Analysis of Epidemics of Northern Leaf Blight on Sweet Corn in Israel

Yehouda Levy

Department of Life Sciences, Bar-Ilan University, Ramat Gan 52900, Israel.
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ABSTRACT

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Epidemics of northern leaf blight of corn incited by the fungus *Exserohilum turcicum* were monitored in five corn fields (cv. Jubilee) during 1986–1988 at various locations in Israel. Infection efficiency, sporulation, and lesion expansion of isolates collected in these fields were measured in growth chambers. Apparent infection rate (r) in the field varied from 0.05 to 0.20/day. There was a low correlation between temperatures and dew periods favorable for disease development and r in the field. A significant and high correlation was found between r and components of fitness measured in the growth chambers. A simple northern leaf blight simulator used to examine the influence of fitness of the pathogen on development of disease indicated that the importance of weather conditions decreases when fields are infected with a highly aggressive population of the pathogen.

Northern leaf blight of corn (*Zea mays* L.), incited by the fungus *Exserohilum turcicum* (Pass) Leonard & Suggs, occurs frequently in Israel during the corn growing season (3). The severity of disease varies between years and locations. Many studies have related the disease severity directly to weather conditions (1,4,5). Various phases of the disease cycle are affected by light, temperature during dew, dew period, plant age, and inoculum concentration (2,4,5). If inoculum is present, duration of the dew periods is the most important environmental factor influencing infection (5). Thus, Berger (1) developed a system to forecast northern leaf blight based on the blight favorable hours, i.e., the number of hours for which temperature is above 15 C and relative humidity is higher than 90%. However, great variability in severity of northern leaf blight was observed in infected fields in Israel, even when blight favorable hours values were similar (Levy, *unpublished*). The results presented in this study show that severity of northern leaf blight epidemics on sweet corn depended mainly on the fitness of *E. turcicum*, which was found to vary greatly among isolates collected from infected fields at various locations in Israel.

MATERIALS AND METHODS

Field observations. All field observations were carried out in commercial sweet corn fields planted with the northern leaf blight-susceptible cultivar Jubilee. Fields of approximately 5 ha were located at various regions of Israel and planted during August-September (Table 1). In all fields, certified seed was planted in 100-m-long rows, spaced 1 m apart. Fertilizers, herbicides, and insecticides were applied according to the usual recommendations. No fungicides were applied. Plants were infected naturally by *E. turcicum*.

After the onset of the disease, 20 plants were randomly sampled from each field once a week until harvest. Total leaf area and infected leaf area of each leaf were measured with the aid of a Delt-I area meter system (Delta-T Device Ltd, Cambridge, England). Temperature and relative humidity were recorded with a hygrothermograph placed in the middle of each field, 0.5 m above ground level. Blight favorable hours were calculated for each field for the entire epidemic. Apparent infection rates (r) (= growth rate) of the blight were calculated by using disease data recorded as a proportion. The rate was expressed as the slope of $\ln(x/[K - x])$ on time in which x represents disease severity, and K maximum disease. The parameters r and K were determined by using a nonlinear regression analysis of the observed data with the aid of a nonlinear regression procedure (7). The area under disease progress curve (AUDPC) was calculated according to the formula described by Tooley and Grau (8).

Growth chamber experiments. Sweet corn cultivar Jubilee was used in all experiments. Plants were grown in the greenhouse in pots containing 1 kg of a mixture of soil:peat:vermiculite (1:1:1, v/v). The cultivar Jubilee was chosen because it is planted in Israel in all regions in which sweet corn is produced. A representative population of each field was collected at random from the infected fields (30 lesions/field) and grown on lactose-casein agar (LCA). Conidia produced from the 30 isolates from each field were mixed, incorporating equal amounts of conidia from each site, and used for plant inoculations.

Five-week-old plants with five or six leaves were inoculated with conidial suspensions prepared by washing conidia from 10-day-old cultures grown in an incubator at 25 C in the dark. Concentration of the conidial suspension was adjusted as desired and measured with a hemacytometer. Plants were inoculated by placing 10-μl droplets of the conidial suspension along the adaxial surfaces of the leaves (10 droplets per leaf, 20 conidia/droplet). At least 10 sites were inoculated on each plant. Inoculated plants were incubated overnight in a dew chamber at 20 C in the dark and then transferred to a growth chamber calibrated to 15, 20, or 25 C and a day length of 12 hr at light intensity of 150 μE $m^{-2}sec^{-1}$.

The following components of fitness were measured: Infection efficiency = the number of lesions formed as a percentage of the number of sites inoculated; lesion expansion = daily increase (mm^2) in lesion area; and sporulation number of spores produced per square centimeter of infected area at 10 days after inoculation. Measurements of lesion expansion were done every other day as lesions appeared over a 10-day period. To estimate sporulation, infected leaves with lesions of a known area were placed on wet filter paper in plastic trays. Trays were covered with polyethylene bags and incubated in the dark for 30 hr at 22 C. At the end of the sporulation period, the spores produced were brushed off into a fixative solution (Formalin:acetic acid:alcohol, 5:5:90, v/v) and filtered through a Millipore filter (pore size 8 μm). Spores on the filter were counted microscopically.

Each experiment was repeated three times with at least 10 plants per location. A composite index of fitness was calculated for each isolate as the product of infection efficiency, lesion area 10 days after inoculation, and sporulation (9). The index gives an indication of the number of lesions produced from a single parent lesion (9). Analysis of variance was performed on the AUDPC, the fitness index, and the components of fitness to compare isolates and locations. The Waller-Duncan k-ratio-t-test was used for mean separation of isolates in cases where the treatment *F*-test was significant. Correlations among size of lesions, sporulation, infection efficiency, and the fitness index, were calculated by location of isolates. Another correlation analysis was performed between AUDPC, *r*, and the fitness index, by location of isolates.

A deterministic simulation model developed earlier (6) was used to examine interactions among fitness of the fungal population, weather conditions, and disease progress. The simulator uses a daily time-step. Simulated epidemics started with an initial disease severity of 1% and continued over a 100-day period. (For more details of the simulator, see reference 6). Epidemics were simulated for the populations with the highest and lowest fitness. A basic simulation was performed by using values of components of fitness as measured in this study. A second simulation was performed in which components of fitness were reduced by 30% to mimic suboptimal environmental conditions. AUDPC and *r* were calculated for each simulated epidemic.

RESULTS

Disease progress over time was variable among the five infected fields (Fig. 1). At Biqat HaYarden and Erez, disease severity reached 85 and 88%, respectively, whereas at Yad Mordekhay (1988), Ayyelet HaShahar, and Yad Mordekhay (1987), final disease severity was only 45, 40, and 30%, respectively. Likewise, AUDPC and *r* were both significantly higher at Biqat HaYarden and Erez than at the other locations. The average blight favorable hours per day during the growth period was lower at Biqat HaYarden and Yad Mordekhay (1987) than at the other locations (Table 1).

Components of fitness measured in growth chambers show that the rate of lesion enlargement and the sporulation of the representative fungus population from Biqat HaYarden and Erez were significantly higher than those of the other (Table 2). Analysis of variance showed that locations had a significant effect on the rate of lesion expansion ($P < 0.001$), but not on the infection efficiency ($P = 0.23$). Size of lesion and sporulation were highly correlated (correlation coefficient = 0.96; $P = 0.007$). The correlation between size of lesion and infection efficiency, and between sporulation capacity and infection efficiency, were 0.61 and 0.53, respectively. Also a high and significant correlation occurred between the fitness index and *r* (correlation efficiency = 0.98, $P = 0.001$), and between the fitness index and AUDPC (0.99; $P = 0.001$) but not between AUDPC and the blight favorable hours. Lesions produced by the representative fungus population from Biqat HaYarden and Erez were significantly larger than those produced by the other populations at 20, 25, and 30 C. For all the five fungal populations, maximal lesion size was obtained at 25 C (Table 3).

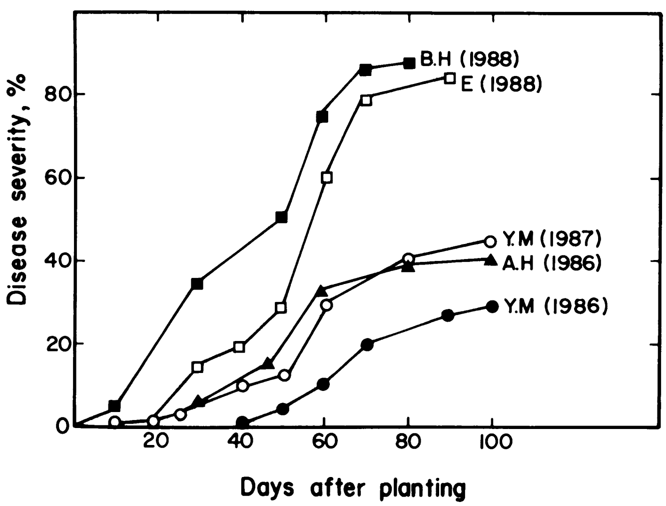

Fig. 1. Disease progress over time in five sweet corn fields (cultivar Jubilee) infected by *Exserohilum turcicum*. Points represent means of observation.

TABLE 1. Area under disease progress curve (AUDPC), apparent infection rate (*r*), and blight favorable hours (BFH) for northern leaf blight in sweet corn at five locations in Israel during 1986–1988

Location and year	Sowing date	BFH[a]	AUDPC[b]	r[c]
Biqat HaYarden (B.H.) 1988 (eastern)	1 August 1988	7	3,576	0.20
Erez (E) 1988 (western)	12 August 1988	11	3,258	0.16
Yad Mordekhay (Y.M.) 1987 (western)	1 September 1987	8	1,010	0.08
Yad Mordekhay (Y.M.) 1986 (western)	10 August 1986	10	961	0.08
Ayyelet HaShahar (A.H.) 1986 (northern)	15 August 1986	10	785	0.05

[a] According to Berger (1), average over growing season.
[b] AUDPC according to Tooley and Grau (8).
[c] Estimated with nonlinear regression. Units = day^{-1}.

TABLE 2. Size of lesion, sporulation, infection, and index for fitness (CFI) of five populations of *Exserohilum turcicum*

Location	Fitness components			
	LS[a]	SC[b]	IE[c]	CFI[d]
Biqat HaYarden (1988)	7.16 a[e]	12,560 a	0.70 a	62,951
Erez (1988)	6.02 a	12,510 a	0.67 a	50,458
Yad Mordekhay (1987)	1.04 b	6,937 b	0.67 a	6,739
Yad Mordekhay (1986)	0.36 c	2,645 c	0.65 a	618
Ayyelet HaShahar (1986)	1.45 b	5,196 b	0.62 a	3,350

[a] LS (cm^2), measured 10 days after inoculation.
[b] SC (number of spores/cm of infected leaf area), 10 days after inoculation.
[c] IE, proportion of lesions formed out of sites inoculated.
[d] CFI, according to Tooley et al (9).
[e] Means followed by the same letter within a column are not significantly different according to the *k*-ratio *t*-test ($P = 0.05$; $k = 100$).

TABLE 3. Effect of temperature and location on lesion enlargement of *Exserohilum turcicum* on sweet corn (cultivar Jubilee)

Isolate source	Lesion size (cm) at		
	20 C	25 C	30 C
Biqat HaYarden	2.7 a[a]	7.1 a	3.3 a
Erez	2.4 a	6.3 a	1.4 b
Yad Mordekhay (1987)	0.4 b	1.4 b	0.2 c
Yad Mordekhay (1986)	0.2 b	0.3 c	0.1 c
Ayyelet HaShahar (1986)	0.4 b	1.1 b	0.1 c

[a] Means followed by the same letter within a column are not significantly different according to the *k*-ratio *t*-test ($P = 0.05$; $k = 100$).

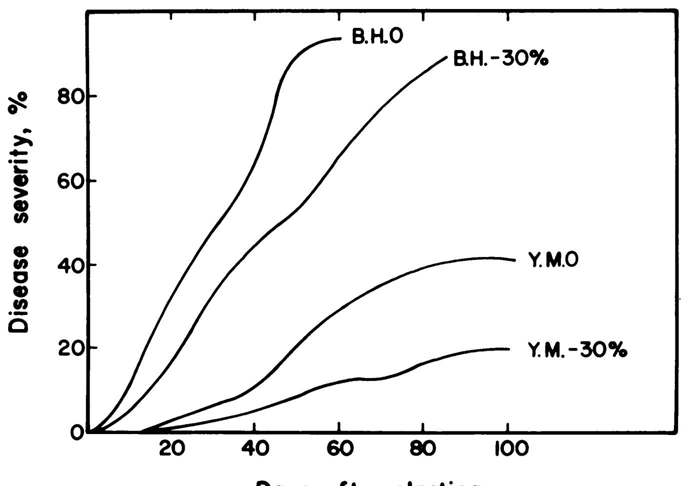

Fig. 2. Simulated epidemics of *Exserohilum turcicum* for pathogen populations with fitness found for Biqat HaYarden and Yad Mordekhay (1986). O = Simulation with the original values of components of fitness; 30% = a reduction of 30% in the values of the fitness components.

In the simulated epidemics, final disease levels were 90 and 40% for the fungal populations from Biqat HaYarden and Yad Mordekhay, respectively. AUDPC and *r* for the fungus from Biqat HaYarden were 4,000 and 0.196/day, respectively. AUDPC and *r* for the fungal population from Yad Mordekhay were lower (Fig. 2). Reducing the components of fitness (sporulation, lesion size, and infection efficiency) of the fungal population from Biqat HaYarden by 30% caused a decrease of 10 and 17% in AUDPC and *r*, respectively. A similar reduction in the fitness components of the fungal population from Yad Mordekhay resulted in decrease of 30 and 45% in the AUDPC and *r*, respectively (Fig. 2).

DISCUSSION

Epidemics of the northern leaf blight depend on the ability of *E. turcicum* to infect, grow, and sporulate on corn plants. The dependence of these processes on weather conditions has been well documented. The infection process is affected by light, dew temperature, dew period, plant age, and inoculum concentration (1,5). The duration of the dew period and the dew temperature are the most important environmental factors influencing infection and sporulation (5). According to Berger (1), a daily average of 6.5 blight favorable hours or less resulted in little blight and not enough disease to justify fungicidal control, while 7–8 blight favorable hours/day required occasional sprays to prevent light to moderate blight in unsprayed fields. Eight or more blight favorable hours/day required a regular fungicide program to avoid serious losses, and 11 blight favorable hours/day often resulted in high disease severity regardless of spray schedules. Our results show that the intensity of northern leaf blight was dependent mainly on fitness of the population of *E. turcicum* at a particular location. A highly fit pathogen, such as the one from Biqat HaYarden, caused a severe epidemic with only 7 blight favorable hours, while a less fit population, such as that from Yad Mordekhay or Ayyelet HaShahar caused only a low level of disease even with 10 blight favorable hours. Variability in fitness of the population of *E. turcicum* at a particular location was due to differences in sporulation and rate of lesion expansion. No differences in infection efficacy were found between populations of *E. turcicum*.

Situations rarely occur in which all phases of the life cycle proceed in an orderly succession, under optimal conditions. The role of the simulated epidemics was to mimic suboptimal conditions for the development of the pathogen by reducing the components of fitness. Results of simulations showed that conditions that will reduce the intensity of sporulation and lesion enlargement by 30%, will not significantly affect disease development of a highly fit population of *E. turcicum* while a similar reduction in the components of fitness will have a severe effect on the development of disease of a less fit population. In practice, under natural conditions, the epidemics caused by the population of *E. turcicum* from Biqat HaYarden were severe in spite of a relatively low blight favorable hours.

In conclusion, our results emphasize the importance of considering components of fitness in addition to weather conditions, in determining severity of northern leaf blight severity. Information on the characteristics of the pathogen population may add to the accuracy of forecasting northern leaf blight by simulation models.

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