneum* accessions were collected.

The percentage of *H. spontaneum* accessions exhibiting resistance to *Puccinia hordei* was high (70%) and very high (90%) in Jordan and Israel, respectively. The alternate host of *Puccinia hordei* is *Ornithogalum* (Star of Bethlehem lily), which is endemic to Israel and co-exists with *H. spontaneum* in many regions of the country (3). Strong co-evolutionary forces between the host and pathogen (as mediated by the alternate host) have been operating for several millennia and likely contributed to the great diversity found in *H. spontaneum* for leaf rust reaction. Leaf rust resistance was more common in accessions

from collection sites with higher rainfall and humidity, as revealed in the correlation analysis. Anikster et al. (2) found that leaf rust resistance was common in *H. spontaneum* accessions from central and northern Israel, but not in the arid regions of the south. Similarly, Moseman et al. (30) found leaf rust resistance common in accessions from the Coastal Plains of Israel, where the environmental conditions are more conducive for disease development (i.e., higher rainfall and humidity) and *Ornithogalum* is present. Manisterski et al. (27) speculated that *H. spontaneum* originating from dry regions in Israel would likely be universally susceptible to leaf rust. However, in this study, we identified highly resistant accessions (IT of 0;) from the arid sites of Revivim and Sede Boqer in the northern Negev Desert. This finding highlights the great diversity for disease resistance in *H. spontaneum* across the center of origin (51). Our study also confirms and extends previous studies (17,27,30) documenting the large reservoir of unexploited leaf rust resistance in this wild progenitor species. Indeed, four of the seven most recently described leaf rust resistance genes in *Hordeum* (*Rph10*, *Rph11*, *Rph15*, and *Rph16*) were derived from *H. spontaneum* (13). Future leaf rust research on *H. spontaneum* should include evaluations to more widely virulent cultures of *Puccinia hordei* and genetic tests to determine the allelic relationships of resistance genes to those already described.

About two-thirds of the *H. spontaneum* accessions evaluated in this study exhibited intermediate to high levels of resistance to *Pyrenophora teres* f. *teres*. Similar results were found for accessions from the Middle East by several other research groups (14,22,28,38). Kenneth et al. (20) reported a high degree of diversity for net blotch reaction in *H. spontaneum* and for virulence in *Pyrenophora teres* f. *teres* in Israel. It is therefore likely that Israel is an important center of diversity for the pathogen and that co-evolutionary forces are operating in this pathosystem. In this study, accessions with high levels of net blotch resistance were found in the higher moisture areas of the Mediterranean coast to the arid region of the Negev Desert. It was interesting to note that the number of accessions that were susceptible to net blotch was high in the Golan Heights—a region where leaf rust and powdery mildew resistance was common.

In contrast to the diseases described above, the frequency of resistance to spot blotch in *H. spontaneum* was lower (46 to 53%). Other investigators have reported a low frequency of spot blotch resistance in this species. This result is in agreement with previous investigations. Jana and Bailey (14) evaluated 291 *H. spontaneum* accessions to *C. sativus* and found only 13 with resistance (4.5% of total). Metcalfe et al. (28) and Legge et al. (22) evaluated a

collection of 43 accessions from Turkey, Iraq, Lebanon, and Syria, but found no resistance. In this study, six accessions exhibited high levels of spot blotch resistance (IR = 2), four from Israel (Gadot 6-35, Bet Shean 21-46, Mehola 22-42, and Avedat 33-28) and two from Jordan (Shūna N. 1-43 and Irbid 2-14). All but one (Avedat 33-28) of these accessions was from northern Israel and Jordan.

Resistance to stem rust was extremely rare in *H. spontaneum* accessions from Israel and Jordan. This result is in agreement with those of Metcalfe et al. (28) and Legge et al. (22), who found no promising levels of stem rust resistance in *H. spontaneum* from the Middle East. The alternate hosts of *Puccinia graminis* f. sp. *tritici* (i.e., *Berberis* and *Mahonia* spp.) originated in Asia (3,23); thus, strong co-evolutionary forces were apparently not operating between the pathogen and *H. spontaneum* in this region of the Fertile Crescent. Accessions from Damon, Gadot, and Shechem in Israel did exhibit high levels of resistance (ITs = 0;1 to 120;) to pathotypes MCCF and QCCJ, but only at the low-temperature environment. These accessions should be evaluated in the field to determine whether they carry broad-based adult plant resistance against *Puccinia graminis* f. sp. *tritici* pathotypes commonly found in North America.

One of the primary objectives of this research was to identify accessions of *H. spontaneum* that possessed high levels of resistance to all six pathogens of importance in the Upper Midwest region of the United States and central provinces of Canada. Such accessions could then be crossed with adapted breeding lines to simultaneously transfer genes for multiple disease resistance, possibly by marker-assisted selection. Two of the 116 accessions (Shechem 12-32 and Damon 11-11) evaluated were resistant to all of the pathogens tested. These accessions were collected from fairly divergent sites in north-eastern and north-central Israel. Only a small fraction (~3%) of the available accessions from the Institute of Evolution was evaluated in this study; thus, it is likely that additional sources of multiple disease resistance will be identified. Crosses have been made between the two *H. spontaneum* resistance sources and advanced barley breeding lines to elucidate the number, effect, and chromosomal position of the resistance genes by molecular mapping techniques. Identification of molecular markers closely linked to the resistance genes will facilitate their introgression in breeding lines by marker-assisted selection. Six-rowed malting barley cultivars in the Upper Midwest region of the United States have adequate levels of spot blotch resistance and stem rust resistance (except to pathotype QCCJ). The incorporation of SSLB, powdery mildew, leaf rust, and net blotch resistance will allow pro-

ducers to attain more stable yields in their barley cultivars without the threat of disease losses.

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