Influence of Temperature and Rainfall on the Development of Tobacco Black Shank

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ABSTRACT

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The incidence of tobacco black shank, which is induced by *Phytophthora parasitica* var. *nicotianae,* increased rapidly 6–8 wk after transplanting in North Carolina. Precipitation, daily air temperature, and number of drought days were associated with rapid disease progression after 6–8 wk in resistant and moderately resistant cultivars and prior to 6–8 wk in susceptible cultivars. No single meteorological parameter was found to influence disease progression more than any other. Models relating meteorological variables to disease progression explained 61–78% of the disease progression variation and can be useful to predict conditions favorable for black shank development.

Black shank is a destructive disease of tobacco (*Nicotiana tabacum* L.) induced by *Phytophthora parasitica* (Dast.) var. *nicotianae* (Breda de Haan) Tucker. The disease was first reported in Georgia in 1915 and spread rapidly throughout most of the flue-cured, Burley, and shade-grown tobacco regions of the United States (6). Losses due to black shank are limited by resistant cultivars to about a 1% yearly reduction in the total harvested crop, but severe losses occur in certain areas (6).

The assessment and prediction of losses related to black shank of tobacco are confounded by the limited experimental information on the effects of temperature and moisture on the disease. The prediction of disease development and determination of losses would be aided by a model relating soil moisture and temperature to disease progression. This information on moisture and temperature is available indirectly via meteorological data bases.

Historical observations suggest that high soil moisture favors black shank development (3). Lucas (6) reported that high moisture favored the growth, production, and dissemination of sporangia and zoospores. Soil moisture apparently is not a limiting factor for infection, but it can affect disease development (7). McCarter (7) reported results of greenhouse and field studies, which indicated that infection can occur on plants grown in soil ranging from 19 to 100% of moisture-holding capacity. Plants of susceptible cultivars were killed more quickly at high moisture contents than at low moisture contents, while more plants of resistant cultivars were killed at lower moisture contents. Other workers (4,11) also have observed that drought conditions favored higher disease incidence in resistant cultivars, especially when drought stress was followed by periods of high rainfall and soil moisture.

Black shank develops only after the mean daily soil temperature reaches 16–24 C (5,7,10). Optimum temperatures for growth and production of sporangia and zoospores are reported to be between 24 and 30 C (6,7,10). The optimal temperature for infection depends on plant age and cultivar susceptibility (5,10). Resistant cultivars apparently require higher temperatures for infection than susceptible cultivars (7); however, disease severity in both resistant and susceptible cultivars increases with increasing temperature (7).

The objectives of this study were to determine what phases of disease development could be used in critical-point model assessment of disease incidence and loss, and to examine the quantitative relationships between available environmental data (rainfall and air temperature) and the progression of black shank.

MATERIALS AND METHODS

Black shank incidence data were obtained from Regional Small Plot Tests, planted yearly in North Carolina to evaluate tobacco breeding lines and commercial cultivar lines for resistance to *P.*

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parasitica var. *nicotianae*. The plots were established in a sandy loam soil naturally infested with the pathogen during 1975, 1976, and 1978 near the North Carolina Tobacco Research Station at Oxford. In 1974, 1977, and 1979 the small-plot tests in naturally infested sandy loam soil were located at the Upper Coastal Research Station at Rocky Mount, NC.

Fifteen commercial cultivars were studied; these were grouped into three relative resistance classes, based on performance in experimental plots and commercial fields. Two cultivars (Hicks and Virginia Gold) were rated susceptible, nine cultivars (NC-95, NC-2326, NC-79, Coker-319, Coker-411, Coker-347, Speight G-140, McNair-914, and Va-115) were moderately resistant, and four cultivars (Coker-86, Coker-298, Speight G-28, and NC-1071) were resistant.

For each cultivar, 20–22 transplants, 20.3 cm tall, were planted (0.56 m spacing) in each of three randomly located rows spaced 1.1 m apart. An initial stand count was made 7–10 days after transplanting, and disease incidence was then recorded at 2-wk intervals for an additional 12–14 wk. Data from the three rows of a cultivar were combined for each year and the percentage (Y) of diseased plants was calculated as Y = [(total cumulative number of irreversibly wilted or dead plants)/(total number of plants in the initial stand count)] × 100. The rate of disease increase was calculated by dividing the number of plants that had become diseased since the previous reading by the number of days since the last reading.

Temperature and rainfall data were obtained from the National Oceanic and Atmospheric Administration reporting stations at the respective experiment stations. Daily maximum (max) and minimum (min) temperatures, and amount of rainfall were utilized to generate other environmental variables possibly related to black shank development. Number of days with an occurrence of an environmental variable were tallied for the intervals between disease readings beginning 2 wk before the initial disease reading. Soil temperature data were obtained from a recording site near Raleigh, NC, the closest (~ 60 km) recording station to the field sites. Based on experimental evidence (5,7,10), disease development was assumed to begin when the soil temperature warmed to the 16–24 C range. The average 4-yr daily max air temperature consistently resulting in a 20 C temperature at a 10.2-cm depth under bare soil was 26.7 C. Counts were made of those days with a max air temperature ⩾23.9 and 26.7 C and those with an average of the max and min temperatures at or above 26.7 C. Days with a max temperature ⩾23.9 or 26.7 C and no rain that followed 0 or 3 days of the same conditions were used to define drought periods. Total rainfall and number of days with rain were recorded.

Relationships between disease percentage and meteorological data were examined by using Pearson's product-moment correlation technique (9). Multiple regression techniques employing the STEPWISE procedure with MAXR option (9) were utilized to develop equations relating disease development to meteorological parameters.

RESULTS

Disease progression. Disease progression was similar for resistant and moderately resistant classes of cultivars over all years and increased moderately at each 2-wk interval, reaching an average maximum of 23.0 and 38.0%, respectively (Fig. 1A and B). The rate of disease increase for the cultivars was fairly constant until 6 wk after the initial stand count, when the rate essentially doubled (Figs. 1A and B, and 2). The susceptible cultivar class had an early and rapid increase in disease resulting in the death of most plants before 6 wk (Figs. 1C and 2). The disease increase for resistant and moderately resistant groups was generally similar among the 6 yr, whereas there was more variability in the susceptible group (Fig. 1).

Linear regression equations, utilizing model V-3 of Nelson and Anderson's (8) linear plateau family of equations, fit the disease progression data with coefficient of determination (R^2) values ranging from 0.84 to 0.99. Model V-3, by the use of vectors, describes curves that consist of essentially two straight lines. Logit transformations of the disease data decreased R^2 values for regression equations over what was obtained by the Nelson and Anderson (8) vector models. All curves for each resistant group in individual years, except four, were explained by equations describing lines that changed slopes at 6 wk after the initial stand count (Fig. 1).

Disease and environmental variable correlations. The correlation coefficients for disease incidence averaged over all years and environmental variables are generally higher for the susceptible group and lower for moderately resistant and resistant groups (Table 1). No single environmental variable that was analyzed appears to be more important than any other (Table 1). However, all the environmental variables are in some degree

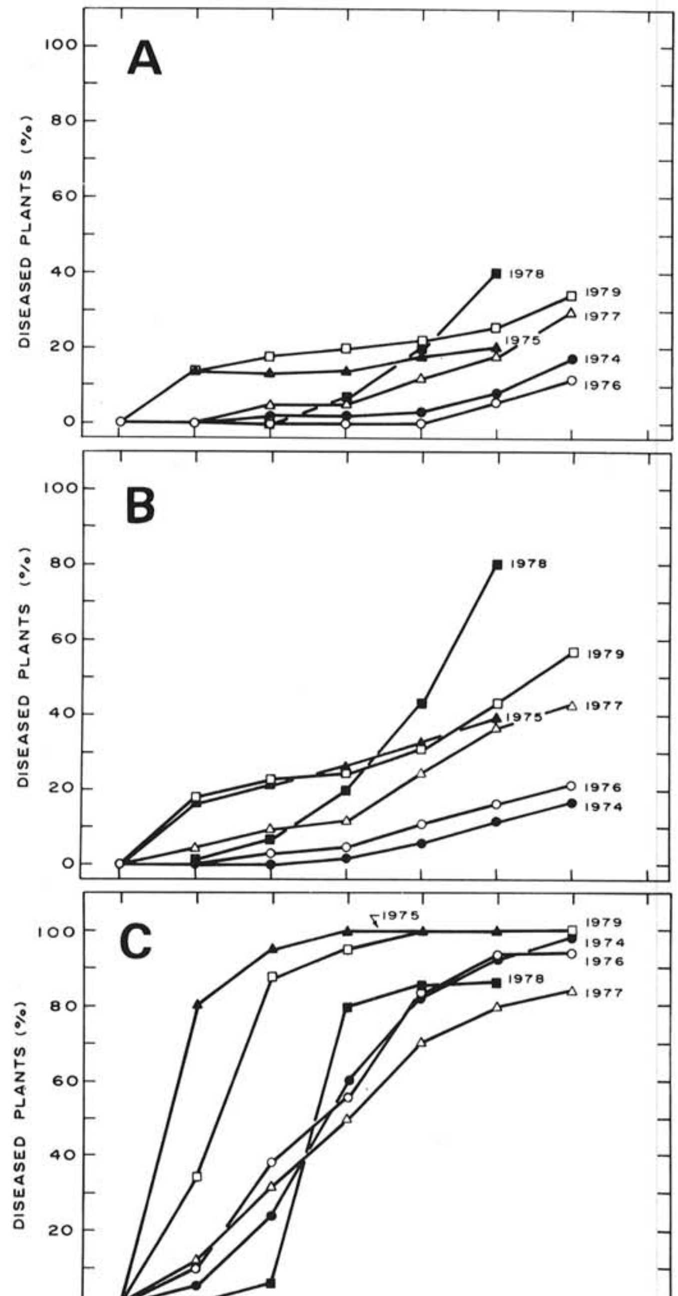

Fig. 1. Disease progression of black shank on tobacco by individual years. Data points represent an average of cultivars in a resistant group. Disease progression in the **A**, resistant cultivar group; **B**, moderately resistant cultivar group; and **C**, susceptible cultivar group.

correlated with disease progression since their cumulative counts increased over time as did disease (Figs. 1 and 3).

Correlation coefficients by individual years indicate a close association (0.85 average correlation) between disease incidence of the susceptible group and weather variables. Resistant and moderately resistant groups had lower correlations with the weather variables, with average correlations of 0.76 and 0.57, respectively ($P \leqslant 0.05$).

Gradual, but small, disease increases in the resistant and moderately resistant groups during weeks 0–6 resulted in few significant correlations of yearly disease incidence (averaged by 2-wk periods) with the cumulative environmental data. Only total precipitation and days with rain were correlated with disease progression in the resistant group (0.56, 0.44, $P \leqslant 0.05$). Disease progression in the moderately resistant cultivars was correlated with total precipitation, days of rain, 23.9 C, 26.7 C, days and drought days at 23.9 C (0.56–0.65, $P \leqslant 0.05$). The susceptible group exhibited good correlations (0.42–0.72, $P \leqslant 0.05$) with all except three of the variables before the sixth week.

Precipitation, temperature, and drought variables were associated with disease progression after the sixth week in resistant and moderately resistant cultivars (0.42–0.61, $P \leqslant 0.05$). Only total precipitation, days of rain and 23.9 C days were correlated with susceptible cultivars after the sixth week (0.53–0.75, $P \leqslant 0.05$). Correlations were made with untransformed data because the curves of disease progression and environmental variables were similar.

Multiple linear regression. Multiple regression models relating disease progression with one to six of the selected environmental variables explained 32–95% ($P \leqslant 0.001$) of the variation in disease progression in individual years (Table 2). Models for individual years within a resistance group had high coefficient of determination (R^2) values (0.53–0.95) except for the resistant group (0.32–0.70) (Table 2). Combining all years into a generalized model for each resistance group reduced the R^2 values because of the variation in disease progression and environmental variables between years (Table 2). Analysis by multiple linear regression of the relationship of disease progression and environmental variables before and after 6 wk revealed that total precipitation, drought days, and days $\leqslant$26.7 C gave the best fit in both phases.

Averaging the incidence of black shank (by 2-wk intervals and resistance group) over all 6 yr removed variation and increased the fit of the selected models from R^2 values of 0.32, 0.56, and 0.67 to 0.61, 0.66, and 0.78 for resistant, moderately resistant, and susceptible groups, respectively (Tables 2 and 3). Adding time (2-wk interval) to the independent portion of the models allows the involvement of time and thus growth status of the plants in regression equations (Table 3). The equations presented in Tables 2 and 3 were selected for high R^2 and the fewest and most significant ($P \leqslant 0.05$) environmental parameters.

Most variation in disease progression related to the cumulative weather parameters can be explained by year to year variation and 2-wk interval within year variation. This is seen for year to year variation in Table 3 in which adding year as an independent value increased the R^2 values for resistant and moderately resistant groups.

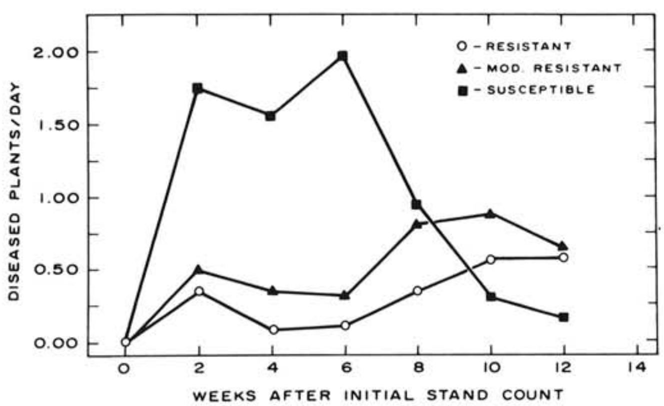

Fig. 2. Six-year average for rate of disease increase over 2-wk intervals for cultivars grouped by resistance to black shank.

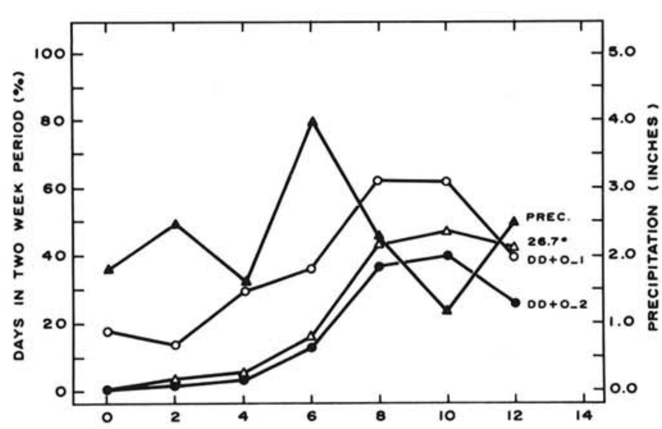

Fig. 3. Six-year averages for selected weather parameters given as the percentage of days with those conditions in a 2-wk period. Prec. = the amount of rain over the preceding 2-wk period. DD + 0_1 and DD + 0_2 = days with no rain and $\geqslant$ 23.9 C or $\geqslant$ 26.7 C maximum temperature, respectively.

DISCUSSION

The progression of the black shank disease implicates the existence of a compound interest type disease (1). This type of disease increase is usually associated with multiplying inoculum during a single season. An analysis, however, of the spatial distribution of dead plants in the field does not indicate a multiplication effect (2). Thus, other factors may be responsible for the disease increase.

A drought period usually occurs 6–8 wk after transplanting in North Carolina along with a dramatic increase in the daily

TABLE 1. Correlation coefficients[a] of various environmental variables with the average incidence of black shank in resistant, moderately resistant, and susceptible cultivar groups[b] (1974–1979)

Environmental variable[c]	Resistance group: Resistant	Moderately resistant	Susceptible
Total precipitation	0.72	0.66	0.76
Rain days	0.68	0.65	0.81
23.9 max days	0.70	0.74	0.83
26.7 max days	0.68	0.74	0.77
26.7 avg days	0.67	0.68	0.58
Drought days + 0_1	0.67	0.73	0.74
Drought days + 3_1	0.44	0.48	0.55
Drought days + 0_2	0.63	0.68	0.57
Drought days + 3_2	0.44	0.47	...[d]

[a] N = 42. The average, over all cultivars in a group, of the cumulative incidence of dead plants in successive 2-wk periods were correlated with cumulative values of the previous 2-wk of environmental information. All values highly significant at $P \leqslant 0.0001$.

[b] Resistant cultivars: Coker-86, Coker-298, Speight G-28, NC-1071. Moderately resistant cultivars: NC-95, NC-2326, NC-79, Coker-139, Coker-411, Coker-347, Speight G-140, McNair-914, Va-115. Susceptible cultivars: Hicks and Va. Gold.

[c] Environmental variables: Rain days = number of days with measureable precipitation, 23.9 max days = days with maximum temperature $\geqslant$ 23.9 C, 26.7 max days = days with maximum temperature $\geqslant$ 26.7 C, 26.7 avg days = days with average maximum and minimum temperature $\geqslant$ 26.7 C, Drought days + 0_1 = no rain and $\geqslant$23.9 C maximum temperature, Drought day + 3_1 = days of no rain and $\geqslant$ 23.9 C after 3 days of the same conditions, Drought days + 0_2 and Drought day + 3_2 are the same as above, but at 26.7 C.

[d] No significant correlation.

temperature (Fig. 3, and W. R. Jacobi, *unpublished*). Drought conditions along with high temperatures would increase the stress on infected plants, resulting in death. After 6–8 wk, plants are also approaching cessation of their rapid vegetative growth stage and beginning to flower. Growth diminishes and plant senescence begins soon after. Thus, the plants may be able to resist the pathogen and secondary root rotting pathogens during rapid growth, but succumb when they become physiologically and environmentally stressed. The elucidation of a critical-point period around 6–8 wk following transplanting helps to focus future efforts in developing a loss assessment system for this important soilborne tobacco disease.

No single meteorological variable studied was found to regulate black shank disease progression, but temperature, precipitation, and number of drought days were consistently related. The drought periods of 3 days and longer at 23.9 C were initially assumed to represent sufficient plant stress to cause noticeable increase in disease, particularly wilt symptoms. The correlations, however, for all cultivars and resistance group means indicated more association between drought periods of 1 day and disease incidence than drought periods of 3 days or more.

The activity of *P. parasitica* should be related to air temperature since air and soil temperatures are correlated. This effect may be important, not only at a critical infection period in the disease process, but also may affect disease progression. Temperature appears to be well correlated with disease incidence, which may be meaningful in terms of stress on the host plant during drought days (Fig. 3 and Table 1).

The regression equations presented here are primarily useful in demonstrating the types of relationships that exist between black shank incidence and temperature and rainfall. The negative or positive sign, or absolute value of the partial regression coefficients, probably does not have any real meaning in the biological process of diseased tobacco. The predictive power of these equations may

TABLE 2. Analysis by multiple linear regression of black shank incidence on tobacco and certain environmental variables (1974–1979)

Resistance group[a]	Year	Equation[b]	R^2[c]
Resistant	1974	Y = −4.87−112.24 (26.7) − 164.22 (RD) + 150.60 (DD + 0_1)	0.32
	1975	Y = −16.14 − 3.92 (TP) + 302.77 (RD)	0.42
	1976	Y = 0.69 + 50.89 (26.7 avg)	0.35
	1977	Y = 0.97 + 60.26 (26.7 avg)	0.44
	1978	Y = 0.26 + 305.40 (DD + 0_2)	0.70
	1979	Y = −7.80 + 2.23 (TP)	0.38
	1974–1979	Y = 0.50 + 40.20 (26.7 avg) + 0.90 (TP)	0.32
Moderately resistant	1974	Y = −3.42− 176.62 (26.7 avg) + 146.37 (DD + 0_1)	0.59
	1975	Y = −4.95− 154.86 (26.7 avg) + 118.55 (DD + 0_1)	0.66
	1976	Y = 0.61 + 48.20 (DD + 0_1)	0.53
	1977	Y = 3.5 + 105.67 (26.7 avg)	0.63
	1978	Y = −3.61 + 455.38 (26.7 avg)	0.89
	1979	Y = −7.89 + 2.49 (TP) + 104.77 (DD + 0_2)	0.69
	1974–1979	Y = −2.37 + 395.98 (26.7 avg) + 0.81 (TP)	0.56
Susceptible	1974	Y = 3.00 + 548.94 (26.7 avg)	0.85
	1975	Y = −8.93 − 954.23 (26.7 avg) + 486.37 (DD + 0_1)	0.75
	1976	Y = 8.94 − 350.10 (26.7 avg) + 378.48 (DD + 0_1)	0.92
	1977	Y = −1.87 + 262.38 (RD)	0.72
	1978	Y = −16.60 + 257.90 (DD + 0_1)	0.82
	1979	Y = −17.30 − 2,352.76 (26.7 avg) + 2,079.70 (DD + 0_1)	0.95
	1974–1979	Y = −8.08 − 99.37 (26.7 avg) + 231.42 (RD) + 106.35 (DD + 0_1)	0.67

[a] Resistant cultivars: Coker-86, Coker-298, Speight G-28, and NC-1071. Moderately resistant cultivars: NC-95, NC-2326, NC-79, Coker-319, Coker-411, Coker-347, Speight G-140, McNair-914, and Va-115. Susceptible cultivars: Hicks and Va. Gold.
[b] For each year N = 28 for resistant, 54 for moderately resistant, and 14 for susceptible. For combined years N = 168 for resistant, 324 for moderately resistant and 84 for susceptible. Equations selected for high R^2, significant terms within equation ($P \leq 0.05$) and those with the fewest environmental variables. Environmental variables: 26.7 = days with maximum temp. ≥ 26.7 C, 26.7 avg = days with average maximum and minimum temperature ≥ 26.7 C, TP = total precipitation, RD = number of days of measureable precipitation, DD + 0_1 or 0_2 = days with no rain and ≥ 23.9 C or ≥ 26.7 C maximum temperature.
[c] All R^2 values highly significant at $P \leq 0.01$.

TABLE 3. Analysis by multiple linear regression of the average incidence[a] of black shank of tobacco by resistance groups and other parameters (1974–1979)

Resistance group[b]	Parameters	Equation[c]	R^2[d]
R	Environmental	Y = 1.10 + 0.95 (TP) + 39.37 (26.7 avg)	0.61
MR	Environmental	Y = 1.18 + 60.74 (DD + 0_1) − 459.22 (DD + 0_2) + 431.9 (26.7 avg)	0.66
S	Environmental	Y = −6.72 − 339.60 (26.7) + 352.81 (23.9) + 132.38 (DD + 0_1)	0.78
R	Environmental + Period	Y = −0.28 − 0.54 (P*) + 1.04 (TP) + 44.82 (26.7 avg)	0.61
MR	Environmental + Period	Y = −8.54 + 3.95 (P) − 152.64 (DD + 3_1) + 84.00 (DD + 0_1)	0.61
S	Environmental + Period	Y = −12.71 + 27.91 (P) − 121.06 (26.7) + 235.89 (DD + 0_1) − 219.47 (26.7 avg)	0.81
R	Environmental + Year	Y = −17.50 + 2.34 (yr) 0.77 (TP) + 29.75 (DD + 0_1)	0.72
MR	Environmental + Year	Y = −33.72 + 5.08 (yr) + 91.98 (DD + 0_1)	0.75
S	Environmental + Year	Y = −15.43 + 1.72 (yr) + 98.61 (23.9)	0.69

[a] The incidence of black shank in all cultivars in a resistance group, averaged within a year, N = 42.
[b] Resistant (R) cultivars: Coker-86, Coker-298, Speight G-28, and NC-1071. Moderately resistant (MR) cultivars: NC-95, NC-2326, NC-79, Coker-319, Coker-411, Coker-347, Speight G-140, McNair-914, and Va-115. Susceptible (S) cultivars: Hicks and Va. Gold.
[c] Equations selected for high R^2, significant terms within equation ($P \leq 0.05$) and those with the fewest environmental variables. Those variables with (*) are not significant at $P \leq 0.05$. Variables: TP = total precipitation, 26.7 avg = days when average maximum and minimum temperature ≥ 26.7, 23.9, or 26.7 = days when maximum temperature ≥23.9 C or 26.7 C, DD + 0_1 or 0_2 = days with no rain and ≥23.9 C or 26.7 maximum temperature, DD + 3_1 = days of no rain and ≥ 23.9 C after 3 days of the same conditions. Y = year, P or Period = 2-wk interval period.
[d] All R^2 values significant at $P \leq 0.001$.

help in developing a loss assessment system. Specific equations and further information are available from the senior author. However, many data gaps still remain to be investigated. In particular, the influence of initial inoculum density, actual measurement of soil moisture, and temperature during the course of several epidemics would help select weather parameters with good predictive value. The use of physiological growth stages rather than basing time as calendar time would allow the involvement of the physiology of the host plant and should also improve and refine future models.

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