Assessment of Interactions Between Cultivated and Wild Wheats and *Septoria tritici*

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ABSTRACT

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Populations and accession lines of diploid and tetraploid wild *Triticum* species with different genomes and cultivars of bread and durum wheats were evaluated for seedling resistance to seven isolates of *Septoria tritici*. Bulk populations of wild wheats expressed pathogenicity patterns ranging from highly resistant to susceptible and exhibited specific population × isolate interactions regardless of species, genomes, or environmental-climatological parameters. Of 22 *T. monococcum boeoticum* lines (genome *AA*), only two were susceptible. Accession lines of diploid wheats with genomes *BB* and *DD* exhibited several pathogenicity patterns. Of 47 wild emmer (*T. turgidum dicoccoides*) lines, 25 were resistant to all seven isolates of *S. tritici*, while the rest exhibited 14 identifiable pathogenicity patterns. Ten different pathogenicity patterns were identified among 17 cultivated wheats. Nine complementary interacting resistance-virulence genetic components were estimated by subjecting a reaction matrix involving 44 wheat lines (wild and cultivated) × seven isolates of *S. tritici* to EPIDAT analysis according to Person's incomplete gene-for-gene scheme. The number of resistance components ranged from eight in some lines of *T. longissimum, T. speltoides*, and *T. turgidum dicoccoides* to one in some *T. turgidum dicoccoides* lines. As many as seven resistance components were estimated in spring wheat line H574 and a similar number of virulence components were found in some isolates of *S. tritici*. Some pathogenicity patterns expressed by the wild wheats were unmatched by the tested cultivated wheats, and vice versa. This genetic variation in wild *Triticum* species is a utilizable germplasm reservoir for resistance to Septoria leaf blotch of wheat.

Additional key words: resistance, Septoria leaf blotch of wheat.

The "wild gene pool" of species closely related to cultivated wheat has been used as a germplasm reservoir for improving agronomic traits, as a source of tolerance to abiotic stresses (drought and salt), and to provide cytoplasmic male sterility (9,16,20). Several genes for rust resistance have been transferred from wild and primitive forms to cultivated wheat (4,11,12,18). Variation in resistance to *Septoria tritici* in diploid, tetraploid, and hexaploid wheats has been reported. Many durum wheats (genome *AABB*) and triticale (genome *AABBRR*) were immune to *S. tritici* in California (14). Whereas very few durum wheat cultivars were resistant in Tunisia (5). Arsenijevic (1) reported resistance in *T. monococcum* and *T. timopheevi*, and Rosielle (23) observed a high level of resistance in *T. dicoccum, T. carthlicum, T. polonicum*, and *T. pyramidale*. Brokenshire (2) reported that the hexaploid wheats (genome *AABBDD*) *T. aestivum, T. spelta*, and *T. compactum* were more susceptible than tetraploid species, except for a highly susceptible selection of *T. dicoccum*, and confirmed the immune reaction of *T. timopheevi* (genome *AAGG*). Eyal (6) reported a higher frequency of resistance among *T. durum* and triticale accessions than among accessions of *T. aestivum* subjected to a highly virulent mixture of isolates of *S. tritici* in Israel.

Rillo et al (22) used a wheat-*Agropyron elongatum* derivative (Purdue 39120A4) as a source of resistance to *S. tritici* in crosses with the susceptible hexaploid wheat cultivar Riley sib. Retrogression of Septoria leaf blotch resistance occurred in mature plants of Purdue 39120A4 and F_1 plants, which, according to the authors, could have resulted from irregular chromosome transmission of resistance or from subsequent testing with more virulent cultures of the pathogen.

Among disomic lines of the wheat cultivar Chinese Spring in which each chromosome pair of *A. elongatum* had been added separately, only lines with chromosomes I and VII from *A. elongatum* were resistant to isolates of *S. tritici* from Oklahoma and Montana (13). The chromosome VII line appeared to be the most stable, and it was concluded that the stability of line VII carrying resistance to *S. tritici* should facilitate efforts to transfer resistance from *A. elongatum* to wheat. Jahier and Trottet (16) reported that line 33 of *Aegilops squarrosa* was weakly attacked by *S. nodorum*, but its thousand-kernel weight was not altered. In crosses between line 33 of *Ae. squarrosa* and hexaploid wheat, plants were recovered that exhibited resistance similar to that of the resistant *Ae. squarrosa* line.

The objective of this study was to assess the variation in resistance to *S. tritici* within and among diploid and polyploid wheat species.

MATERIALS AND METHODS

Bulk populations and accession lines of diploid and tetraploid species of wild *Triticum* species with different genomes (*AA, BB, DD*, and *AABB*), and cultivars of cultivated wheats were evaluated for seedling resistance to several isolates of *S. tritici*.

The hosts. *Wild diploid species.* Selections of wild einkorn, *T. monococcum boeoticum* (genome *AA*), used in this study originated from Greece and Turkey. Origins of populations and accession lines of four diploid species of the section Sitopsis, provided by D. Zohary and S. Mendlinger of the Hebrew University of Jerusalem, were as follows: *T. speltoides* (genome *SS*) from Israel and Turkey, and *T. longissimum* (genome S^lS^l), *T. searsii* (S^sS^s), and *T. sharonensis* (genome S^lS^l) from different ecogeographic habitats in Israel. The genomes of these four species are related to the *BB*

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genome of the tetraploid and hexaploid wheats (9,20,26). Accession lines of *T. tauschii* (= *Ae. squarrosa*), the donor of the *DD* genome to hexaploid wheat, also were obtained from D. Zohary. The nomenclature or the genus *Triticum* used in this work is according to Morris and Sears (20) and Feldman and Sears (9).

Wild emmer wheat. Accession lines of wild emmer-*T. turgidum dicoccoides* (genome *AABB*), from diverse ecological habitats in Israel, were obtained from a collection screened by Z. K. Gerechter-Amitai of the Volcani Center for resistance to stripe rust caused in wheat by *Puccinia striiformis*. In addition, several accession lines from Turkey and populations from Israel were used.

Cultivated wheat. Seventeen wheat cultivars, categorized by their response to virulent isolate IS398A1 of *S. tritici*, were used as comparative checks. The spring bread wheat cultivars were: susceptible cultivars—Barkai (V238-8822-11/Miriam 2), Bet Dagan (Yaktana//Norin 10/Brevor 21-1C/3/Florence Aurore), Lakhish (Yaktana//Norin 10/B21-1C/3/Florence Aurore), and Miriam (Chapingo 53//Norin 10/B26/3/Yaqui 54/4/2* Merav); resistant cultivars—Colotana (CI 13556), Olaf (CI 15930), Klein Titan (CI 12615), and H574-1-2-6. Resistant winter bread wheats included Bezostaya 1(Lutescens 17/Skorospelka 2), Kavkaz (Lutescens 314 H 147/Bezostaya 1), NE 7060 (Favorit/5/Cirpiz/4/Jang Kwang/2/Atlas 66/Commanche/3/Velvet), and Trakia (Bezostaya 1/Elia//Rousalka). Durum wheat cultivars used were: susceptible cultivars—Inbar (D27534/Jori "S"×Langdon 357E-TC^2), Giorgio VZ 331 (Mexican cross/Capelli); resistant cultivars—Nursit 163, and Zenati-Bouteille. The susceptible Australian triticale accession LI 217 was included in the study.

Pathogen. Twenty-one single pycnidium isolates of *S. tritici* were screened for pathogenicity patterns on the comparative cultivar set to which six selected accession lines of wild wheat were added. Twelve of the isolates of *S. tritici* were obtained from bread wheat samples from Israel, Oklahoma, Montana, Morocco, and Tunisia, and nine were from durum wheat samples from Israel, Italy, and Tunisia. All isolates were maintained on malt agar slants at 18 C and were periodically reisolated from leaves of infected seedlings in the greenhouse. *S. tritici* isolate IS398A1 was used as a check isolate in all trials.

Inoculation. For each selected line or wheat cultivar, 20–30 seeds were sown around the periphery of 30 × 30 × 10-cm plastic trays, eight to nine accessions per tray with the cultivar Miriam serving as a check in each tray. Ten-day-old seedlings were inoculated uniformly with a 10^7 spores per milliliter suspension (15 ml per tray) of each isolate (8). The inoculated trays were placed for 72 hr in a humidity chamber equipped with fine-mist humidifier, which was built within a temperature-controlled (18–20 C) greenhouse room. The trays were later removed to benches in the same room for 21 days prior to disease assessment. Disease severity (estimation of maximum pycnidial density of first and second leaves) was visually assessed with the aid of standard drawings (7). In each inoculation trial, isolate IS398A1 of *S. tritici* was used as a check isolate and tested on the comparative cultivar set.

Sixty-five to seventy-five seeds from each bulk population of wild wheat collections were used in the population studies along with the check cultivar Miriam, and the comparative cultivar set.

TABLE 1. Mean pycnidia coverage and regression coefficients of wheat cultivars and wheat progenitors to isolate IS398A1 of *Septoria tritici* compared to the susceptible cultivar Miriam

Wheat cultivars and wild accessions	Genome	Growth habit[a]	Mean pycnidia coverage[b](%)	Regression coefficient[c]
Trakia	*AABBDD*	W	0.7 ± 0.1	−79.9
Bezostaya 1	*AABBDD*	W	2.5 ± 0.9	−78.1
N-163	*AABB*	S	2.5 ± 0.7	−77.9
NE 7060	*AABBDD*	W	3.3 ± 0.9	−77.2
Zenati-Bouteille	*AABB*	S	3.8 ± 0.9	−76.8
Kavkaz	*AABBDD*	W	4.9 ± 0.7	−75.6
Titan	*AABBDD*	S	7.0 ± 0.6	−73.4
H574-1-2-6	*AABBDD*	S	8.8 ± 0.9	−76.1
Inbar	*AABB*	S	27.8 ± 0.9	−52.5
Giorgio 331	*AABB*	S	39.3 ± 0.7	−47.2
Olaf	*AABBDD*	S	40.3 ± 0.5	−39.7
Colotana	*AABBDD*	S	41.3 ± 0.9	−38.8
Triticale LI 217	*AABBRR*	S	72.8 ± 1.0	− 7.7
Barkai	*AABBDD*	S	76.8 ± 1.2	− 3.8
Bet Dagan	*AABBDD*	S	77.0 ± 0.9	− 2.9
Lakhish	*AABBDD*	S	79.9 ± 0.7	− 0.6
Miriam	*AABBDD*	S	80.4 ± 1.0	0.0
Triticum speltoides (Ashdod)	*SS*	S	3.2 ± 0.7	−77.3
T. monococcum boeoticum G-24	*AA*	S	5.3 ± 0.1	−75.3
T. longissimum(Gilat)	S^lS^l	S	22.6 ± 0.9	−57.8
T. dicoccoides G-7-2-4	*AABB*	S	31.0 ± 0.9	−44.4
T. tauschii 0.18B	*DD*	S	39.4 ± 0.7	−41.0
T. turgidum dicoccoides G-40-2B-1	*AABB*	S	58.9 ± 1.0	−21.3

[a] W = winter wheat and S = spring wheat.
[b] The mean pycnidia coverage of primary leaf and standard error.
[c] Computed regression coefficients compared to the regression coefficient (b) of Miriam weighted to zero.

RESULTS

Selection of isolates of *S. tritici*. To study the effect of isolate and cultivar on percent pycnidial coverage, the following regression model was fitted to the data from the individual plants:

$$y = \sum_i a_i I_i + \sum_j b_j V_j + \sum_i \sum_j c_{ij} I_i V_j + d$$

in which:

y is the percent pycnidial coverage for a plant.

I_i (for i = 1,2,...) are a set of dummy variables that represent the isolate associated with the plant. Each isolate, except IS398, is represented by a distinct dummy variable I_i which has the value of one when that isolate is associated with the plant, and otherwise is zero. That is, the coefficient a_i represents the average difference between the percent pycnidial coverage for a plant with isolate i to that of IS398.

V_j (j = 1,2,...) are a set of dummy variables that represent the cultivar of the plant. Each cultivar, except Miriam, is represented by a distinct dummy variable V_j which has the value one when the jth cultivar is present and zero otherwise. That is, the coefficient b_j represents the average difference between plants of the jth cultivar and those of Miriam.

I_iV_j is the product of the dummy variables for the ith isolate and jth cultivar. It is zero unless both the ith isolate and jth cultivar are present in the plant (when it is one). When the coefficient c_{ij} is zero, it indicates that the effects of the isolate and cultivar are additive (or independent).

d is the intercept of the regression equation.

a_i, b_j, c_{ij} (for i = 1,2,..., and for j = 1,2,...) are the slopes of the regression lines and are described above.

The percent pycnidial coverage (y) is the average coverage of several plants. Different numbers of plants were recorded under the varying conditions. Therefore, the variance of y is inversely proportional to the number of plants used to compute the average. As a result, when fitting the regression model, the number of plants were used to weight each average in the estimation of the coefficients and sums of squares.

Coefficients of the regression model (for comparing the relevant values of a_i, b_j, c_{ij} and d) were estimated by the computer program BMDP9R (10). The negative coefficients (b) indicate the response of a specific cultivar relative to that of the susceptible response (b = 0) of Miriam (Table 1). A large negative regression coefficient indicates a low percent pycnidial coverage.

Severity classes were established on the basis of the response of the cultivars to isolate IS398, separated into two groups based on the regression coefficient (b) of 50.0, which corresponded to about 30% pycnidial coverage (resistant 0–30%, susceptible >30%).

Seven of the twenty-one isolates of *S. tritici* that expressed distinct differential response on the comparative cultivar set and on the wild wheats were selected for further studies. The isolates screened were as follows: IS398A1 (isolated from the bread wheat Hazera 84, Israel), IS7901 (from Hazera 895, Israel), IS8036 (from Hazera 895, Israel), MT-3 (from A. L. Scharen, Montana), TUN8051 (bread wheat Tunisia), IS7798 (durum land cultivar, Israel), and IS8046 (from the durum wheat cultivar Inbar from Israel).

A factorial analysis of variance (cultivars, isolates, and trials) was used to analyze interactions among the different components. The interaction between the seven selected isolates and the 17 cultivars was statistically highly significant ($F = 1,851.8$). A test for the repeatability of the method was conducted by analyzing the interaction between isolates × trials, which resulted in nonsignificant interaction ($F = 2.71$) while the interaction between cultivars × trials indicated a statistically significant value ($F = 4.56$).

The durum wheat cultivar Zenati-Bouteille was resistant to all seven isolates (Table 2). The durum wheats Inbar and N. 163 were susceptible only to isolates originating from *T. durum* (IS7798 and IS8046). Cultivars Bezostaya 1 and Kavkaz, which have common parentage, were susceptible to IS8036 and MT-3 while Trakia, which contains Bezostaya 1 germplasm, expressed a different pathogenicity pattern. The Brazilian accession H574-1-2-6 (obtained from R. M. Caldwell, Purdue University) and the Argentinian cultivar Klein Titan were highly resistant to most isolates. The susceptible Israeli commercial wheats (Barkai, Bet Dagan, Lakhish, and Miriam) were resistant to the *S. tritici* isolate from Montana (MT-3) and to another from Oklahoma (OK 80-17).

Response of wild wheat populations. Eleven bulk populations of wild wheats: four *Triticum longissimum*; two *T. sharonensis*; one *T. speltoides* and four *T. turgidum dicoccoides*, collected from different geographic locations in Israel, were inoculated with the seven isolates of *S. tritici*. The mean pycnidia coverage on the 11 bulk populations indicated different pathogenicity patterns among the isolates (Table 3). Standard errors in Table 3 reveal that some populations were uniformly resistant or susceptible to specific isolates of *S. tritici*, whereas other populations were heterogeneous. Nine of the bulk populations were highly resistant to isolate MT-3 (Table 3). Variation in four populations is presented in Fig. 1A to D, where the population response was expressed for both pycnidia coverage percentage and the corresponding response classes (VR to S) as established for isolate IS398A1 of *S. tritici* in Table 1. Two types of population × isolate interactions were expressed: one in which only two distinct response groups occurred, resistant and susceptible (ie, *T. longissimum* from Givat Brenner to isolates IS8046 and MT-3 (Fig. 1A), which may indicate a low number of interacting genes; and one in which there was a continuous array of resistant, intermediate, and susceptible responses of the population to specific isolates (ie,

TABLE 2. Cultivar seedling response to selected *Septoria tritici* isolates of diverse origin, based on pycnidia coverage

Wheat cultivar	Growth habit	*S. tritici* isolate						
		IS398[a]	IS7901	IS8036	MT-3	TUN8051	IS7798	IS8046
Zenati Bouteille	TDS[b]							
Inbar and N163	TDS						S[c]	S
Giorgio 331	TDS	S				S	S	S
Bezostaya 1 and Kavkaz	TAW			S	S			
Trakia	TAW		S	S				
NE 7060	TAW		S	S		S		
H574-1-2-6	TAS		S					
Klein Titan	TAS		S			S		
Colotana	TAS	S	S	S		S		
Barkai and Miriam	TAS	S	S	S		S	S	
Bet Dagan and Lakhish	TAS	S	S	S		S		S
Olaf	TAS	S	S	S	S	S		S
LI 217	TCL	S	S	S		S		S

[a] Isolated from bread wheat: IS398A, IS7901, IS8036, MT-3, and TUN8051; from durum wheat: IS7798 and IS8046.
[b] TDS = spring durum wheat; TAW = bread winter wheat; TAS = bread spring wheat; TCL = triticale.
[c] Susceptible host response (pycnidia density >30%); blanks = resistant host response (pycnidia density <30%).

TABLE 3. Mean pycnidia coverage of populations of wild wheats inoculated with seven isolates of *Septoria tritici*

Triticum species	Source	Mean pycnidia coverage (%) of isolates of *S. tritici*						
		IS398A1	IS7901	IS8036	TUN8051	MT-3	IS7798	IS8046
Triticum longissimum	Beit Lid	4.7 ± 0.7[a]	12.2 ± 2.3	3.4 ± 0.3	5.7 ± 0.3	0.6 ± 0.1	3.6 ± 0.5	2.2 ± 0.4
T. longissimum	Givat Brenner	0.4 ± 0.2	1.1 ± 0.3	1.4 ± 0.1	1.4 ± 0.2	30.6 ± 4.2	5.3 ± 0.3	25.5 ± 2.8
T. longissimum	Yeruham	25.3 ± 3.6	2.9 ± 0.2	2.2 ± 0.1	16.3 ± 1.4	5.0 ± 0.1	3.4 ± 0.6	25.3 ± 3.6
T. sharonensis	Ashdod	0.2 ± 0.7	4.1 ± 0.8	0.1 ± 0.1	5.2 ± 0.7	0.2 ± 0.1	38.9 ± 5.4	2.1 ± 0.1
T. sharonensis	Kfar Vitkin	23.5 ± 3.1	40.5 ± 3.7	0.2 ± 0.0	27.4 ± 4.4	3.2 ± 0.1	12.3 ± 3.5	13.8 ± 3.1
T. turgidum dicoccoides	Bet Hakerm	30.1 ± 4.7	23.8 ± 3.7	18.9 ± 3.7	46.0 ± 0.2	4.7 ± 0.6	78.8 ± 0.8	13.4 ± 3.7
T. turgidum dicoccoides	Kochav Hayarden	56.9 ± 1.3	39.5 ± 4.5	34.5 ± 3.7	47.9 ± 4.8	49.0 ± 0.2	44.1 ± 5.7	0.3 ± 0.2
T. turgidum dicoccoides	Gamla 1	9.9 ± 1.7	10.8 ± 4.2	24.1 ± 3.7	6.5 ± 0.5	0.4 ± 0.1	5.5 ± 1.2	18.8 ± 2.7
T. turgidum dicoccoides	Gamla 2	25.8 ± 3.4	5.7 ± 0.4	32.3 ± 0.6	5.0 ± 0.6	0.3 ± 0.0	35.7 ± 2.1	28.3 ± 3.7
T. turgidum dicoccoides	Mt. Kabir	23.0 ± 1.2	5.9 ± 1.1	27.3 ± 3.7	25.4 ± 1.5	4.4 ± 0.1	3.4 ± 0.1	48.6 ± 0.5
T. turgidum dicoccoides	Rimonim	24.6 ± 0.9	64.5 ± 1.5	5.1 ± 0.3	23.7 ± 4.0	0.8 ± 0.1	61.3 ± 0.6	40.5 ± 0.5

[a] ± Standard error.

T. longissimum from Yeruham in the arid Negev to isolates IS8046 and IS398 (Fig. 1B), *T. sharonensis* from Kfar Vitkin to isolates IS7091, IS7798, and IS8046 (Fig. 1C), and *T. turgidum dicoccoides* from Gamla in the Golan to isolates IS8046, IS7798, and IS398 (Fig. 1D).

Response of wild wheat accession lines. Of 22 lines of *T. monococcum boeoticum* (genome *AA*) that were tested, only two were susceptible to one (IS7798) of the seven isolates (Table 4). The remaining 20 lines were resistant to all of the isolates of *S. tritici*. Five different pathogenicity patterns were exhibited by seven accession lines of *T. longissimum* of which two lines were from the central coastal plains (Binyamina 679 and Beit Lid), and the remaining from arid regions (Table 4). The five pathogenicity patterns were not associated with geographic regions. The selection of *T. searsii* showed a pathogenicity pattern similar to that of *T. longissimum* collected in Gilat located in the arid Negev. Of the two lines of *T. speltoides* collected on Mt. Carmel range (Mt. Carmel and Technion 7701) the Mt. Carmel and a Turkish line were both susceptible only to an isolate from Tunisia (TUN8051), whereas the latter was susceptible also to isolate IS398. The three *T. tauschii* (= *Ae. squarrosa*) lines exhibited three different pathogenicity patterns; however, all the lines were resistant to isolates MT-3, TUN8051, and IS7798. Fourteen different patterns were exhibited by 47 accession lines of wild emmer (*T. turgidum dicoccoides*) of Israeli (41 lines) and Turkish (six lines) origin. Of the tested wild emmer accessions, 25 (53%) were resistant to all seven isolates of *S. tritici*. The majority of selected wild emmer lines originated from bulk collections from northern Israel and accession G-140-1-1 was secured from an arid habitat in southern Samaria. Some of the pathogenicity patterns expressed on the tetraploid wild emmer lines had been observed previously in some diploid wild wheats. Most of the wild emmer lines were resistant to isolates MT-3 and IS8036 of *S. tritici*, both virulent on Bezostaya 1 and Kavkaz. More than 50% of the lines were susceptible to the two isolates (IS7798 and IS8046) from durum wheat and also to isolate IS7901 from bread wheat.

Analysis of reaction matrices. Assuming that gene-for-gene interactions exist in the system involving *Septoria tritici* and *Triticum* (including triticale), the *Triticum* (wild and cultivated) × *S. tritici* isolates reaction matrices were subjected to the EPIDAT analysis according to an incomplete (17) Person's scheme of cultivar × isolate reaction matrix. This analysis estimates the minimum number of resistance or virulence components (hereafter termed genes) operating in a gene-for-gene system, without a prior knowledge about the genetic composition of the host or parasite. Thus, it permits one to predict genotypes without performing genetic tests. A reaction matrix of 44 wheat lines (27 patterns from 46 wild wheats and 17 cultivated accessions) × seven isolates of *S. tritici* was subjected to the EPIDAT analysis. The reaction matrix analysis estimated the presence of nine corresponding interacting

TABLE 4. Pathogenicity patterns of selected lines of *Triticum* species to seven *Septoria tritici* isolates

Species and lines	Genome	*S. tritici* isolates						
		IS398	IS7901	IS8036	MT-3	TUN8051	IS7798	IS8046
Triticum monococcum[a]	A							
Turkey 7-5							S	
Turkey 8-1							S	
Triticum longissimum	S^l (=B^l?)							
Binyamina 679		S[b]	S					
Dimona						S		
Urim								S
Beit Lid, Sderot, Hebron		S						S
Gilat		S			S	S		
Triticum searsii	S^s(=B^s?)							
Taiyiba		S		S	S	S		
Triticum speltoides	S(=B?)							
Mt. Carmel, G-14 Ceyhan, Turkey					S			
Technion 7701		S				S		
Triticum tauschii (=*Aegilops squarrosa*)								
6619 Ilam Iran	D	S						S
018B K-36 Leningrad		S	S	S				
030 2115-4 Japan				S				
Triticum turgidum dicoccoides	AB							
G-7-2-4,G-40-1-2B-1,[c] G-117-1-1-1-3M,G-487		S	S				S	S
G-7-2-6B-3,G-416-2, G-422-1,G-436-1,G-480-6								S
G-25-4M,G-29-1M,G-90-1-1-BM, G-193-1M,G-194-3M,TUR 7-5								S
G-28-2B-1BM							S	S
G-114-5-7B-1,G-148-1-2M		S					S	S
G-283-10M						S		
G-313-9M,TUR8-15			S			S	S	S
G-314-6,G-410-1-1		S						
G-316-2M					S			
G-332-1-3-5,G-348-M					S			
G-363-4-4B		S	S					S
G-395-7M			S					S
TUR 7-8			S		S	S		S
TUR 7-40			S	S	S	S	S	S

[a] According to the nomenclature of the genus *Triticum* used by Feldman and Sears (10) and Morris and Sears (20).

[b] S = susceptible response (pycnidia density >30%): blanks indicate a resistant host response.

[c] Accession lines with designations preceded by the letter G were collected or selected by Z. K. Gerechter-Amitai of the Volcani Center in Israel and those with designations preceded by TUR originated from Turkey.

resistance and virulence genes in the 44 hosts and the seven isolates of *S. tritici*. Based on the EPIDAT analysis (Table 5), 18 distinct interaction patterns could be derived from the 44 wild wheat accession lines. The number of resistance genes (tentatively designated by the letters *ST* followed by arabic numerals) ranged from eight in some lines of *T. longissimum, T. speltoides*, and *T. turgidum dicoccoides* to one in lines of *T. turgidum dicoccoides* from Israel and Turkey. In the selected comparative cultivar set, 10 distinct interaction patterns could be derived from the 16 bread, durum, and Triticale cultivars (Table 5). As many as seven resistance genes were estimated in the spring bread wheat H574-1-2-6, the same as that estimated for lines of *T. turgidum dicoccoides* G-332-1-3-5 and G-348-M. Six resistance genes were estimated in the Argentinian cultivar Klein Titan (CI 12615) with no matching combination in wild wheat. In the winter wheat Trakia, which possesses Bezostaya 1 germplasm, only two (*ST*1 and *ST*4) of the three resistance genes (*ST*1, *ST*4, and *ST*7) estimated for Bezostaya 1 were indicated. Matching combinations between the durum cultivars Inbar and Nursit 163 were found in the wild emmer line G-28-2B-1BM. Two different resistance genes were indicated in the susceptible Israeli commercial bread wheat cultivars Barkai-Miriam and Bet Dagan-Lakhish each possess common parentage.

The seven isolates of *S. tritici* differed in numbers and combinations of virulence genes (tentatively designated by the italic letters *VST* followed by arabic numerals) (Table 6). Isolate TUN8051, from a bread wheat in Tunisia, possessed seven virulence genes and differed from the Israeli isolates IS398A1, IS7901, and IS8036 secured from bread wheat at three, two, and two loci, respectively. Isolates IS7798 and IS8046 which were secured from durum wheats, did not possess the *VST*7 virulence component. The isolate from Montana (MT-3), despite giving a susceptible reaction with Bezostaya 1, possessed fewer virulence genes than any of the other isolates of *S. tritici* secured from bread wheat. It is significant that isolates TUN8051, IS398A1, and IS7901 lacked the *VST*1 or the *VST*7 virulence genes needed to overcome the seedling resistance of Bezostaya 1-Kavkaz complex since these cultivars are being used as sources of resistance in breeding programs.

DISCUSSION

The considerable genetic variation encountered within populations of wild wheat indicates a large reservoir of genes for reaction interacting with a variable pathogen population. Populations of diploid and tetraploid wild wheats showed different interactive patterns regardless of species, genomes, and geographical sources. Interactive patterns were observed even in populations collected in arid habitats (*T. longissimum* and *T. turgidum dicoccoides*) where infections by *S. tritici* are rare. Little information is available on the occurrence and magnitude of Septoria leaf blotch epidemics in wild *Triticum* species in natural habitats. Pycnidia of *S. tritici* occurred in varying densities in plants of *T. turgidum dicoccoides* at several natural habitats in northern Israel and the Judean foothills (6). The tested accession lines were obtained following selections for resistance to *Puccinia striiformis*, which is more abundant in the cooler northern regions (11); thus, no definite conclusion can be drawn about the association between the frequency of resistance and environmental factors associated with geography.

Protection against powdery mildew in *Hordeum spontaneum* in Israel has shown definite geographic patterns, being more prevalent in cool regions than in hot, dry ones (24). Mendlinger (19) suggests that the large amount of genetic variation present in most of the wild diploid *Triticum* species that he studied (the same Israeli diploid populations examined in this study) might indicate the operation of microhabitat natural selection, or an outcome of frequency dependent selection. The established specific interactions between *Septoria* and wild *Triticum* spp. may serve as a tool for studying the resistance structure and variation in these populations and its association with environmental and climatic factors.

The comparative analysis of interacting host-pathogen matrices assumed a gene-for-gene relationship although there is no direct evidence that such exists in systems involving *Septoria* and *Triticum*. The analysis of severity-dependent response classes hypothesized nine interacting genes common to wild and cultivated *Triticum* species. The Person (17) analysis of the gene-for-gene scheme theory assumes that the presence of a resistance gene can be determined only when compatible and incompatible host responses occur (21). Thus, wild accession lines and cultivars resistant to all seven isolates were initially excluded from the EPIDAT analysis (17). The relatively large number of populations and accession lines of wild wheats that developed uniformly low numbers of pycnidia (resistant host response) in response to infection by the seven isolates of *S. tritici* (most of the accessions from *T. monococcum boeoticum* and 53% of those from *T. turgidum dicoccoides*), is indicative of the magnitude of untapped resistance in the wild wheat relatives. Only durum wheat cultivar Zenati-Bouteille exhibited uniform resistance to all the seven isolates of *S. tritici* (Table 2).

The relatively few predicted resistance genes attributed to winter bread wheat cultivars Bezostaya 1 and Kavkaz is important because they have been used extensively in spring × winter breeding programs (3,6). Isolate IS8036, which was secured from the susceptible wheat cultivar Hazera 895 (which does not possess Bezostaya 1 - Kavkaz germplasm) and isolate MT-3, both being virulent on Bezostaya 1 - Kavkaz germplasm differed in virulence spectrum on all other cultivars. The presence of specific host-pathogen interactions may provide a means for evaluating distributions and frequencies of pathogenicity patterns and facilitating designing strategies in breeding for resistance.

Danon et al (3) estimated the presence of a dominant and (probably) also a recessive gene for resistance to the Israeli isolate IS398A1 of *S. tritici* in Bezostaya 1. It is possible that these resistance genes were those predicted by the EPIDAT analysis as

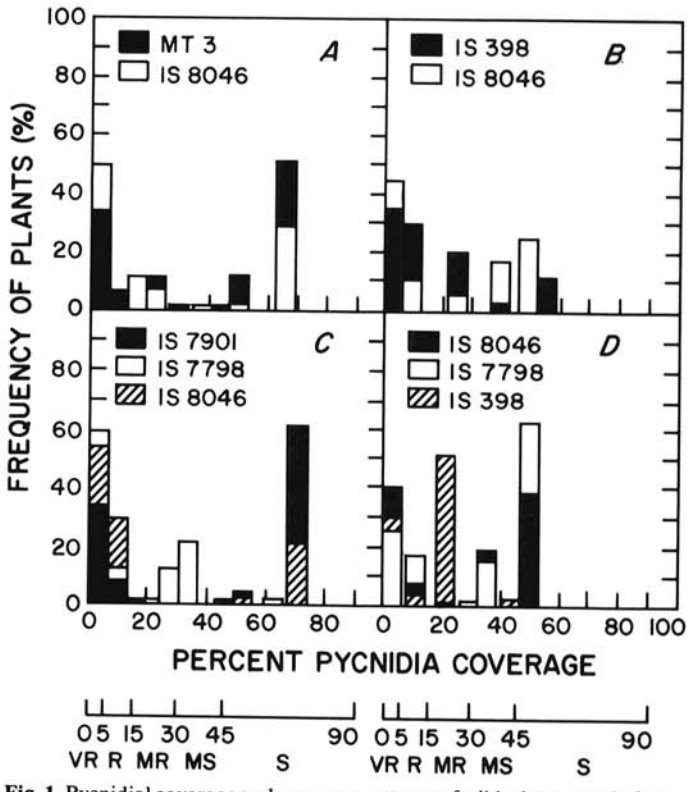

Fig. 1. Pycnidial coverage and response patterns of wild wheat populations from Israel in response to seedling inoculation with specific isolates (see legend with each graph) of *Septoria tritici*. Only resistant and susceptible patterns were detected in **A,** a population of *Triticum longissimum* from Givat Brenner in the coastal plains. An array of resistant, intermediate, and susceptible (respectively) responses were detected in **B,** a population of *T. longissiumum* from Yeruham in the Negev Desert; **C,** a *T. sharonensis* from Kfar Vitkin in the central coastal plains; and **D,** a population of *T. turgidum dicoccoides* from Gamla in the Golan Heights.

TABLE 5. Hypothesized resistance genes derived from analysis of reaction matrix in selected lines of *Triticum* species and wheat cultivars inoculated with seven *Septoria tritici* isolates

Wheat species and accessions	Hypothesized resistance genes								
	*ST*1	*ST*2	*ST*3	*ST*4	*ST*5	*ST*6	*ST*7	*ST*8	*ST*9
Wild wheats:									
T. longissium: Dimona	+[a]	+		+	+	+	+	+	+
T. speltoides: Mt. Carmel, G-14 Turkey	+	+		+	+	+	+	+	+
Triticum dicoccoides[b]: G-283-10M	+	+		+	+	+	+	+	+
T. dicoccoides: G-314-6, G-410-1-1		+	+	+	+	+	+	+	
T. dicoccoides: G-332-1-3-5, G-348-M	+		+	+	+	+		+	+
T. boeoticum[c]: TUR 7-5, TUR 8-1	+	+	+		+			+	+
T. dicoccoides: G-25-4M, G-29-1M, G-90-1-1-BM, G-193-1M, G-194-3M, TUR 7-5	+	+	+		+			+	+
T. longissimum: Urim	+	+	+	+		+			+
T. dicoccoides: G-7-2-6B-3, G-416-2, G-422-1, G-436-1, G-480-6	+	+	+	+		+			+
T. speltoides: Technion, 7701		+		+	+	+	+	+	
T. tauschii: 030 2115-4 Japan	+			+	+	+	+	+	
T. dicoccoides: G-395-7M	+			+	+	+	+	+	
T. longissimum: Binyamina 679			+	+	+	+		+	
T. longissimum: Beit Lid, Sderot, Hebron		+	+	+		+			
T. tauschii: 6619 Ilam, Iran		+	+	+		+			
T. tauschii: 018B K-36 Leningrad				+	+	+		+	
T. dicoccoides: G-28-2B-1BM	+	+	+						+
T. dicoccoides: G-316-2M	+			+			+		
T. dicoccoides: G-363-4-4B	+			+		+			
T. longissimum: Gilat				+			+		
T. searsii: Taiyiba				+			+		
T. dicoccoides: G-114-5-7B-1; G-148-1-2M		+	+						
T. dicoccoides: G-313-9M, TUR 8-15	+								
T. dicoccoides: G-7-2-4, G-40-1-2B-1, G-117-1-1-1-3M, G-487			+						
T. dicoccoides: TUR 7-8, TUR 7-40	+								
Wheat and triticale cultivars:									
Trakia and NE7060	+			+	+	+		+	
Bezostaya 1 and Kavkaz	+			+			+		
N-163 and Inbar	+	+	+						+
Klein Titan	+		+	+	+			+	+
H574-1-2-6	+		+	+	+	+		+	+
Giorgio 331		+							
Olaf				+					
Colotana				+	+	+		+	
Triticale LI 217				+		+			
Barkai and Miriam					+			+	
Bet Dagan and Lakhish				+		+			

[a] Presence of resistance genes based on P. Kampmeijer's EPIDAT (17) analysis of incomplete Person scheme of a variety × isolate reaction matrix.
[b] *Triticum dicoccoides* = *T. turgidum dicoccoides.*
[c] *Triticum boeoticum* = *T. monococcum boeoticum.*

TABLE 6. Hypothesized virulence genes derived from analysis of reaction matrix in seven *Septoria tritici* isolates tested on 44 accessions of bread and durum wheats, wild *Triticum* species, and triticale

S. tritici isolate	Hypothesized virulence genes								
	*VST*1	*VST*2	*VST*3	*VST*4	*VST*5	*VST*6	*VST*7	*VST*8	*VST*9
TUN8051	+[a]	+		+	+	+		+	+
IS398A1		+	+	+	+	+	+	+	
IS7901	+		+	+	+	+		+	+
IS8036	+			+	+	+	+	+	
IS7798	+	+	+		+			+	+
IS8046	+	+	+	+		+			+
MT-3	+			+			+		

[a] Presence of virulence genes based on P. Kampmeijer EPIDAT (17) analysis of incomplete Person scheme of a cultivar by isolate reaction matrix.

*ST*4 and *ST*7. In the same study (3), the presence of at least two recessive genes for resistance to isolate IS398A1 were estimated for the South American bread wheat cultivars Colotana and Klein Titan. The EPIDAT analysis predicted three common resistance genes (*ST*4, *ST*5, and *ST*8) that complement the virulence genes of isolate IS398A1 (Table 5). Genetic tests designed to elucidate and estimate the genes for resistance and virulence in some of the studied wheat lines and isolates of *S. tritici*, respectively, are currently being carried out.

Resistance to Septoria leaf blotch combined with resistance to *P. graminis* and *P. striiformis* and other traits (protein content, drought tolerance, etc.) can be found in *T. turgidum dicoccoides* and diploid wheats (11,12). Accumulating evidence indicates the presence of minor gene resistance to *P. striiformis* in wild emmer populations in Israel (25), some of which were used in the present study.

Using the untapped wild genetic reservoir to improve cereal crops is becoming more attractive, providing that techniques can be found to transfer the qualitative and quantitative genetic entities from the wild wheats into agronomically desirable ones (15,18) without affecting productivity.

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