Inheritance of Tolerance to Septoria Leaf Blotch of Wheat

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ABSTRACT

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The effect of Septoria leaf blotch on yield components and plant height was investigated in parents, segregating populations, and selected lines of crosses between tolerant and nontolerant (Miriam × Bet Dagan 233) and tolerant and moderately resistant (Miriam × Yafit) cultivars. The unselected F_3 and F_4 bulks were susceptible and suffered moderate losses in yield components. Selection in segregating F_3 and F_4 populations produced susceptible semidwarf lines that were as tolerant and high yielding as Miriam under severe Septoria epidemics. Selection for low kernel weight produced dwarf lines with low kernel weight and kernel number that phenotypically resembled the vulnerable dwarf cultivar Bet Dagan 233. Tolerance derived from Miriam seemed to be incompatible with dwarf plant stature. The rapid achievement of tolerance by selection implied a trait controlled by a small number of additive loci. In contrast, the resistance of Yafit appeared to be controlled by the joint action of several loci. Plants of cultivar Miriam and the selected lines from crosses with Miriam maintained high 1,000-kernel weight and yield under dry conditions. Tolerance may represent a compensatory response mechanism to physiological stresses that affect the grain-filling process. Breeding for tolerance appears to be possible if the selection goals are high kernel weight and semidwarf or taller plant stature. Selection for high kernel number per head should be done among promising tolerant lines.

Additional key words: Septoria tritici, Triticum aestivum.

Septoria leaf blotch of wheat, which is caused by *Septoria tritici* Rob. ex Desm., is a worldwide disease that causes appreciable economic loses to wheat crops (19, 20, 24, 29). Germ plasm resistant to *S. tritici*, especially in short-strawed wheats, is not abundant (4).

Little is known about the mode of inheritance, or the manipulation and accumulation of resistance to *S. tritici* (4,8,22). Some susceptible wheat cultivars display tolerance and can endure high levels of Septoria leaf blotch without sustaining appreciable losses in yield (31,32). The rate of Septoria leaf blotch progress on plants of the tolerant cultivar Miriam was similar to that on plants of the vulnerable short-statured cultivars of similar maturity (1).

The continuous stability of the tolerant spring wheat cultivar Miriam under severe Septoria epidemic was due to its nonspecific response in yield components to the damaging effect of the pathogen (32).

Tolerance of some oat cultivars to the crown rust fungus (*Puccinia coronata*) and of wheat cultivars to Septoria glume blotch (caused by *Septoria nodorum*) was attributed to an additive polygenic mode of inheritance (2,27).

The damage caused to the photosynthesizing tissue by Septoria diseases disrupts the grain-filling process (2,4,22). Kernel weight, which is the main yield component affected by the disease, is a useful measure of tolerance in both spaced plants and in regularly spaced plots (2,3,5,18,26).

Selection for tolerance based on kernel weight in segregating diseased populations produced lines with superior kernel weight, but not necessarily higher yields (28,30). Several reports indicated that kernel weight would be the easiest character to improve by direct selection procedures, and that selection for kernel weight could be effective in increasing grain yield (9,10,11,15,25). McNeal et al (14) reported that selection for high kernel weight in the offsprings of the cross of CI 13242 and Thatcher gives increased grain yield accompanied by a decrease in the number of kernels per head. Several reports also indicated that kernel weight and plant height are positively correlated (7,10,16). Brönnimann et al (3) concluded that the original tolerance to *S. nodorum* of the cultivar Zenith is not retained in the mutation-shortened lines.

The objectives of this study were to examine selection methods for tolerance to *S. tritici* in spring wheat and to assess the relationship between tolerance and plant stature.

MATERIALS AND METHODS

Experimental populations were derived by crossing the Septoria-tolerant, early maturing, semidwarf, spring wheat cultivar Miriam (Ch 53//Nrn 10/B26/3/Yq 54/4/2 Merav) with the vulnerable dwarf cultivar Bet Dagan 233 (Yt//Nrn 10/B21-1C/3/FA) and

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with the moderately resistant, semidwarf cultivar Yafit (2193/Ch 53-An × Gb 56 × An 64).

Field trials were conducted for a 5-yr period beginning in 1974 at the Bet Dagan Experiment Station. Parental cultivars; F_2, F_3, and F_4 segregating bulks; and selected lines were grown in a split plot design. The kernels were hand sown 10 cm apart in rows spaced at 20 cm. One of the split plots was inoculated uniformly several times during the season (terminating at the end of the milk state) with a suspension containing 1×70^7 spores of virulent *S. tritici* isolates per milliliter, while the other was protected by several applications of benlate fungicide.

Selections were made in infected and protected F_3 and F_4 bulk populations on the basis of 1,000-kernel weight (TKW). In the infected populations two groups of plants were selected, those with TKW exceeding 40 g and with TKW less than 20 g, while in the protected populations only plants with TKW greater than 40 g were selected.

Parents and selected lines were further tested in advanced generations from infected and disease-free trials. The following data were collected for each plant: disease severity (the percentage of the green area of the top three leaves and sheath covered with pycnidia of *S. tritici* at the early dough stage) and phenotypic traits and yield components (each plant was measured for plant height [cm], yield per head [g], TKW [g], and the number of kernels per head). Data from the four replications were pooled and means and variances for each population were computed.

RESULTS

Table 1 presents the 3-yr record of the parent cultivars and the segregating bulks of the tolerant cultivar Miriam crossed to the vulnerable Bet Dagan 233 and to the moderately resistant Yafit. The averages for yield components and disease severity for the parents, F_3, and F_4 represent 3, 2, and 1 yr, respectively, of observation under both epidemic and disease-free conditions. In the 1976–1977 trials, the F_3 and F_4 populations were tested only under epidemic conditions and their values are not included in Table 1. The correlations between TKW and plant height in both the protected and unprotected segregating bulks were high (0.75–0.81), positive, and statistically significant. The correlations between disease severity and TKW in the infected bulks are small, positive, and not statistically significant (0.01–0.15).

Tables 2 and 3 present the selected lines, unselected bulks, and parent cultivars grown in the 1976–1977 season under *S. tritici* epidemic. The cultivar Miriam retained its tolerance, but the resistance of the cultivar Yafit was not maintained in the 1976 trials (6% pycnidia coverage in 1974 compared to 49% in 1976). Selected lines derived from infected or protected bulks when placed under disease stress showed a large significant gain in TKW over the unselected bulks. Selection for low TKW drastically reduced all yield components.

Realized gains and realized heritabilities of TKW and plant height are shown in Table 4. Realized gain (ΔG) is estimated as the

TABLE 1. A 3-yr summary of the relationship of Septoria leaf blotch of wheat to yield components and plant height of parents and segregating populations of the cross Miriam (tolerant) × Bet Dagan 233 (vulnerable) and Miriam × Yafit (moderately resistant)

Cultivar or lines	Number of years	Yield head		1,000-Kernel weight		Kernels/head		Plant height		Disease severity
		g	loss (%)	g	loss (%)	no.	loss (%)	cm	loss (%)	(%)[a]
Miriam	3	1.97[b]	4[c]	38.3	5	51.9	(−)[c]	103	−1	73
Bet Dagan 233	3	1.51	46*[d]	36.7	34*	40.9	20*	77	−1	77
Yafit	3	1.80	13*	34.2	13*	52.8	(−)	104	−3	27
Miriam × Bet Dagan F_3	2	1.49	1	35.4	7*	41.5	−3	103	5	75
Miriam × Bet Dagan F_4	1	1.62	14*	39.4	16*	41.0	(−)	101	3	68
Miriam × Yafit F_3	2	1.78	17*	42.0	17*	41.5	3	100	5	65
Miriam × Yafit F_4	1	1.60	20*	40.7	18*	39.0	5	97	−9*	60

[a] Mean pycnidia coverage (%) of the green area of the top three leaves and sheath, recorded at the 10.5.4 stage (12).

[b] Values from benlate-protected plots.

[c] Percent loss = [(benlate protected plots − Septoria infected plots)/benlate protected plots] × 100; (−) indicates a loss less than 1%; and asterisks indicate a statistically significant loss, $P < 0.05$.

[d] Single asterisks indicate a statistically significant loss, $P < 0.05$.

TABLE 2. The relationship of Septoria leaf blotch of wheat to yield components and plant height of parents, segregating populations, and selected lines of the cross Miriam × Bet Dagan 233 (1976–1977)

Cultivar or lines	No. of lines	Yield/head (g)	1,000-Kernel weight (g)	Kernels/head (no.)	Plant height (cm)	Disease severity (%)
Miriam		1.70 ± 0.02[a]	33.1 ± 0.3	51.3 ± 0.4	102 ± 0.3	78 ± 0.5
Bet Dagan 233		0.72 ± 0.02	22.9 ± 0.3	31.0 ± 0.6	78 ± 0.5	75 ± 0.6
Miriam × Bet Dagan 233 F_3		1.41 ± 0.05	30.6 ± 0.6	44.7 ± 0.9	95 ± 1.2	79 ± 3.0
Miriam × Bet Dagan 233 F_4		1.54 ± 0.04	32.1 ± 0.6	47.9 ± 1.2	110 ± 1.2	71 ± 0.4
Selected high F_3[b]	11	1.70 ± 0.05	38.6 ± 0.4	44.5 ± 0.7	111 ± 0.6	73 ± 0.7
Selected high F_4[b]	8	1.50 ± 0.05	36.8 ± 0.7	39.9 ± 0.8	111 ± 1.1	72 ± 0.9
Protected F_4[c]	2	1.70 ± 0.05	36.3 ± 0.9	47.4 ± 1.4	102 ± 1.5	75 ± 1.5
Selected low F_3[d]	9	0.85 ± 0.02	21.9 ± 0.4	37.6 ± 0.7	77 ± 0.6	77 ± 0.7
Selected low F_4[d]	3	0.98 ± 0.06	26.1 ± 1.0	36.0 ± 1.3	93 ± 1.5	70 ± 1.2
Mean bulks		1.47 ± 0.03	31.4 ± 0.4	46.3 ± 0.8	102 ± 0.8	75 ± 1.5
Mean high lines[e]		1.63 ± 0.03	37.3 ± 0.4	43.9 ± 0.6	108 ± 0.6	73 ± 0.6
Mean low lines		0.92 ± 0.03	24.0 ± 0.5	36.8 ± 0.7	85 ± 0.8	74 ± 0.7

[a] Standard error.

[b] The average of lines selected from infected bulks of Miriam × Bet Dagan 233 with 1,000-kernel weight > 40 g.

[c] The average of lines selected from protected bulks of Miriam × Bet Dagan 233 with 1,000-kernel weight > 40 g.

[d] The average of lines selected from infected bulks of Miriam × Bet Dagan 233 with 1,000-kernel weight < 20 g.

[e] The average of F_3, F_4 selected high and F_4 protected high lines.

difference between selected lines and their unselected bulks of the 1976–1977 season. The selection differential (SD) is the average of the selected lines minus the average of their unselected bulks in the 1975–1976 season. Realized heritability (h^2) is estimated as realized gain in current generation divided by selection differential in the parental generation ($h^2 = \Delta G/SD$). Realized heritability is the proportion of the selection intensity that is realized in the following generation (6).

In the cross between Miriam and Bet Dagan 233, selection for high TKW in both infected and protected bulk populations resulted in significant gains in the selected lines with heritability values of 0.70–0.85. Selection for low TKW sharply reduced this character in the selected lines with heritability values of 0.47–0.62. Similar results were obtained for the cross between Miriam and Yafit.

Selected lines, their parent cultivars, and two leading commercial cultivars Barkai (early maturing, short strawed [70 cm]) and

TABLE 3. The relationship of Septoria leaf blotch of wheat to yield components and plant height of parents, segregating populations, and selected lines of the cross Miriam × Yafit (1976–1977)

Cultivar or lines	No. of lines	Yield/head (g)	1,000-Kernel weight (g)	Kernels/head (no.)	Plant height (cm)	Disease severity (%)
Miriam		1.70 ± 0.02[a]	33.1 ± 0.3	51.3 ± 0.4	102 ± 0.3	78 ± 0.5
Yafit		1.28 ± 0.02	26.6 ± 0.3	48.9 ± 0.8	105 ± 0.3	49 ± 1.2
Miriam × Yafit F_3		1.43 ± 0.05	30.4 ± 0.8	46.6 ± 1.2	106 ± 2.0	70 ± 1.4
Miriam × Yafit F_4		1.57 ± 0.04	32.0 ± 0.5	48.7 ± 0.7	113 ± 1.4	61 ± 1.1
Selected high F_3[b]	14	1.28 ± 0.03	34.4 ± 0.4	37.5 ± 0.5	116 ± 0.5	69 ± 0.7
Selected high F_4[b]	11	1.47 ± 0.03	36.7 ± 0.4	39.3 ± 0.6	119 ± 0.7	55 ± 1.1
Protected F_3[c]	19	1.44 ± 0.02	35.0 ± 0.3	41.1 ± 0.5	111 ± 0.7	73 ± 0.7
Protected F_4[c]	6	1.59 ± 0.08	38.3 ± 1.0	41.7 ± 1.8	106 ± 1.3	72 ± 1.4
Selected low F_3[d]	4	0.65 ± 0.03	19.1 ± 0.6	32.8 ± 1.0	77 ± 0.9	82 ± 0.8
Selected low F_4[d]	4	0.75 ± 0.04	22.1 ± 0.8	32.9 ± 1.0	83 ± 0.9	63 ± 1.7
Mean bulks		1.50 ± 0.03	31.2 ± 0.5	47.2 ± 0.7	110 ± 1.2	66 ± 0.8
Mean high lines[e]		1.44 ± 0.02	36.1 ± 0.3	39.9 ± 0.5	112 ± 0.4	67 ± 0.5
Mean low lines		0.70 ± 0.03	20.6 ± 0.5	32.8 ± 0.7	80 ± 0.6	72 ± 0.5

[a] Standard error.

[b] The average of lines selected from infected bulks of Miriam × Yafit with 1,000-kernel weight > 40 g.

[c] The average of lines selected from protected bulks of Miriam × Yafit with 1,000-kernel weight > 40 g.

[d] The average of lines selected from infected bulks of Miriam × Yafit with 1,000-kernel weight < 20 g.

[e] The average of F_3, F_4 selected high and F_3, F_4 protected high lines.

TABLE 4. Realized gain and realized heritability of 1,000-kernel weight and plant height in two crosses with the wheat cultivar Miriam (1976-1977)

	Miriam × Bet Dagan 233						Miriam × Yafit					
	1,000-Kernel weight			Plant height			1,000-Kernel weight			Plant height		
Lines	ΔG[a]	SD[b]	h^2[c]	ΔG	SD	h^2	ΔG	SD	h^2	ΔG	SD	h^2
Selected high lines F_3	8.0	10.8	0.74	16	7	2.30	5.0	10.1	0.50	9	15	0.60
Selected high lines F_4	4.7	9.6	0.70	2	10	0.20	4.4	8.8	0.50	6	10	0.60
Protected lines F_3	...[d]	...	...	...	...	...	4.9	7.6	0.64	5	7	0.71
Protected lines F_4	6.2	7.3	0.85	−7	3	−2.30	6.3	10.5	0.60	−7	11	−0.64
Selected low lines F_3	−8.7	−14.1	0.62	−18	−27	0.67	−11.0	−19.2	0.57	−29	−26	1.12
Selected low lines F_4	−6.0	−12.7	0.47	−16	−11	1.40	−11.0	−14.2	0.77	−30	−32	0.94
Mean high lines	6.3	9.2	0.68	4	7	0.55	5.2	9.2	0.56	3	11	0.30
Mean low lines	−7.4	−13.4	0.54	−17	−19	0.90	−11.0	−16.7	0.66	−30	−29	1.02

[a] The realized gain due to selection (ΔG); the difference between the mean of all the selected lines and the mean of the unselected 1976–1977 bulk populations.

[b] The selection differential (SD); the difference between the mean of the selected parents and the mean of the 1975–1976 bulk population from which they were drawn.

[c] The realized heritability = ΔG/SD

[d] No selection was made in the F_3 protected bulk.

TABLE 5. Yield components of wheat parents and selected lines in the Septoria leaf blotch epidemic in 1976 and in the disease-free drought conditions in 1978

	1,000-Kernel weight			Kernels/head (no.)			Yield/head (g)		
Cultivar or lines	1976[a]	1978[b]	Δ[c]	1976	1978	Δ	1976	1978	Δ
Miriam	33.1	37.3	4.2 ± 0.5	51.3	48.0	−3.3 ± 0.7	1.70	1.79	0.09 ± 0.03
Bet Dagan 233	22.9	27.9	5.0 ± 0.9	31.0	38.4	7.4 ± 0.7	0.72	1.08	0.36 ± 0.04
Yafit	26.6	27.6	1.0 ± 0.9	48.9	47.6	−1.3 ± 1.3	1.28	1.28	0.00 ± 0.04
Miriam × Bet Dagan 233 — high lines[d]	39.1	42.4	3.3 ± 1.7	41.9	41.4	−0.5 ± 2.0	1.64	1.77	0.13 ± 0.10
Miriam × Yafit — high lines[d]	38.6	47.0	8.4 ± 1.5	40.9	37.8	−3.1 ± 2.0	1.58	1.77	0.19 ± 0.11
Barkai[e]	...	29.9	...	...	43.1	...	...	1.30	...
Lakhish[e]	...	38.7	...	...	36.9	...	...	1.43	...

[a] Means of yield components from Septoria-infected yield trials in 1976.

[b] Means of yield components from disease-free yield trials in 1978.

[c] The differences (Δ) between the values for 1976 and 1978 plus-minus their standard errors.

[d] Selected F_4 (F_5) lines and their selected F_6 (F_7) sublines.

[e] Commercial cultivars Barkai (early maturing, short strawed [70 cm]) and Lakhish (moderate maturity, semidwarf [100 cm]) were grown only in the 1978 season.

Lakhish (moderate maturity, semidwarf [100 cm]) were grown under disease-free conditions in the 1978–1979 season. Yield components of these lines and their 1976 counterparts under Septoria epidemic conditions are presented in Table 5. The 1978 high lines come from six superior F_3 and F_4 lines of the Miriam × Bet Dagan 233 cross and from seven superior F_4 lines of the Miriam × Yafit cross. These superior lines were selfed for two generations and produced 11 (F_6) lines from the cross Miriam × Bet Dagan 233 and 16 (F_5 and F_6) lines from the cross Miriam × Yafit. Several lines of both crosses maintained or exceeded the tolerant cultivar Miriam in yield and TKW, yet with lower number of kernels per head, under both Septoria epidemic and disease-free conditions. The commercial cultivars Barkai and Lakhish had lower yield components than Miriam under the adverse dry conditions of 1978.

DISCUSSION

Susceptible wheat cultivars that were able to endure the damaging effects of Septoria diseases are classified as tolerant (2,4,18,21,26).

Difficulties in detection, transmission, and utilization of tolerance in breeding programs have not been overcome (2,18,21,32).

Maintenance of high kernel weight under severe Septoria epidemics reflects tolerance to the disease (31). The results in Table 1 further suggest that TKW maintenance under Septoria leaf blotch epidemics can be used as a selection criterion when breeding for tolerance.

The segregating populations afford an interesting comparison between tolerance and resistance. The F_3 and F_4 bulks show some degree of tolerance judging by their intermediate percentage losses. These reduced losses are accompanied by as high a pycnidial coverage as that of the tolerant cultivar Miriam or the vulnerable cultivar Bet Dagan 233. The resistance of Yafit is virtually lost in the Miriam × Yafit cross. Apparently resistance of Yafit requires the joint action of a number of loci, whereas tolerance in Miriam appears to be controlled by additive loci.

TKW in the selected lines diverges markedly from the average of the unselected bulks (Tables 2 and 3). Selection for high TKW appears to be equally effective in populations exposed or unexposed to Septoria leaf blotch. Yield performance of the high lines under high disease coverage is as good as that of the tolerant parent Miriam. Average plant height has increased slightly in the high-TKW lines and has declined sharply in the low-TKW lines. One generation of selection for high-TKW has produced high lines that yield as well as Miriam and low-TKW lines that resemble the vulnerable cultivar Bet Dagan 233 in yield components and plant height. Selection for high-TKW has produced high-TKW lines very similar to each other that somewhat exceed Miriam in both traits. Selection for high-TKW in segregating bulks of the cross Miriam × Yafit, significantly increased TKW in the selected lines. However, in this cross the number of kernels per head and yield per head was significantly lower than those of Miriam under the Septoria epidemic (Table 3). This reduction is mainly due to a low rate of head proliferation of lateral tillers in the cultivar Yafit (31). The selected low-TKW lines are very similar to each other and strikingly resemble the vulnerable dwarf Bet Dagan 233 (Tables 2 and 3). Since a single generation of selection for high (or low) TKW can seemingly produce tolerant (or vulnerable) semidwarf (or dwarf) lines, expression of TKW under Septoria epidemics would appear to be governed by a small number of additive loci, and quite conceivably by a single locus. These results are in contrast with the reports for *S. nodorum* in wheat (2) and for *P. coronata* in oats (27), that tolerance is governed by a large number of contributing loci.

The realized heritability values reported in this work (Table 5) are in good agreement with theoretical estimates of TKW in both crosses, and with heritability estimates for TKW in both diseased and nondiseased trials reported elsewhere (2,13,23,27).

Yield per head in a Septoria leaf blotch epidemic is clearly related to plant height. An examination of the infected segregating bulks revealed that plants with dwarf stature (<70 cm) had poor yield, but plants with high TKW (>40 g) and high kernel number (>50 kernels per head) could be found among semidwarfs. Bahat et al (1) reported that pycnidia of *S. tritici* appear on the leaves of a dwarf cultivar immediately after the leaves emerged from the sheath, while in the semidwarf cultivars of similar receptiveness there was a 10–20 day lag between leaf emergence and pycnidia formation. The association between vulnerability to Septoria leaf blotch and dwarfness may be the result of a longer pathogen stress exerted on the receptive photosynthesizing tissue of the dwarf cultivars prior to and during grain filling. Those considerations lead to an improvement program that would first screen for tolerance using high kernel weight as a criterion and only aim for semidwarf plant stature with large kernel number per head. These results concur with those of Brönnimann et al (3) and suggest that a program for tolerant-dwarf cultivars would not be likely to succeed for either Septoria glume blotch or leaf blotch diseases.

Several of the superior F_3 and F_4 high lines were tested under disease-free conditions in 1978, which was a rather dry season. The depressed yields in 1978 are in fact due to drought, and it is of interest that Miriam and its high-TKW lines exhibit tolerance to these adverse conditions. The stability in yields of the high-TKW lines are comparable to those of Miriam for 1976 and 1978: under the Septoria leaf blotch epidemic in 1976 and the disease-free (but dry) conditions in 1978 (Table 5). The high-TKW lines are clearly as well buffered as Miriam. Lines from both crosses display (relative to Miriam) increased TKW which is offset by reduced numbers of kernels per head, but additional selection can improve the latter trait (11,14,17). Indeed, one line from the Miriam × Bet Dagan 233 cross exceeded Miriam in both yield components. Pinthus and Millet (17) also show that differences in individual kernel weight and number of kernels per head in certain cultivars were not necessarily negatively correlated.

The susceptible spring wheat cultivar Miriam and selected high-TKW lines from crosses with this cultivar responded similarly to Septoria stress and drought, retaining high yield components (Table 5). The genetically controlled endurance of yield components of tolerant cultivars may represent a general compensatory response mechanism that results in the stability in performance of these cultivars under stress conditions.

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