Factors Affecting the Vertical Progression of Septoria Leaf Blotch in Short-Statured Wheats

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ABSTRACT

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The meteorological factors affecting the development and vertical progress of Septoria leaf blotch of wheat were assessed for equally susceptible dwarf (70–80 cm) and semi-dwarf (100–120 cm) spring wheat cultivar pairs of different maturity in both an arid and a rainy region in Israel. In the dwarf cultivars, pycnidia of *Septoria tritici* were found immediately after leaf emergence; in the semi-dwarf cultivars there was a 10- to 20-day lag between the emergence of the four upper leaves and pycnidia formation on those leaves. The time lag increased for plants of both dwarf and semi-dwarf cultivars in the rain-sparse region. The vertical progress of the pathogen from lower to higher leaves was affected by the distances between consecutive leaves—the "ladder effect". The rate of vertical progress on the dwarf wheats under the severe epidemics was similar to the rate on the equally receptive semi-dwarf cultivars despite the difference in plant architecture and maturity. Functions were developed to analyze the net contribution of climatological factors on the progress of the disease within the temperature range of 10–25 C. The vertical progress of the disease was correlated with the number of rainy and dewy days and temperature indices 7–21 days prior to disease observation and disease severity was correlated mainly with the number of dewy days and temperature indices 7–21 days prior. There were lower correlations in the arid region which was characterized by less rainfall, prolonged rainless periods, and hot spells toward the end of the growing season than in the rainy coastal plains.

Additional key words: Septoria tritici, Triticum aestivum, epidemiology.

Septoria leaf blotch of wheat, which is caused by *Septoria tritici* Rob. ex Desm., is a major wheat disease in many parts of the world, particularly on the Mediterranean seacoast, in South America, in the highlands of East Africa, and in Australia (11,13,17,18). Severe Septoria leaf blotch epidemics which caused significant economic crop losses in the recently introduced semi-dwarf wheats (4,11,13,18) occurred in North Africa during the unusually wet and cool 1968-1969 growing season. Although Septoria leaf blotch was reported in Israel on indigenous emmer (*Triticum dicoccoides* Koern.), on some 'land varieties' of bread (*T. aestivum* L.), and on durum wheats (*T. durum* Desf.), only occasionally were appreciable yield losses sustained by the 'classical' commercial bread wheat cultivars (3,4,6). The widespread and rapid replacement of the local wheats by the high-yielding cultivars, combined with favorable environmental conditions and changes in agronomic practices, contributed to the recent occurrence of severe leaf blotch epiphytotics (4,11,13,18).

There is little specific information on the relation of weather to the epidemics of Septoria leaf blotch. Saari and Wilcoxson (13) reported that epidemics caused in wheat by *S. tritici* occurred in countries in the Mediterranean basin in areas receiving 700 mm or more of rainfall annually, and that with decreased rainfall, the disease becomes progressively less of a problem. Severe Septoria leaf blotch epidemics causing substantial losses in yield occur in the semiarid southern plains of Israel with average annual rainfall of 300 mm or less (3,6). All stages of the infection cycle, from pycnidiospore liberation, dispersal, penetration, lesion development, and pycnidial formation, are dependent on moisture, both as rainfall and dew (7,8,15,17,19). Shaner and Finney (16) reported that severe epidemics of Septoria leaf blotch occurred at Lafayette, Indiana in seasons with 40 or more rainy days from 1 April to 14 June. Renfro and Young (12) observed that two consecutive days with a minimum temperature of 7 C or less inhibited infection. Many investigators suggested 20–24 C as the optimum range for disease development, but disease development usually proceeds well over the range of 16–27 C (17,18). Certain phases in pathogen development probably are temperature dependent; however, specific information on the relationship between disease development and temperature during the wheat-growing season are lacking (15,16)

The objective of this study was to determine the relationship between environmental factors and the vertical progress of Septoria leaf blotch on susceptible short-statured spring wheat cultivars differing in maturity and plant height.

MATERIALS AND METHODS

The trials were conducted during the 1975–1976 growing season at the Lakhish Experiment Station (situated in the semiarid southern coastal plains [average rainfall of 300–400 mm] and duplicated at the Bet-Dagan Experiment Station (situated in the rainy central coastal plain [average rainfall of 500–600 mm]). Five high-yielding, short-strawed, autumn-sown spring wheat cultivars were sown: susceptible early-maturing cultivars, the dwarf 'Barkai' (V238-8822-11/Miriam 2; V238-8822-11 = Yt//Nrn10/B21-1C/3/FA), the semi-dwarf cultivars 'Miriam' (Ch53/2/Nrn 10/B26/3/Yq 54/4/2 Merav), and 'Hazera 337' (Inia "s" [Son 64-Tzpp/Yq 54]); and two susceptible wheats with intermediate maturity date, the dwarf, 'Bet-Dagan 131' (Yt//Nrn10/B21-1C/3/FA), and the semi-dwarf 'Lakhish', a sib selection of the same cross. All cultivars originated at the Volcani Center except Hazera 337, which originated at the Hazera Seed Co., Israel.

Wheat plots (5m × 9m) were sown in four replications, each plot separated from adjacent plots by 2-m-wide buffer strips to reduce interplot interference. The mean number of seedlings per square meter was about 250 for each of the wheat cultivars tested. Septoria leaf blotch epidemics were established by spreading wheat straw infested with viable pycnidia of *S. tritici* that contained viable pycnidiospores, just after seedling emergence. Finely chopped

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infested straw was spread over the wheat canopy twice during the rainy days, approximately 10 days following the first straw application.

Standard meteorological stations were placed at the center of the wheat plots at the two locations. Each station contained a standard rain gauge, a minimum-maximum thermometer, a thermohygrograph (Model 594, The Bendix Corporation, Baltimore, MD) fitted with a dew duration recorder (Machine Shop, Iowa State University, Ames). The dew duration apparatus operated on the principle of recording changes in the length of a lamb gut membrane (Gold-beater's skin method) fitted between two levers connected to a microswitch and an electromagnet. The membrane, which expanded when wet and contracted when dry, was located at plant height level in the wheat plot.

Twenty randomly selected plants in each wheat plot were marked for future observations on plant and disease development. The disease development throughout the season was assayed at 7-day intervals from the detection of Septoria leaf blotch symptoms on the main culms of each marked plant. The following parameters were determined:

(a) Disease severity: the percent of green area of each leaf covered by pycnidia of *S. tritici* (5).
(b) The maximum height (centimeters) above ground level at which pycnidia of *S. tritici* could be found on green plant tissue.

The phenology for each plant was recorded throughout the season in parallel with disease development observations according to the

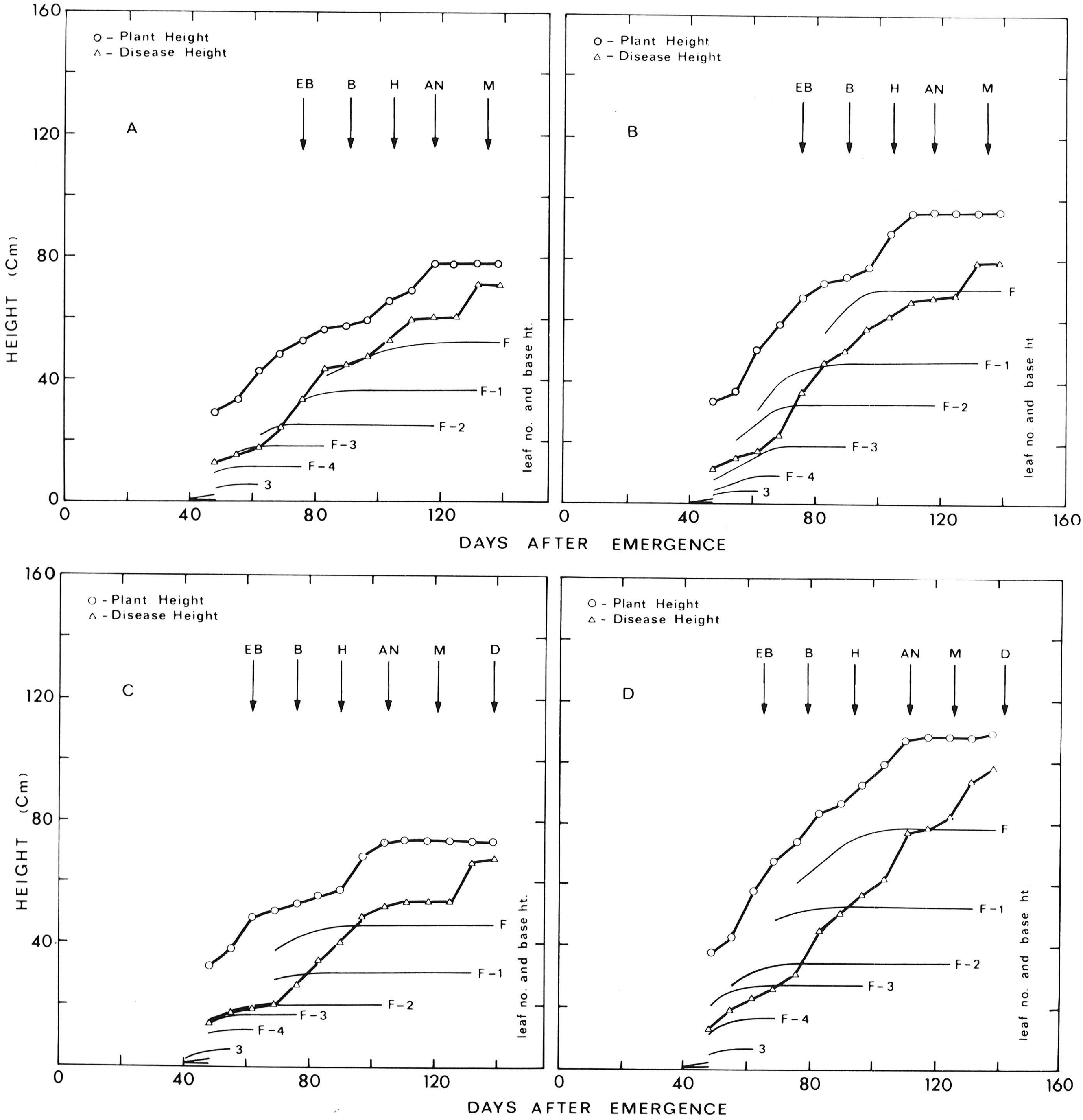

Fig. 1. Septoria leaf blotch in short-statured wheats. The progress of the disease (Δ) and plant height (O) related to the height of leaf bases (F = flag leaf, F−1 = flag minus one, F−2 = flag minus two, etc.) and growth stages in four wheat cultivars: **A** = Bet-Dagan 131, **B** = Lakhish, **C** = Barkai, and **D** = Miriam at the Bet-Dagan Experiment Station in Israel. Growth stages: EB = early boot, B = boot, H = heading, AN = anthesis, and M = milk stage.

following parameters:

(c) The height (centimeters) of the wheat plant and its developmental growth stage (6,10).
(d) The time of leaf emergence from the sheath and the height (centimeters) of each leaf base from the ground level.

The climatological variables derived from meteorological station records of daily maximum and minimum temperatures and precipitation were summarized for each 7-day period by: average maximum daily temperature (AVMAXT); average minimum daily temperature (AVMINT); absolute minimum temperature (ABSMINT) and the sum of the daily temperature indices (ΣT). A daily temperature index (T) was computed as the ratio of the daily temperature range restricted to the optimal *S. tritici* growth interval of 12–25 C, to the observed temperature range; ie, $T = (t_1 - t_2)/(t_{max} - t_{min})$ in which t_1 is the maximum temperature but not >25 C, and t_2 is the minimum temperature but not <12 C. The value T ranges from zero to one, zero if the temperatures that day were never in the range of 12 to 25 C and one if they never were outside the 12–25 C range. This measure is related to the temperature equivalent developed by Schrödter (9,14). The temperature index is summarized for each recording interval by summation of T. The rain parameters used were: the number of rainy days (DAYS OF RAIN); the cumulative rainfall (mm) during the recording interval (RAIN) and the sum of T for rainy days (ΣT_R). The number of dewy days (DAYS OF DEW) and the sum of T for dewy days during the recording interval (ΣT_D) also was included in the analysis.

RESULTS

Septoria progress and plant architecture. The relationship between the vertical progress of *S tritici* exemplified by disease height and plant architecture parameters such as plant height, the date of leaf emergence and height of the leaf base, and the developmental growth stages, is shown in Fig. 1A–D for the Bet-Dagan trials in the 1975–1976 season. The height of leaf bases and the distances between consecutive leaves differ markedly between the dwarf and the semi-dwarf wheats. In the intermediate-maturing dwarf Bet-Dagan 131 (Fig. 1A) and in the early-maturing dwarf Barkai (Fig. 1C) leaf emergence is followed by the almost immediate incidence of pycnidia on the new leaf blade. In the corresponding semi-dwarf cultivars, the intermediate-maturing Lakhish (Fig. 1B) and the early-maturing Miriam (Fig. 1D), there is a 10–20 day lag between emergence of the upper leaves and the time pycnidia were detected at these leaves. In plants of the semi-dwarf cultivars this time lag increases on the upper leaves toward the end of the growing season when the rainfall is less frequent. Pycnidia were found on the uppermost parts of plants of all four cultivars as the plants reached dough stage. In the more arid region the time lag between leaf emergence and the appearance of pycnidia on the leaf blade is pronounced even on the dwarf wheats (eg, Fig. 2A); this lag is much longer on the semi-dwarf cultivars (eg, Fig. 2B). In this region, pycnidia reached the uppermost plant parts toward the end of the season primarily on the dwarf cultivars.

Evaluation of disease. The relative vertical progress of the disease in relation to plant height is expressed in SPC values (Septoria Progress Coefficient). This coefficient is the ratio between the maximum height above ground level at which pycnidia of *S. tritici* are found on green plant tissue (regardless of its severity on the plant part) to the height of the wheat plant at the time of observation (6). The progress of SPC over time for the intermediate-maturing pair of cultivars (Fig. 3A) was similar to that of the three early-maturing wheats in the arid region and to that of the same cultivars in the more rainy region (eg, Fig. 3B). The SPC values were higher in the trial conducted in the rainy, central coastal plain. In the rainy region, the shape of the SPC curve resembles somewhat the shape of the cumulative rainfall curve (Fig. 3A). The correlation coefficients (r) between SPC and time (weeks after emergence) for the cultivars in the arid and rainy region were 0.93 and 0.90 ($P < 0.001$) respectively (Table 1).

Pycnidial coverage was estimated by the percent green leaf area covered with pycnidia of *S. tritici.* On each day of observation disease severity was assessed as the sum over all green leaves of the pycnidial coverage plus the last recorded pycnidial coverage for each of the dead leaves. The cumulative disease severity percentages were higher in the rainy region (Fig. 3B) than in the more arid region (Fig. 3A). The shape of the rainfall curve was not similar to the shape of the disease severity curve in both regions. The correlation coefficients for disease severity and time for the cultivars in the arid and rainy regions were 0.89 and 0.83 ($P <$

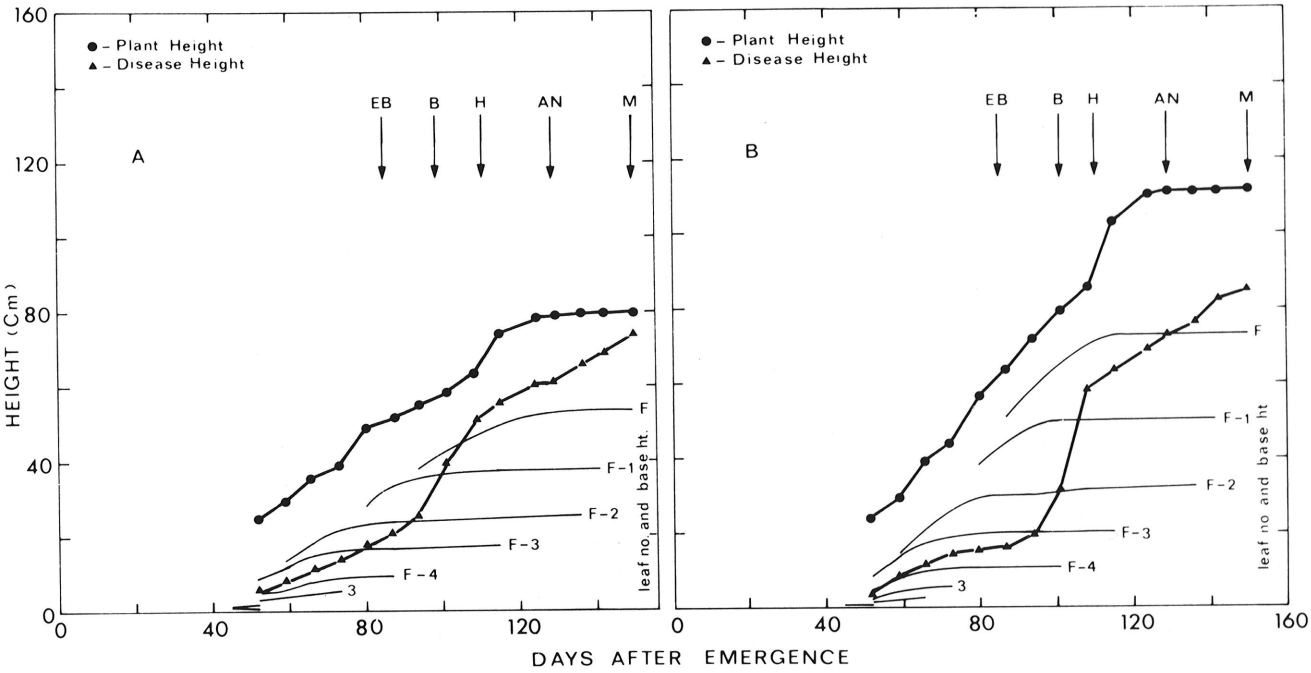

Fig. 2. Septoria leaf blotch in short-statured wheats. The progress of the disease (▲) and plant height (●) related to the height of leaf bases (F = flag leaf, F−1 = flag minus one, F−2 = flag minus two, etc.) and growth stages in two wheat cultivars: **A** = Bet-Dagan 131, and **B** = Lakhish at the Lakhish Experiment Station in Israel. Growth stages: EB = early boot, B = boot, H = heading, AN = anthesis, and M = milk stage.

0.001) respectively (Table 1).

The high correlation coefficients between the meteorological variables and both time and disease parameters (Table 1) cause considerable difficulty in evaluating the net effect of any meteorological variable on the disease progress. Therefore, we chose to analyze the following disease development parameters: ΔSPC = change in SPC values between successive recording times and $\Delta \log$ percent disease coverage = change in $\log_{10}$ disease coverage between successive recording dates. $\log_{10}$ disease coverage was preferred to percent disease coverage in order to have greater homogeneity of variance. At the Bet-Dagan trial the correlation coefficients between ΔSPC and $\Delta \log$ disease coverage was −0.02, between ΔSPC and time was 0.07 and 0.25 between $\Delta \log$ disease coverage and time. At the Lakhish trial the correlation coefficients between ΔSPC and $\Delta \log$ disease coverage was 0.11, between ΔSPC and time was −0.07, and 0.13 between $\Delta \log$ disease coverage and time.

These low correlations enable us to study the net effect of the meteorological variables on disease progress. For each region, a repeated-measures Analysis of Variance was performed for the variables: cultivar, plant, and time, where plant was the replicate, and time was the repeated measure. The analysis of variance revealed a large significant time effect on both SPC and percent disease coverage for both regions. There was a moderate cultivar effect, for which the sum of squares for percent disease coverage attributed to cultivars varied from 2.9 in the more arid region to 14.6 in the rainy central coastal plain trial. The week × cultivar interaction is relatively small; the sum of the squares attributed to this interaction does not exceed 2.4% of the total sum of squares for both the SPC and percent coverage parameters. This small interaction allows us to study all five cultivars by adjusting each observation for its mean value by the use of dummy variables.

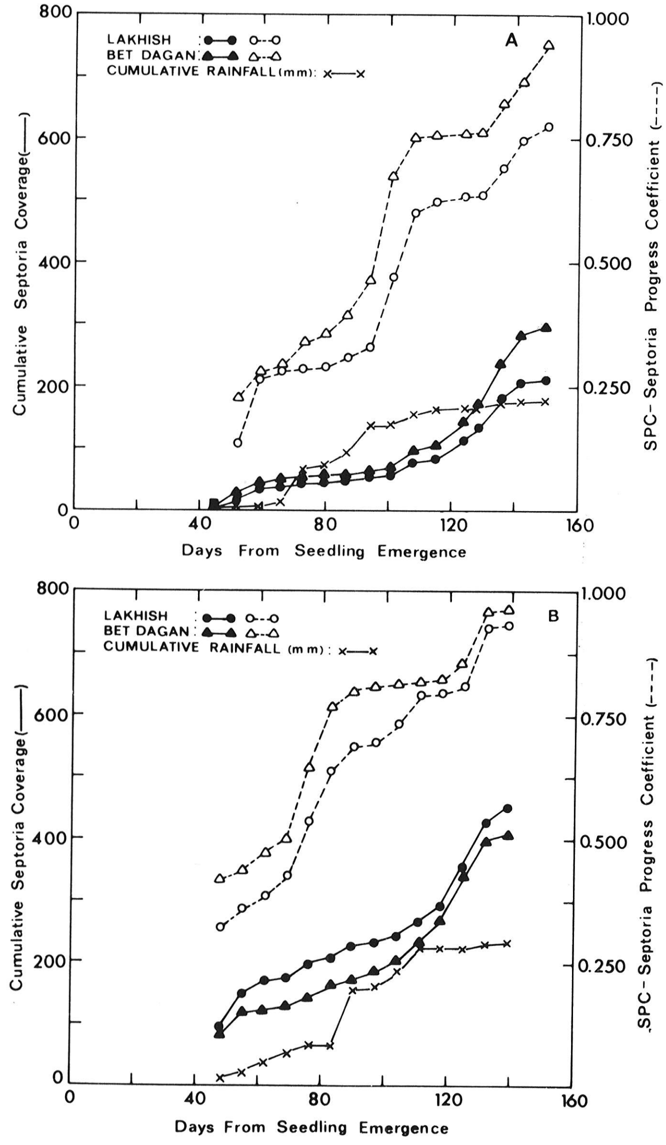

Fig. 3. Septoria leaf blotch in short-statured wheats. The progress of the cumulative percentage coverage by pycnidia (——), the Septoria Progress Coefficient (- - - -), and rainfall(×———×) in the semi-dwarf cultivar Lakhish (△) and the dwarf cultivar Bet-Dagan 131 (o) at **A,** the Lakhish Experiment Station and at **B,** the Bet-Dagan Experiment Station, both in Israel.

The two regions differed in both the macro and microclimatic conditions. In the rainy central coastal plain there were 9 more rainy days (total of 27 days) for the 90 observed days, than in the more arid southern coastal plain region. There were 61 dewy days in the rainy region as compared to 66 dewy days in the more arid region, for the same recorded period. In the rainy region the average minimum temperature (AVMINT) was higher than 7 C during the last 30 days of recording compared to 45 days in the arid region. The average maximum temperature (AVMAXT) in the arid region for the last 25 days was higher than 25 C reaching 31 C compared to an average of 24 C at the rainy region with a high of 25 C for some recording intervals. The mean ΣT_R for the central coastal plain region was 1.00 (standard deviation 0.85) while the mean ΣT_R for the semiarid region was 0.46 (SD 0.38). The disease development parameters (ΔSPC, and $\Delta \log$ disease coverage) usually had higher correlations with the biometeorological indices (ΣT, ΣT_R and ΣT_D) than with the meteorological variables (Table 2). In order to investigate the relationships between ΔSPC and $\Delta \log$ disease coverage to the biometeorological variables, Stepwise Multiple Regression analysis was performed. Table 3 indicates the significant coefficients found in the regressions. For example, ΣT_R and ΣT_D estimated 14 days prior to disease recording has significant coefficients when used to estimate the rate of vertical progress of the disease (ΔSPC) in the more rainy region. Separate analyses of the disease parameters for the 13–15 recording intervals for each wheat cultivar showed no significant differences between cultivars in the effect of meteorological variables on either disease progress or disease severity. Thus, the regional equations are adaptable to the five susceptible short-statured wheats.

The simple coefficients of determination (r^2) in Table 2 are not always indicative of its importance as shown in Table 3. This apparent disagreement is due to the interrelationships between the biometeorological variables. For example, during part of the growing season the coastal plain has either rain or dew almost every day and therefore $\Sigma T_R + \Sigma T_D$ is almost ΣT. Also, the difference between ΣT, ΣT_R, or ΣT_D between the two consecutive 7-day periods is a measure of the week-to-week change in the climatic conditions. Hence, the partial correlation of a biometeorological variable with disease development after other variables are in the regression equation can differ greatly from the simple correlation. Similarly, more than one set of variables may be used to explain a similar amount of variation in the dependent variable (disease development).

DISCUSSION

Epiphytotics of Septoria leaf blotch in countries along the Mediterranean seacoast were associated with favorable weather conditions (rainy, cold season) and the wide-spread distribution of susceptible short-strawed wheat cultivars (3,11,13,18). Severe outbreaks of the disease occurred in geographic regions with ample rainfall in South America (11) and in rain-sparse countries in the Mediterranean basin (3,11,13,18). The susceptible tall wheat cultivar 'Florence Aurore' was grown for many years over most of the bread wheat acreage in the Mediterranean region. This cultivar was known to harbor high numbers of pycnidia without its yield being affected (3,11,13,18). The replacement of the local tall wheats with susceptible short-statured cultivars enhanced development of the pathogen resulting in Septoria epidemics with high economic impact (3,13,18). The vertical progress of the pathogen from lower to higher leaves is affected by the distance between consecutive leaves—the "ladder effect". The distances between the first and the third leaf of both the dwarf (70–80 cm) and semi-dwarf cultivars (100–120 cm) are similar, but increase progressively between the upper leaves (Fig. 1 and 2). We suggest that the close proximity of the leaves in the dwarf cultivars allows the newly emerging leaves to be more readily exposed to splashing pycnidiospores or to direct contact with infected lower leaves resulting in earlier appearance of pycnidia, than would be the case for the same higher-placed leaves of plants of the semi-dwarf cultivars.

In a similar experiment conducted during the 1974–1975 season, plants were randomly chosen at each time interval; this resulted in large week-to-week changes in the disease parameters due to plant-

TABLE 1. Simple correlation coefficients (r) for Septoria leaf blotch disease and time and weather variables

Location and independent variables	Dependent variables										
	Disease coverage	Time	AVMINT[a]	ABSMINT	AVMAXT	ΣT	RAIN	DAYS RAIN	ΣT_R	DAYS DEW	ΣT_D
Bet-Dagan											
SPC[b]	0.75	0.90	0.39	0.04	0.52	0.34	−0.06	−0.38	−0.30	0.21	0.32
Disease coverage		0.83	0.66	0.44	0.71	0.58	−0.25	−0.36	−0.16	−0.01	0.31
Time			0.64	0.33	0.74	0.60	−0.20	−0.44	−0.25	0.18	0.47
Lakhish											
SPC	0.83	0.93	0.66	0.33	0.83	0.57	−0.54	−0.61	0.11	−0.17	0.15
Disease coverage		0.89	0.72	0.44	0.87	0.45	−0.47	−0.52	0.03	−0.32	0.06
Time			0.65	0.33	0.88	0.51	−0.53	−0.65	−0.01	−0.21	0.10

[a] AVMINT = average daily minimum temperature; ABSMINT = absolute minimum daily temperature; AVMAXT = average maximum daily temperature; ΣT = the sum of the daily indices for temperature; RAIN = cumulative rain (mm) for the recording interval; DAYS OF RAIN; ΣT_R = the sum of the daily indices for rainy days; DAYS OF DEW; ΣT_D = sum of the daily indices for dewy days.

[b] SPC = Septoria Progress Coefficient.

TABLE 2. Simple coefficients of determination (r^2) for meteorological variables affecting *Septoria tritici* on wheat at the Bet-Dagan and Lakhish trials

Locations and predictive periods (days)	Meteorological variables								
	AVMINT[a]	ABSMINT	AVMAXT	ΣT	RAIN	DAYS RAIN	ΣT_R	DAYS DEW	ΣT_D
BET-DAGAN TRIAL:									
Δ log percent coverage									
0–7	0.048	0.073	0.084	0.102	0.002	0.078	0.073	0.006	0.084
7–14	0.029	0.012	0.168	0.130	0.102	0.185	0.137	0.336	0.449
14–21	0.022	0.010	0.004	0.014	0.008	0.000	0.005	0.008	0.019
Δ SPC									
0–7	0.053	0.129	0.014	0.053	0.006	0.003	0.014	0.005	0.029
7–14	0.062	0.129	0.019	0.044	0.014	0.022	0.004	0.026	0.005
14–21	0.006	0.078	0.053	0.029	0.062	0.000	0.000	0.002	0.026
LAKHISH TRIAL:									
Δ log percent coverage									
0–7	0.123	0.090	0.040	0.176	0.032	0.001	0.314	0.053	0.001
7–14	0.001	0.000	0.044	0.109	0.129	0.185	0.001	0.012	0.040
14–21	0.001	0.005	0.010	0.036	0.014	0.058	0.019	0.067	0.032
Δ SPC									
0–7	0.000	0.014	0.005	0.001	0.000	0.000	0.040	0.004	0.002
7–14	0.073	0.053	0.044	0.062	0.014	0.000	0.044	0.010	0.010
14–21	0.152	0.090	0.090	0.194	0.053	0.202	0.032	0.006	0.096

[a] AVMINT = average daily minimum temperature; ABSMINT = absolute minimum daily temperature; AVMAXT = average maximum daily temperature; ΣT = the sum of the daily indices for temperature; RAIN = cumulative rain (mm) for the recording interval; DAYS OF RAIN; ΣT_R = the sum of the daily indices for rainy days; DAYS OF DEW; ΣT_D = sum of the daily indices for dewy days.

TABLE 3. Analysis of the contribution of ΣT indices to Δ SPC and Δ log disease coverage by partial regression analysis

Locations and disease parameter	F-value	R^2	ΣT for predictive periods								
			ΣT			ΣT_R			ΣT_D		
			0–7	7–14	14–21	0–7	7–14	14–21	0–7	7–14	14–21
Bet-Dagan											
Δ SPC	7.42**	0.47	++	++	+			++		+	++
Δ log coverage	53.0 **	0.50		+						++	
Lakhish											
Δ SPC	7.8 **	0.29		+	+[a]	+					+[a]
Δ log coverage	31.0 **	0.51	++			++	+				

[a] Indicates that either ΣT or ΣT_D could be included in this regression.

** = significant at $P < 0.01$.

++ = high significant contribution to coefficient of determination.

+ = moderate significant contribution to coefficient of determination.

to-plant variation. Therefore, the following season we modified the design to use the same plants throughout the experiment, as reported in this article. In this earlier trial the progress of *S. tritici* from lower onto upper parts of plants of the semi-dwarf cultivars was slow, resulting in low SPC and pycnidial density values compared to higher values for the dwarf cultivars. The low frequency of rainy days and the long rainless intervals with high temperatures towards the end of the season interrupted the pathogen's progress to the upper plant parts of the semi-dwarf cultivars. In the trial reported here (1975–1976), the rate of vertical progress of the disease on dwarf wheats was similar to the rate of progress on the semi-dwarf wheats despite 30- to 50-cm difference in total plant height. There were no significant differences in disease severity between the susceptible cultivars that differed in plant architecture and maturity. The number of infection cycles of the pathogen on a particular leaf may be greater on the dwarf than on semi-dwarf cultivars under low to moderate epidemics; this would then result in faster progress and greater area affected by the pathogen. The epidemiological disadvantages of the dwarf cultivars are more pronounced under low to moderate epidemics associated with unfavorable weather conditions. The total height to which pycnidia can reach under such conditions may include the flag leaves of the dwarfs at 50–60 cm, a height corresponding to flag leaf minus one in the semi-dwarf wheats (Fig. 1), and thus result in greater losses in yield. Under favorable epidemic conditions the differences in plant architecture are readily overcome by the pathogen. The rates of change in both SPC and disease severity were similar in the two regions, thus reinforcing the results of our previous reports that Septoria epidemics may occur in regions with rainfall of 200–300 mm with moderate temperatures provided ample inoculum and susceptible germplasm are available (6).

Attempts to forecast outbreaks of Septoria leaf blotch were made by Shaner (15) and Shaner and Finney (16) who analyzed 20 yr of weather and Septoria records in Indiana. The number of rainy days and minimum temperature used in their prediction model may not be sufficient to explain the recent outbreaks of Septoria leaf blotch in the Mediterranean basin. The epidemics reported here have resulted from a combination of meteorological factors favorable for host and pathogen development, and the provision of ample primary inoculum and susceptible germplasm.

The high correlations usually found between any index of disease development and meteorological variables may by an artifact due to the relationship between the cumulative disease development and the unidirectional change in meteorological variable due to the changing season (Table 1). For this reason we have chosen to analyze the rate of disease progress and disease coverage; these measures have very low correlations with time. Even so, we still found some significant relationships with the biometeorological variables, although the correlations were greatly reduced (Table 2). When data is accumulated from seasons it will be possible to utilize these biometeorological variables in a model to predict the development of Septoria leaf blotch epidemics in the Mediterranean basin (1,2).

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