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Genetical and Biological Control of Septoria Diseases of Wheat

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Contents

ABSTRACT

1. A combined effort was directed toward the development of methodology, germplasm and concepts which enable the elevation of the level of protection of wheat agianst the adverse effect of septoria diseases on wheat productivity.

Methods were evaluated by which the chemical desiccant, magnesium chlorate, could be used as a simulator of postanthesis stress exerted by septoria tritici blotch. Wheat cultivars were identified which express endurance in kernel weight to both biotic (septoria tritici blotch) and abiotic (chemical desiccation) stresses. The effect of these stresses on processes involved in kernel growth and mobilization of assimilates from the affected source to the sink was evaluated. It is possible that tolerant cultivars have a capacity to mobilize assimilates from reservoirs and non-affected tissue and maintain the rate and duration necessary to endure the efect of those stresses.

Wheat cultivars differ in the rate by which the photosynthesizing tissue is being depleted in septoria-affected plants. Infrared thermometry is capable of sensing plant canopies and assessing the relative resistance of wheat cultivars to Mycosphaerella graminicola. Wheat cultivars differ in their capacityto retain residual green leaf tissue under septoria-stress. Cultivars which maintain a high green leaf area, despite severe septoria coverage are capable of continuing to produce and mobilize assimilates for kernel growth.

Investigations onm the protection of crop yield through low disease coverage (resistance), endurance of yield components (tolerance) and biological control were pursued in this project.

Effective resistance to septoria tritici blotch was revealed in winter and spring bread wheats and in durum wheats. The inheritance of

resistance in bread and durum wheats was assessed to virulences in the co-operating Institutions. Biological antagonists were isolated which were able to significantly reduce the development of M. graminicola symptoms.

A method was developed to assess virulence patterns in the sexual state of M. graminicola and relate the findings to the efect of the sexual state on the virulence spectrum of the asexual state.

GENETICAL AND BIOLOGICAL CONTROL OF SEPTORIA DISEASES OF WHEAT

2. Introduction

Septoria tritici botch of wheat incited by the fungus Mycosphaerella graminicola (Fuckel) Schroeter (anamorph, Septoria tritici Rob. ex Desm.) and septoria nodorum blotch of wheat caused by Leptosphaeria nodorum E. Muller (anamorph, Septoria nodorum (Berk.) Ber.) have been studied considerably in recent years because of the damage they cause to wheat in several parts of the world (1, 3). Vulnerability of wheat to the diseases has been enhanced by the wide-spread adoption of susceptible cultivars and by changes in cultural practices (1).

Breeding for disease resistance is the most economical control measure, yet little is known about its utilization and the mode of protection and its durability. The effectiveness of the limited resistance sources is being threatened by the diversity of virulence in both pathogens (2, 4).

The utilization of lasting protection hs been hampered by deficiency in methodology for its incorporation and understanding of its mode of action (1). Alternative protection measures (biological control) have been suggested to reeduce the increasing use of fungicide in the wheat management systems (3). Biocontrol agents of the pathogens of the phyllo-plane would offer a distinct advantage in reducing losses and pollution of the environment,if operative.

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3. RESULTS AND DISCUSSIONS

Chemical desiccation of Wheat Plants as a Simulator of Postanthesis Speckled Leaf Blotch Stress by M. Zilberstein, A. Blum and Z. Eyal (enclosed)

The Effect of Septoria tritici Blotch and Chemical Desiccation on Grain Filling of Spring Bread Wheat by Z. Eyal (enclosed)

The Effect ofSeptoria tritici Blotch on Wheat Productivity by Z. Eyal (enclosed)

Infrared Thermal Sensing of Plant Canopies as a Technique to Assess the Relative Resistance of Wheat Cultivars to Mycosphaerella graminicola by A. Blum and Z. Eyal (enclosed)

The Development of Agronomic Breeding Lines which Possess Combined Resistance and Tolerance to Septoria tritici Blotch of Wheat by Z. Eyal. (enclosed)

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3.1

Resistance

Chemical Desiccation of Wheat Plants as a Simulator of Postanthesis Speckled Leaf Blotch Stress

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ABSTRACT

Zilberstein, M., Blum, A., and Eyal, Z. 1985. Chemical desiccation of wheat plants as a simulator of postanthesis speckled leaf blotch stress. Phytopathology 75:226-230.

Field trials were conducted over 2 yr to evaluate whether the postanthesis destruction of the photosynthetic source by chemical desiccation may be used to detect wheat cultivars that sustain kernel growth in the presence of speckled leaf blotch. Spring wheat cultivars of diverse origin were subjected to three treatments: inoculation with virulent isolates of *Septoria tritici* until an epidemic was initiated, postanthesis application of magnesium chlorate (4% a.i.) solution to destroy most of the plant's green tissues, and a control in which a fungicide was applied to protect against loss of green tissue. Grain yield components, kernel growth curves, and harvest index were determined. The progress of the pathogen on the four uppermost leaves was monitored at weekly intervals. For similar Septoria progress values (area under the disease progress curve), various cultivars manifested different rates of loss in kernel weight (as percent of the fungicide-treated control), and harvest index. Cultivars differed in the rate of loss in kernel weight and harvest index when treated with the chemical desiccant. Significant correlations were revealed across the same five cultivars in losses in kernel weight between plants infected by *S. tritici* and those that had been chemically desiccated in 1 yr ($r = 0.925$) but not in the other ($r = 0.804$). Correlation between the two parameters was highly significant ($r = 0.626$) across 16 (out of 18) cultivars that had similar Septoria progress values. The correlations in losses in kernel weight between plants infected by *S. tritici* and those that had been mechanically defoliated (postanthesis) in the five cultivars in 1981-1982 were $r = 0.733$. The potential for utilizing postanthesis chemical desiccation as a measure for revealing wheat cultivars tolerant to speckled leaf blotch in the absence of infection by *S. tritici* is discussed.

Additional key words: tolerance, *Triticum aestivum*, yield components.

Speckled leaf blotch, which is caused in wheat by the fungus *Septoria tritici* Rob. ex Desm. (perfect state: *Mycosphaerella graminicola* (Fuckel) Schroeter), may impose severe limitations on crop yield. In certain environments and years the impact is more pronounced than in others (7).

Under certain environments, early buildup of infection by *S. tritici* on lower plant parts may adversely affect root biomass and plant development (19). Early infection of lower leaves also may reduce yield, especially by altering sink development (the number of tillers per plant, the number of spikes per plant, and the number of grains per spike) and consequently affect assimilate distribution (16,17,19).

Infection of the upper plant parts that are responsible for grain filling is considered to be the most significant factor contributing to losses in yield (18). Infection on upper plant parts usually affects kernel weight and grain number (6,9,22,24). The magnitude of reduction in yield components depends on the pre- and postanthesis level of disease affected plant tissues, disease progress relative to plant growth stage, and cultivar response to disease stress (1,5,18). Wheat cultivars of similar phenotypic characters may express differential loss in yield under similar apparent disease severity and disease progress (4,22–24). Wheat cultivars may vary in ability to endure (tolerate) severe Septoria epidemics without sustaining significant losses in yield when compared to vulnerable (nontolerant) cultivars (5). This endurance or the tolerance of plants to pathogen-generated stress (10,11,14), though widely mentioned, is poorly understood. One of the major obstacles in evaluating plant responses to disease stresses relates to the inherent difficulties in establishing equivalent disease stresses across cultivars and characterizing the nature and magnitude of the imposed stresses. Accumulating evidence suggests that wheat genotypes vary in capacity to utilize stored assimilates as a source for kernel growth in the absence of postanthesis photosynthesis (2,3,20,21). The differential capacity of wheat cultivars to sustain translocation-based kernel growth in the absence of transient photosynthesis was revealed (3) through postanthesis destruction of the photosynthetic source by chemical desiccation. Since the major effect of postanthesis infection by *S. tritici* is expressed by reduction in the photosynthetic source, it was hypothesized that postanthesis chemical desiccation of the wheat canopy may simulate a uniform disease stress in testing for tolerance. Tolerance is thus estimated as the plant's capacity to sustain appreciable

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kernel growth following destruction of the photosynthetic source by chemical desiccation or speckled leaf blotch of wheat.

The present study was undertaken to test the possibility that chemical desiccation can be used as a simulator of postanthesis speckled leaf blotch infection in the detection of tolerance to the disease.

MATERIALS AND METHODS

The experiments were conducted at the Bet-Dagan Experimental Farm during the 1979-1980 and 1981-1982 growing seasons. Eight spring wheat (*Triticum aestivum* L.) cultivars (commercial and advanced lines) and 18 wheat cultivars, were tested in the first and the second year, respectively. All cultivars were of similar phenology and growth habit. Five wheat cultivars susceptible to *S. tritici* were included in both years: the early-maturing, dwarf (75-cm) cultivar Barkai (V238-8822-11/Miriam 2), the early-maturing semidwarfs (95-cm): Ceeon (Yaktana $65A^3$//Norin 10/Brevor), Hazera 337 (Inia "S" × Sonora 64-Tezanos Pentos Precoz/Yaqui 54), Miriam (Chapingo 53//Norin 10/Brevor/3/Yaqui 54/4/2 Merav), and the somewhat later-maturing (by 10 days) semidwarf cultivar Lakhish (Yaktana//Norin 10/Brevor/3/Florence Aurore). The experimental design was in split plots, with treatments in main plots and cultivars in subplots in four replications. Each subplot was 2 m wide and 12 m long. The plots were drill-seeded at a 30-cm row spacing. Three treatments were performed on all cultivars: fungicide-protected (three applications of Tilt-Propiconazole, CGA 64250) control, inoculation with *S. tritici*, and chemical desiccation. Speckled leaf blotch epidemics were incited by inoculating the plant canopy weekly with a suspension of 10^7 spores per milliliter starting at the emergence of the flag-minus-2 leaf and finishing at the end of the milk stage. The suspension was prepared from a mixture of virulent isolates of *S. tritici*. Inoculation was performed during rainy days and/or dewy nights by using a low-volume low-pressure sprayer (Ulva 8-Micron Co., Bromyard, England). In the chemical desiccation treatment, magnesium chlorate was used as a commercial formulation (Machteshim Works, Ltd., Beer-Sheva, Israel) 18% active ingredient (a.i.) formulation routinely used for foliar defoliation in cotton (2). The desiccant was applied as a solution of 4% a.i. at a rate of 35 cm^3/m^2. Each cultivar was sprayed once at 14 days after anthesis. The 30-cm row spacing allowed penetration of the spray into the canopy. Weekly assessment of percent disease coverage was initiated on the uppermost four leaves upon the emergence of the flag-minus-2 leaf in 15 randomly selected plants per treatment across cultivars in all replications (8). These plants were marked for disease assessment and later for yield components evaluation.

The five uppermost leaves in 15 randomly selected plants were mechanically defoliated 14 days after anthesis in the untreated fungicide-protected control plots of the five cultivars in all replications (1981-1982 trial).

In the kernel growth studies, 15 main tillers were randomly sampled at weekly intervals between anthesis and the late dough stage, from a population of main tillers with a common anthesis date, in each plot. Disease blotch and kernel number were assessed for each plant separately. Kernel and shoot dry weights were determined for each main tiller after drying for 48 hr at 90 C. Harvest index was calculated as the dry weight ratio of grain to shoot.

RESULTS

Kernel weight. Most of the green tissues were dead within 2 days after the chemical desiccant was applied. Awns, glumes, leaf laminae, and parts of the spike-peduncle and leaf sheaths were bleached and killed. For all practical purposes, the desiccant-treated plants were devoid of photosynthetic source (3). During the 1981-1982 growing season disease progress was somewhat slower than the previous season (1979-1980), with consequent respective lower losses in 1,000-kernel weight (Table 1). Furthermore, the effect of the desiccant on kernel weight was somewhat higher in the 1979-1980 trial than in the 1981-1982 trial. Other than in Hazera 337 and Miriam, the response in kernel weight to speckled leaf blotch was the same for both years. Plants of cultivars Lakhish, Miriam (1981-1982 only), and Hazera 337 (1981-1982 only) sustained less losses in kernel weight due to speckled leaf blotch, chemical desiccation, and defoliation (1981-1982 only) than did cultivars Barkai and Ceeon (Table 1).

In both years, the mean effect of chemical desiccant on kernel weight was greater than the effect of Septoria, most probably due to a more drastic effect and a greater reduction in photosynthetic tissue in the former. Cultivars significantly differed in the rate of kernel weight loss due to chemical desiccation. These differences could be ascribed to differences in mobilization of plant reserves to the kernels (3). The correlation across the means of the five cultivars in percent kernel weight loss between Septoria-infected and chemically desiccated plants was significant in 1979-1980 ($r = 0.925$), but not in the 1981-1982 trial ($r = 0.804$). The relationship between kernel weight loss due to speckled leaf blotch and weight loss due to chemical desiccation across the 18 cultivars tested in 1981-1982 is presented in Fig. 1. The wheat cultivars Hazera 2218 and Hazera 2230 expressed almost a 1:1 loss ratio between Septoria and chemical desiccation under similar disease coverage. Their vulnerability to speckled leaf blotch was higher than that of the nontolerant cultivar Barkai (0.64 loss ratio—Septoria/desiccant). When data for these two cultivars were excluded from the analysis, the association presented in Fig. 1 became statistically stronger ($r = 0.626$**), as compared to $r = 0.478$* for the 18 cultivars.

TABLE 1. The effect of speckled leaf blotch (caused by *Septoria tritici*), chemical desiccation (magnesium chlorate), and defoliation on 1,000-kernel weight in five spring bread wheat cultivars common to the two trials at Bet-Dagan, Israel in 1981-1982

Wheat cultivar	Septoria severity[u] (AUSPC × 10^{-2})		Loss in 1,000-kernel weight (%)				
			S. tritici[v]		desiccant[w]		defoliation[x]
	1979-1980	1981-1982	1979-1980	1981-1982	1979-1980	1981-1982	1981-1982
Barkai	44.7 a	43.0 a[y]	40.4 **	30.3 *	52.8 **	24.4 *	21.1 *
Ceeon	34.2 b	34.1 a	29.7 **	25.0 *	41.7 **	34.7 *	26.5 *
Hazera 337	33.5 b	22.0 b	31.6 **	9.0 ns	39.8 **	30.6 *	1.7 ns
Lakhish	28.7 b	20.8 b	2.3 ns[z]	13.7 ns	18.9 **	18.6 *	9.5 ns
Miriam	30.1 b	25.5 b	21.6 *	10.3 ns	44.3 **	19.0 *	15.6 ns
Mean ± SE	34.2 ± 2.8	29.1 ± 6.3	25.1 ± 6.4	17.7 ± 4.2	39.5 ± 5.6	25.5 ± 3.2	16.7 ± 4.1

[u] Postanthesis Area Under Septoria Progress Curve × 10^{-2} in the inoculated plants.
[v] Percent loss = { [(kernel weight of fungicide protected)−(kernel weight of treated)]/(kernel weight of fungicide protected) } × 100.
[w] Magnesium chlorate (4% a.i.) applied 14 days after anthesis.
[x] Five uppermost leaves were mechanically defoliated 14 days after anthesis.
[y] Means within columns with a common letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.
[z] The abbreviation ns = not significant, and the asterisks (*) and (**) indicate statistical significance $P = 0.05$ and 0.01, respectively, where treated plants were analyzed versus the untreated, fungicide protected control.

The correlation across the means of the five cultivars in percent kernel weight loss between Septoria-infected and defoliated (postanthesis) plants was not significant in 1981-1982 ($r = 0.733$).

Kernel growth. Typical kernel growth curves, as affected by treatments, in two representative cultivars (Miriam [tolerant] and Barkai [nontolerant]) of the same heading date, are presented in Fig. 2. Speckled leaf blotch caused a reduction in kernel growth rate in both cultivars. In Barkai, the pathogen also caused a reduction in kernel growth duration, as compared with Miriam. Chemical desiccation had a greater effect on kernel growth, as compared with Septoria affected plants. It affected both kernel growth rate and growth duration in the two cultivars. The effect of the desiccant was greater in Barkai than in Miriam, especially in the earlier stages of grain development (at ~17–32 days after anthesis). The association across five cultivars between disease progress expressed as Area under Septoria Progress Curve ($\times 10^{-2}$) and losses in kernel growth rate (Area Under Grain Filling Progress Curve [AUGFPC]) in plants affected by *S. tritici* was statistically not significant ($r = 0.621$). The lack of association indicates a differential cultivar response in kernel growth rate and growth duration, namely, some wheat cultivars (Lakhish, Hazera 337, and Miriam) maintained high grain filling rate despite severe Septoria epidemics. The association between losses in kernel growth expressed as AUGFPC in Septoria-affected and chemical desiccation across the five cultivars was $r = 0.497$. This positive, nonsignificant correlation may be due to a differential cultivar loss response in kernel growth rate and growth duration.

Yield components and harvest index. Yield components are often used as indirect selection indices for a high yield potential in wheat breeding. The correlations across cultivars between percent loss in 1,000-kernel weight in Septoria affected plants (as a measure of tolerance) and the potential number of kernels per spike, the potential kernel weight per spike, or the potential 1,000 kernel weight (as indicated by the uninoculated, protected control) were not statistically significant (Table 2). Therefore, tolerance to speckled leaf blotch of wheat in terms of sustained kernel growth in infected plants, appeared to be independent of yield potential or sink size.

Cultivars in the control treatment did not differ in harvest index (Table 3). Septoria and chemical desiccation reduced harvest index, by an average of 16.3 and 22.5%, respectively. For a very similar level of disease severity, the relative reduction in harvest index by the pathogen was less in the three more tolerant cultivars (Hazera 337, Lakhish, and Miriam) than in Barkai and Ceeon. While the relative reduction in harvest index by chemical

TABLE 2. Coefficients of correlation between potential yield components (uninoculated control) and tolerance to speckled leaf blotch (percent loss in 1,000-kernel weight) across cultivars (cvs) in 2 yr

Yield component	Correlation coefficient (r)			
	1979-1980 (8 cvs)[y]	1979-1980 (5 cvs)	1981-1982 (5 cvs)	1981-1982 (15 cvs)
Number of kernels per spike	0.202 ns[z]	−0.016 ns	−0.216 ns	-
Kernel weight per spike	−0.557 ns	−0.494 ns	−0.248 ns	-
1,000-kernel weight	−0.395 ns	−0.539 ns	−0.011 ns	0.007 ns

[y] Number of wheat cultivars tested.
[z] Abbreviation ns = not significant $P = 0.05$.

TABLE 3. The effect of speckled leaf blotch (caused by *Septoria tritici*) and chemical desiccation on harvest index progress in five spring wheat cultivars, compared to fungicide-protected controls. Bet-Dagan Experiment Station, Israel, 1979-1980

Wheat cultivar	Disease severity (AUSPC $\times 10^2$)	Harvest index (control)[w]	Loss in harvest index (%)[x]	
			S. tritici	Desiccant
Barkai	44.7 a[z]	60.1 a	22.3 *[y]	25.9 *
Ceeon	34.2 b	57.0 a	23.5 *	31.9 *
Hazera 337	33.5 b	54.7 a	12.7 ns	16.9 ns
Lakhish	28.7 b	55.1 a	12.8 ns	22.0 *
Miriam	30.1 b	60.9 a	10.3 ns	15.6 ns
Mean ± SE	34.2 ± 2.8	57.6 ± 2.2	16.3 ± 3.1	22.5 ± 2.8

[v] Postanthesis Area Under Septoria Progress Curve $\times 10^{-2}$.
[w] Harvest index = grain yield/shoot yield (Area Under Harvest Index Progress Curve $\times 10^{-2}$).
[x] Percent loss in Harvest Index Progress Curve from anthesis to ripeness.
[y] Means within columns with a common letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.
[z] ns and asterisk (*), not significant and significant, $P = 0.05$, respectively, where plants were analyzed versus the fungicide-protected control.

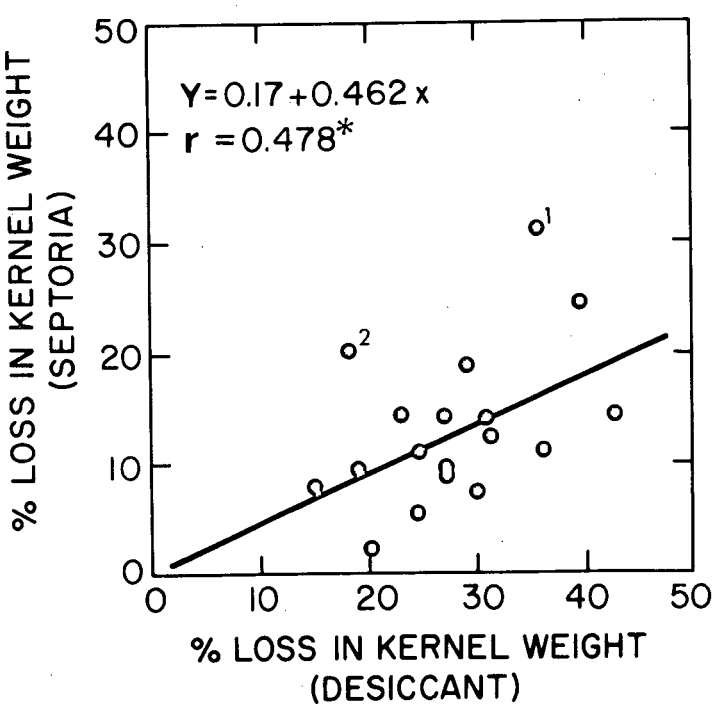

Fig. 1. The linear relationship between losses in 1,000 kernel weight of chemically desiccated and speckled leaf blotch-affected plots across 18 wheat cultivars. Bet-Dagan, Israel, 1981-1982. (1—Hazera 2218 and 2—Hazera 2230).

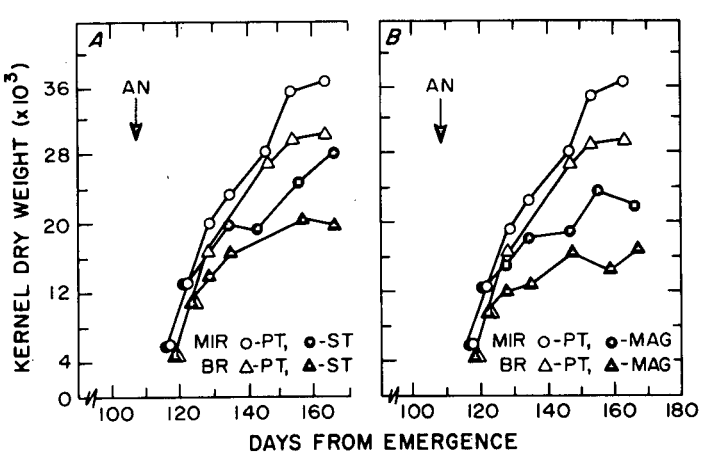

Fig. 2. Kernel growth rates for wheat cultivars Barkai (BR) and Miriam (MIR). **A**, Plants inoculated with *Septoria tritici* (ST) or protected by fungicide treatment (PT), and **B**, plants chemically desiccated with magnesium chlorate (MAG) or protected by fungicide treatment. AN = anthesis.

desiccation was greater in Lakhish than in Hazera 337 and Miriam, the overall response of the five cultivars to chemical desiccation was similar in this respect to their response to Septoria. The correlation across cultivars between loss in harvest index due to disease and loss in harvest index due to chemical desiccation was statistically significant ($r = 0.926$). Thus, the relative capacity of speckled leaf blotch-tolerant cultivars to sustain the least reduction in harvest index was expressed quite well under chemical desiccation.

DISCUSSION

The explanation of plant tolerance to speckled leaf blotch, in terms of sustained development of yield components, could not be derived from information obtained in studies on photosynthesis (16,17), and redistribution of ^{14}C (19). It is possible that the apparent storage of stem reserves in wheat and the capacity of the plant to translocate reserves to the growing kernel when the photosynthetic source is limited, may provide the explanation for postanthesis tolerance to Septoria.

Postanthesis chemical desiccation of the canopy causes stem reserve mobilization into the growing kernels (3). It was further shown (2) that in terms of the ability to sustain kernel growth in the absence of transient photosynthesis, plant response to chemical desiccation was similar to the response to postanthesis drought stress. The association across cultivars in the reduction in kernel growth between Septoria stress and chemical desiccation stress is not simple. While both stresses are apparently induced by (or do not interfere with) plant reserve mobilization to the growing kernel, Septoria stress is not as severe as chemical desiccation stress (Tables 1 and 3 and Fig. 1) and is not imposed abruptly at a given stage of kernel growth. While chemical desiccation destroys the plant's photosynthetic source almost totally, residual transient photosynthetic green area must still exist in plant parts that are unaffected by Septoria, such as the spike.

These differences between the two stresses may reduce the strength of the correlation across cultivars in the reduction of kernel growth between Septoria and chemical desiccation. Thus, for example, cultivars such as Lakhish (Table 3), that were relatively less affected by Septoria than by chemical desiccation may possess a surpassing capacity for ear photosynthesis. In spite of such complexities, significant associations were revealed in most of the tests between Septoria stress and chemical desiccation stress in the rate of loss in kernel growth and harvest index, across cultivars. As argued above, chemical desiccation of the canopy is not a perfect simulator of Septoria epiphytotics in that it does not result in the same pattern of foliar destruction (leaf laminae, sheaths, spike-peduncle, glumes, and awns). It is, however, a simulator of Septoria speckled leaf blotch stress in the sense that it reveals the genotypic capacity for translocation-based kernel growth when the photosynthetic source is severely affected.

The effect of mechanical defoliation on the supply of assimilates to the grain resembled that of speckled leaf blotch where sheath, spike-peduncle, glumes and awns are not as severely affected as chemically desiccated tissue. Differential response in kernel weight of wheat cultivars to defoliation of the upper leaves was also observed by Hendrix et al (12). Kernel weight of plants inoculated with stripe rust were more severely affected than of mechanically defoliated plants (12). While the removal of organs supplying photosynthetic assimilates to the grain may contribute to the understanding of the redistribution of plant reserves (15), it is difficult to employ as a rapid and simple screening technique for tolerance.

It is of interest to note that the cultivars Lakhish and Miriam, classified as tolerant to speckled leaf blotch in terms of kernel growth and harvest index, behaved similarly in a previous study (2,3) with respect to their response to chemical desiccation and postanthesis drought stress. It is, therefore, proposed that a superior capacity for translocation-based kernel growth is probably the common denominator for plant tolerance to various postanthesis stresses that affect the photosynthetic source, such as certain plant diseases or drought.

The question whether this mechanism of tolerance is associated with a reduced sink size and yield potential was raised (5,13) and addressed (2,24). It has been shown (2) that wheat cultivars that sustain the least reduction in kernel growth under conditions of postanthesis stress by drought or by chemical desiccation did not have a small sink size. Such cultivars tended to have a different sink geometry, in that they had a relatively larger number of kernels per spike and smaller kernels, relative to nontolerant cultivars. The results of this study also do not support an association between tolerance and small sink size (potential kernel number and kernel weight per spike) or low yield potential (13). Thus, the results obtained in this study, as well as those obtained previously (2,24), show that plant tolerance to postanthesis stress (either by speckled leaf blotch or by drought) in terms of translocation-based kernel growth, can be developed in high-yielding genotypes. Postanthesis chemical desiccation of the wheat canopy and the subsequent measurement of its effects on the relative reduction in kernel weight, may serve as a useful screening technique for tolerance to speckled leaf blotch of wheat.

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The effect of septoria tritici blotch and chemical desiccasion on grain filling of spring bread wheat

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ABSTRACT

Eyal, Z. 1986. The effect of septoria tritici blotch on grain filling of spring bread wheat.

Field trials were conducted over 2 yr to evaluate the effect of Septoria tritici blotch infection and chemical desiccation on kernel growth. Spring wheat cultivars of diverse origin were subjected to three treatments: inoculation with virulent isolates of Mycosphaerella graminicola (anamorph: Septoria tritici) until an epidemic was initiated, postanthesis application of magnesium chlorate (4% a.i.) solution to destroy most of the plants green tissues, and a control in which a fungicide was applied to protect against loss in green tissue.

The effect of sink-size was assessed in spikes where half of the spikelets were removed prior to anthesis in the 3 major treatments. Kernel weight in reduced spikes was significantly greater than kernel weight of intact spikes, indicating no limitation in reserves and trans-

location of assimilates for kernel growth in stress affected plants. The glumes and awns were responsible for 6-30% of kernel weight in chemically desiccated plants.

Kernel growth was supported by the accumulation of preanthesis assimilates and their utilization at postanthesis. The nonstructural carbohydrates and fructosan followed a corresponding accumulation and depletion trend. The stem thus may act as a temporary reservoir organ for nonstructural carbohydrates to enable them to overcome the phase between the time of maximum assimilate production and the time of increased requirement for carbohydratre by the developing grain. The balance between loss in kernel weight under septoria-infected plants and the translocation of nonstructural carbohydrates to support kernel growth may in part explain the differential loss response among cultivars. The tolerant cultivar Miriam is capable of supporting kernel growth by translocating more nonstructural carbohydrates from reservoires and from non-affected plant tissue.

Additional keywords: tolerance, Triticum aestivum, yield components.

Mycosphaerella graminicola (Fuckel) Schroeter, (anamorph, Septoria tritici Rob. ex Desm.), the causal agent of septoria tritici blotch, reduces yield of wheat in several parts of the world (6). Breeding for resistance has not always been successful in protecting wheat cultivars from the damaging effects of the disease (6, 21). Morphological traits (plant height and ccanopy architecture), physiological traits (photoperiod and vernalization requirements) and growth habit, all influence expression of symptoms and signs (chlorosis, necrosis and pycnidial density). Differentiation of cultivar response to the pathogen is usually based on quantitative assessment of symptoms.

The pathogen affects leaf tissue, causing large coalescing necrotic lesions, which in many cases harbour pycnidia. Pycnidia often can be found on sheath and also on peduncles, glumes and awns, depending on cultivar susceptibility and receptivity (6).

Wheat cultivars have expressed maintenance of high kernel weight under severe septoria tritici blotch epidemics (21, 22). The endurance of kernel weight under septoria tritici blotch epidemics appears to be governed by a small number of additive loci (22). The measurement of tolerance ["that quality that enables a susceptible plant to endure severe attacl by a pathogen without sustaining severe losses in yield" (13)] is based on the comparison between Septoria infected on non-infected plots of the same cultivar and on the relative performance of tolerant to intolerant check cultivars included in the same trial (21).

Gaunt (7) has argued that green leaf area, rather than diseased leaf tissue, should be used as an estimator of yield losses. The effectof the disease on yield components can be postulated when the duration and onset of the epidemics are known. the integration of yield loss, disease intensity and crop growth stage has been used by Teng and Gaunt (17) and by Teng and Bowen (18) in proposaing a conceptual yield loss model.

Buddenhagen (3) confined the term 'tolerance' to an expression of performance by a host when infected by pathogens causing systemic disease, rather than for leaf spot diseases, as argued by Schafer (13). Yet, the author indicated that the innovative technique that has been developed to select for tolerance to drought stress (2) and to Septoria leaf blotch (20) seems to satisfy a logical definition of tolerance and the need to have a uniform challenge applied at a specific phenological stage. The utilization of magnesium chlorate on a specific day after flowering enables the selection of lines that more effectively fill the grain.

Ellis (5) has postulated that the tolerance of local corn cultivars to Puccinia polysora is related to the accumulation of sugars in insoluble form in the stems and their remobilization when needed.

Zilberstein et al. (20) proposed that a superior capacity for translocation-based kernel growth is probably the common denominator for plant tolerance to various postanthesis stresses that affect the photosynthetic source, such as certain plant diseases or drought. Moreover, the authors have shown that wheat cultivars that sustain the least reduction in kernel growth, under conditions of postanthesis stress by drought or by chemical desiccation, did not have a small sink size. The results of the study by Zilberstein et al. (20) did not support an association between tolerance and small sink size (potential kernel number and kernel weight per spike) or low yield potentia, as previously suggested by Kramer et al. (9).

The present study was undertaken to investigate the effect of source capacity (leaf area) and sink size on the grain filling process in Septoria infected and chemically desiccated spring wheats.

MATERIALS AND METHODS

The experiments were conducted at the Bet-Dagon Experimental Farm during the 1982-1983 and 1983-1984 growing seasons. Six spring wheat (Triticum aestivum L.) cultivars were tested in the trials. All cultivars were of similar phenology and growth habit. The cultivars were as follows : the early-maturing, dwarf (75 cm) cultivar Barkai (V238-88222-11/Miriam 2), the early-maturing semidwarfs (95 cm) - Bet Lehem (H574-1-2-6/Lakhish 212), Ceeon (Yaktana $65A^3$//Norin 10/Brevor), Hazera 337 (Inia "S" x Sonora 64. Tezanos Pentos Precoz/Yaqui 54), Miriam (Chapingo 53//Norin 10/Brevor/3/Yaqui 54/4/2 Merav), and the somewhat later-maturing (by 10 days) semidwarf cultivar Lakhish (Yaktana//Norin 10/ Brevor/3/Florence Aurore). The experimental design was in split plots, with treatments in main plots and cultivars in subplots in four replications. Three treatments were performed on all cultivars: fungicide-protected (three applications of Tilt-Propiconazole, CGA 64250) control, inoculation with M. graminicola (anamorphic form) and chemical desiccation. Septoria tritici blotch epidemics were incited by inoculating the plant canopy weekly with a suspension of 10^7 spores per milliliter, starting at the emergence of the flag-minus-2 leaf and finishing at the end of the milk stage. The suspension was prepared from a mixture of virulent isolates of the pathogen. Inoculation was performed during rainy days and/or dewy nights, by using a low-volume low-pressure sprayer (Ulva 8-Micron Co., Bromyard, England). In the chemical desiccation treatment magnesium chlorate was used as a commercial formulation (Machteshim Works, Ltd., Beer-Sheba, Israel), 18% active ingredient (a.i.) formulation routinely used for foliar defoliation in cotton. The desiccant was applied as a solution of4% a.i. at a rate of

35 cm^3/m^2. Each cultivar was sprayed once at 14 days after anthesis. Weekly assessment of percent disease coverage was initiated on the uppermost four leaves upon the emergence of the flag-minus-2 leaf in 15 randomly selected plants across cultivars in all replications.

Sink-source relations . In each of the three major treatments (control, Septoria and desiccant), 15 randomly selected plants bearing the same anthesis date in each cultivar, were kept intact, while in another 15 plants half of the spikelets/spike were removed. In the desiccated plots additional plants were covered with paper bags during the magnesium chlorate application and were removed thereafter. The schematic presentation of the experimental design is presented in Figure 1. In each one of the plants which was harvested when ripe, the following parameters were assessed : shoot dry weight, kernel number and kernel weight.

Non-structural carbohydrates analysis . The carbohydrate analysis was conducted during the 1983-1984 season for the cultivars : Barkai, Ceeon, Hazera 337, Lakhish and Miriam. Six plants per cultivar in each replica were harvested in the three major treatments : control, Septoria infected and chemical desiccation. Sampling was started prior to anthesis for 6 weekly intervals thereafter. Each main tiller was assessed for disease severity, residual green leaf tissue, stem dry weight, number of kernels and kernel dry weight. Stems of main tiller were dried for 48 hr at 70°C. The dried stem portion was ground and immersed in 50 ml of 80% ethanol. The sample was shaken for 24 hr at 55°C. This fraction included the sugars soluble in organic solvents (lower molecular weight carbohydrates, i.e. mono- and disaccharides). Following evaporation of the ethanol, 100 ml of H_2O were added and the residue was boiled for 1 hr to remove the oligosaccharides and fructosans (10, 12, 14). Total carbohydrate was

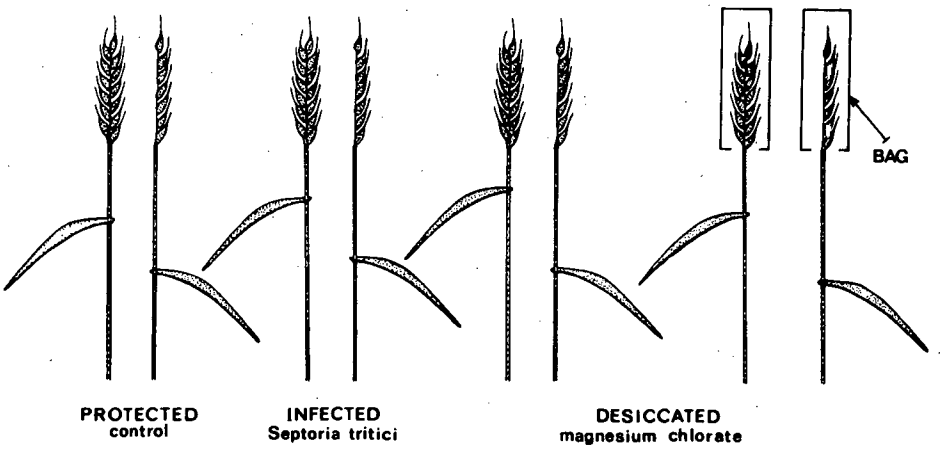

Figure 1. Schematic presentation of treatments performed in Source-Sink trials, Bet Dagan, 1982-1984.

determined for each fraction bythe phenol-sulfuric acid method (4) with a glucose standard. The monosaccharides and fructosans were determined according to Smith (15). Total nonstructural carbohydrates (TNC) thus included monosaccharides + polysaccharides + starches.

RESULTS

Source-sink relations. During the 1982-1983 growing season, disease progress was slower than that of the following season (1983-1984), with consequently lower losses in 1,000-kernel weight (Table 1). The effect of the desiccant on kernel weight was similar in both trials. The effect of septoria tritici blotch and chemical desiccation on total biomass (stem weight) was significant, though greater in the latter, as expected. The cultivar Miriam expressed the lowest loss in biomass under chemical desiccation. Destruction of assimilates source by abiotic (magnesium chlorate) or by biotic (septoria tritici blotch) stresses greatly affected kernel weight. The great differences in loss response between the two seasons prevented the drawing of specific conclusions as to the endurance of a specific cultivar under these stresses. Manipulations of sink size by reducing spikelets number prior to anthesis was performed, to evaluate the capability of source affected plants to mobilize assimilates when needed. Reduction in sink size by half, in all treatments, significantly incrased the kernel weight as compared to kernel weight in non-reduced spikes, yet the compensation in kernel weight due to reduction in sink size was assessed by calculating the loss in 1000-kernel weight in treated plants, as compared to reduced spikes in the control (Table 1). Loss in 1000-kernel weight due to septoria in the reduced spikes was significantly lower than losses in non-reduced spikes in all cultivars. This is partly due to the ability of the septoria affected plants to mobilize assimilates

Table 1.

THE EFFECT OF SEPTORIA TRITIC BLOTCH AND THE DESICCANT MAGNESIUM CHLORATE (MAG) ON 1000-KERNEL WEIGHT IN WHOLE AND HALF SPIKES AND ON BIOMASS AND HARVEST INDEX IN 6 SPRING BREAD WHEATS DURING THE 1982-1984 SEASONS.

		Loss in TKW[a]		Loss in TKW[b] from Control (half)		Gain in Tkw[c] from self (half)		Loss in Biomass[d]		Loss in Harvest[e] Index		Contribution of Glumes[f] + Awns	
WHEAT CULTIVAR	YEAR	Septoria	MAG[g]	Septoria	MAG	Septoria	MAG	Septoria	MAG	Septoria	MAG	Self (whole)	Self (half)
BARKAI	1982/83	7.09	23.20	3.28	27.07	16.86	12.02	8.77	16.29	10.76	17.09	12.65	22.36
	1983/84	27.00	27.52	10.90	24.55	38.27	23.96	18.96	25.98	26.02	29.82	19.78	16.99
BET-LEHEM	1982/83	6.30	10.13	3.41	19.33	6.67	13.42	8.77	16.29	10.76	26.02	13.41	17.62
	1983/84	26.29	28.43	2.94	30.56	25.06	12.34	7.71	25.97	1.39	21.73	8.65	25.75
CEEON	1982/83	6.13	27.69	2.24	36.03	9.82	9.12	5.90	22.59	8.24	26.63	11.25	33.09
	1983/84	12.59	38.31	5.58	39.44	16.86	6.31	9.99	29.49	5.14	40.52	29.15	47.66
HAZERA 337	1982/83	6.54	13.22	7.93	25.29	6.36	7.84	4.05	12.64	1.96	21.08	6.17	20.49
	1983/84	18.27	18.87	1.53	19.76	24.63	8.57	11.26	20.33	9.74	18.89	7.69	13.99
LAKHISH	1982/83	4.68	19.77	0.74	20.03	1.69	1.00	7.52	7.98	5.61	11.73	5.59	16.59
	1983/84	21.85	16.75	7.46	18.36	27.68	8.65	18.08	19.49	9.68	8.34	10.32	16.82
MIRIAM	1982/83	3.04	11.25	6.62	14.97	9.42	13.81	7.65	3.86	3.79	20.93	7.13	2.04
	1983/84	25.80	18.37	4.00	29.36	32.52	6.19	18.26	12.94	11.56	20.81	8.77	18.96

a) Tkw = 1000-Kernel weight [(Protected control - infected)/Protected] x 100
b) [(Protected half spike-infected half spike)/Protected half spike] x 100
c) [(half spike-whole spike)/Half spike] x 100
d) [(Stem weight protected-Stem weight infected)/Stem weight protected] x 100
e) HI = Kernel weight/Stem dry weight
f) [(MAG treated with covered spike -MAG treated uncovered)/MAG treated with covered spike] x 100
g) MAG = magnesium chlorate

from non-affected foliar tissue, and also from non-affected peduncles, glumes and awns.

The gain in 1000-kernel weight in reduced septoria infected plants, as compared to non-reduced septoria infected plants was greater in Barkai and Miriam than in the other cultivars. The similar magnitude of losses in 1000-kernel weight in non-reduced plants as compared to gains in 1000-kernel weight in reduced spikes suggests again that assimilates in the infected plants are available from residual green tissue. Part of the compensation is explained by the contribution of glumes and awns as expressed in the desiccated plants (Table 1).

The relationships between % loss in kernel weight and % loss in kernel weight from the control in reduced spike across cultivars in the two years, were positive in both stresses. A slope, b = 0.9109, was calculated in the desiccated plants (Figure 2) as compared to b = 1.613 in the septoria infected plants (Figure 3). The gain in kernel weight from reduced sink across cultivars in the two years (1982/1983 and 1983/1984) was positively correlated with % loss in kernel weight in infected plants (Figure 4) but with poor positive correlation in desiccated plants (Figure 5). The losses in kernel weight were positively and strongly correlated withlosses in total biomass in the abiotic (magnesium chlorate) and biotic (septoria tritici blotch) stresses (Figure 6, Figure 7, respectively).

The reduction in sink size prior to anthesis has significantly increased stem dry weight in the control plants and the septoria infected plants (Table 2). In the latter, no increase in stem weight was recorded in the cultivars Bet-Lehem, Lakhish and Miriam, although disease severity was high and no significant differences were recorded between reduced and non-reduced spikes.

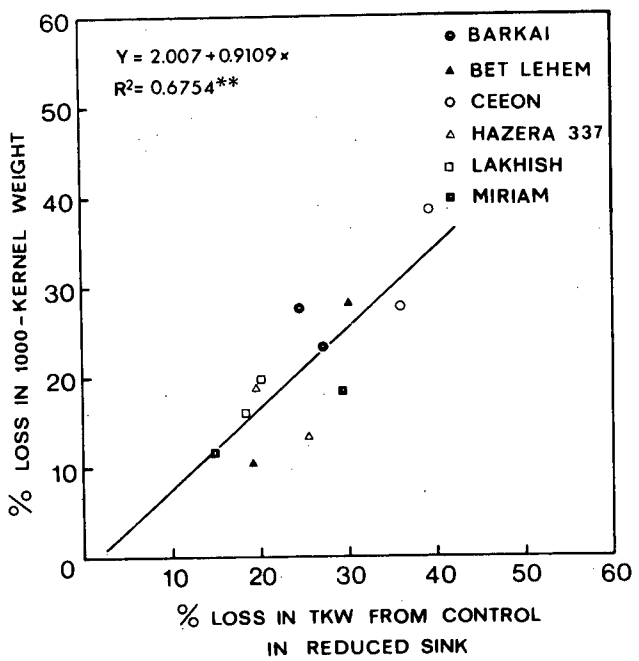

Figure 2.

Chemical desiccation
(magnesium chlorate)

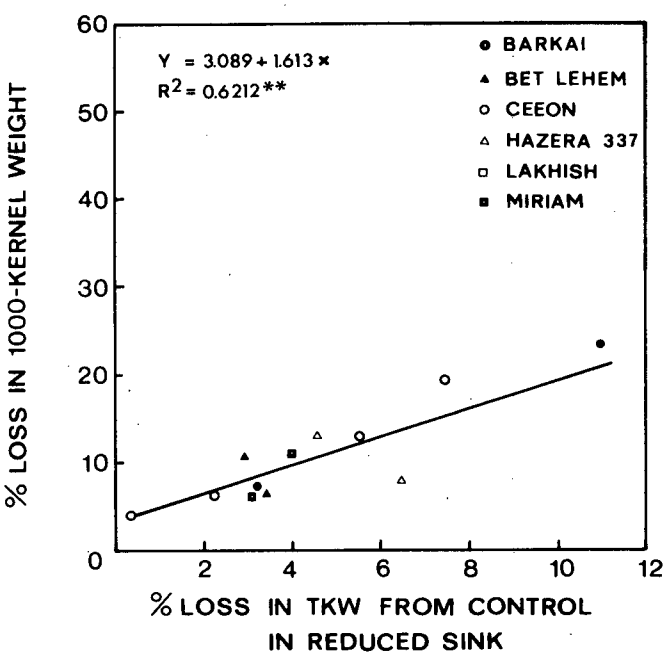

Figure 3.

Septoria tritici blotch

The linear relationship between loss in 1000-kernel weight (TKW) in half-spike of treated plants from that of half-spike of non-treated control and percent loss in 1000-kernel weight of treated whole spike across 6 spring bread wheat cultivars during 1982/1983 and 1983/1984.

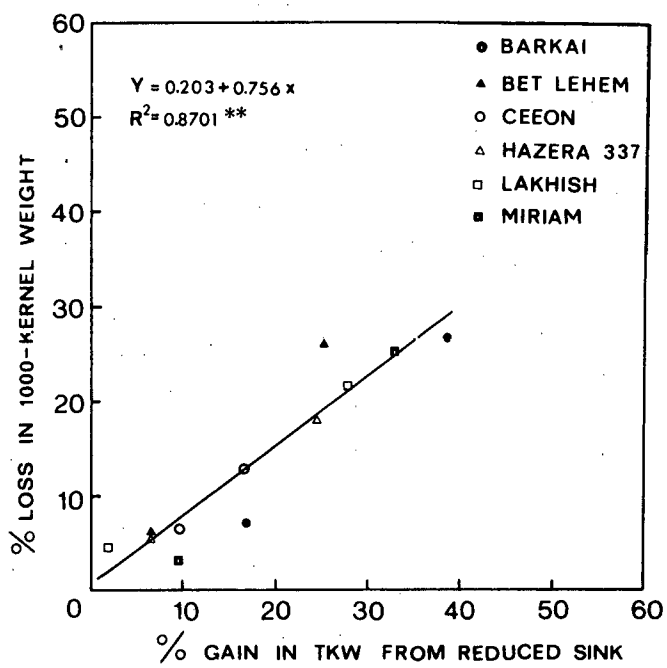

Figure 4.

Septoria tritici blotch

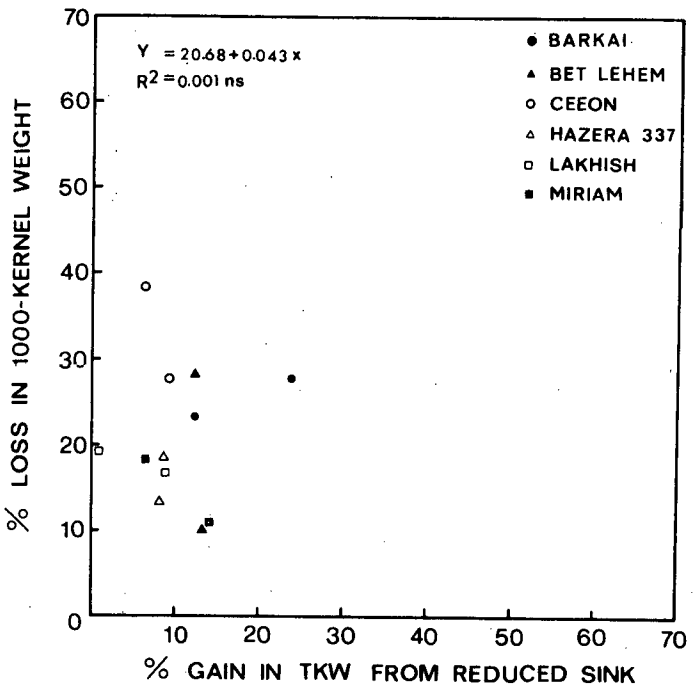

Figure 5.

Chemical desiccation
(magnesium chlorate)

The relationship between gain in 1000-kernel weight (TKW) of half-spike from whole spike in treated plant and percent loss in 1000-kernel weight of treated whole spike across 6 spring bread wheat cultivars during 1982/1983 and 1983/1984.

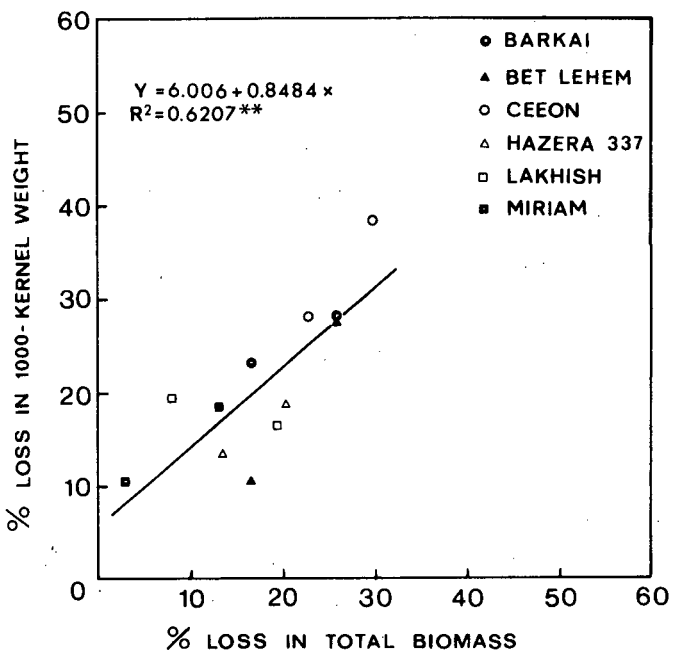

Figure 6.

Chemical desiccation (magnesium chlorate)

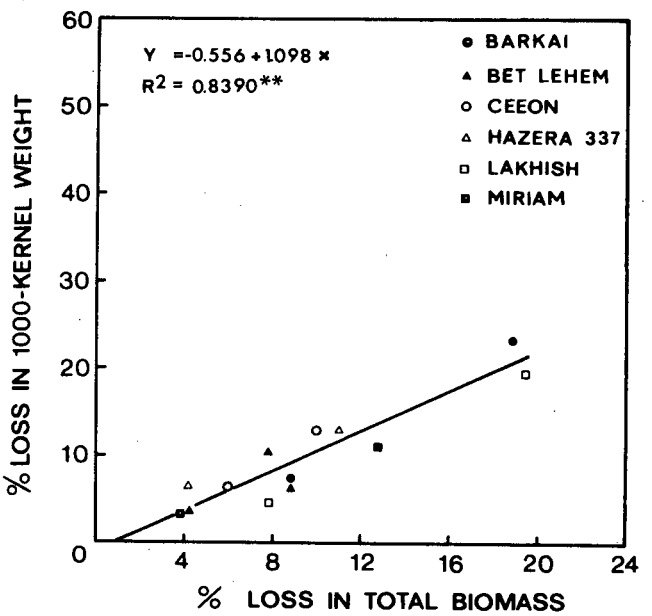

Figure 7.

Septoria tritici blotch

The linear relationship between loss in total biomass in treated plants and loss in 1000-kernel weight across 6 spring wheat cultivars during 1982/1983 and 1983/1984.

Table 2.

EFFECT PF REDUCED SPIKE SIZE ON STEM DRY WEIGHT, NUMBER OF KERNELS PER HEAD AND 1000-KERNEL WEIGHT IN 6 SPRING BREAD WHEAT CULTIVARS INOCULATED WITH MYCOPHAERELLA GRAMINICOLA AND NON-INOCULATED, FUNGICIDE-TREATED CONTROL PLOTS. BET DAGAN 1983/1984.

CULTIVAR	STEM DRY WEIGHT				NUMBER OF KERNELS/HEAD				1000-KERNEL WEIGHT				% DISEASE COVERAGE	
	Control[a]		Septoria[b]		Control		Septoria		Control		Septoria		Septoria	
	Whole[c]	1/2[c]	W	1/2	W	1/2	W	1/2	W	1/2	W	1/2	W	1/2
BARKAI	1.08	1.14 ns	0.99	1.06 *	45.6	21.5 **	45.3	22.9 **	46.6	55.6 **	35.8	49.5 *	86.3	88.0 ns
BET LEHEM	1.74	1.94 **	1.62	1.67 ns	52.6	25.7 **	54.3	27.4 **	45.3	52.4 **	40.7	50.9 **	88.8	89.5 ns
CEEON	1.39	1.56 **	1.29	1.39 *	37.2	17.6 **	37.7	19.3 **	48.8	52.9 **	42.7	49.9 **	87.8	88.4 ns
HAZERA	1.49	1.74 **	1.49	1.53 **	52.2	25.1 **	51.0	25.1 **	38.8	42.7 **	33.7	42.0 **	87.3	87.7 ns
LAKHISH	1.41	1.58 **	1.20	1.29 ns	39.9	21.1 **	38.6	20.5 **	49.9	55.4 **	40.1	51.2 **	85.5	88.5 ns
MIRIAM	1.38	1.48 ns	1.28	1.37 ns	44.8	19.0 **	41.5	20.2 **	41.6	51.0 **	36.9	48.9 **	89.7	89.8 ns

a) NON-INOCULATED, FUNGICIDE-PROTECTED (PROPICANAZOLE, TILT, CIBA GEIGY)
b) SEPTORIA TRITICI BLOTCH INFECTED
c) WHOLE SPIKE; 1/2 = HALF SPIKE
* SIGNIFICANT AT P = 0.05; ** P = 0.01; NS = NOT SIGNIFICANT

An increase in stem weight in spike-reduced plants was recorded in chemically desiccated plants (Table 3). However, the stem weight of reduced spikes in desiccated plants was lower than that of stem weight of intact control plants.

Kernel growth . Typical progress curves for disease severity (PCD), residual green leaf area in septoria-infected plants (GRN), green leaf area decline in non-infected plants and kernel growth curves (1000-kernel weight) are given for the early-maturing cultivars Barkai (non-tolerant) and Miriam (tolerant) in Fig. 8 and Fig. 9 resperctively. The progress of M. graminicola in the dwarf cultivar was faster than that of Miriam and the consequent residual green area in Barkai from anthesisfward was significantly lower than that in Miriam. The disease progression in the cultivars Hazera 337 and Lakhish resembled that of Miriam, while the cultivar Ceeon resembled the progression of Barkai (Fig. 10).

Nonstructural carbohydrates . The accumulation and depletion of stem dry weight, nonstructural carbohydrates and fructosans in control and septoria-infected plants of the cultivars Barkai and Miriam, are presented in Fig. 11 and Fig. 12 respectively. The weight of stem dry weight reached its peak at about 10-14 days following anthesis and thereafter started to decline with corresponding increase in kernel yield. The non-structural carbohydrates and fructosans followed a similar progression scheme. The comparison between cultivars in the three major treatments (control, septoria and desiccant) was conducted on the area under the curve for kernel weight, stem dry weight, nonstructural carbohydrates, fructosans, % disease coverage and residual green leaf in septoria-infected plants (Table 4). Percent loss in the above parameters was calculated for septoria-infected and desiccated plants from that of the

Table 3.
EFFECT OF REDUCED SPIKE SIZE ON STEM DRY WEIGHT, NUMBER OF KERNELS PER HEAD AND 1000-KERNEL WEIGHT IN 6 SPRING BREAD WHEAT CULTIVARS INOCULATED WITH MYCOSPHAERELLA GRAMINICOLA AND TREATED WITH MAGNESIUM CHLORATE. BET DAGAN 1983/1984

CULTIVAR	STEM DRY WEIGHT				NUMBER OF KERNELS/HEAD				1000-KERNEL WEIGHT				% DISEASE COVERAGE	
	SEPTORIA[a]		DESICCANT[b]		SEPTORIA		DESICCANT		SEPTORIA		DESICCANT		SEPTORIA	
	Whole[c]	1/2[c]	W	1/2	W	1/2	W	1/2	W	1/2	W	1/2	W	1/2
BARKAI	0.99	1.06 *	0.99	1.01 ns	45.3	22.9 **	40.9	17.7 **	35.8	49.5 **	33.8	41.9 **	86.3	88.0 ns
BET LEHEM	1.62	1.67 ns	1.47	1.49 ns	54.3	27.4 **	48.8	21.4 **	40.7	50.9 **	32.4	36.4 *	88.8	89.5 ns
CEEON	1.29	1.39 *	1.28	1.39 *	37.7	19.3 **	32.7	16.4 **	42.7	49.9 **	30.1	32.0 ns	87.8	88.4 ns
HAZERA 337	1.40	1.53 **	1.33	1.39 ns	51.0	25.1 **	45.8	20.2 **	33.7	42.0 **	31.5	34.2 ns	87.3	87.7 ns
LAKHISH	1.20	1.29 ns	1.21	1.34 *	38.6	20.5 **	38.2	18.1 **	40.1	51.2 **	41.6	45.2 *	88.5	88.5 ns
MIRIAM	1.28	1.37 ns	1.28	1.37 *	41.4	20.2 **	40.2	19.5 **	36.9	48.9 **	33.9	36.0 *	89.7	89.8 ns

a) SEPTORIA TRITICI BLOTCH INFECTED WHEAT CULTIVARS

b) POSTANTHESIS TREATMENT WITH MAGNESIUM CHLORATE

c) WHOLE SPIKE; 1/2 = HALF SPIKE

* SIGNIFICANT AT P = 0.05; ** P = 0.01; ns = NOT SIGNIFICANT

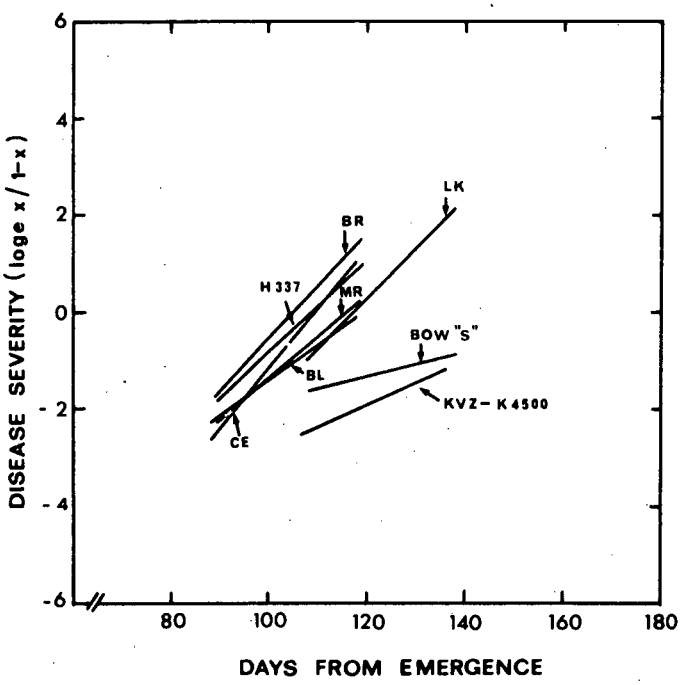

Figure 10. The linear progression of septoria tritici blotch 30 days from the onset of anthesis in the spring wheat cultivars Barkai (BR), Bet Lehem (BL), Bobwhite "S" (BOW "S"), Ceeon (CE), Hazera 337 (H337), KVZ-K4500, Lakhish (LK), and Miriam (MR) during 1983/1984.

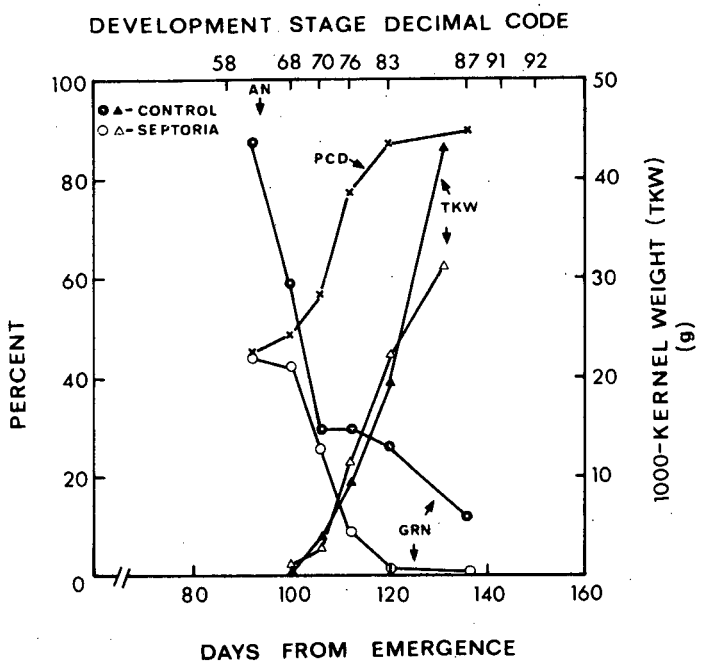

Figure 8.

Cultivar: Barkai
(early-maturing, dwarf)

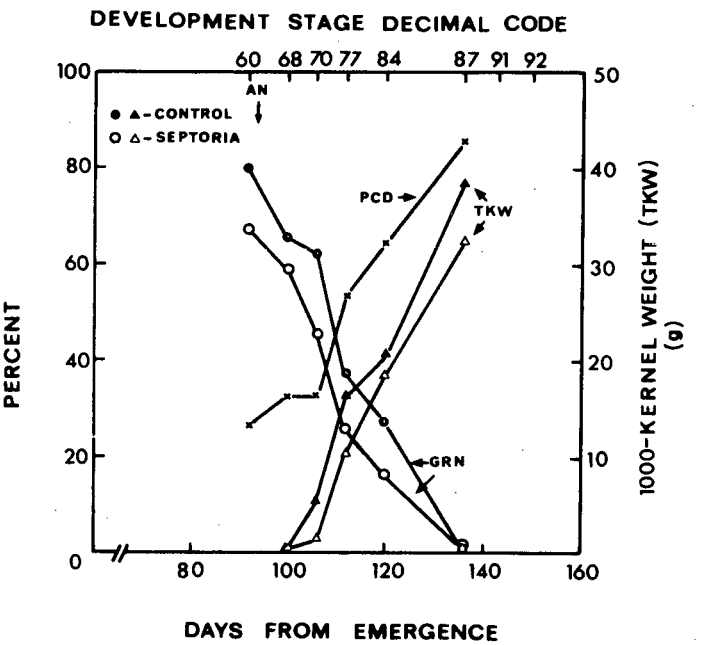

Figure 9.

Cultivar: Miriam
(early-maturing, semi-dwarf)

The relationship between percent disease coverage (PCD), the decline in green leaf area (GRN) in Septoria-nfected (○) and non-infected (●) plants and kernel growth (TKW) in Septoria-infected (△) and non-infected control (▲).
AN=anthesis.
Decimal growth stage code according to Zadoks et al 1974. Weed Research 14:415-421.

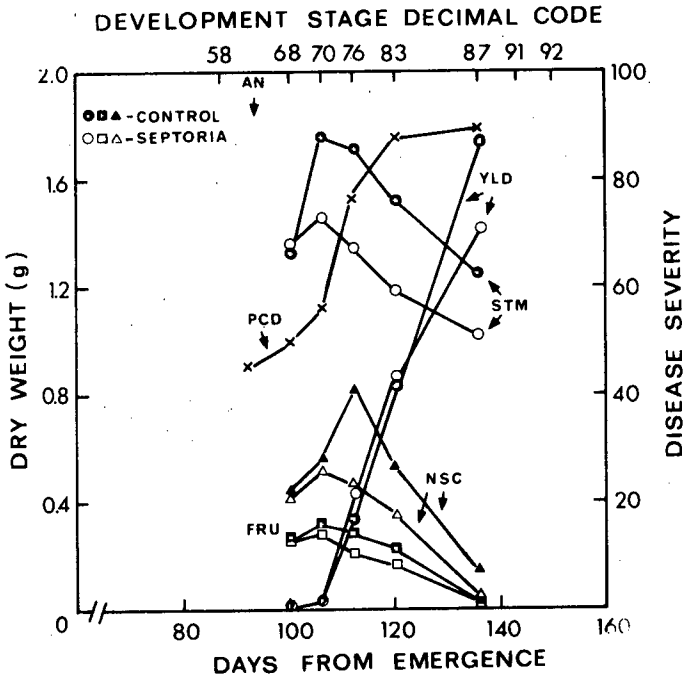

Figure 11.

Cultivar: Barkai

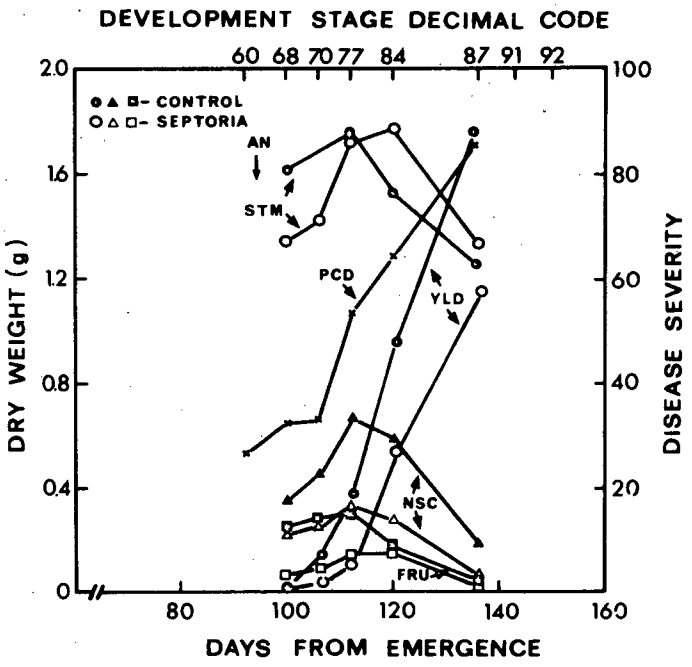

Figure 12.

Cultivar: Miriam

The relationship betwee percent disease coverage (PCD); Stem dry weight (STM) in Septoria-infected (○) and non-infected control (●); Non-structural carbohydrates (NSC) in Septoria-infected (△) and non-infected control (▲); Fructosans (FRU) in Septoria-infected (□) and non-infected control (■); and yield (YLD) in Septoria-infected (○) and non-infected control (●). AN = Anthesis. Decimal growth stage code according to Zadoks et al 1974. Weed Research 14:415-421.

Table 4.

AREA UNDER PROGRESS CURVE CALCULATED FOR THE PERIOD OF 100-136 DAYS AFTER SEEDLING EMERGENCE FOR THE PARAMETERS : KERNEL WEIGHT, STEM DRY WEIGHT, NON-STRUCTURAL CARBOHYDRATES, FRUCTOSAN, PYCNIDIAL COVERAGE AND GREEN LEAF TISSUE IN SEPTORIA INFECTED, DESICCANT TREATED AND NON-INOCULATED, FUNGICIDE PROTECTED CONTROL PLANTS. BET DAGAN 1983/1984.

WHEAT CULTIVAR	KERNEL WEIGHT			STEM DRY WEIGHT			NSC[a]			FRUCTOSANS			SEPTORIA	
	C[b]	S[c]	M[d]	C	S	M	C	S	M	C	S	M	PCD[e]	GREEN TISSUE
BARKAI	695.3	564.9	486.5	54.8	44.6	43.3	17.7	12.2	11.2	7.6	6.2	6.0	2782	369
CEEON	719.2	569.8	478.5	58.4	55.3	51.9	17.1	8.6	14.4	7.3	2.3	4.7	2704	523
HAZERA 337	638.9	374.9	385.3	62.8	49.6	59.4	12.7	11.7	10.6	5.8	4.6	4.1	2272	695
LAKHISH	552.0	309.4	359.8	50.3	39.5	47.7	16.1	12.8	15.0	6.2	6.1	7.3	2264	939
MIRIAM	703.5	557.7	506.8	56.1	56.7	56.1	16.9	8.5	13.4	7.1	3.5	5.8	2088	830

a) NON-STRUCTURAL CARBOHYDRATES

b) CONTROL : NON-INOCULATED FUNGICIDE-PROTECTED (Tilt)

c) INFECTED WITH Septoria tritici BLOTCH

d) MAG - MAGNESIUM CHLORATE DESICCANT

e) PERCENT DISEASE COVERAGE

non-infected, fungicide-protected control (Table 5). The lossin kernel weight in septoria infected plants was the lowest in the tolerant Miriam cultivar, but was not significant from that of the non-tolerant cultivars Barkai and Ceeon, while the highest losses in kernel weight were recorded inthe cultivars Hazera 337 and Lakhish, which previously expressed a high degree of endurance to the pathogen. The differences in losses in kernel weight among cultivars in desiccated plants, was of low magnitude. The depletion in stem dry weight in septoria-infected plants was the lowest in the cultivars Ceeon and Miriam with correspondingly high losses in the nonstructural carbohydraets and fructosans. This trend was not expressed inthe desiccated plants. The relationship between loss in sugars (non-structural carbohydrates and fructosans) and loss in kernel weight expressed as differences in area under progress curves of the treated (septoria-infected) from the non-infected control, is presented in Fig. 13. The ability of the host plant to mobilize nonstructural carbohydrates and fructosan during the post-anthesis grain filling period, is partly explained by the relation represented in this figure.

DISCUSSION

The explanation of plant tolerance to septoria tritici blotch and chemical desiccation, in terms of sustained development of yield components, was proposed to be based on superior capacity for translocation-based kernel growth in the tolerant cultivars (21, 20). Other explanations related this phenomenon to genotype-environment interactions (9). Their interpretation of this interaction led to the hypothesis that cultivars which develop a relatively small skink in relation to the source, may react as tolerant. When the sink-source ratio is high, namely, greater demand (kernel number and/or size) is

Table 5.

PERCENT LOSS IN WEIGHTS (AUPC) FROM THE CONTROL CALCULATED OVER THE PERIOD FROM 14 DAYS POSTANTHESIS AND ADDITIONAL 22 DAYS, FOR THE PARAMETERS : KERNEL WEIGHT, STEM DRY WEIGHT, NON-STRUCTURAL CARBOHYDRATES, FRUCTOSANS AND GRAIN YIELD PER SPIKE, IN SEPTORIA INFECTED AND CHEMICALLY DESICCATED PLANTS, BET DAGAN, 1983/1984.

WHEAT CULTIVAR	KERNEL WEIGHT		STEM DRY WEIGHT		NSC[a]		FRUCTOSANS		GRAIN YIELD PER SPIKE	
	S[b]	M[c]	S	M	S	M	S	M	S	M
BARKAI	23.4	28.8	20.4	22.9	36.5	43.2	22.1	24.5	5.2	37.1
CEEON	21.3	34.3	7.6	13.0	51.1	17.9	68.5	37.9	51.8	37.2
HAZERA 337	40.9	39.9	20.3	6.4	2.7	21.1	8.6	32.7	16.6	24.9
LAKHISH	43.9	34.8	23.5	6.8	23.5	8.9	17.3	14.9	43.7	63.4
MIRIAM	19.5	27.9	5.0	4.0	51.0	24.5	45.1	21.1	41.5	33.8

a) NON-STRUCTURAL CARBOHYDRATES

b) SEPTORIA TRITICI BLOTCH

c) MAG-MAGNESIUM CHLORATE DESICCANT

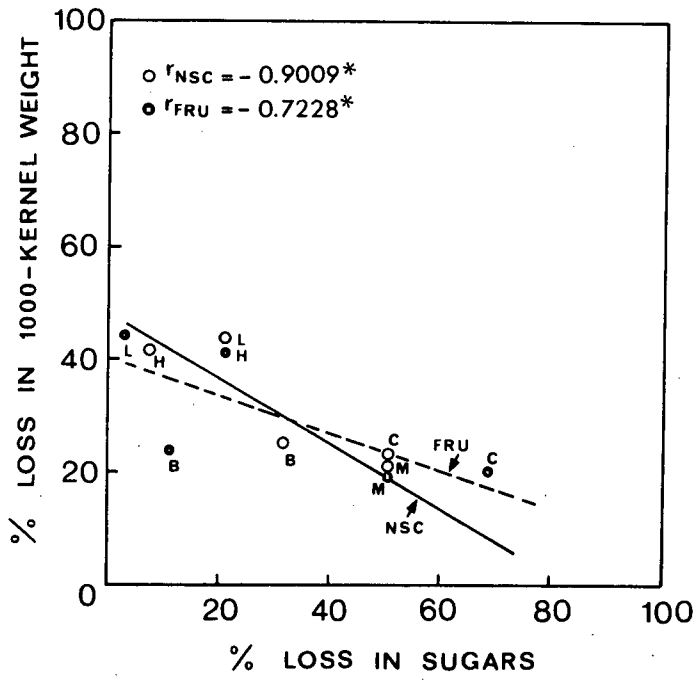

Figure 13. The linear relationship between loss in non-structural carbohydrates (NSC, -O-) , and Fructosans (FRU, -O-) and loss in 1000-kernel weight in septoria tritici blotch infected plants across cultivars (B = Barkai , C = Ceeon, H = Hazera 337, L = Lakhish, and M = Miriam).

greater than assimilate supply in healthy plants, any loss in photosynthetic capacity of the source cannot be compensated for by translocation of reserves, because these have already been utilized by sink-filling. As a result of this, a loss in yield is imminent. High sink-source ratio cultivars will, therefore, behave as non-tolerant. Ellis (5) related tolerance to the capacity of a cultivar to supply assimilates from a reservoir until exhaustion, more or longer than a non-tolerant cultivar. It was thus important toverify whether intolerant and non-tolerant cultivars sink-source relation and translocation of reserves offer the explanation to the differential response in kernel weight under stress conditions. Zilberstein et al. (20) were able to show that plant tolerance to pthanthesis stress (either by septoria tritici blotch or by drought) in terms of translocation-based kernel growth, can be developed in high-yielding genotypes. The compensation in kernel weight in source-limited plants, when sink-size was reduced by half, indicates that the 6 tested spring wheat genotypes had the capacity to translocate reserve assimilates during kernel growth.

This capacity was of higher magnitude in septoria-infected plants probably due to a rather large residual green leaf area, which continues to produce assimilates despite loss in photosynthesizing apparatus of the necrotic leaves. This translocation can be derived from stored reserves and fromphotosynthesis of non-affected plant tissue, i.e. sheath, peduncle, glumes and awns. The contribution of glumes and awns to kernel weight in desiccated intact spikes was inthe range of 5-20%.

The above findings do not support or disprove the notion of whether there is a stimulation of photosynthesis or translocatin by sink demand in stressed (abiotic and biotic) plants. The bell shape of stem dry weight curve in non-infected control plants is typical of pre- and post-anthesis

accumulation and depletion processes (11, 12). This may be due to enhanced transpiration and to mobilization of reserves.

The potential for photosynthate production was at a maximum level around anthesis. Stoy (16) has pointed out that stem carbohydrate reserve could contribute to grain filling or energy requiring processes within the plants. No attempt was made to calculate the balance between stem weight depletion and nonstructural carbohydrate utilization and accumulation of dry matter in the grain. There is a general agreement that vegetative nonstructural carbohydrates contribute only 7-12% of the final grain yield under nonstressed growing conditions (18, 19). It is clear that pre-anthesis assimilates were responsible for the provision of stored reserves to kernel growth, especially in chemically desiccated plants. Vegetative dry weight loss in septoria-infected plants ranged from 5-24% and 4-23% in desiccated plants, while loss in kernel weight ranged from 20-44% in the former and from 28-40% in the latter, counted for the period of 100-136 days from seedling emergence, or from around anthesis to 30 days post-anthesis.

Losses in kernel weight were correlated tolosses in nonstructural carbohydrates and fructosans. The cultivar Miriam which manifested the lowest loss in kernel weight expressedthe greatest loss in sugars. It is suggested that this cultivar has a greater capacity to translocate sugars for kernel growth under biotic stress. However, in the cultivar Lakhish, which in the past has shown a capacity for stress endurance, low losses in sugars were recorded. Such discrepancy may be derived from the somewhat late maturity of this cultivar. The balance between translocation of assimilates and kernel growth may provide a proper measure for better

understanding of the differential loss response of wheat cultivars to septoria sterss, yet there was no clear indication that septoria stress increased the contribution of pre-anthesis assimilates to grain yield.

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3.3

THE EFFECT OF SEPTORIA TRITICI BLOTCH ON WHEAT PRODUCTIVITY

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ABSTRACT

Field trials were conducted during the 1984/1985 season to evaluate the relations between disease severity, green leaf area and losses in kernel weight. Bread, durum wheats and triticale cultivars of diverse origin, differing in maturity, plant stature and response to septoria tritici blotch were subjected to two treatments : inoculation with virulent isolates of Mycosphaerella graminicola (anamorph : Septoria tritici) until an epidemic was initiated, and a control in which a fungicide was applied to protect against loss of green tissue. The progress of the pathogen on the four uppermost leaves was monitored at weekly intervals. The wheat and triticale cultivars were classified according to the following maturity classes : early-maturing, moderate-

maturing and late-maturing cultivars. The early-maturing cultivars expressed high level and rapid progress of the disease, with consequent rapid decline in residual green leaf area. Some moderate and late-maturing cultivars expressed rapid decline in the residual green leaf area in the septoria tritici blotch infected area and also in the green leaf area in protected plots. The late-maturing cultivars Giorgio VZ 331 and Polk/Waldron senesce rapidly regardless of infection. The rate of decline in the residual green leaf area is faster in the late-maturing cultivars due mainly to postanthesis environmental constraints. The net loss in green leaf area revealed wheat cultivars expressing differential yield loss. Loss in green leaf area and disease severity expressed as the area under disease progress curve resembled an estimated loss in kernel wheat.

Septoria tritici blotch, which is caused in wheat by the fungus Mycosphaerella graminicola (Fuckel) Schroeter (Anamorph : Septoria tritici Rob. ex Desm.), may impose severe limitations on cropyields in several parts of the world (3). The annual average losses in yield due to septoria diseases of wheat in the U.S.A. were estimated at 1% in a 1965 report (3). With severe epidemics, some vulnerable wheat cultivars may suffer 30-50% losses in yield, resulting in shrivelled grain unfit for milling (3).

Under certain environments, early build-up of infection by M. graminicola on lower plant parts may adversely affect root biomass and plant development (1, 7). Early infection of lower leaves also may reduce yield, especially by altering sink development (the number of tillers per plant, the number of spikes per plant and the number of grains per spike)

and consequently affect assimilate distribution (7, 13). Infection of the upper plant parts that are responsible for grain filling is considered to be the most significant factor contributing to losses in yield (13). Infection on upper plant parts usually affects kernel weight and grain number (3, 13). The magnitude of reduction in yield components depends on the pre- and post-anthesis level of disease-affected plant tissues, disease progress relative to plant growth stage and cultivar response to disease stress (13). Gaunt (6, 7) has pointed ouit that disease is rarely measured by physiological parameters but rather by a pathogen based character such as lesion number, lesion size, spore number, etc.

Gaunt (7) and Hooker (10) suggested that absolute green leaf area was correlated with yield loss. They suggested that disease should be measured by several different parameters, including host-based parameters such as total leaf area, senescence, etc. (6).

Evans et al. (2) stated that under most circumstances, 90-95% of the carbohydrate in grain is derived from carbon dioxide fixation after anthesis. Grain yield may, therefore, bear a close relation to the duration and rate of photosynthesis after anthesis. Photosynthesis before anthesis and particularly during ear development, may profoundly influence yield through effects on the components of storage capacity (2, 5, 8, 9).

There is a close correlation between disease severity of septoria tritici blotch expressed in terms of percent leaf area covered with pycnidia and loss in kernel weight (3). Some cultivars express differential loss in yield under apparently similar disease severity and disease progress (3). This differential loss expression of some cultivars was recorded in chemically desiccated plants where the desiccant (magnesium chlorate) was applied 14 days post-anthesis (13). In the case of septoria-affected plants, kernel growth was achieved through the

genotypic capacity to translocate reserve when photosynthetic source is limited and via residual transient photosynthetic green area (unafected leaf area, peduncle and spike).

The present study was undertaken to assess the relationships between septoria-affected and residual green areas and loss in kernel weight

MATERIALS AND METHODS

The trial was conducted at the Bet-Dagan Experimental Farm during the 1984-1985 growing season. Forty-two wheat and triticale cultivars were evaluated. The bread wheat, durum and triticale cultivars included accessions varying in plant height, maturity and response to septoria tritici blotch. The experimental design was in split plots, with treatments in main plots and cultivars in subplots in four replications. Each subplotwas 2 m wide and 6 m long. Two treatments were performed on all cultivars: fungicide-protected (three applications of Tilt-Propiconazole, CGA 64250) control, and inoculation with Mycosphaerella graminicola (anamorphic state : Septoria tritici). Septoria tritici blotch epidemics were incited by inoculating the plant canopy weekly with a suspension of 10^7 spores per milliliter, starting at the emergence of the flag-minus-2 leaf and finishing at the end of the milk stage of the moderately maturing accessions. The suspension was prepared from a mixture of virulent isolates of M. graminicola, which included isolate ISR 8036, whichis virulent on Aurora-Bezostaya 1-Kavkaz varietal complex. Inoculation was performed during rainy days and/or dewy nights, by using a low-volume low-pressure sprayer (Ulva 8 - Micron Co., Bromyard, England). Weekly assessment of percent disease coverage was initiated on the four uppermost leaves upon the emergence of the flag-minus-2 leaf in 10 randomly selected plants per treatment, across cultivars in all

replications (4, 13). These plants were also assessed for residual green leaf area. The plots wre combine-harvested and 1000-kernel weights were determined.

RESULTS

The classification of the wheat and triticale accessions which were included in the trial into maturity classes are presented in Table 1. The majority of the Israeli bread and durum wheat cultivars are of early-maturity (90-105 days to anthesis) and of short plant stature (80-105 cm). Some of the better known CIMMYT cultivars (Bobwhite, Genaro, Glennson, Pavon 76 and Seri) are of moderate maturity (110-113 days to anthesis) and of short stature (95-110 cm). Most of the late maturing accessions (125-132 days to anthesis) are also of tall plant stature (130-150 cm). Disease severity and the residual green leaf area were assessed in all cultivars 6 times during the season. Since accessions varied in maturity, the calculations were performed for the above parameters for the 30 days period from the onset of anthesis in the plot. The data is presented as a logit transformation for groups of cultivars with a common denominator with the following cultivars serving as checks : Barkai (early-maturing, short-stature, susceptible); Bobwhite "S" (moderate-maturing, semidwarf, resistant); and Kvz-k4500 L.A.4 (moderate-maturing, semidwarf, resistant).

Israeli bread wheats - The Israeli commercial bread wheat cultivars tested in the trial are susceptible to septoria tritici blotch. The cultivars Bet Lehem (BL) and Miriam (Mir) expressed the slower disease progress (Fig. 1), while Barkai (BR), Bet-Hashita (BH), Ceeon (CE), Hazera 337 (H337), Lakhish (Lk) and Shafir (SH) all expressed similar regression coefficients.

Table 1. The classification of wheat and triticale accessions according to maturity classes. Bet-Dagan, 1984-1985.

CULTIVAR	SOURCE	GROWTH HABIT	DAYS TO ANTHESIS	PLANT HEIGHT (cm)
EARLY MATURITY				
BARKAI	V*	SBW[1]	97	80
BET LEHEM	V	SBW	95	105
BET HASHITAH	V	SBW	102	87
BEAGLE	C	TCL[3]	102	130
CEEON	H	SBW	91	102
CIANO 79	C	SBW	105	102
DGANIT	W	SBW	100	80
HAZERA 337	H	SBW	95	100
HAZERA 870	H	SDW[2]	100	100
HAZERA 2230	H	SBW	105	102
IAS-20	M	SBW	105	125
LAKHISH	V	SBW	102	105
MAPACHE	C	TCL	102	120
MARCOS JUAREZ INTA	C	SBW	105	110
MIRIAM	V	SBW	95	105
SHAFIR	H	SBW	95	100
V 392-304	V	SBW	97	105
V 447	V	SDW	105	100
V 979-28	V	SBW	105	100
V 8828-233	V	SBW	105	85
ZENATI BOUTEILLE	M	SDW	105	125

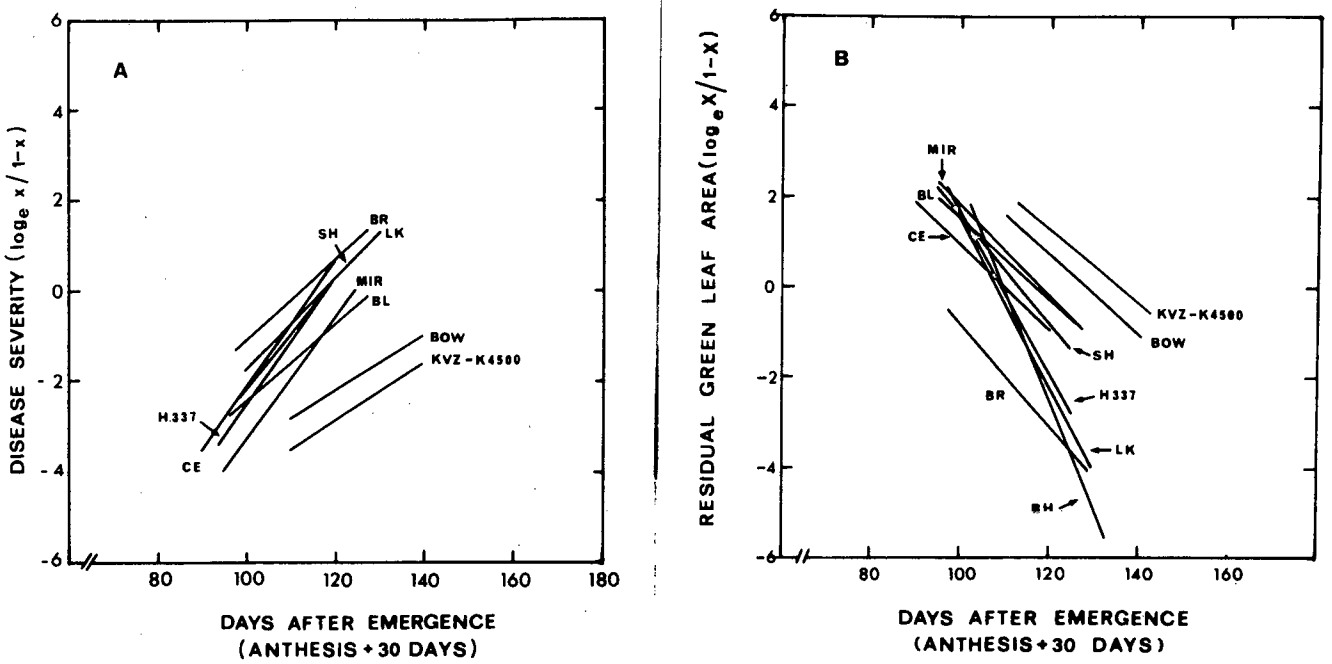

Figure 1. A, the linear progression of septoria tritici blotch 30 days from the onset of anthesis and B, the decline in green leaf area in septoria-infected plots in Israeli spring bread wheat cultivars: BR = Barkai, BH = Bet Hashita, BL = Bet Lehem, CE = Ceeon, H337 = Hazera 337, LK = Lakhish, MIR = Miriam, SH = Shafir and the resistant check cultivars BOW = Bobwhite "S" and KVZ-K4500.

	SOURCE	GROWTH HABIT	DAYS TO ANTHESIS	PLANT HEIGHT (cm)
MODERATE MATURITY				
BOBWHITE "S"	C	SBW	111	100
GENARO 81	C	SBW	110	102
GLENNSON	C	SBW	110	110
INBAR	V	SDW	107	90
KVZ/7C	C	SBW	120	122
KVZ-K4500 L.A.4	C	SBW	112	110
KVZ-UP 301	C	SBW	120	107
LI 217	M	TCL	107	132
MUSALA "S"	C	SBW	120	105
PAVON 76	C	SBW	112	105
SERI 82	C	SBW	112	95
VERANOPOLIS	M	SBW	114	130
LATE MATURITY				
COLOTANA	M	SBW	125	147
ETIT 38	M	SDW	125	132
FORTALEZA-1	M	SBW	125	148
GIORGIO VZ 331	M	SDW	125	90
OLAF	M	SBW	125	115
POLK/WALDRON	M	SBW	132	135
TITAN	M	SBW	125	150
TOROPI	M	SBW	125	140
ZT 7551	M	SBW	125	130

1 - SBW : Spring bread wheat

2 - SDW : Spring durum wheat

3 - TCL : Triticale

* - V = Volcani Center

H = Hazera seed Co.

W = Weizmann Institute

C = CIMMYT

M = Miscellaneous

The cultivars Dganit and Bet-Dagan (V8828-233), V392-304, V979-28 and Hazera 2230 resembled the pattern expressed by most of the other Israeli cultivars.

The decline n residual leaf area was rapid in Barkai, somewhat slower in Bet Hashita, Hazera 337 and Lakhish (Fig. 1-2). In the cultivars Bet Lehem, Ceeon, Miriam and Shafir the slope of the regression line was not as steep and resembled that of the resistant cultivars Bobwhite "S" (BOW) and Kvz-k4500.

Tall-late bread wheats - The regression coefficients of the tall-late cultivars resembled that of the resistant cultivars, but differed markedly from that of the susceptible cultivar Barkai (Fig. 2-1). The onset of anthesis of Veranopolis (VER) resembled that of Bobwhite "S" (BOW) and Kvz-k4500 was very similar in the level of disease of the other cultivars to the two resistant checks. The decline in green leaf area was rapid in Polk/Waldron (P/W) despite low level of disease (Fig. 2-2). The regression coefficients of the cultivars Colotana, Olaf (Olf), Toropi (TP) and Veranopolis (VER) all resembled that of Bobwhite "S" (BOW) and Kvz-k4500.

Durum and triticale - The regression coefficient of disease progress of the durum and triticale varied considerably within the group (Fig. 3-1), Giorgio VZ 331 (G331) expressing high level of symptoms, despite its lateness. Inbar (IN) and V 447 exhibited moderate level of disease, higher than that of Bobwhite "S". Zenati-Bouteille (ZB) expressed somewhat higher level of diseae than the triticale Beagle (BGL) but less than the triticale Mapache (MP). The decline in residual green leaf area was very rapid in the durum wheat Giorgio VZ 331 (Fig. 3-2). The rest of the accessions had similar regression coefficients, although they differed in the level of the residual area.

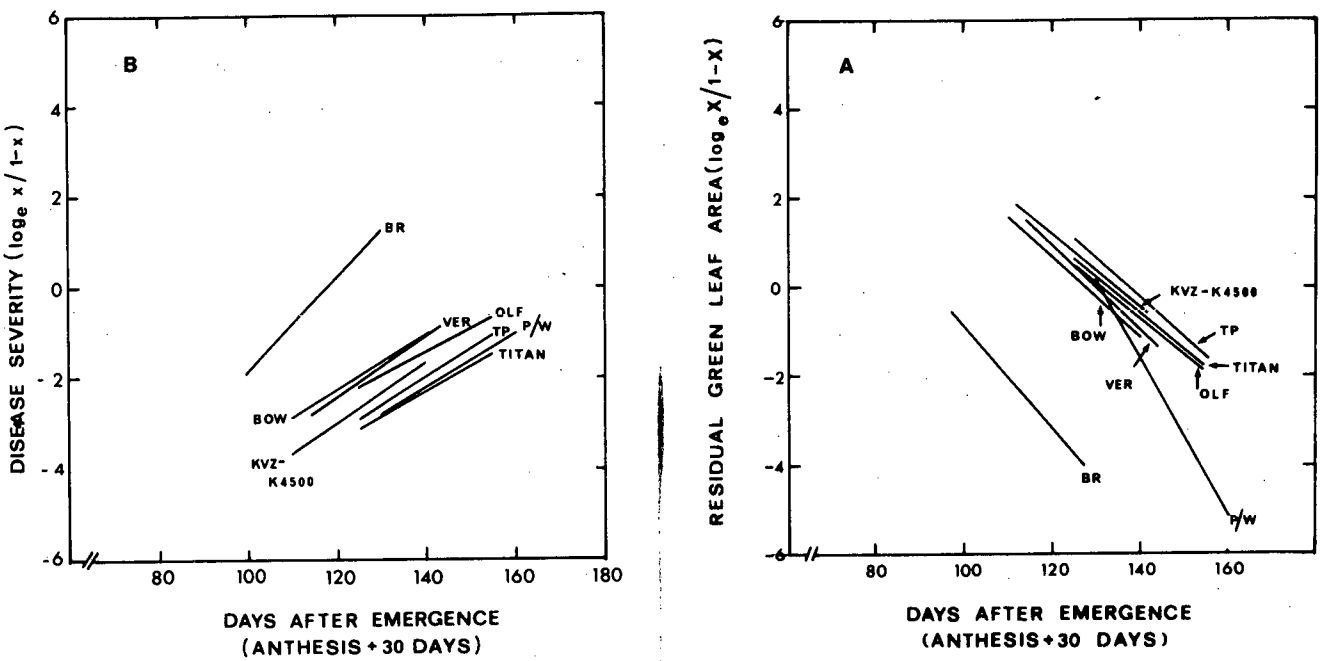

Figure 2. A, the linear progression of septoria tritici blotch 30 days from the onset of anthesis and B, the decline in green leaf area in septoria-infected plots in tall-late maturing spring bread wheat cultivars : OLF = Olaf, P/W = Polk/Waldron, Titan, TP = Toropi, VER = Veranopolis and the susceptible check cultwvar Barkai (BR) and the resistant check cultivars Bobwhite "S" (BOW) and KVZ-K4500.

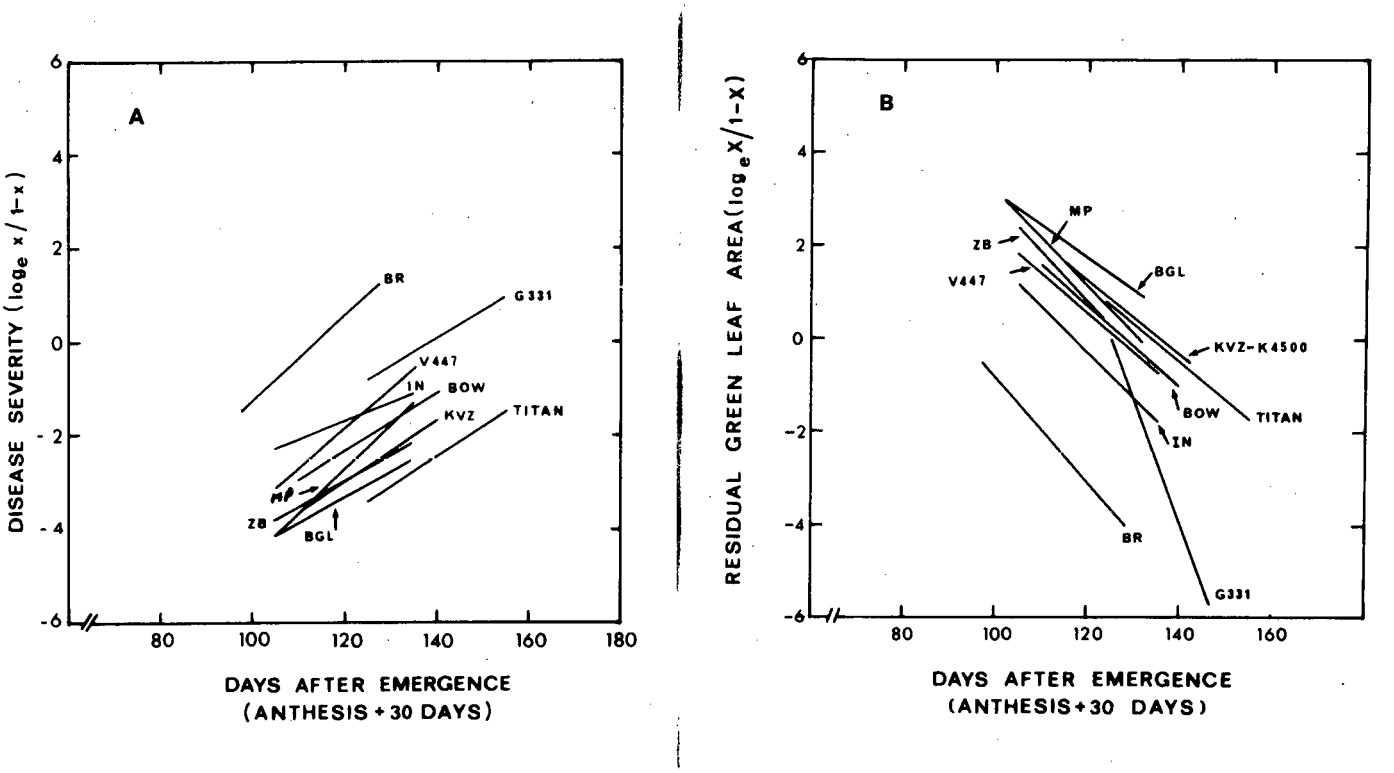

Figure 3. A, the linear progression of septoria tritici blotch 30 days from the onset of anthesis and B, the decline in green leaf area in septoria-infected plots in durum wheat and triticale cultivars: BGL = Beagle, IN = Inbar, G331 = Giorgio VZ331, MP = Mapache, V447 = Volcani 447, ZB = Zenati-bouteille, and the susceptible check cultivar Barkai (BR) and the resistant cultivars BOW = Bobwhite "S", KVZ = Kvz - K4500, and Titan.

CIMMYT cultivars - The level of disease coverage of the CIMMYT cultivars was lower than that of the susceptible, somewhat late cultivar Lakhish (LK). The cultivar Seri 82 expressed a slower disease progress than Ciano 79 (CNO), Genaro 81 (GEN), Glennson (GLN), Marcos Juarez Inta (MJI), Musala "S" (MUS) and Pavon 76 (PVN). All the above cultivars had higher disease levels than Bobwhite "S" (BOW) and Kvz-k4500 (Fig. 4-1). The regression coefficients of the residual green leaf area were similar for all CIMMYT cultivars, with the exceptiono of Pavon 76 (PVN) which retained a higher green leaf area for the 30 days post anthesis (Fig. 4-2).

A summary of the trends in disease progression and residual green leaf area across cultivars is presented in Figures 5-1 and 5-2.

Relation to yield

A significant linear correlation was expressed between the green leaf area in infected plots and that in the protected (Fig. 6). The cultivars Polk/Waldron (P/W) and Giorgio VZ 331 (G331), which express low to moderate levels of symptoms, expressed a rapid decline in green leaf area even in non-inoculated, protected control plots. The relationship between disease progress and residual green leaf area during the 30 days post anthesis revealed that the retained green area is cultivar dependent (Fig. 7). Late maturing cultivars under Israeli growing conditions encounter high temperatures and/or water stress towards the end of the season, which strongly affect the senescence of the green tissue. However, the capacity to retain green leaf duration is genotype dependent. Some late maturing cultivars, i.e Zenati-Bouteielle (ZB) and Beagle (BGL) express high green leaf retention capability, whereas the cultivars Polk/ Waldron (P/W), Giorgio VZ 331 (G331), Kvz-UP301, ZT 7551 (ZT) and to a lesser extent : Ettit 38 (ET), Colotana (CL), Titan (T), Olaf (Olf), Fortaleza-1 (F), Toropi (TP) and IAS 20 (I20), do not. If the above 11 accessions

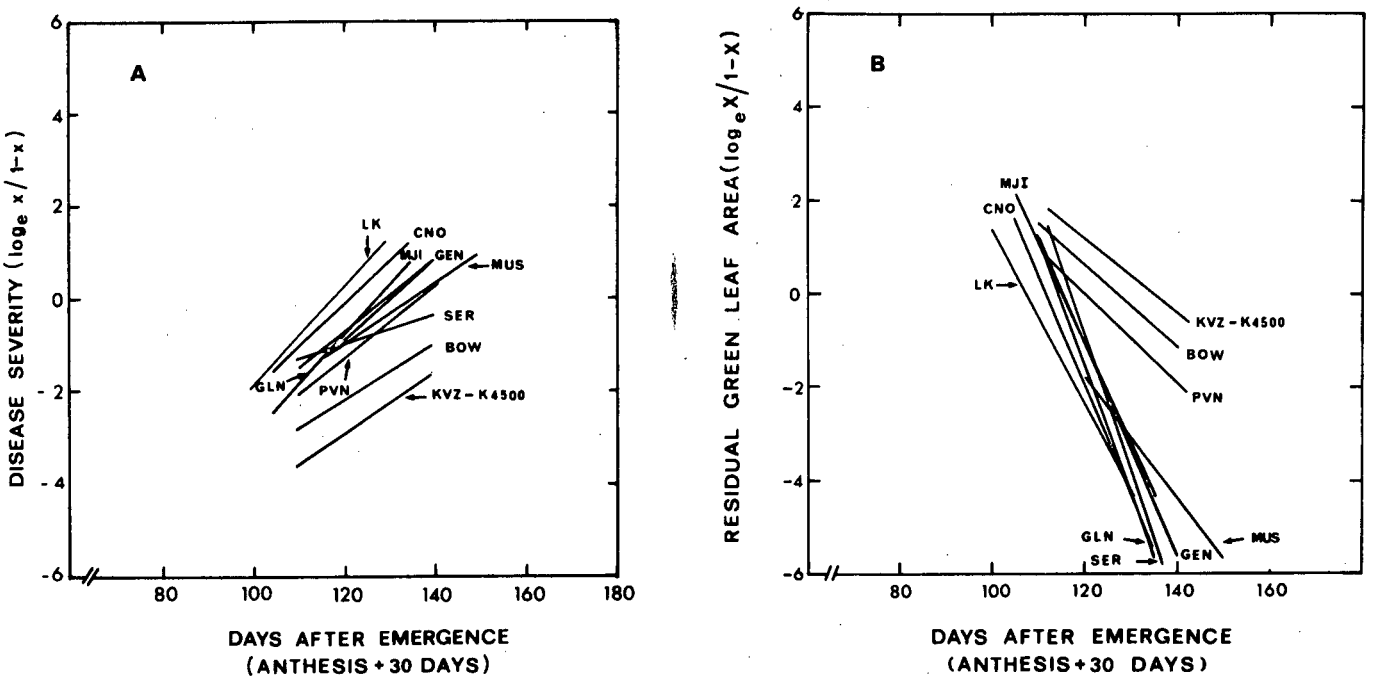

Figure 4. A, the linear progression of septoria tritici blotch 30 days from the onset of anthesis and B, the decline in green leaf area in septoria-infected plots in CIMMYT cultivars: CNO = Ciano 79, GEN = Genaro 81, GLN = Glennson, MJI = Marcos Juarez Inta, MUS = Musala "S", and PVN = Pavon 76 and the susceptible cultivar Lakhish (LK) and the resistant cultivars Bobwhite "S" (BOW) and KVZ_K4500.

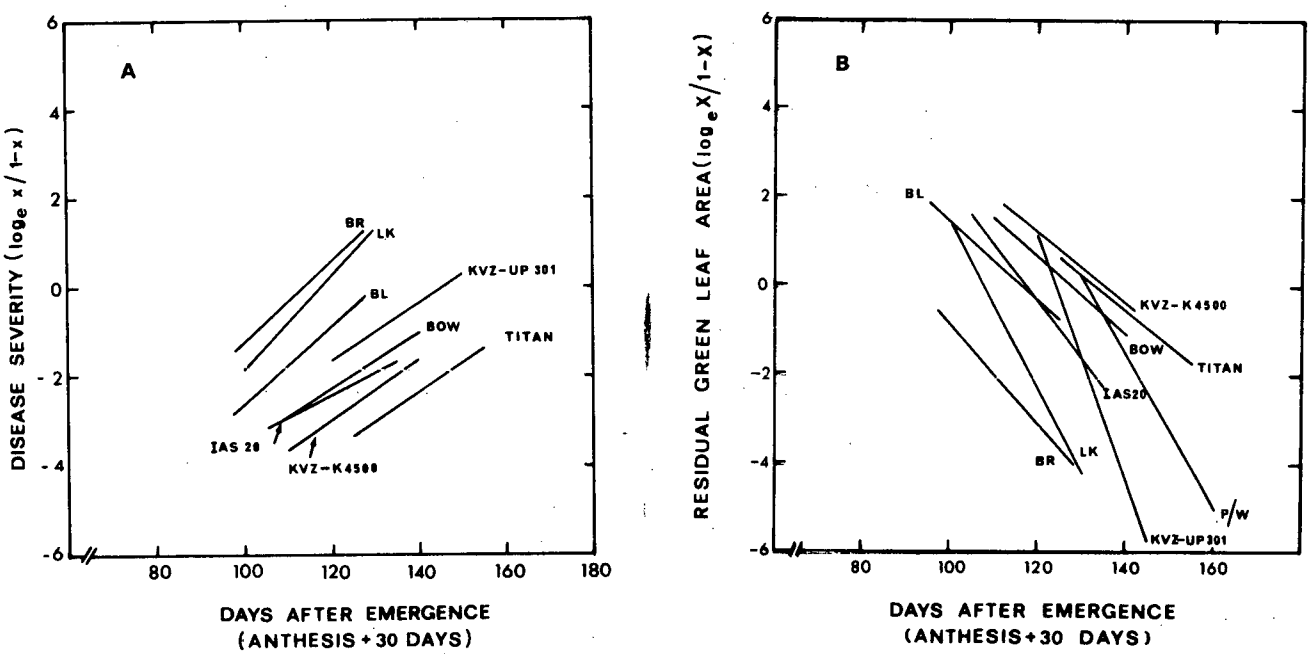

Figure 5. A, the linear progression of septoria tritici blotch 30 days from the onset of anthesis and B, the decline in green leaf area in septoria-infected plots in cultivars representing the major trends: BR = Barkai, BL = Bet Lehem, BOW = Bobwhite "S", IAS 20 = IASSL, LK = Lakhish, P/W = Polk/Waldron and Titan.

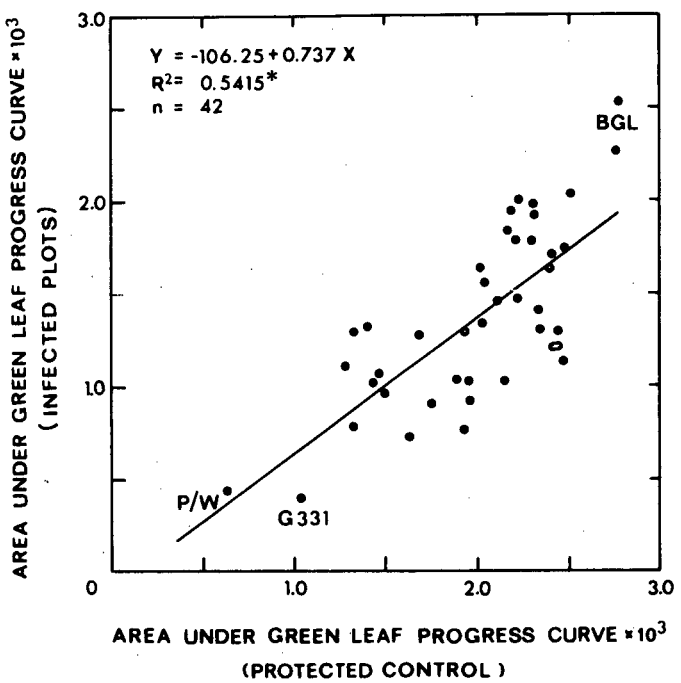

Figure 6. The linear relationship between the area under green leaf progress curve in the protected control and the area under green leaf progress curve in Septoria-infected plots across 42 cultivars. BGL = Beagle, G331 = Giorgio VZ331, and P/W = Polk/Waldron.

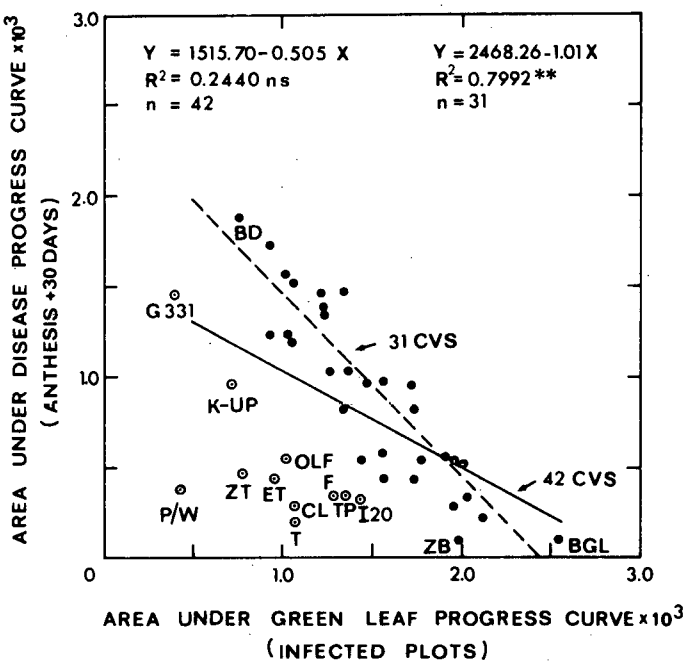

Figure 7. The linear relationship between the area under green leaf progress curve in Septoria-infected plots and area under disease progress curve in Septoria-infected plots 30 days from the onset of anthesis. Regression line for 31 cultivars (dotted line), regression line for 42 cultivars (full line).
BD = Bet Dagan, BGL = Beagle, CL = Colotana, ET = Etit 38, F = Fortaleza-1, G331 = Giorgio VZ331, I20 = IAS 20-IASSUL, K-UP = KVZ-UP301, OLF = Olaf, P/W = Polk/Waldron, T = Titan, TP = Toropi, ZB = Zenati Bouteille, and ZT = ZT7551.

are excluded from the analysis the correlation between the necrotic area and the residual greenleaf area markedly improves (R^2 = 0.7992) from that of the regression across the 42 accessions (R^2 = 0.2440). This may be indicative that in the case of septoria tritici blotch, the effect of the pycnidia-bearing necrotic leaf area is confined to the lesion and does not affect the residual green leaf tissue.

The relation between disease progress and loss in 1000-kernel weight is presented in Figure 8. Some accessions express differential yield response, namely, lower loss with equivalent disease level or higher vulnerability with equivalent disease level. Similar relationship is expressed between loss in green leaf area to loss in 1000-kernel weight (Fig. 9). The loss in green leaf area during the 30 days post anthesis, was calculated from the difference in the area under the green leaf area curve in the protected control and that of the residual green leaf area in the infected plot of each accession.

DISCUSSION

Increase in the yield of crop plants can come from many quarters, such as better adaptation to environmental conditions, greater resistance to pests and diseases, improved agronomic practices, increased genetic yield potential and interactions between these. In a system where the balance between the source, transport and sink capacities is being disrupted by septoria tritici blotch, through the adverse effect on the ability of the source (photosynthesizing capacity) to produce assimilates, special attention should be given to the relation between source magnitude and losses in yield. Under at least some well-defined conditions, grain growth rates are not limited by photosynthetic rate, since carbohydrate balance sheets reveal that more assimilate is available for grain filling

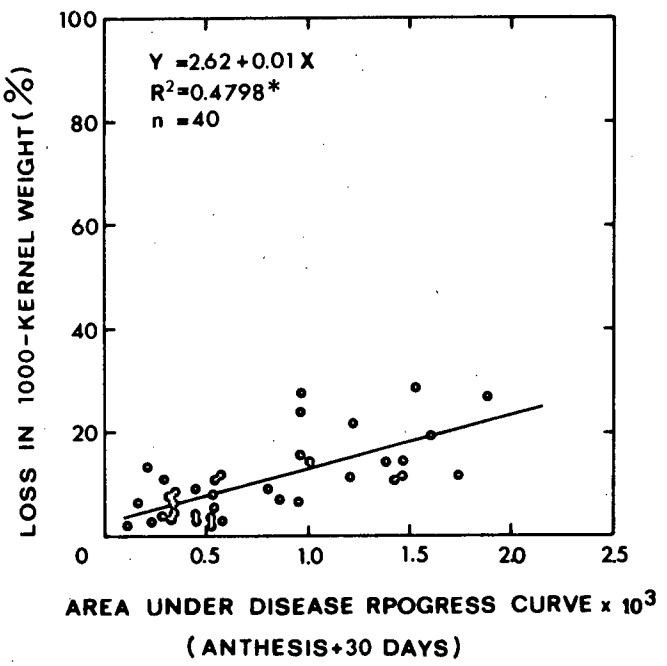

Figure 8. The linear relationship between the area under Septoria progress curve 30 days from the onset of anthesis and loss in 1000-kernel weight across 40 wheat and triticale cultivars.

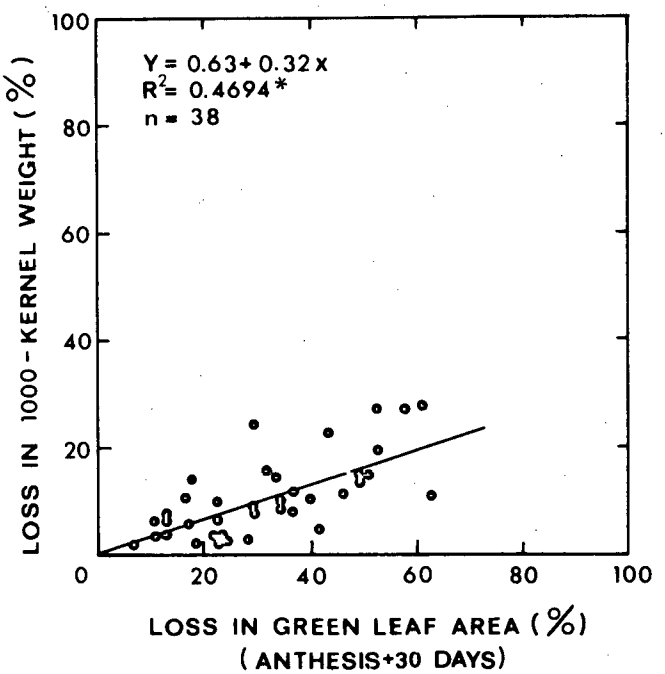

Figure 9. The linear relationship between loss in green leaf area (protected-infected/protected) 30 days from the onset of anthesis and loss in 1000-kernel weight across 38 wheat and triticale cultivars.

than is used (2, 11, 12). Reserves built up at the time of anthesis, especially in the lower internodes of the stem, are not drawn on as fully as they are when the plants are under stress (2). In previous work presented in this BARD report, no such upgrading in build up of reserves was found. Septoria tritici blotch significantly decreased the amount of accumulated assimilates.

The significant reductions in kernel weight under septoria tritici blotch epidemics are therefore the result of the affected reserves built up prior to and post anthesis and its translocation to the grain. The confinement of septoria tritici blotch symptoms to the necrotic lesion leaves residual green leaf area which, together with non-affected photo-synthesizing tissue (peduncles, glumes and awns) is insufficient to support grain filling (rate and duration) as is the case in the disease-unaffected plants. The expression of losses in terms of residual green leaf area reveals additional constraints in addition to the pathogen. During the 1984/1985 growing season the cultivars Giorgio VZ 331 and Polk/ Waldron expressed decline in green leaf area devoid of septoria tritici blotch infection. Most late-maturing cultivars are confronted with adverse post anthesis environmental conditions (temperatures and water stress), which may serve as yield constraints. In most of these late-maturing cultivars the yield potential under Israeli conditions is low as compared to better adapted early-maturing cultivars. In terms of the relationship between maturity and losses in yield, under severe septoria tritici epidemics the moderate-maturing accessions (i.e. CIMMYT derived cultivars) express relatively high disease severity and consequent losses.

The expression of losses in kernel weight in terms of losses in net green leaf area during the 30 days post anthesis, still exhibited differential yield losses similar to that between lossesi n kernel weight

and disease severity. Kernel weight endurance under septoria tritici blotch epidemics expressed in terms of loss in green leaf area in the tolerant cultivars Lakhish and Miriam reveals that these two cultivars retained sufficient photosynthesizing leaf area. This phenomenon was not unique only to the tolerant cultivars. The estimation of losses in yield components on the basis of loss in green leaf area did not improve the correlation coefficient (R^2) over that of disease severity expressed as the area under disease progress curve.

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3.4

INFRARED THERMAL SENSING OF PLANT CANOPIES AS A TECHNIQUE TO ASSESS THE RELATIVE RESISTANCE OF WHEAT CULTIVARS TO MYCOSPHAERELLA GRAMINICOLA

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Septoria leaf blotch of wheat, which is inated by the fungus Mycosphaerella graminicola (Fuckel) Schroet () (anamorph: Septoria tritici Rob. ex Desm.), may impose severe limitations on crop yield.
Wheat cultivars of similar phenotypic characters may express differential yield response under similar apparent septoria severity and disease progress (4). Wheat cultivars may vary in their ability to endure (tolerate) severe epidemics without sustaining significant losses in yield when compared to vulnerable (non tolerant) cultivars (4). This endurance or the tolerance of plants to pathogen generated stress (4, 8), though widely mentioned, is poorly understood. One of the major obstacles in evaluating plant responses to disease stresses relates to the inherent difficulties in establishing equivalent disease stresses across cultivars and characterizing the magnitude and nature of the imposed stresses. Difficulties in detection, transmission, and utilization of tolerance have so far limited its usefulness in breeding programs. In theory, the characteristic of not placing selective pressure on the pathogen, the projected durability, and the reduced need for fungicide make tolerance an attractive concept to exploit as means of protecting plants from disease damage (4).

Postanthasis chemical desiccation has been utilized as a measure for revealing wheat cultivars tolerant to septoria tritici blotch in the absence of infection by m. graminicola (8). Chemical desiccation has been used to simulate postanthesis drought stress (2,3). Wheat cultivars tolerant to both septoria tritici blotch and drought could also tolerate postanthesis chemical desiccation stress.

Leaf-canopy temperatures were found to be a reliable indicator of plant water stress (5, 6). The close association between leaf temperature and

plant water stress stems from the reduction in transpirational cooling of the leaf upon stomatal closure at low leaf water potential (1).

Leaf-canopy temperature obtained by infrared (IR) thermometer were correlated with leaf water potential across cultivars and thus can be used as a screening method for dehydration avoidance (1). Septoria leaf blotch causes leaf necrosis and leaf dehydration, the rate of which depends on disease severity and cultivar resistance.

It was therefore hypothesis that infrared sensing of canopy temperature under disease conditions may serve as an indirect relative measure of damage caused by septoria and the resistance of varieties. This experiment was performed to evaluate the hypothesis in a preliminary manner.

Materials and Methods

The experiment was conducted at the Bet Dagan Experiment farm during the 1983-1984 growing season. Forty six wheat and triticale cultivars were sown in a split plot design, with treatments in main plots and cultivars in subplots in four replications. Each subplot was 2 m wide and 6 m long. Two treatments were employed: fungicide-protected (three applications of Tilt-Propiconazole, CGA 64250) non-inoculated control, and inoculation with M. graminicola (anamorph: Septoria tritici). Septoria tritici blotch epidemics were incited by inoculating the plant canopy weekly with a suspension of 107 spores per milliliter starting at the emergence of the flag-minus-2 leaf and finishing at the end of the milk stage. The suspension was prepared from a mixture of virulent isolates of M. graminicola (anamorphic stage: S. tritici). Inoculation was performed during rainy days and/or dewy

nights by using a low-volume low-pressure sprayer (Ulva 8-micron Co., Bromyard, England). Weekly assessments of percent disease coverage was initiated on the uppermost four leaves upon the emergence of the flag-minus-2 leaf. In each disease assessment the growth stage of the cultivar was recorded using the Zadoks et al decimal code (7).

Leaf temperatures were measured twice during the season at 117 and 145 days after seedling emergence, in conjunction with disease severity assessments. Measurements were made from the ground, using a hand-held, "Everest" IR thermometer with a 2^{o} angle of view. The viewing target consisted only of plants, avoiding the imaging of the ground. Temperatures were recorded at solar-noon.

Results and Discussion

Septoria tritici blotch epidemic developed rather fast during the 1983-1984 season. The progress of the disease on eight representative cultivars was calibrated to 30 days past-anthesis for non-transformed (Figure 1) and logit transformation of log x/1-x where x = disease severity (Figure 2). The cultivars included: early maturing, short stature wheats - Barkai, Bet-Lehem, and the somewhat later maturing wheat Lalhich; medium-maturity, short stature wheats-Bobwhite's, KVZ-UP301, and KVZ-K4500 L.A.4 and the tall cultivar IAS 20-IASSUL, and the late maturing, tall cultivar Titan. Disease progress on the early maturing short wheats was fast and the pathogen reached upper plant parts early during the season. The cultivar KVZ-UP301 represent a group of moderate-maturity cultivars with moderate level of disease as compared to Bobwhite "S" (BOW"S") and KVZ-K4500 L.A.4.

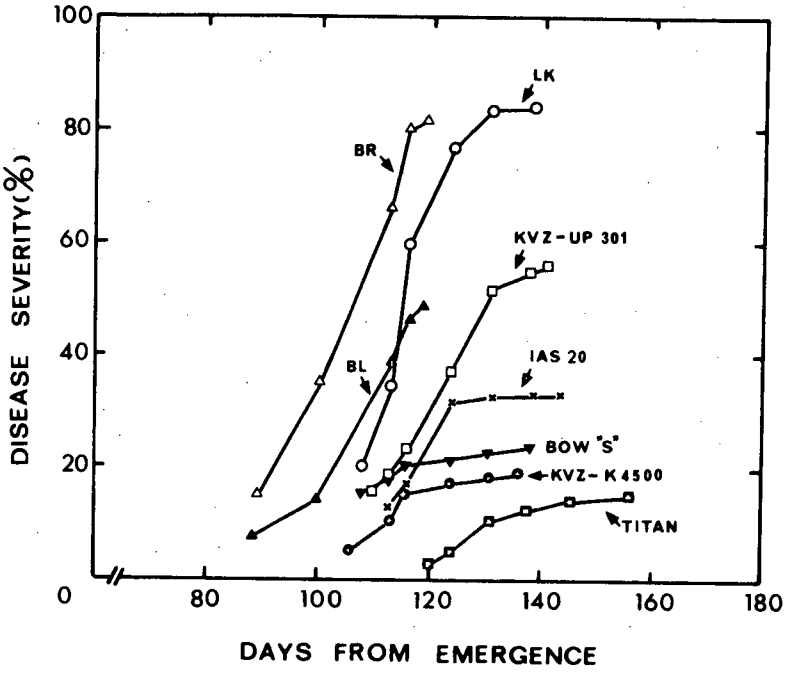

Figure 1. The progression of septoria tritici blotch on the four uppermost leaves 36 days from the onset of anthesis on eight spring wheat cultivars. BR=Barkai, BL = Bet Lehem, LK = Lakhish.

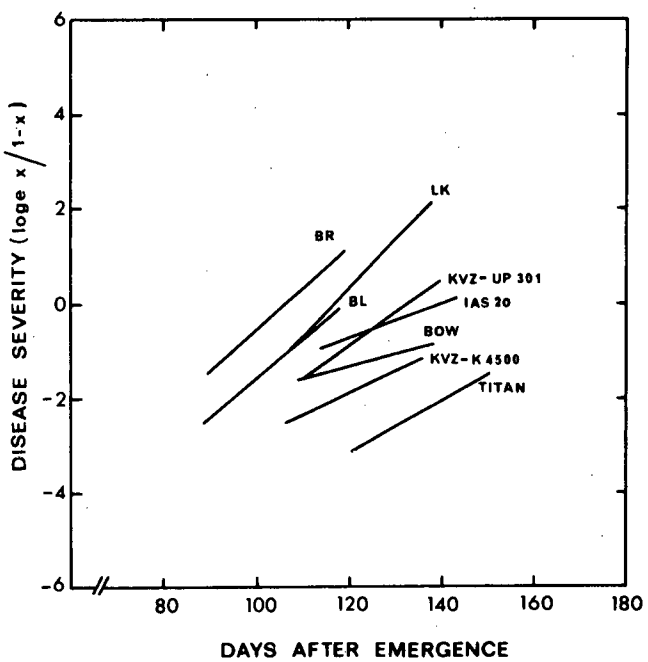

Figure 2. The progression of septoria tritici blotch where disease severity expressed as the logarithmic transformation of percent coverage on the four uppermost leaves. BR = Barkai, BL = Bet Lehem, and LK = Lakhish.

which are resistant. The tall, late cultivar Titan harbored low level of symptoms.

The relationship between disease severity expressed as the Area under disease progress curve for the period from anthesis plus 30 days thereafter and loss in 1000-Kernel weight [(1000-kernel weight in protected plots - 1000-kernel weight in infected plots)/ 1000-kernel weight in protected plots] x 100 is presented in figure 3.

A Significant association existed between disease severity and losses in Kernel weight, whereas Miriam and Lakhish expressed low losses in kernel weight despite high pycnidia coverage.

The relation between percent disease coverage and leaf temperatures recorded by IR thermometer 117 and 145 days after anthesis for 46 cultivars are presented in Figure 4.

Five wheat cultivars are marked for identification: Barkai (BR), KVZ-K4500. L.A.4, Lakhish (LK), and the tall late cultivars Titan and Toropi,: The vulnerable cultivar Barkai expressed higher temperatures during the 117 recording, however, the tolerant cultivar Lakhish expressed high canopy temperature during the late recording (145). The range of differentiation across cultivars was greater with respect to disease coverage while the range of temperatures across cultivar was of lower differentiating magnitude.

It is clear that the cultivar's growth stage, and residual green tissue are of influencing the interpretation of the results with regard to the association between disease severity, consequent losses in Kernel weight and canopy temperature.

While the gross association between disease and leaf temperature indicates the potential of infrared thermal measurements, much more work is

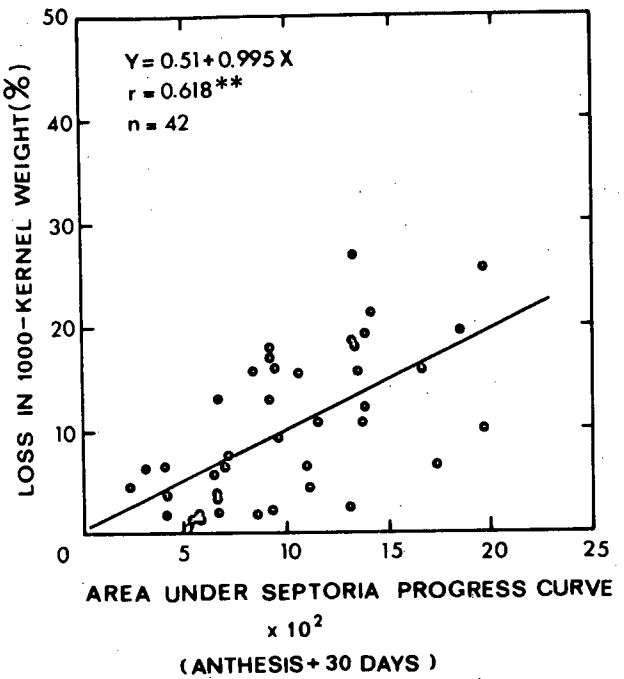

Figure 3. The relationship between disease severity expressed as the area under septoria progress curve 30 days from the onset of anthesis and loss in 1000-kernel weight across 42 wheat and triticale cultivars.

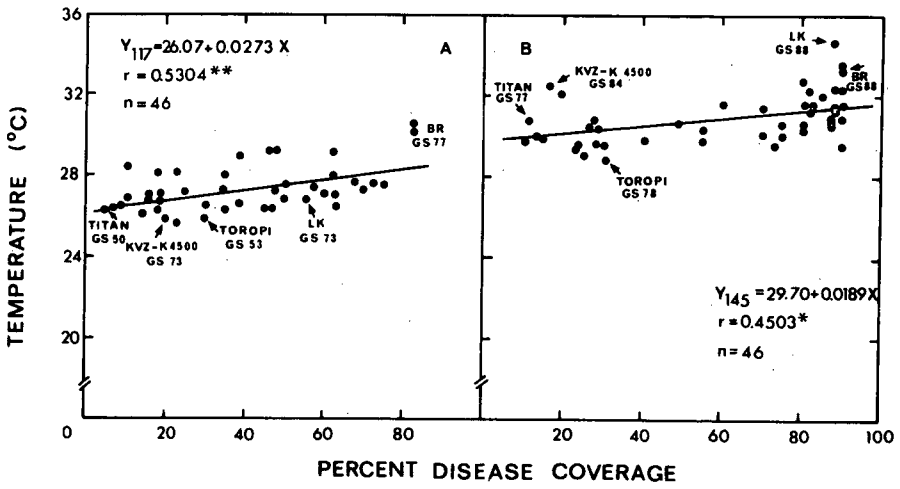

Figure 4. The relation between percent disease coverage on the four uppermost leaves and the temperature recorded by a hand held "Everest" Infrared thermometer across 46 cultivars. 4 A - recording conducted 117 days from seedling emergence, 4 B - recording at 145 days from emergence. BR = Barkai, LK = Lakhish. Growth Stages (GS) according to the Zadoks et al decimal code (Eucarpia Bull. 7:45-52, 1974).

needed in order to increase the sensitivity of the test and to elucidate the factors involved in this association across varied genetic materials.

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3.5

The development of agronomic breeding lines which possess combined resistance and tolerance to Septoria tritici blotch of wheat

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Septoria tritici blotch of wheat incited by Mycophaerella graminicola (Fuckel) Schroeter (Anamorph : Septoria tritici Rob. ex. Desm.) causes serious yield reductions in certain parts of the world (6, 19). The annual average losses in yield due to septoria diseases - leptoshaeria nodorum blotch and septoria tritici blotch, in the United States, were estimated at 1% in the report of 1965 (6). With severe epidemics some vulnerable wheat cultivars maysuffer 30-50% losses in yield, resulting in shrivelled grain unfit for milling.

Some susceptible wheat cultivars display tolerance and can endure high levels of septoria tritici blotch epidemics without sustaining appreciable losses in yield (6, 18, 19).

Selection for tolerance, based on kernel weight in segregating diseased populations in crosses between nontolerant cultivars x tolerant cultivars, produced lines with superior kernel weight, but not necessarily higher yields (1, 7, 9, 12, 14, 15, 16, 19). 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 (19). Ziv et al. (19) reported that tolerance derived from the cultivar Miriam seemd to be incompatible with dwarf plant stature. This 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 (19). It was suggested that breeding for tolerance would be possible if the selection goals are high kernel weight among semidwarf plants and trying to avoid dwarf and tall lines. Despite these findings, difficulties in detection, transmission and utilization of tolerance in breeding programs have not been overcome. This can be attributed in part to the reluctance in using susceptible-tolerant germplasm in breeding programs and to release of cultivars with such characteristics to wheat growers.

Fassati et al. (7) used a mutagenesis technique to improve tolerance or resistance to S. nodorum in the cultivar Fermo. The technique was valuable but many genotypes had to be treated because mutants could not be selected from allthe genotypes. All the isolated mutants expressed reduction of yield potential. These authors suggest that the best way of obtaining plants which resist S. nodorum would be the association of partial resistance and tolerance in the same plant.

MATERIALS AND METHODS

The septoria-tolerant, high-yielding, early-maturing, short-statured cultivars Lakhish (Yaktana//Norin 10/Brevor/3/Florence Aurore) and Miriam (Chapingo 53//Norin 10/Brevor/3/Yaqui 54/2 Merav) were crossed with each of the followingf septoria-resistant cultivars : the winter, early-maturing, semidwarf cultivar Bezostaya 1 (PI 345685); the spring,

moderate-maturing, semidwarf accession Musala "S" (Lee x kvz/CC x Ron-Cha, CIMMYT accession CM 16780-J-1M-2Y-501M-0Y, from 7 ISEPTON # 56); the spring, late-maturing, semidwarf cultivar Olaf (CI 15930); and the spring, late-maturing, tall stature cultivar Titan (CI 12615).

In each of the above 8 basic crosses, the F_1 were backcrossed once to the resistant parent and once back to the tolerant parent. In the F_2 and the BCF_2 of each cross, resistant and susceptible plants expressing high kernel weight under severe septoria tritici blotch epidemics were selected.

During 1982/1983 and 1984/1985 each population was split into septoria-infected and fungicide-protected subplots. Septoria tritici blotch epidemics were incited by inoculating the plant canopy weekly with a suspension of 10^7 spores per milliliter, starting at the emergence of the flat-minus-2 leaf and finishing at the end of the milk stage. The suspension was prepared from a mixture of virulent isolates of M. graminicola. Inoculation was performed during rainy days and/or dewy nights by using low-pressure sprayer (Ulva 8 - Micron Co., Bromyard, England). Protected subplots were sprayed 3 times during the season with Tilt (Propiconazole CGA 64250). Selection for resistant and susceptible F_2 plants was performed in populations inoculated with the M. graminicola isolate ISR 398A1. This isolate is virulent on both Lakhish and Miriam, avirulent on Bezastaya 1 and Titan and may induce moderate level of symptoms on Musala "S" and Olaf. In the following years the isolate mixture included isolate ISR 8036 which is also virulent on Bezostaya 1 (5, 17).

Assessment of percent coverage of the uppermost four leaves, plant height and kernel weight were performed on plants within each of the families or on advanced lines. In selecting high kernel weight lines under septoria epidemic, a 1000-kernel weight of 40 gm was established as the selection cut-point. Thus, lines exceeding this cut-point were selected for further testing.

RESULTS

The scheme for the development of tolerant populations to septoria tritici blotch of wheat is presented in Fig. 1. Two directives were taken : a) develop populations from a single cross between resistant and tolerant parents and select among them resistant and susceptible lines with high kernel weight, and continue to select for high kernel weight and plant height under disease epidemic in following generations; and b) develop populations in which the portion of the resistant and the tolerant parents was enhanced via backcrossing with selection for high kernel weight and plant height in future generations.

Tolerant lines from the two directives would then be subjected separately to two M. graminicola isolates : isolate ISR 398A1, lacking gene(s) for virulence on Bezostaya 1-Kavkaz-Titan, and isolate ISR 8036 possessing virulence gene on the Bezostaya 1-Kavkaz parents and derivatives (Musala "S").

Bezostaya 1 x Lackhish - This cross between the resistant, early, semi-dwarf, winter wheat Bezostaya 1 and the tolerant cultivar Lakhish, yielded rather high kernel weight populations with a low mean loss in the F_3 and BC_2F_2 (Table 1). In this cross there was no backcross to Bezostaya 1.

Figure 1.

DEVELOPMENTAL SCHEME OF POPULATIONS TOLERANT TO SEPTORIA TRITICI BLOTCH

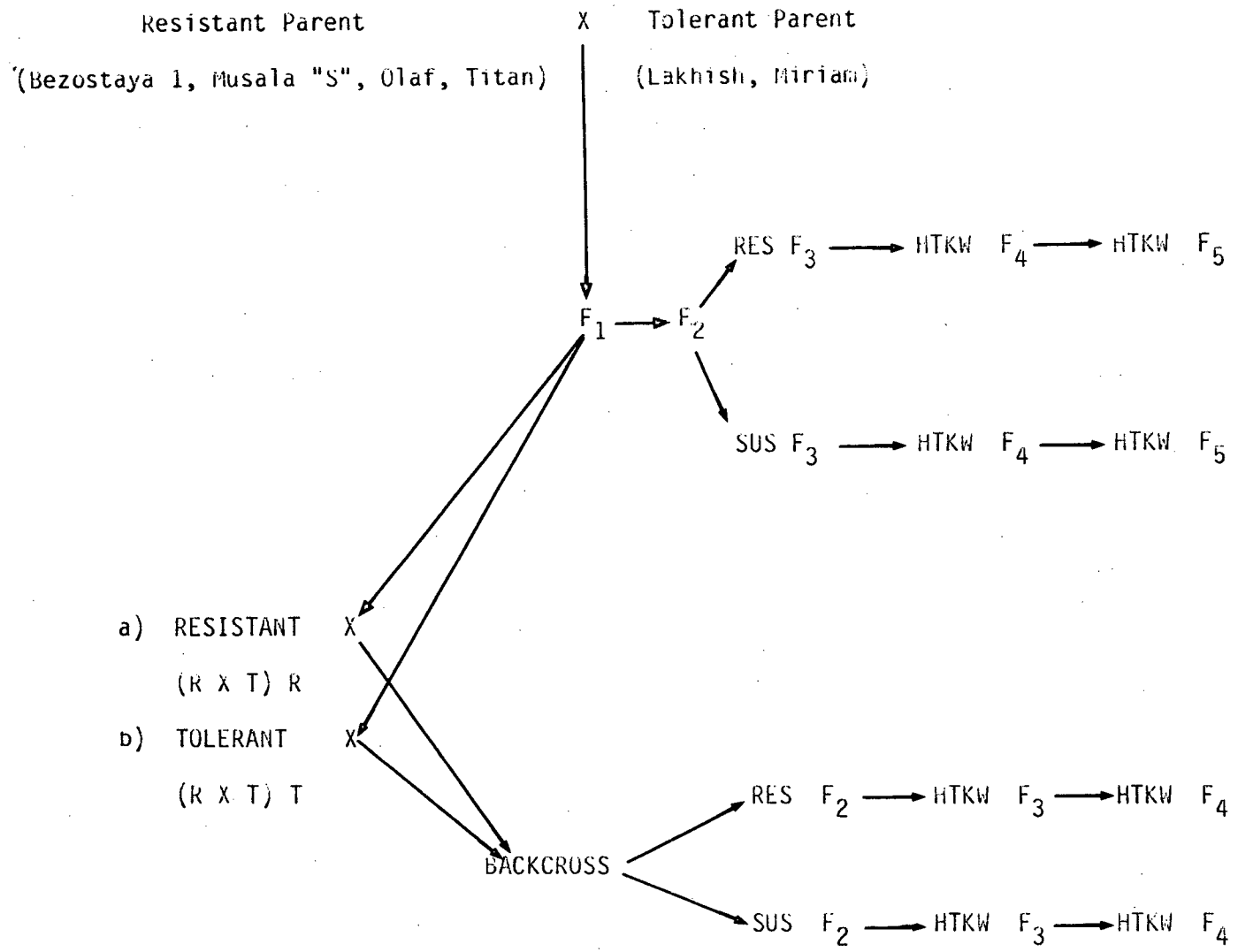

Table 1. Observed generation means for 1000-kernel weight, disease severity and plant height in septoria tritici blotch infected families of the cross Bezostaya 1/Lakhish and backcross to Lakhish.

CROSS	GENERATION	NUMBER OF LINES	1000 - KERNEL WEIGHT			DISEASE SEVERITY (%)	PLANT HEIGHT (cm)
			MEAN	RANGE	LOSS (%)		
BEZOSTAYA 1/LAKHISH	F_1	-	47.0	21.5-54.1	-	28.2	120.6
	F_2	132[c]	39.8	24.1-58.1	-	25.2	113.7
	F_3	115	43.2	15.8-61.7	11.93	64.3	-
BEZOSTAYA 1/LAKHISH//LAKHISH	BC_2[d]	-	36.8	24.7-45.8	-	50.1	105.8
	BC_2F_2	56	41.5	28.3-56.6	4.61	48.6	-

a) Mean loss from corresponding non-inoculated, fungicide-protected family
b) Mean pycnidia coverage of the 4 upper leaves recorded at dough stage
c) Number of plants
d) Backcross to P_2 (Lakhish)

The range of kernel weight under sever septoria epidemics was very high (61.7 gm). The progress of the breeding scheme was terminated at F_3 and BC_2F_2 due to severe susceptibility to stem rust (Puccinia graminis) and leaf rust (Puccinia recondita) of wheat.

Bezostaya 1 x Miriam - This cross between Bezostaya 1 and the early, semi-dwarf, tolerant cultivar Miriam yielded susceptible, semidwarf populations with high kernel weight. The losses in kernel weight were lower in F_3 populations than in backcrosses with Miriam (Table 2). Backcrosses to Bezostaya 1 yielded late, more resistant populations with corresponding low losses in kernel weight (2.21%). The progress of this breeding scheme was terminated as the previous cross, due to susceptibility to leaf and stem rusts of wheat.

Musala "S" x Lakhish - The cross between the semidwarf, somewhat late, moderately-resistant CIMMYT accession Musala "S" and Lakhish yielded agronomically suitable populations and lines, among which were some in the maturity range of Lakhish and plant height similar to both parents (Table 3). The resulting F_5 lines were susceptible to the mixture of the virulent isolates of M. graminicola. The range of the kernel weight in the single cross and backcross to Musala "S" was higher than that of lines derived from backcross to Lakhish, yet with similar mean loss. Families from this cross yielded 38 tolerant lines for further evaluation.

Musala "S" x Miriam - The mean loss in kernel weight in the 56 F_5 lines was in the range of 4.7 x 7.6% (Table 4). The mean kernel weight of the tolerant F_5 lines was similar to the previous cross. Lines of this cross yielded somewhat taller plants, though within the range of the early, tolerant parent Miriam (90-110 cm.). This cross yielded grains with

Table 2. Observed generation means for 1000-kernel weight, disease severity and plant height in septoria tritici blotch infected families of the cross Bezostaya 1/Miriam and backcrosses to both parents.

CROSS	GENERATION	NUMBER OF LINES	1000 - KERNEL WEIGHT			DISEASE SEVERITY (%)	PLANT HEIGHT (cm)
			MEAN	RANGE	LOSS (%)		
BEZOSTAYA 1/MIRIAM	F_1	-	45.6	36.6-51.4	-	18.3	116.1
	F_2	82[c]	38.9	30.0-50.8	-	32.3	110.4
	F_3	121	41.7	30.0-52.5	4.05	58.9	-
BEZOSTAYA 1/MIRIAM//BEZOSTAYA 1	BC_1[d]	-	43.6	34.2-63.2	-	1.2	121.0
	BC_1F_2	51	46.6	37.1-53.9	2.21	39.6	-
BEZOSTAYA 1/MIRIAM//MIRIAM	BC_2[e]	-	30.8	18.9-52.6	-	18.3	116.1
	BC_2F_2	17	38.5	31.7-46.5	13.89	61.2	-

a) Mean loss from corresponding non-inoculated, fungicide-protected family
b) Mean pycnidia coverage of the 4 upper leaves recorded at dough stage
c) Number of plants
d) Backcross to P_1 (Bezostaya 1)
e) Backcross to P_2 (Miriam)

Table 3. Observed generation means for 1000-kernel weight, disease severity and plant height in septoria tritici blotch infected families of the cross Musala"s"/Lakhish and backcrosses to both parents.

CROSS	GENERATION	NUMBER OF LINES	1000 - KERNEL WEIGHT			DISEASE SEVERITY (%)	PLANT HEIGHT (cm)
			MEAN	RANGE	LOSS (%)		
MUSALA/LAKHISH	F_1	-	45.8	36.7-51.2	-	23.6	96.7
	F_2	176[c]	39.9	23.8-56.0	-	33.6	98.4
	F_3	91	46.9	37.1-56.2	11.42	62.3	-
	F_4	71	36.6	25.3-51.3	-	-	102.6
	F_5	13	42.3	31.8-59.0	12.82	85.3	105.9
MUSALA/LAKHISH//MUSALA	BC_1[d]	-	45.3	31.2-49.3	-	6.2	90.0
	BC_1F_2	60	49.4	35.7-60.9	5.18	53.9	-
	BC_1F_3	56	37.7	26.8-49.6	-	-	98.6
	BC_1F_4	18	42.9	32.7-54.8	10.45	79.7	98.1
MUSALA/LAKHISH//LAKHISH	BC_2[e]	-	37.2	28.9-49.6	-	61.7	98.3
	BC_2F_2	65	46.6	33.0-60.5	16.04	61.3	-
	BC_2F_3	63	31.7	21.7-45.9	-	-	102.2
	BC_2F_4	7	41.5	36.8-45.8	11.23	87.5	101.7

a) Mean loss from corresponding non-inoculated, fungicide-protected family
b) Mean pycnidial coverage of the 4 upper leaves recorded at dough stage
c) Number of plants
d) Backcross to P_1 (Musala"s")
e) Backcross to P_2 (Lakhish)

Table 4. Observed generation means for 1000-kernel weight, disease severity and plant height in septoria tritici blotch infected families of the cross Musala "s"/Miriam and backcrosses to both parents.

CROSS	GENERATION	NUMBER OF LINES	1000- KERNEL WEIGHT			DISEASE SEVERITY (%)	PLANT HEIGHT (cm)
			MEAN	RANGE	LOSS		
MUSALA/MIRIAM	F_1	-	44.9	39.6-49.4	-	44.9	113.3
	F_2	31[c]	36.5	28.2-43.6	-	36.5	107.2
	F_3	98	42.5	30.2-58.1	14.91	65.9	-
	F_4	97	36.3	22.9-48.2	-	-	95.7
	F_5	32	43.1	37.4-48.8	4.70	83.7	111.3
MUSALA/MIRIAM//MUSALA	BC_1[d]	-	40.1	29.2-62.1	-	40.1	112.7
	BC_1F_2	23	46.9	28.4-61.0	10.81	65.1	-
	BC_1F_3	21	38.4	18.9-46.2	-	-	95.1
	BC_1F_4	21	42.9	31.1-47.2	7.64	84.4	103.7
MUSALA/MIRIAM//MIRIAM	BC_2[e]	-	33.3	22.9-49.9	-	33.3	116.6
	BC_2F_2	34	39.9	26.2-53.7	10.29	79.6	-
	BC_2F_3	31	35.7	29.9-42.6	-	-	104.1
	BC_2F_4	3	41.5	35.1-44.9	5.12	90.0	110.0

a) Mean loss from corresponding non-inoculated, fungicide-protected family
b) Mean pycnidia coverage of the 4 upper leaves recorded at dough stage
c) Number of plants
d) Backcross to P_1 (Musala"s")
e) Backcross to P_2 (Miriam)

kernel weight smaller than lines obtained with cross with Lakhish, due to higher kernel weight Lakhish. This cross yielded lines as early-maturing as Miriam with excellent agronomic types, which are being tested for yield and introduced to re-breeding.

Olaf x Lakhish - The cross between the semidwarf, late-maturing, moderately resistant cultivar Olaf and the tolerant cultivar Lakhish yielded late populations and lines with a relatively small kernel weight under septoria epidemics similar to that of the cultivar Olaf (Table 5). The number of agronomically suitable lines with high kernel weight was small as well (2). This cross was also characterized by weak straw and lodging, thus the breeding scheme was not continued beyond the F_4 generations of the backcross populations.

Olaf x Miriam - The cross between these two parents yielded small kernel weight populations and lines, with no single line which yielded 1000-kernel weight above the 40 gm, which was the selection cut-point. This is rather surprising since even the backcross to the tolerant cultivar Miriam yielded a surprisingly low kernel range in the BC_2F_3 which terminated further selection and progress (Table 6).

Titan x Lakhish - The cross between the tall, late-maturing, resistant cultivar Titan and Lakhish resulted in rather tall, late-maturing populations and lines with relatively high kernel weight and relatively low losses (Table 7). Two lines with a short stature, but with a kernel weight lower than 40 gm were kept for further evaluation. The relatively high kernel weight range dictates that a severe selection for plant height under septoria should be continued.

Titan x Miriam - This cross yielded tall populations and lines with relatively low disease coverage and correspondingly high kernel weight

Table 5. Observed generation means for 1000-kernel weight, disease severity and plant height in Septoria tritici blotch infected families of the cross Olaf/Lakhish and backcrosses to both parents.

CROSS	GENERATION	NUMBER OF LINES	1000 - KERNEL WEIGHT			DISEASE SEVERITY (%)	PLANT HEIGHT (cm)
			MEAN	RANGE	LOSS (%)		
OLAF/LAKHISH	F_1	-	43.9	37.2-53.6	-	51.7	113.3
	F_2	43[c]	37.9	25.3-51.6	-	49.2	118.5
	F_3	26	44.7	35.0-51.9	6.91	72.6	-
	F_4	26	39.5	28.9-49.0	-	-	113.9
	F_5	2	46.1	41.6-50.6	1.35	81.2	115.0
OLAF/LAKHISH//OLAF	BC_1[d]	-	45.1	39.2-49.1	-	28.9	118.7
	BC_1F_2	34	41.4	27.5-49.7	11.97	32.6	-
	BC_1F_3	34	33.4	27.1-42.4	-	-	105.3
	BC_1F_4	-	-	-	-	-	-
OLAF/LAKHISH//LAKHISH	BC_2[e]	-	40.5	30.0-51.1	-	82.3	111.8
	BC_2F_2	60	40.8	21.5-53.0	10.47	75.3	-
	BC_2F_3	60	32.9	19.4-43.5	-	-	97.3
	BC_2F_4	-	-	-	-	-	-

a) Mean loss from corresponding non-inoculated, fungicide-protected family
b) Mean pycnidia coverage of the 4 upper leaves recorded at dough stage
c) Number of plants
d) Backcross to P_1 (Olaf)
e) Backcross to P_2 (Lakhish)

Table 6. Observed generation means for 1000-kernel weight, disease severity and plant height in septoria tritici blotch infected families of the cross Olaf/Miriam and backcrosses to both parents.

CROSS	GENERATION	NUMBER OF LINES	1000 - KERNEL WEIGHT			DISEASE SEVERITY (%)	PLANT HEIGHT (cm)
			MEAN	RANGE	LOSS (%)		
OLAF/MIRIAM	F_1	-	48.9	37.9-57.7	-	62.5	113.3
	F_2	64[c]	32.3	20.4-43.1	-	63.6	111.8
	F_3	103	37.6	23.0-57.0	10.33	56.2	-
	F_4	98	28.9	26.0-38.6	-	-	100.1
	F_5	0	-	-	-	-	-
OLAF/MIRIAM//OLAF	BC_1[d]	-	42.0	31.3-59.5	-	44.7	96.2
	BC_1F_2	42	34.5	24.2-40.8	6.25	30.8	-
	BC_1F_3	26	28.9	20.9-41.4	-	-	105.4
	BC_1F_4	-	-	-	-	-	-
OLAF/MIRIAM//MIRIAM	BC_2[e]	-	39.2	27.3-49.4	-	69.9	107.0
	BC_2F_2	51	37.4	23.6-47.5	7.90	61.6	-
	BC_2F_3	39	26.5	20.3-33.2	-	-	99.1
	BC_2F_4	-	-	-	-	-	-

a) Mean loss from corresponding, non-inoculated, fungicide-protected family
b) Mean pycnidial coverage of the 4 upper leaves recorded at dough stage
c) Number of plants
d) Backcross to P_1 (Olaf)
e) Backcross to P_2 (Miriam)

Table 7. Observed-generation means for 1000-kernel weight, disease severity and plant height in septoria tritici blotch infected families of the cross Titan/Lakhish and bacrosses to both parents.

CROSS	GENERATION	NUMBER OF LINES	1000 - KERNEL WEIGHT			DISEASE SEVERITY (%)	PLANT HEIGHT (cm)
			MEAN	RANGE	LOSS (%)		
TITAN/LAKHISH	F_1	-	44.4	33.5-52.7	-	39.8	140.2
	F_2	95[c]	40.0	24.9-59.0	-	41.0	140.1
	F_3	85	36.4	23.7-53.9	9.88	30.4	-
	F_4	83	37.8	22.0-50.7	-	-	107.8
	F_5	3	37.9	35.2-41.5	2.41	73.3	96.7
TITAN/LAKHISH//TITAN	BC_1[d]	-	39.1	34.4-43.3	-	15.6	131.5
	BC_1F_2	49	47.1	36.5-52.4	3.51	15.4	-
	BC_1F_3	48	42.9	30.3-50.7	-	-	136.3
	BC_1F_4	-	-	-	-	-	-
TITAN/LAKHISH//LAKHISH	BC_2[e]	-	39.8	30.5-48.4	-	79.2	122.1
	BC_2F_2	55	38.3	26.0-52.0	16.02	72.3	-
	BC_2F_3	55	36.7	27.1-49.0	-	-	106.5
	BC_2F_4	-	-	-	-	-	-

a) Mean loss from corresponding non-inoculated, fungicide-protected family
b) Mean pycnidia coverage of the 4 upper leaves recorded at dough stage
c) Number of plants
d) Backcross to P_1 (Titan)
e) Backcross to P_2 (Lakhish)

(Table 8). Severe selection for shorter plant stature would determine the future of this cross.

The performance of the parents involved in the breeding scheme (with the exception of Bezostaya 1) in the 1984/1985 season when advanced lines were selected, is presented in Table 9. The cultivar Miriam continued to express kernel weight endurance under high disease severity with significant losses (14%) in Lakhish. The accession Musala "S" expressed high disease severity to the virulent M. graminicola isolate mixture which included the virulent isolate ISR 8036, yet, with statistically not significant losses in kernel weight. The two late-maturing cultivars Olaf (semi-dwarf) and Titan (tall) expressed low disease severity and resulting lowlosses. In the same trial, the non-tolerant, dwarf cultivar Barkai expressed a loss in kernel weight of 35%.

DISCUSSION

Susceptible wheat cultivars that were able to endure the damaging effects of septoria and rust diseases are classified as tolerant (1, 2, 10, 11, 12, 14). It is generally accepted that tolerance describes a phenomenon in which less yield loss or less quality loss occurs with equal pathogen or insect infestation when two cultivars are compared (1, 4, 8, 12). This interpretation is a retrospective analysis since it is not possible to measure or see the phenomenon in segregating early generations in breeders' plots (4). Buddenhagen (2, 3, 4) considered that selecting in segregating generations for tolerance to non-systemic diseases (leaf spots or rusts) is not really possible. His main objectives relate to the establishment of 'equal disease infestation' and to the reliability of

Table 8. Observed generation means for 1000-kernel weight, disease severity and plant height in septoria tritici blotch infected families of the cross Titan/Miriam and backcrosses to both parents.

CROSS	GENERATION	NUMBER OF LINES	1000 - KERNEL WEIGHT			DISEASE SEVERITY (%)	PLANT HEIGHT (cm)
			MEAN	RANGE	LOSS (%)		
TITAN/MIRIAM	F_1	-	47.6	44.1-51.0	-	27.9	135.2
	F_2	85[c]	42.5	35.9-58.1	-	4.1	142.3
	F_3	74	42.7	30.0-50.8	5.36	9.5	-
	F_4	74	43.1	32.5-51.9	-	-	130.3
	F_5	-	-	-	-	-	-
TITAN/MIRIAM//TITAN	BC_1[d]	-	41.8	26.2-51.7	-	1.7	125.7
	BC_1F_2	49	47.1	35.4-51.9	8.68	19.3	-
	BC_1F_3	49	39.3	25.8-53.6	-	-	128.5
	BC_1F_4	-	-	-	-	-	-
TITAN/MIRIAM//MIRIAM	BC_2[e]	-	35.8	28.0-41.6	-	59.5	111.3
	BC_2F_2	53	40.6	21.7-54.1	9.36	57.6	-
	BC_2F_3	53	35.6	23.0-43.9	-	-	120.2
	BC_2F_4	-	-	-	-	-	-

a) Mean loss from corresponding non-inoculated, fungicide-protected family
b) Mean pycnidial coverage of the 4 upper leaves recorded at dough stage
c) Number of plants
d) Backcross to P_1 (Titan)
e) Backcross to P_2 (Miriam)

Table 9.

THE PERFORMANCE OF 6 SPRING WHEAT CULTIVARS IN SEPTORIA TRITICI BLOTCH INFECTED TRIALS, BET-DAGAN 1984/1985.

CULTIVAR	PLANT HEIGHT (cm)	DISEASE [a] SEVERITY (%)	1000-KERNEL WEIGHT[b] (PROTECTED)	LOSS IN TKW[c] (%)
LAKHISH	90.0	86.7	46.7 ± 0.81[d]	13.95*
MIRIAM	91.2	90.0	43.3 ± 0.76	9.07 ns
MUSALA "S"	96.7	73.3	34.5 ± 0.19	8.89 ns
OLAF	120.0	35.0	33.5 ± 0.52	9.78 ns
TITAN	140.0	7.5	39.8 ± 0.41	1.94 ns
BARKAI	81.0	90.0	44.9 ± 0.87	34.73 **

a) PYCNIDIA COVERAGE ON UPPER 4 LEAVES

b) 1000-KERNEL WEIGHT IN NON-INOCULATED, FUNGICIDE-PROTECTED PLOTS

c) TKW = 1000-KERNEL WEIGHT

d) STANDARD ERROR

* SIGNIFICANT AT P = 0.05

** SIGNIFICANT AT P = 0.01

ns STATISTICALLY NOT SIGNIFICANT

ascribing a certain yield loss to a certain percent leaf area diseased across cultivars which have different ratios of sink/source limitation of yield.

Ziv et al. (19) have shown that selection for tolerance to septoria tritici blotch in segregating populations is possible in advanced generations and when certain a priori considerations are being followed. Selection of proper parents is of crucial importance, since a negative correlation was found between kernel weight endurance and dwarfness in septoria infected trials (19). Ziv et al. (19) suggested that this association may be the result of a longer (in time) pathogen stress exerted on the receptive photosynthesizing tissue of the dwarf cultivars prior to and during grain filling. The difficulties associated with disease stress are thus related to the question of measuring the effect of disease stress in terms of physiologifcal systems of the host affecting kernel growth. Different factors affecting the measurable disease parameters, namely disease severity and disease progress, associated with host growth dynamics (6, 13), plant stature (tall vs. dwarf), maturity (growth stage) and genotype, affect the final expression of disease on kernel growth. Kernel weight endurance under severe septoria epidemics could be readily selected for in populations where the two parents, the tolerant and the resistant, were selected within a relatively agronomically similar germplasm. The introduction of extermities, such as stature (tall or dwarf) and late maturity require the investment of genetical corrections difficult to encounter in breeding for tolerant lines. Thus, crosses with Bezostaya 1 would require selection for tolerance or resistance not only under septoria tritici blotch, but also under leaf and stem rust epidemics. This would interfere with the philosophy of combing frontal protection via low disease coverage,

together with kernel weight endurance whenever this protection is being succumbed.

This hypothesis that backcrosses to the recurrent tolerant parent would increase the probability of selecting more readily for kernel weight endurance, was disproven in the present study. In all combinations the range of kernel weight under septoria tritici blotch epidemics was the same or even higher than the range and the means of the backcrossed populations and lines, when subjected to isolate mixtures. The level of retained resistances in these combinations has to be tested. It is conceivable that the level would be significantly higher in lines derived from backcrosses to the recurrent resistant parent.

In the populations which were subjected to a mixture of virulent isolates the initial resistance which was selected for at early generations (Fig. 1) was over ome by virulence of ISR 8036. In order to test whether resistance was retained in the selected tolerant lines they are being evaluated during the 1985/1096 seasons by the following treatments : 1) inoculations with isolate ISR 398A1, which is avirulent to Bezostaya 1-Kavkaz-Titan and thus would reveal resistant lines in crosses with Musala "S" and Titan; 2) inoculations with isolate ISR 8036 which is virulent to the Bezostaya 1-Kavkaz genes, and would serve as the equivalent check for tolerance whenever resistance is overcome; and 3) a non-inoculated, fungicide-protected control. Thus, each line is grown in 3 replicated subplots (treatments). The scheme for future development of agronomic advanced lines which combine frontal resistance to septoria tritici bloch and tolerance in the background, is presented in Figure 2.

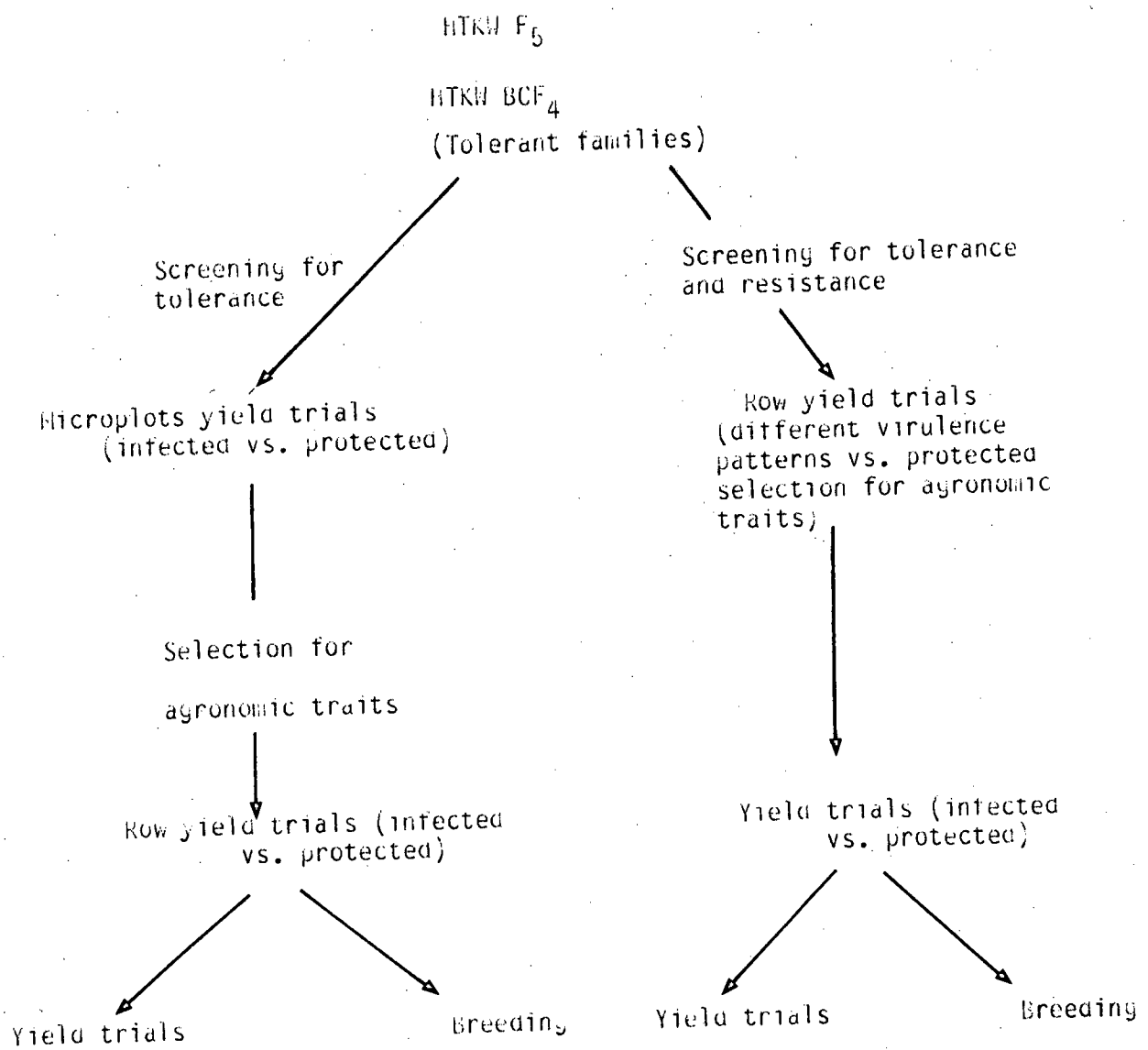

Figure 2. Procedures to be followed in testing and developing agronomic lines possessing "frontal" resistance and tolerance in the background.

This scheme would enable breeding for agronomic lines which possess resistance to the prevalent virulences and selelection for tolerance by means of chemical desiccation (magnesium chlorate) and virulent combinations which overcome the introduced resistance.

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Selection of winter wheat lines for resistance to S. tritici at Stillwater, Oklahoma, and Tel-Aviv, Israel.

A total of 99 winter wheat lines, having resistant cultivars Carifen-12 and Primepi in their pedigrees, were evaluated for resistance at Stillwater and Tel-Aviv. At Stillwater, the seed were sown in the field in late November. Vernalization, growth, and infection by S. tritici followed naturally. The lines were evaluated in growth stage 10.5, and classed susceptible if the third leaf (F-3) below the flag leaf was more than 50% necrotic and supported pycnidia. Conversely, lines in which the F-3 leaves were less than 50% necrotic were classed resistant. At Tel-Aviv, seedlings were started in a greenhouse, vernalized at 3C for 8 wk, and transplanted into the field on December 10. The transplant date was considered as the emergence date. Plants were spray-inoculated in the spring with a mixture of conidia from five virulent Israeli isolates of S. tritici (designated ISR398, ISR8036, ISR7801, ISR7901, and ISR TD). The lines were evaluated by estimating the amount of necrosis in the flag leaves and the first three lower ones. Additionally, plant height (cm), upward spread height of disease (cm), and heading date (days after emergence) were recorded.

To obtain a commonality for scoring disease reaction at both Stillwater and Tel-Aviv, we classed lines susceptible if their F-3 leaves were more than 50% necrotic. On this basis, 12 lines were resistant at both Stillwater and Tel-Aviv, 13 were resistant at Stillwater and susceptible at Tel-Aviv, 16 were susceptible at Stillwater and resistant at Tel-Aviv, and 58 were susceptible at both locations (Table 1).

All lines resistant in both the USA and Israel will be entered into the breeding nurseries at Stillwater, Oklahoma. One line, Payne/3/Primepi/Exile//Payne, because of its resistance and early heading at

Tel-Aviv, will be incorporated into the breeding program at Tel-Aviv University.

Table 1. Reaction of selected winter wheat lines to Septoria tritici in Israel and in Oklahoma, USA. (a)

Row No.			% infection on leaves (d)				Dis. Ht.	Plant Ht.	Head Date
USA	Israel	Lines and Cultivars (b,c)	F	F-1	F-2	F-3	(cm)	(cm)	(e)
		Resistant in the USA and Israel							
5035	895	PYN/3/PMP/EXILE//PYN	t	5	10	20	70	110	112
5039	899	PYN/3/PMP/VONA//VONA	5	5	10	20	90	110	111
5049	963	TAM101//TAM101/CAR-12	5	10	20	30	100	135	+112
5057	971	"	0	5	20	30	60	105	+112
5065	979	TAM101/3/OK72-2721*2//TAM101/CAR-12	5	10	20	30	95	125	+112
5066	980	"	0	5	20	30	85	125	+112
5073	987	"	5	10	20	30	80	110	+112
5079	993	TAM105//TAM101/CAR-12	5	10	20	30	80	100	+112
5086	1001	CSM//TAM101/CAR-12	10	20	30	40	90	110	+112
5088	1003	VONA//TAM101/CAR-12	5	10	20	30	85	120	+112
5096	1011	"	10	20	30	40	80	100	103
5098	1013	"	5	20	30	40	70	100	+112

Resistant in the USA, Susceptible in Israel

5028	888	PYN/3/PMP/VONA//VONA	50	60	70	80	75	100	109
5029	889	PYN/3/PMP/NWT//NWT	70	70	80	90	80	105	109
5043	956	PYN/3/PMP/VONA//VONA	20	30	40	50	90	120	106
5044	957	PYN/3/PMP/VONA//VONA	20	30	50	60	75	105	110
5067	981	TAM101/3/OK72-2721*2//TAM101/CAR-12	60	70	80	90	85	105	+112
5068	982	"	30	40	50	60	85	115	107
5069	983	"	20	30	40	50	80	110	109
5077	991	"	20	30	40	50	90	130	+112
5084	998	CSM//TAM101/CAR-12	60	70	70	80	80	105	+112
5089	1004	VONA//TAM101/CAR-12	50	60	70	80	85	110	106
5090	1005	"	40	50	60	70	90	115	+112
5091	1006	"	40	50	60	70	80	110	106
5093	1008	"	40	50	60	70	85	110	106

Susceptible in the USA, Resistant is Israel

5002	862	TAM101/3/PMP/VONA//VONA	10	20	20	30	90	125	105
5004	864	"	5	10	20	30	85	110	110
5005	865	"	0	0	5	10	80	105	+112
5007	867	"	20	30	40	50	80	110	+112
5010	870	TAM101/3/PMP/TX71A-562-6//OK72-2721	5	10	20	30	90	120	+112
5013	873	"	5	10	20	30	90	115	110
5022	882	VONA/3/PMP/VONA//VONA	5	10	20	30	80	105	-
5036	896	PYN/3/PMP/EXILE//PYN	5	10	10	20	75	115	111
5039	897	PYN/3/PMP/VONA//VONA	5	10	20	30	90	115	-
5041	954	"	5	10	30	40	80	120	106
5054	968	TAM101//TAM101/CAR-12	0	5	10	30	60	100	+112
5058	972	"	0	5	20	30	60	105	+112

5052	973	"	0	5	40	50	65	90	+112
5062	976	"	0	5	20	30	70	115	+112
5073	987	TX71A-562-6//TAM101/CAR-12	5	10	20	30	80	110	+112
5078	992	TAM105//TAM101/CAR-12	5	10	20	30	80	120	+112
	1030	KAVKAZ (check)	40	50	60	70	100	120	-
	1031	AURORA (check)	60	70	80	90	100	130	110

(a) Entries with less than 50% leaf necrosis at or below 20 cm of stem height were scored resistant at Stillwater, Oklahoma.

(b) A total of 101 entries were grown both at Stillwater, Oklahoma, and at Tel-Aviv. Entries at Tel-Aviv were inoculated with five Israeli cultures (ISR398, ISR8036, ISR7801, ISR7901, and ISR TD). Infection occurred naturally at Stillwater.

(c) Cultivar names abbreviated as follows: CAR-12 = Carifen-12; CSM = Chisholm; EXILE = Exile; PYN = Payne; PMP = Primepi; TAM101 = TAM W-101; TAM105 = TAM 105; OK72-2721 and TX71A-562-6 = experimental lines.

(d) The % infection (necrosis) was recorded for the flag leaf (F) and on three lower ones (F-1, F-2, F-3) at Tel-Aviv.

(e) Heading date (at Tel-Aviv) is shown as days following emergence (Dec. 10, 1984).

Selection of winter x spring wheat lines for resistance to S. tritici at Tel-Aviv, Israel.

Thirty-four lines derived from crosses made at Stillwater among winter x spring wheats were tested in 1985, using the same cultures and inoculation techniques applied to the winter wheat lines. Of the 34 lines tested, four were selected for incorporation into the breeding program at Tel-Aviv University (Table 2).

Table 2. Selected winter x spring wheats which will be incorporated in the Israeli spring wheat breeding program. (a)

Row No.		% infection on leaves (c)				Dis. Ht.	Plant Ht.	Head
Israel	Material (b)	F	F-1	F-2	F-3	(cm)	(cm)	Date (d)
913	CSM//GALLO-CUCKOO/KVZ-SX	t	5	10	20	100	130	100
918	EXILE//CONDOR"S"-MUSALA"S"	10	20	30	60	80	105	95
921	"	5	10	20	30	75	105	89
928	CSM/BOBWHITE"S"	10	20	30	40	80	100	96

(a) Thirty-four winter x spring wheats were grown at Tel-Aviv and data collected in the spring of 1985. The entries were inoculated with five Israeli cultures (ISR398, ISR8036, ISR7801, ISR7901, and ISR TD).

(b) Cultivar names abbreviated as follows: CSM = Chisholm; and KVZ = Kavkaz.

(c) The % infection (necrosis) was recorded for the flag leaf (F) and for three lower ones (F-1, F-2, and F-3).

(d) Heading date is shown as days following emergence (Dec. 10, 1984).

Inheritance of resistance to S. tritici, culture St83A, in winter wheats.

We stated in the initial report that in winter x winter wheat crosses performed at OSU, data from F_2 populations indicated that resistance to S. tritici, culture St83A, was conditioned by single dominant genes in cvs. Cappelle Deprez and Vilmorin 27 and by a recessive gene pair in Atlas 66. Although the crosses were made prior to the grant award date, the objective was consistent with that of the BARD grant. Thus, the testing was made an integral part of the grant effort. Of the three resistance sources, Vilmorin 27 appeared most useful because it was also highly resistant to tan spot

(caused by Pyrenophora tritici-repentis) than the other cultivars. Only Vilmorin 27 derivatives were retained in the BARD program. Subsequent F_3 tests confirmed that resistance of Vilmorin 27 to culture St83A was conditioned by a single dominant gene that is probably associated (P = 0.02-0.05, chi square test for independence) with a single gene for resistance to our test cultures of P. tritici-repentis. Lines were recovered from Vilmorin 27/Chisholm that were singly resistant to the test cultures of S tritici (St83A) and P. tritici-repentis, and one line that was resistant to both organisms. We anticipate that this dually resistant line, tentatively designated 'Septan,' will be released as germplasm.

Resistant winter wheat cvs. Dur Concur, Hadden, and H574-1-2-6 were each crossed with the commercially grown susceptible cv. TAM W-101. Additionally, Dur Concur and Hadden were crossed with the susceptible cv. Chisholm, and Hadden with the susceptible cv. Newton.

The F_1 and F_2 plants derived from the crosses were grown in the greenhouse during the winter of 1983-84. Three attempts to inoculate the plants with St83A were unsuccessful. Although infections occurred on some plants with each inoculation, the incidence was too low to establish the mode of inherited resistance. The F_3 families descended from the F_2 plants were space-planted in rows in the field in the fall of 1984. Rows of a very suceptible cv., Danne, were grown between those of the F_3 families.

The F_3 families and susceptible Danne were inoculated on March 27, 1985, and twice thereafter at weekly intervals with culture St83A. The inoculum was produced by flooding V-8 agar in petri dishes with conidial suspensions of St83A and incubating the cultures under fluorescent lamps for 7 days. Conidial colonies on the agar were collected in water poured into each plate and the resulting suspensions combined in a common container to derive a

suspension of about 40 x 10^6 conidia per ml. This required 100-200 petri dish cultures to produce 1 L of inoculum. The inoculum was applied to the plants with a back-pack mist blower.

The families were scored for reaction to St83A on April 30 and again on May 10. Counts of resistant and susceptible plants on April 30. On May 10 the scoring was limited to confirming the description of each family as either homozygous for resistance, segregating for resistance and susceptibility, or homozygous for susceptibility.

Results of the F_3 test indicated that resistance was conditioned by a single gene in each of the cultivars (Table 3). Although the number of families tested from each cross was small, their reaction to infection was very distinct. Similarly, reactions of plants within segregating families were discrete and indicated that resistance in each of the three resistant cultivars was dominant.

Table 3. An F_3 analysis of the inheritance of resistance to Septoria tritici (culture St83A) in resistant winter wheats Dur Concur, Hadden, and H574-1-2-6.

Cross	Numbers of F_3 families: Homoz. Res.	Seg. Res. and Susc.	Homoz. Susc.	Total	Probability of fit to a 1:2:1 ratio (a)
TAM W-101/Dur Concur	17	36	6	59	0.02-0.05
Chisholm/Dur Concur	4	12	11	27	0.10-0.20
TAM W-101/Hadden	5	19	15	39	0.05-0.10
Chisholm/Hadden	9	11	0	20	0.01-0.02
Newton/Hadden	4	23	13	40	0.05-0.10
TAM W-101/H574-1-2-6	10	43	19	72	0.05-0.10

(a) chi-square test for goodness of fit.

Biological Control:

Effect of streptomycin on development of Septoria leaf blotch.

The effect of streptomycin on development of Septoria leaf blotch in flag leaves of winter wheat cv. TAM W-101 was tested in the field in the spring of 1984 and again in 1985. In 1984, plots were established within large (30 m x 15 m) no-till plots (having a full complement of residue from the previous wheat crop) used in a crop residue management study. In 1985, the plots were established within both no-till and clean-till plots of the crop residue study. A randomized complete block design with four replications was used in all tests. The treated and untreated plots were each 1 m^2, and so arranged that they occupied diagonally opposed quadrants of 2 m x 2 m squares. This

arrangement permitted maximum access to the plots, minimized spray drift, and maintained close proximity of the treated and check plots.

Streptomycin HCl (125 ppm) in distilled water containing a drop of Tween 20/L was applied to runoff with a hand-held CO_2 pressurized mist sprayer. In 1984, applications were made on May 8, 14, 21, and 31, when the plants were in growth stages (Feekes' scale) 9.0, 10.0, 10.3, and 10.5, respectively. In 1985, streptomycin was applied on April 13 and 20 and on May 1 and 11; plant growth stages were not recorded.

Ten flag leaves were collected randomly from each plot on June 6, 1984, and on May 20, 1985. The number of Septoria leaf blotch lesions/g of dry leaf tissue was determined.

Attempts were made each year, during the time the streptomycin was being applied, to isolate bacteria antagonistic to growth of S. tritici from leaves collected from plants adjacent to the plots. Nutrient agar and V-8 agar were used as the isolation medium in 1984, and nutrient agar and Pseudomonas isolation medium were used in 1985.

The application of streptomycin resulted in a 52.6% increase in number of lesions/g of dry leaf tissue in 1984, and in a 14.2% and 22.1% increase, respectively, in similar tissue from plants in the no-till and clean-till plots in 1985 (Table 4). These data strongly indicate that naturally occurring bacteria inhibit infection by S. tritici. Attempts to isolate bacteria antagonistic to S. tritici failed in 1984. However, two bacteria, identified as Bacillus subtilis and Pseudomonas fluorescens biovar I, which inhibited growth of S. tritici were isolated in 1985.

Table 4. Effect of streptomycin on the development of Septoria leaf blotch lesions in flag leaves of a winter wheat cv. TAM W-101.

Crop year	Tillage practice (a)	Lesions/g of dry leaf		% Increase	LSD
		Streptomycin	Check		
1984	No-till	11.9	7.8	52.6	1.08
1985	No-till	43.4	38.0	14.2	0.84
1985	Clean-till	45.8	37.5	22.1	1.25

(a) No-till = all residue from prior wheat crop left on soil surface; clean-till = residue buried with a moldboard plow.

Isolation and testing bacterial antagonists of S. tritici.

Bacterial antagonists of S. tritici were isolated from soil and from nylon mesh dipped in budding cultures of S. tritici in liquid V-8 medium and buried in a wheat field for 48 hr. Efforts to isolate antagonists from wheat leaves were unsuccessful during the 1983-84 crop season, but were successful during the spring of 1985 (see preceding section). Soil samples, nylon mesh V-8 medium baits, and leaf segments were shaken vigorously in sterile distilled water with either a vortex mixer or a sonic bath. Standard serial dilutions of the wash water were spread on V-8 agar and nutrient agar in 1984 and on Pseudomonas isolation agar and nutrient agar in 1985. Individual bacterial colonies taken directly from the dilution plate series or from secondary cultures were used to point-inoculate fresh media in petri dishes. After 48 hr the medium was sprayed with S. tritici conidia suspended in sterile water. Growth inhibition of S. tritici around the bacterial colonies

was the criterion for selecting antagonists. Two bacteria from soil which appeared most inhibitory to growth were identified as Bacillus pumilus and B. subtlis.

Beginning on April 4, 1984, B. pumilus and B. subtlis were suspended in water and sprayed on 1-m^2 plots of TAM W-101 wheat seven times at 7-day intervals at the rate of 125 ml per plot. Concentrations of the suspensions ranged from 770 to 1100 million cfu/ml for B. pumilus and 90 to 930 for B. subtlis. The experimental design was a randomized complete block with eight replications.

The experiment was repeated in 1985 with some variations: namely, plots were established within large no-till and clean-till plots with four replication in each; two check plots were included in each replication--one sprayed with water and one with V-8 liquid medium--;and LSD values rather than Duncan's multiple range tests were determined to indicate significant differences between treatments. The bacterial suspensions, water, and V-8 liquid medium were applied to the foliage on April 13 and 20 and on May 1 and 5. Rates of application on the consecutive dates for B. pumilus were 790, 656, 805, and 863 million cfu/ml, and for B. subtlis were 830, 723, 1001, and 775 million cfu/ml.

Ten flag leaves were randomly collected from each plot on June 20. Lesions per gram of dry leaf tissue were determined.

Results of the tests were reasonably similar in both years (Tables 5 and 6). Both B. pumilus and B. subtlis significantly reduced the number of Septoria leaf blotch lesions in the flag leaves of the wheat cv. TAM W-101.

Table 5. Development of Septoria leaf blotch lesions in flag leaves of wheat cv. TAM W-101 treated with two bacteria in 1984 (a).

Bacteria and check	Lesions/g of dry leaf tissue (b)
Bacillus pumilus	58.6 a
Bacillus subtlis	49.6 a
water spray (check)	218.3 b

(a) Plots were established in a wheat plot under no-till management

(b) Values followed by the same letter are not significantly different (P = 0.01) according to Duncan's multiple range test.

Table 6. Development of Septoria leaf blotch lesions in flag leaves of wheat cv. TAM W-101 grown under two tillage systems and treated with two bacteria in 1985.

	Lesions/g of dry leaf tissue in indicated tillage plots (a)	
Bacteria and check	No-till	Clean-till
Bacillus pumilus	21.1	22.4
Bacillus subtlis	20.0	21.0
water spray (check)	38.0	37.4
V-8 liquid medium (check)	36.9	38.3

(a) LSD = 3.32 for no-till and 2.04 for clean-till.

INHERITANCE OF RESISTANCE TO *S. TRITICI* IN DURUM WHEAT

Overview for BARD report (Maarten van Ginkel)

In 1983 and 1984, crosses and related generations were produced between thirteen durum wheat varieties obtained from wheat research and breeding programs in North Africa and Israel.

Varieties were selected based on one or more of the following criteria:

a. field resistance to *S. tritici*

b. high yielding

c. good agronomic type

d. proven local adaptation

e. good combining ability

Seedling disease reactions were assessed of these varieties and the subsequent progenies, following inoculation with 34 different *S. tritici* isolates, originating from countries in the Mediterranean region including Israel, Italy, Spain, Syria, Tunisia, and Turkey.

Various genetic parameters, including those on mode of inheritance and number of genes involved in disease expression were estimated. Close agreement was observed between the data presented by Eyal et al. (1985) on the variety-isolate disease matrix and results obtained in this genetic study of durum wheat varieties.

The implications of the analyses regarding breeding and selection strategies directed toward increasing resistance to *S. tritici* in durum wheat, as well as a complete report of the various analyses will be presented in the form of a pending doctoral thesis.

3.8

Virulence patterns in ascospores-derived cultures of *Mycosphaerella graminicola*

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INTRODUCTION

The first step in formulating any control strategy is to establish the life cycle of the organism, especially the source and timing of the primary infection. It is generally assumed that the primary inoculum is by windblown or trashborne pycnidiospores (4, 5, 6). Because of the difficulty, even for the trained eye, in detecting pseudothecia of Mycosphaerella graminicola (Fuckel) Schroeter on stubble or crop debris, there are few recors of this organism in the literature. The importance of the perfect state as the source of primary inoculum is being greatly underestimated (6, 7).

The contribution of the perfect state of M. graminicola to the virulence spectrum of the pathogen in regions where it is operative, has not been investigated. The ineffectiveness of Bezostaya 1 - Kavkaz complex in conferring resistance to septoria tritici blotch in Oregon ws attributed to the presence of corresponding virulence in the pathogen. The detection of pseudothocia of M. graminicola on trash of wheat, together with pycnidia of the asexual state has drawn attention to the inter-relations between the two states (asexual and sexual) operating concurrently in the same location.

RESULTS AND DISCUSSION

Leaf samples bearing perithecia of Mycosphaerella graminicola were collected at Hyslop Agronomy Farm, Oregon State University, Corvalis, Oregon, in the spring of 1982. Leaf segments were attached to the inside of upper part of a petri plate containing 1% potato dextrose agar. Ascospores were removed in order and transferred to malt agar slants (1). The marked cultivars were grown in liquid medium for 5 days and thereafter the spore suspension was used after equilibration to 1-2 x 10^7 conidia per milliliter to inoculate trays containing seedlings of 8 cultivars. The cultivars used in the study were as follows : Aurora x Kalyansona-Bluebird/Woodpecker "S" (CM 33203-k-9M-2Y-1M-1Y-1M-0Y), Siete Cerros (7C) CI 14493, Bobwhite "S", Bezostaya 1 (PI 345685), Fortuna (CI 13596), Colotana (CI 13556), Wampum, 81M UWWMN 2024 (Palmaress/(TF 1035) Fauereau/4/Martin/K3/Hohen 77/Uro/2/Capelle/Magdalena) sel.1) and Weibull 7389.

The inoculated plants were scored for percent necrotic leaf area on a 0-9 scale. The response of the wheat cultivars was determined by using a cluster analysis where 6 response groups were arbitrarily established : very susceptible (VS), susceptible (S), moderate susceptible (MS), moderate resistant (MR), resistant (R) and very resistant (VR). The distribution of the means of the 8 (cultivars) x 20 (isolates) is presented in Table 1. The 20 isolatres included three check anamorphic isolates, one from the same location (ORG 82076), an isolate from Stillwater, Oklahoma (OK 83106) and an isolate from New Zealand (NZ1). Three ascospore-derived isolates were used in the study: isolate 46 with 6 subcultures; isolate 48 with 3 subcultures, and isolate 53.1 with the full ascospore-derived subcultures.

The cutpoint betwen resistant and susceptible host response was determined by adding the standard deviation of the moderately resistant response group to its mean. The cutpoint between resistant and susceptible was thus 1.8351 + 0.2166 = 2.05.

A cultivar (8) by isolate (20) matrix was formed using resistant (R) and susceptible (S) calculated values (Table 2). This matrix was analyzed bythe GENEALOGY computer analysis which estimates the minimum number of interacting genes assuming a gene-for-gene analysis (2, 3, 8). The gene-for-gene analysis identified 6 hypothetical different interacting genes in the 20-isolate x 8-cultivar matrix. The cultivar 81 MUWWMN 2024 which was resistant toall 20 isolates of M. graminicola and thus was not possible to assign any specific genes for resistance to it. The hypothetical genes for resistance assigned to the 7 cultivars are presented in Table 3. The cultivars Siete Cerros, Bezostaya 1, Fortuna and Colotana possesseach one different gene for resistancer. The cultivar Bobwhite "S" passes 3 genes, with one common gene for resistance with Bezostaya 1. The cultivar Weibull 7389 possess two genes for resistance, one common with Bobwhite "S". The hypothesized genes for virulence assigned to the 20 isolates are presented in Table 4. The isolate Oregon 82076 was assigned a gene virulent on Siete Cerros but not on Bezostaya1 and Bobwhite "S" to which this isolate was virulent in a previous study (2). The distribution of virulence genes according to their ascospore distribution did not follow an organized pattern. The attempt to follow virulence patterns according to ascospore arrangement can be more readily done according to reaction types (susceptible or resistant) as presented in Table 1. In isolate 46 an ascospore arrangement fitted a 2 : 4 : 2 combination on Bezostaya 1 assuming that this cultivar possess one gene for resistance. The same 2 : 4 : 2 combination was found in isolate 53.1 on this cultivar.

There was agreement in virulence arrangement for isolate 53.1 on gene for virulence VST 3 which was identified by the GENEALOGY analysis (Table 4). Such a combination (2 : 4 : 2) may be indicative that the reduction division occurred in the second division and that a crossing over occurred in chromosome segment containing that responsible for virulence. If this assumption is correct, this may led to the conclusion that virulence of those cultures is based on two un-linked loci in those haploid ascospore-derived cultures.

The gene virulent on Bezostaya 1 or any gene for virulence are hypothesized genes and are rather ambiguous markers for use in genetical analysis. This was the first attempt done with Mycosphaerella graminicola to follow distribution of virulence as an outcome of meiosis.

The above suggestion should be carefully checked on a larger number of M. graminicola cultures with more refined genetical markers. The attempts made in the laboratory to produce the sexual state in vitro were not successful.

Table 1. Cluster analysis of six cultivar response classes in a 20-isolate (*Mycosphaerella graminicola*) x 8-cultivar matrix.

Response class	Number of Evaluations	Necrosis (mean %) + standard deviation
Very susceptible	8	5.56 ± 0.49
Susceptible	14	4.00 ± 0.42
Moderately susceptible	18	2.74 ± 0.25
Moderately resistant	35	1.83 ± 0.22
Resistant	34	1.13 ± 0.20
Very resistant	51	0.34 ± 0.24

The analysis forms clusters of variables which are based on a measure of association (similarity) between the variables, or of distance (difference) between them.

Table 2. The distribution of susceptible host response in the 20 isolate (*Mycosphaerella graminicola*) x 8-cultivar matrix.

Isolate \ Cultivar	Siete Cerros	Bobwhite "S"	Bezostaya 1	Fortuna	Colotana	Wampum	81 M 2024	Weibull 7389
Oregon 82076		+	+		+	+		
Oklahoma 83106	+			+	+	+		
N.Z. 1	+		+	+	+	+		+
46A	+	+	+	+	+	+	+	
46B			+	+		+		
46C								
46E								
46F								
46G	+	+	+	+	+	+		+
48A	+		+		+	+		
48B								
48H								
53.1A		+	+		+	+		
53.1	+			+	+	+		
53.1C								
53.1D					+	+		
53.1E						+		
53.1F	+					+		
53.1G	+		+			+		
53.1H	+		+	+		+		

+ = denotes a susceptible host response

Table 3. Hypothetical resistance genes assigned to the 7 cultivars from a gene-for-gene analysis using the GENEALOGY computer analysis on 20-isolatres x 8 cultivar interacting matrix.

Cultivar	Genes for resistance						Hypothetical number of genes
	1	2	3	4	5	6	
Siete Cerros	+[a]						1
Bobwhite "S"			+	+		+	3
Bezostaya 1			+				1
Fortuna		+					1
Colotana				+			1
Wampum							0
81 M 2024	*	*	*	*	*	*	-
Weibull 7389					+	+	2

* resistant to all isolates

a Presence of resistance genes based on P. Kampmeijer's DIFFER and GENEALOGY (3) analysis of incomplete Person scheme of a variety x isolate reaction matrix.

Table 4. Hypothesized virulence genes derived from analysis of reaction matrix in 20 *Mycosphaerella graminicola* isolates tested on 8 cultivars

Mycosphaerella graminicola isolate	Hypothesized virulence genes					
	V1	V2	V3	V4	V5	V6
Oregon 82076	+[a]					
Oklahoma 83106		+	+	+		
N.Z.1	+	+	+	+	+	
46A	+	+	+	+	+	+
46B		+	+			
46C						
46E						
46F						
46G				+	+	
48A	+		+	+		
48B						
48H						
53.1A			+	+		+
53.1B	+	+		+		
53.1C						
53.1D				+		
53.1E						
53.1F	+					
53.1G	+		+			
53.1H	+	+	+			

a - Presence of virulence genes based on P. Kampmeijer (3) analysis of incomplete Person scheme of a cultivar by isolate reaction matrix.

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4. DESCRIPTION OF CO-OPERATION

Germplasm screened and evaluated for septoria tritici blotch in the U. S. and Isrel was incorporated in both countries breeding for resistance programs. Segregating populations and lines where shuttled to both countries for further evaluation and screening. The most promising lines were made available to breeders both in Israel and the U. S.

Resistant germplasm both of bread and durum wheats, was screened to a wide spectrum of virulences of Mycosphaerella graminicola at Montana State University, utilizing techniques developed by the co-operating investigators. Exchange of material and information was performed during visits in the co-operating Institutions by the co-operating scientists.

Evaluation of yield components under septoria tritic blotch and chemical desiccation (magnesium chlorate) was conducted by the Israeli team. In addition, infrared thermometry sensing was evaluated in yield trials conducted by the Israeli investigators.

Resistant germplasm and lines possessing combined frontal resistance and tolerance were made available to the Volcani breeding program and are being evaluated for yield and quality in the ARO breeding program.

Assessmen of virulence patterns of the sexual state was carried out by the Montana team with the aid of Dr. Sanderson, who is noted for his scientific contribution to the subject.

5. BENEFIT TO AGRICULTURE

Germplasm resistant to a wide spectrum of virulences of Mycosphaerella graminicola was identified and incorporated into national breeding programs in the two countries.

Methods were developed to identify and assess wheat cultivars capable of enduring both biotic and abiotic stresses. The understanding of the ability of wheat cultivars to tolerate stresses will enable its better utilization.

A breeding scheme for the incorporation of resistance and tolerance in high yielding wheats was proposed and experimentally evaluated. This novel approach will enable wheat breeders to continue to select for frontal resistance and assess its incorporated endurance for septoria tritici blotch and abiotic stress, using septoria epidemics and chemical desiccation as stress agents.

The understanding of the parameters involved in the endurance of tolerant cultivars under disease and abiotic stresses contributed to its potential use in breeding programs and in wheat production in the future.

Infrared thermometry sensing may offer a rapid technique to assess the relative resistance of wheat cultivars under septoria tritici blotch epidemics. Residual green leaf area of resistant and susceptible cultivars may explain their ability to maintain high yields under disease stress. Selection of wheat cultivars which do not exhibit rapid depletion in green leaf area offer an advantage in protecting yield.

The isolation of biocontrol agents antagonistic to Mycosphaerella graminicola and capable of reducing the level of symptoms offers an opportunity of future use of biological control of this pathogen and possibly of other foliar pathogens.

The understanding of the virulence spectrum of the pathogen and the contribution of the sexual state to the virulence recombination of M. graminicola as pursued for the first time in this project. The implications on breeding for resistance to septoria tritici blotch are far reaching.