Assessment of Yield Component Losses Caused in Plants of Spring Wheat Cultivars by Selected Isolates of Septoria tritici

Oded Ziv and Zahir Eyal

Graduate Assistant and Associate Professor, respectively, Division of Mycology and Plant Pathology, Department of Botany, The George S. Wise Center for Life Sciences, Tel Aviv University, Israel.
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ABSTRACT

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Four spring wheat cultivars expressing different levels of loss-response to *Septoria tritici* and of variable height and maturity each were uniformly inoculated separately with four selected isolates of the pathogen that varied in virulence. The progress and severity of the disease, and also yield per head, 1,000-kernel weight, and number of kernels per head were assessed in randomly selected plants within each plot. Losses in yield for each treatment were evaluated by comparing the yield in inoculated plots to that in fungicide-protected plots. The isolates exhibited differential variations in both virulence and aggressiveness based on disease severity and losses in yield on all four wheat cultivars that were tested. The tolerant cultivar Miriam sustained nonsignificant losses in yield (based on measurements of yield components) in spite of leaf blotch severity similar to that of the nontolerant (vulnerable) cultivars Bet Dagan 131 and Barkai. Vulnerable and tolerant cultivars were evaluated on the basis of the linear relationship between losses in yield per head, 1,000-kernel weight, number of kernels per head, and disease severity. The long-term usefulness of tolerance to *S. tritici* for protecting productivity is discussed in relation to other resistance types and wheat breeding methods.

Additional key words: disease resistance, general resistance, selection pressure, epidemiology.

Septoria leaf blotch of wheat (*Triticum aestivum* L.), which is caused by *Septoria tritici* Rob. ex Desm., is a major disease of wheat in many parts of the world (18, 23, 27). Susceptible wheat cultivars may sustain 30-50% losses in yield and produce shrivelled grain unfit for milling (4, 9, 14). Cultivar resistance, chemicals, and suitable agronomic practices are the major means used to control this disease (5, 18, 23). Breeding for resistance is the most promising, but resistant germplasm is scarce and the mode of inheritance is not well understood (3, 7, 11, 21). Little is known about the types of resistance or their manipulation and accumulation (6). These aspects, together with the presence of physiologic specialization of the pathogen (7), are major obstacles in breeding for resistance.

Among the various control measures that have been used, many have given tolerance a high priority (1, 10, 19, 26). Tolerance may be defined as the inherent or acquired capacity of plants that appear susceptible to a disease, to endure disease and avoid severe losses in yield or quality (15, 19). Simons (25) has suggested that tolerance has a significant theoretical advantage over resistance in that new biotypes of a pathogen have no selective advantage over existing types. Tolerant oat cultivars, when subjected to epidemics caused by races of *Puccinia coronata* or by strains of barley yellow dwarf virus did not exhibit specific interactions in race (strain) - yield response (12, 24). In previous studies in Israel, it was shown that susceptible wheat cultivars expressed different levels of losses in yield under severe epidemics of Septoria leaf blotch (6, 28). The tolerant wheat cultivar Miriam consistently showed nonsignificant losses in yield under severe epidemics in several locations and years, whereas nontolerant (vulnerable) cultivars varied among themselves in the degree of yield losses under similar percents of disease severity (6, 28). The purpose of this study has been to assess the relationship between yield components of nontolerant, tolerant, and resistant wheat cultivars to epidemics incited by selected variants of *S. tritici*.

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MATERIALS AND METHODS

Four spring wheat cultivars that expressed different levels of losses in yield under severe epidemics of *Septoria tritici* and also were of variable height and maturity, were grown in 4-m-square field plots. Each experimental plot was separated from adjacent plots by 3-m-wide oat strips to insure against interplot interference. During the 1973-74 trials the following two wheat cultivars were sown: Bet Dagan 131 (Yt//Nrn10/B21 - 1c/3/FA), a vulnerable, dwarf wheat of moderate maturity date; and Miriam (Ch53/2/Nrn10/B26/3/Yq54/4/2Merav), a tolerant semi-dwarf of early maturity. Both cultivars originated at the Volcani Center, Agricultural Research Organization, Israel. The cultivar Bet Dagan 131 was replaced in the 1974-75 trials by the early maturing (equivalent to Miriam) susceptible dwarf cultivar Barkai (V238-8822-11/Miriam2; V238-8822-11=Yt//Nrn10/B21-1c/3/FA). This cultivar also originated at the Volcani Center. The semi-dwarf cultivar Yafit (2193/Ch53-An × Gb56 × An64) which is of moderate maturity date and was originated at the Hazera Seed Co. in Israel, represented resistant wheat as expressed by a sparse coverage of pycnidia (9, 28).

The isolates of *S. tritici* were grown in modified Fries' liquid medium for 8-10 days at 18 C (7). The spore suspensions were adjusted to approximately 1×10^7 spores/ml. Inoculation of the wheat plots was accomplished by uniformly spraying with 400 ml of spore suspension per plot, six or eight times during the season starting at the end of tillering, and repeated at 8- to 10-day intervals thereafter. The spore suspension was applied with a CO_2-operated sprayer fitted with No. 15 DeVilbiss nozzles.

Three isolates of *S. tritici* of different origins and virulence were used during the 1973-74 trials. Isolate 18 originally was isolated from the moderately resistant cultivar Hazera 84, an Israeli selection of the cultivar Son64A-Tzpp/Yq54 × Napo63, grown in the Plateau of Menashe (7). Culture 213 was isolated from Miriam grown in the southern coastal plan of Israel. Isolate 240 was secured in the Judean mountains from a local durum wheat of unknown pedigree. During the 1974-75 trials, isolate 240 was replaced by isolate 336, which was isolated from the resistant winter wheat cultivar Russian (P.I. 94478-1), and was grown at a nursery and artificially inoculated with infested straw. Isolate 18 previously was recorded as virulent on many bread and durum wheats of diversified background (7). Isolate 213 was virulent on the tolerant cultivar Miriam; isolate 240, from local durum wheat, also was virulent on bread wheats.

Experimental treatments, replicated four times, were: (i) inoculation with the four isolates of *S. tritici* (which varied in their origin and virulence), applied separately or in mixtures; (ii) wheat plots in which infested straw was spread at the tillering stage to achieve conditions similar to natural infection; (iii) protected wheat plots with four to five applications of benomyl (600 g/hectare); and (iv) noninoculated, unprotected wheat plots.

Disease development was recorded at the growth stage 10.5.4, according to Feeke's scale (13), on 25 randomly selected wheat plants per plot. The percentage of green leaf area affected with pycnidia of *S. tritici* was assessed for the three uppermost leaves and sheath (8, 9). Prior to harvest, these plants were removed from all plots for assessment of yield components. The yield per head, 1,000 - kernel weight, and number of kernels per head were recorded and analyzed for each of the harvested wheat plants.

RESULTS

Yield components.—Yield and percent losses per head of four wheat cultivars artificially inoculated with selected isolates of *S. tritici* are presented in Table 1. Losses were 53% and 42% during the 1973-74 and the 1974-75 seasons, respectively, following inoculation of the susceptible cultivars Barkai and Bet Dagan 131 with isolate 18. All other isolates, including a mixture of isolates or inoculation with infested straw, caused less drastic effects on the yield of these two wheat cultivars. The yield of the noninoculated control plots in the 1974-75 season was equivalent to that of the fungicide-protected wheat plots. The tolerant cultivar Miriam exhibited insignificant losses in yield/head for all treatments during the two seasons. Inoculation of Miriam with isolate 18 resulted in a yield loss of 10% during the 1973-74 season, while during the 1974-75 season, the yield/head in the fungicide-protected wheat plots was nonsignificantly higher than that of the inoculated treatments. The moderately resistant cultivar, Yafit, exhibited greater loss during the 1973-74 trials in wheat plots inoculated with isolate 240, and significantly lower losses with isolate 18 (Table 1).

Reduction in 1,000-kernel weight of 32% (Table 2) occurred in the vulnerable cultivar Bet Dagan 131 following inoculation with isolate 18; the visible symptom was shrivelled grain. The 1,000-kernel weight for the tolerant Miriam was reduced 13% by isolate 18, but was still 8 g more than that of the vulnerable Bet Dagan 131, which initially had the same 1,000-kernel weight in the fungicide-protected plots. The moderately resistant

TABLE 1. Assessment of losses in yield (grams per head) caused by *Septoria tritici* isolates on spring wheat cultivars grown at Bet Dagan Experiment Station, Israel, during the 1973-74 and 1974-75 seasons

Treatment	g/head	% loss	g/head	% loss	g/head	% loss
1973-74	Bet Dagan 131		Miriam		Yafit	
Treated check[x]	1.38 a[y]	...	1.39 a	...	1.30 ab	...
Isolate 18	0.65 b	53	1.26 a	10	1.27 abc	2
Isolate 213	0.83 b	40	1.46 a	− 4	1.19 bcd	9
Isolate 240	0.82 b	41	1.27 a	9	1.13 cd	13
Infested straw	0.84 b	39	1.37 a	2	1.34 a	− 3
Isolate mixture	0.77 b	44	1.29 a	7	1.10 d	16
1974-75:	Barkai		Miriam		Yafit	
Treated check[x]	1.57 a	...	1.43 a	...	1.46 a	...
Isolate 18	0.91 c	42	1.48 a	− 3	1.34 a	8
Isolate 213	1.05 bc	33	1.46 a	− 2	1.37 a	6
Isolate 336	1.14 b	27	1.47 a	− 3	1.36 a	7
Noninoculated control	1.56 a	1	1.53 a	− 6	1.39 a	5

[x]Treated with 600 g/hectare benomyl.
[y]Values in each vertical column followed by the same letters do not differ significantly at $P = 0.05$ by Duncan's multiple range test.

cultivar Yafit exhibited little loss in 1,000-kernel weight due to infection by isolates of *S. tritici*.

Losses of about 10 kernels/head (30%) resulted from infection by isolate 18 in the cultivar Bet Dagan 131 (Table 3). The number of kernels per head in Miriam was not affected by the pathogen. Yafit exhibited a lower number of kernels per head in the noninoculated, fungicide-protected plots in the 1973-74 trials, than those of the plots inoculated with isolate 18 or infested wheat straw. This cultivar exhibits a low rate of proliferation of lateral tillers, which is expressed in high ratios of central to lateral tillers (28).

Evaluation of disease.—A high density of pycnidia was recorded on upper plant parts in all treatments on the nontolerant wheat cultivars and the tolerant cultivar Miriam (Table 4). Disease severity recorded for isolate 18 was high and similar in both trial years on all cultivars, but those for isolates 213 and 336 were lower during the 1974-75 trial. The pathogen reached the upper plant parts (the three uppermost leaves and sheath) responsible for

TABLE 2. Assessment of losses in 1,000-kernel weight caused by isolates of *Septoria tritici* on spring wheat cultivars at Bet Dagan Experiment Station, Israel, during the 1973-74 and 1974-75 seasons

Treatment	g/1,000 kernels	% loss	g/1,000 kernels	% loss	g/1,000 kernels	% loss
1973-1974						
	Bet Dagan 131		Miriam		Yafit	
Treated check[x]	43.7 a[y]	...	42.8 a	...	36.6 a	...
Isolate 18	29.6 c	32	37.1 c	13	35.4 a	3
Isolate 213	30.3 c	31	39.8 abc	7	36.7 a	0
Isolate 240	32.2 bc	26	37.7 bc	12	35.4 a	3
Infested straw	36.9 b	16	41.1 ab	4	36.8 a	−1
Isolate mixture	31.8 bc	27	39.4 abc	8	35.8 a	2
1974-75						
	Barkai		Miriam		Yafit	
Treated check[x]	39.0 a	...	42.4 a	...	33.7 a	...
Isolate 18	29.3 c	25	39.7 a	6	32.4 a	4
Isolate 213	34.1 abc	13	40.8 a	4	33.0 a	2
Isolate 336	33.2 abc	15	41.7 a	2	32.3 a	4
Noninoculated control	37.6 ab	4	41.1 a	3	34.8 a	−3

[x]Treated with 600 g/hectare benomyl.
[y]Values in each vertical column followed by the same letters do not differ significantly at $P=0.05$ by Duncan's multiple range test.

TABLE 3. Assessment of losses in number of kernels per head caused by isolates of *Septoria tritici* on spring wheat cultivars grown at Bet Dagan, Experiment Station, Israel, during the 1973-74 and 1974-75 seasons

Treatment	No. kernels/ head	% loss	No. kernels/ head	% loss	No. kernels/ head	% loss
1973-74:						
	Bet Dagan 131		Miriam		Yafit	
Treated check[x]	31.6 a[y]	...	32.5 a	...	35.6 ab	...
Isolate 18	22.0 c	30	33.8 a	− 5	36.1 a	− 1
Isolate 213	27.0 b	14	36.5 a	−12	32.6 bc	8
Isolate 240	25.3 bc	20	33.6 a	− 4	31.9 c	10
Infested straw	22.9 b	27	33.2 a	− 3	36.6 a	− 3
Isolate mixture	24.3 bc	23	32.9 a	− 2	31.0 c	13
1974-75:						
	Barkai		Miriam		Yafit	
Treated check[x]	40.3 ab	...	33.7 a	...	48.2 a	...
Isolate 18	31.1 c	23	37.2 a	−10	41.5 b	14
Isolate 213	30.6 c	24	36.1 a	− 7	41.6 b	14
Isolate 336	35.6 bc	12	35.1 a	− 4	42.2 b	12
Noninoculated control	41.4 a	− 3	37.1 a	− 9	40.1 b	17

[x]Treated with 600 g/hectare benomyl.
[y]Values in each vertical column followed by the same letters do not differ significantly at $P=0.05$ by Duncan's multiple range test.

grain filling, and this resulted in high SPC values (Septoria Progress Coefficient). This epidemiological coefficient expresses the relationship between the maximal height (cm) above ground level at which pycnidia of *S. tritici* could be found on green plant tissue (regardless of the severity of the measured plant part), and

TABLE 4. Severity and progress of Septoria leaf blotch caused by *Septoria tritici* on spring wheat cultivars grown at the Bet Dagan Experiment Station, Israel, during the two seasons

Treatment	Severity[w] (%)	Progress coefficient[x]	Severity (%)	Progress coefficient	Severity (%)	Progress coefficient
1973-74:						
	Bet Dagan 131		Miriam		Yafit	
Treated check[y]	1.7 c[z]	0.405 c	1.0 c	0.506 c	0.8 c	0.341b
Isolate 18	73.2 a	0.948 a	67.3 a	0.765 ab	10.8 ab	0.444 a
Isolate 213	59.8 b	0.910 b	57.4 b	0.719 b	14.5 a	0.492 a
Isolate 240	59.8 b	0.925 ab	57.1 b	0.749 ab	11.1 ab	0.454 a
Infested straw	59.7 b	0.916 b	52.8 b	0.784 a	8.1 b	0.471 a
Isolate mixture	65.1 a	0.928 ab	55.4 b	0.737 ab	8.7 b	0.446 a
1974-75:						
	Barkai		Miriam		Yafit	
Treated check[y]	0.7 e	0.708 d	1.0 e	0.716 c	0.9 c	0.747 a
Isolate 18	73.2 a	0.944 a	69.4 a	0.948 a	11.3 a	0.742 a
Isolate 213	45.7 b	0.888 b	31.9 b	0.884 b	4.0 abc	0.729 a
Isolate 336	37.9 c	0.876 b	27.9 c	0.882 b	7.6 ab	0.756 a
Noninoculated control	6.2 d	0.777 c	3.0 d	0.722 c	1.2 bc	0.724 a

[w]Mean pycnidia coverage (%) of flag leaf, flag leaf minus 1, flag leaf minus 2, and sheath.
[x]Septoria Progress Coefficient (SPC): disease height on plant (cm)/plant height (cm).
[y]Treated with 600 g/hectare benomyl.
[z]Values in each vertical column followed by the same letters do not differ significantly at $P = 0.05$ by Duncan's multiple range test.

TABLE 5. The relationships between losses in yield components and disease severity caused by *Septoria tritici* on the wheat cultivars: Barkai, Bet Dagan 131 (BD 131), and Miriam

Treatment	Yield/head		1,000-kernel weight		No. kernels/head	
1973-74:						
	BD 131	Miriam	BD 131	Miriam	BD 131	Miriam
Isolate 18	0.72[x]	0.14	0.44	0.19	0.41	+
Isolate 213	0.67	+[y]	0.51	0.12	0.24	+
Isolate 240	0.68	0.15	0.44	0.21	0.33	+
Infested straw	0.65	0.04	0.26	0.07	0.46	+
Isolate mixture	0.68	0.13	0.42	0.14	0.35	+
Mean ($\bar{x}$)	0.68		0.41	0.15	0.36	
Regression coefficient (b)[z]	0.711		0.433	0.171	0.386	
Correlation coefficient (r)[z]	0.999**		0.983**	0.954**	0.989**	
1974-75						
	Barkai	Miriam	Barkai	Miriam	Barkai	Miriam
Isolate 18	0.57	+	0.34	0.09	0.31	+
Isolate 213	0.72	+	0.27	0.12	0.52	+
Isolate 336	0.72	+	0.39	0.06	0.30	+
Mean ($\bar{x}$)	0.67		0.33	0.09	0.38	
Regression coefficient (b)	0.633		0.322	0.072	0.337	
Correlation coefficient (r)	0.992**		0.993**	0.928**	0.901**	

[x]Ratio expressing: % loss in yield/disease severity.
[y]Recorded gains in yield components in relation to fungicide-protected check plots. Double asterisks (**) indicate a significant correlation, $P = 0.01$.
[z]Regression coefficient (b) in the linear equation: Y=a+bX (X = disease severity; Y=% loss), and the computed correlation coefficient (r).

the height of the wheat plant (cm) at the time of recording (9). This coefficient enables the proper comparison between wheat cultivars of varying height, and indicates the relative progress of the pathogen from the lower to the upper plant parts (28). In cultivar Yafit, the pathogen remained on the lower leaves; the upper plant parts exhibited low pycnidial coverage in all treatments during the two seasons.

Yield loss and disease severity relationships.—Evaluation of the relationship between losses (based on yield components) and disease severity revealed the relative effect of the isolates of *S. tritici* on the wheat cultivars (Table 5). Linear regression analysis was made to determine whether the relationship between yield loss and disease severity corresponded for both the nontolerant and tolerant wheat cultivars. The means of the loss-severity ratios of the different treatments, are very similar to the calculated values of the regression coefficient (b) in the linear equation $Y = a + bX$, where $Y =$ % loss in yield components, and $X =$ disease severity. The expressed loss-severity ratios are markedly higher in all treatments for the nontolerant wheats than those of the tolerant cultivar.

DISCUSSION

Septoria leaf blotch is one of the factors limiting wheat production in Australia, the Mediterranean basin, and certain regions in North and South America (3, 11, 14, 18, 20, 23, 27). The recent discovery of specialized virulence in cultures of *S. tritici* makes dubious the long-term effectiveness of certain resistance types (7). Attention is now shifting to more generalized types of resistance that confer an acceptable level of protection against a broad spectrum of virulences in the pathogen (3, 10, 15, 16, 17). Certain susceptible wheat cultivars can endure high levels of Septoria leaf blotch without sustaining appreciable losses in yield (6, 9, 28). The advantage is that tolerance in the host does not place selective pressure on the pathogen (17, 19). Our data suggest that tolerance of the wheat cultivar Miriam is nonspecific in nature to the damaging effect of the *S. tritici* cultures tested (Tables 1, 2, 3, 4). Thus, the long-term usefulness of tolerance in protecting productivity is strengthened by its ability to alter nonspecifically the consequence of *S. tritici* infection.

The difficulties in detecting and evaluating tolerance can be partly overcome by analysis of the yield loss and disease severity relationships (Table 5). Such an analysis enabled us to evaluate the relative effect on yield by variants of *S. tritici* that differed in virulence and aggressiveness. In agreement with Schafer's concept of tolerance (19), the nontolerant and tolerant wheats sustained different losses in yield under similar disease severity. The relationship between the nontolerant and the tolerant wheat cultivars is determined by the regression coefficients between the two variables (loss and disease severity) for the cutlivars under comparison.

The evidence suggests that tolerance is inherited additively and is polygenic (2, 22, 26). The stability derived from the nonspecific loss response, makes its use attractive to exploit. Difficulties in detection, evaluation and recovery, present technical problems in the incorporation and use of tolerance in common breeding procedures (2, 6, 19). Fuller understanding of the traits that confer capacity to endure disease, their heritability, and breeding techniques for their use, separately and in combination with other resistance systems, will determine its usefulness in the future (15, 17, 19).

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