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Relationship Between Weather and Soybean Seed Infection by *Phomopsis* sp.

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ABSTRACT

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Five soybean (*Glycine max*) cultivars were planted at three dates in the field for 4 yr to investigate the relationship between seed infection by *Phomopsis* sp. and environmental conditions. Weather data were summarized during two growth periods: seed development (from the beginning of seed filling to physiological maturity) and seed maturation (physiological maturity to harvest maturity). Seed infection by *Phomopsis* sp. ranged from zero to 68% across years, cultivars, and planting dates. The incidence of *Phomopsis* sp. was significantly correlated with air temperature and minimum relative humidity but not with total precipitation or precipitation per day. A regression model was developed that included minimum temperature and minimum relative humidity during both growth periods, precipitation per day during the seed development period, and interactions between growth periods (nine terms, $r^2 = 0.70$). It accurately predicted *Phomopsis* sp. infection when tested with data independent of those used to develop the model. The model predicted low levels (3%) of *Phomopsis* sp. seed infection from long-term average weather data for Lexington, KY, for an early maturing cultivar planted early (mid-May). Predicted levels increased to 39% when all weather variables were increased to 20% above average. Similar increases occurred when only the moisture variables were increased to 20% above average, but little increase occurred if temperature alone was increased by 20%, suggesting that infection of soybean seed by *Phomopsis* sp. depends more on moisture than on temperature at Lexington, KY.

Additional key words: Diaporthe, epidemiology, planting dates, pod and stem blight.

Infection of soybean (*Glycine max* (L.) Merrill) seed by *Diaporthe phaseolorum* (Cke. & Ell.) var. *sojae* Wehm. (anamorph *Phomopsis sojae* Leh.), the pod and stem blight fungus, can result in severe reductions in seed germination (2,6,15). Recent studies with variants of *D. phaseolorum* recognize three distinct types of fungal isolates associated with soybean seed infection (6,8). They are *Phomopsis* sp., along with the teleomorphs *D. phaseolorum* var. *sojae* and *D. phaseolorum* var. *caulivora* Athow and Caldwell. Distinction among these variants is based on the production and morphology of perithecia and on the degree of virulence on seed (6).

The frequency of infection by *Phomopsis* sp. is related to cultivar maturity, planting date, and weather conditions (5,10,11). The frequency of seed infection was less on late maturing cultivars or on early maturing cultivars that were planted late in Kentucky, suggesting that environmental conditions in late fall are less favorable for pod and stem blight development (1). Ross (10) reported lower levels of a *Phomopsis* sp. on late maturing cultivars in North Carolina, and Shortt et al (11) reported similar results in Illinois.

Warm, wet conditions during seed development or maturation favor seed infection (7,10,15). Shortt et al (11) reported that rainfall is more closely associated than temperature with the occurrence of

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seed decay by *Phomopsis* sp. in Illinois. Spilker et al (13) concluded that relative humidity (RH) is more important than temperature in determining the infection of seed by *Phomopsis* sp.

Seed infection by pod and stem blight fungi can be reduced by using foliar fungicides (3,9,10), but application must be made before symptoms are visible. A better understanding of the effect of the environment on soybean seed infection by *Phomopsis* sp. would enable devising a disease forecast model that would be useful for scheduling foliar fungicide applications.

The objectives of this research were to investigate the relationship between environmental conditions during seed development and maturation and the infection of soybean seed by *Phomopsis* sp.

MATERIALS AND METHODS

Soybeans were grown on Spindletop Research Farm near Lexington, KY, for 4 yr, 1976–1979. Cultivars ranging from maturity group (MG) II to V were planted mid-May, mid-June, and early July to provide a wide range of environmental conditions during seed development and maturation. The cultivars included in 1976–1978 were Beeson (MG II), Williams (MG III), Cutler 71 (MG IV), Kent (MG IV), and York (MG V). In 1979, only cultivars Williams, Kent, and York were used. The experimental plots were in the same locations for the duration of the experiments although soybeans had not been grown in the field the year before the experiment was initiated (1975).

In 1978 and 1979, an additional experiment was conducted at the farm at a separate location using the cultivar Williams planted in mid-May, mid-June, and early July. This experiment was in the same area both years, but soybeans had not been grown in the area before 1978. In both years, infested soybean residue was spread on the soil surface after seedling emergence to help insure adequate levels of inoculum.

Individual plots in both experiments consisted of four to six rows (76-cm row spacing), each 6 m long with approximately 33 plants per meter of row. A split-plot design with planting dates as main plots and cultivars as subplots in a randomized complete block design with three replications was used in 1976–1979. A randomized complete block design with three replications was used for the experiment that included only cultivar Williams in 1978 and 1979. In each experiment the plot area was plowed in the spring and a seedbed was prepared according to conventional cultural practices. In 1976, all cultivars in the July planting and cultivar York in the June planting, and in 1979, cultivars York and Kent in the July planting, were killed by a freeze before maturity, and no data were collected from these plots.

Reproductive growth stages were determined on 10 randomly selected plants per plot as described by Fehr and Caviness (4). Physiological maturity (PM, maximum seed dry weight) was taken as the date of growth stage R7 (14). The date of harvest maturity (HM, the first day that seed moisture declined to 14% [wet basis] or less) was determined by taking random samples of pods at 2-day intervals and measuring seed moisture by drying at 105 C for 24 hr. At HM, approximately 30 consecutive plants from a randomly selected portion of an interior row were removed from the field; the seeds were threshed by hand and stored in a controlled environment room (10 C, 50% RH) until seed quality evaluations were made.

The level of seed infection by *Phomopsis* sp. was determined by a modification of the procedure described by Kmetz et al (6). Fifty seeds were surface sterilized by soaking in 0.5% NaOCl for 4 min, washed with 200 ml of sterile distilled water, and plated on acidified (pH 4.5) potato-dextrose agar. Five seeds were placed on each culture plate, and the plates were held under fluorescent light at room temperature (approximately 25 C) for 12–14 days before fungal identification based on colony morphology was made. Because the majority of the fungal isolates in this study were classified as *Phomopsis* sp., this name will be used for all isolates of *D. phaseolorum* from soybean seed.

Daily maximum and minimum air temperatures, maximum and minimum RHs, and precipitation were measured at the Spindletop Research Farm Weather Station about 0.5 km from the experimental plots. The weather data were summarized over two periods of plant growth. The seed development period extended from the beginning of seed filling (growth stage R5) (4) to PM (14). The seed maturation period extended from PM to HM. Temperatures and RH were averaged over the appropriate time period for each production environment (each planting date × cultivar × year combination). Precipitation was expressed both as the total accumulation for the period and precipitation per day (total precipitation divided by the length of the period) to eliminate differences in the length of the periods. Maximum RH at Lexington was frequently near 100%, so only the minimum RH was used in all analyses. Regression and correlation analyses were done using the SAS-80 statistical analysis system. The minimum R^2 procedure was used to develop the regression model.

RESULTS

The combination of planting dates and cultivars of varying maturity resulted in a range in seed infection by *Phomopsis* sp. from 0 or near 0 each year to high levels in 1977, 1978, and 1979 (Table 1). The range was much narrower in 1976. Using three planting dates and cultivars of different maturity groups also provided a range of environmental conditions for both developmental periods in each year (Table 2). The date the plants reached growth stage R5 varied from 2 August to 22 September across the 4 yr, while the dates that the plants reached HM ranged from 11 September to 22 November. Average temperatures were

TABLE 1. Soybean seed infection by *Phomopsis* sp. at Lexington, KY, 1976 through 1979

Year	Observations (no.)	*Phomopsis* sp. (%)	
		Mean	Range
1976	9	2	0–10
1977	15	34	3–68
1978	18	14	0–31
1979	10	23	2–51

TABLE 2. Weather conditions during soybean seed development (R5 to physiological maturity [PM]) and seed maturation (PM to harvest maturity) for all cultivars and planting dates from 1976 through 1979 at Lexington, KY

Year	Sample size	Growth period	Average temperature (C)		Minimum relative humidity (%)		Precipitation per day (mm)	
			Mean	Range	Mean	Range	Mean	Range
1976	9	Seed development	20	17–21	47	44–52	3	2–4
		Seed maturation	15	7–19	51	41–59	3	0–6
1977	15	Seed development	21	13–23	54	50–57	4	3–6
		Seed maturation	16	10–24	53	44–68	2	0–4
1978	18	Seed development	20	15–23	50	45–56	3	0–6
		Seed maturation	17	11–25	44	33–54	2	0–4
1979	10	Seed development	18	14–22	56	53–59	6	3–8
		Seed maturation	14	11–18	52	47–57	3	0–13

higher during seed development (R5 to PM) than during seed maturation (PM to HM) in all 4 yr. In 1977, 1978, and 1979, conditions (precipitation per day and minimum RH) were drier during seed maturation than during seed development, although the difference was not as great as for temperature.

There was a significant correlation between temperature during each of the development periods and the level of seed infection by *Phomopsis* sp. at HM (Table 3). Although the correlation coefficients were all statistically significant, they were not very high. Minimum temperature during seed development and seed maturation showed a slightly higher correlation than maximum or average temperature (Table 3). Minimum RH was also significantly correlated with seed infection by *Phomopsis* sp. during both seed development and seed maturation, but there was no significant correlation between seed infection and total precipitation or precipitation per day for either developmental period (Table 3). Temperature, minimum RH, and precipitation (total and per day) were also summarized over the period from 5 days before PM to 5 days after PM. The resulting correlation coefficients for seed infection by *Phomopsis* sp. were no higher than those reported in Table 3 and they were lower for minimum RH and the two precipitation variables.

To further investigate the relationship between the weather conditions during seed development and maturation and seed infection by *Phomopsis* sp., the data were subjected to multiple regression analysis. Based on the results of the correlation analysis, the weather variables included were minimum air temperature (C) and minimum RH (%) for both developmental periods (seed development and seed maturation). Although in this study precipitation per day (millimeters per day) was not significantly correlated with seed infection by *Phomopsis* sp. (Table 3), it was included in the multiple regression analysis because precipitation has been implicated by other workers (10,11). The dependent variable was the percentage of the seed infected with *Phomopsis* sp. at HM. The linear and quadratic term of each variable for both growth stages and all possible linear interactions were evaluated using the minimum R^2 procedure in SAS-80. The data from 1976, 1978, and 1979 were used to develop the model, and the predictive ability of the model was tested by using the 1977 data. The model was tested with the 1977 data because they show a wide range in seed infection by *Phomopsis* sp. and weather (Tables 1 and 2). The model selected was the one with the minimum number of terms that satisfactorily predicted the levels of seed infection by *Phomopsis* sp. in 1977.

The regression model selected contained nine terms with an R^2 of 0.70 and an $S\hat{y} = 8.0\%$ (Table 4). The eight-term regression model systematically underestimated the levels of seed infection by *Phomopsis* sp. measured in 1977, and regression models with more than nine terms had higher R^2, but none had better predictive abilities. The nine-term model included weather variables from both the seed development and seed maturation periods, and all of the terms, except two, were significant at $\alpha = 0.05$ (Table 4). The eight- and nine-term models had five terms in common; the major difference was that the eight-term model included several terms involving precipitation per day during seed maturation that did not appear in the nine-term model. The selected regression procedure generated several similar, equally predictive nine-term models, which probably reflects the high degree of correlation among the weather variables.

The correlation between the levels of seed infection by *Phomopsis* sp. at HM in 1977 and the levels predicted with the model using 1977 weather data was 0.52 (Fig. 1). There were three observations that the model failed completely to predict; exclusion of these improved the correlation to 0.86, which was statistically significant ($\alpha = 0.01$). The three data points that were not accurately predicted were those for cultivar Cutler 71 in the June planting and cultivars Kent and York in the July planting.

DISCUSSION

The combination of years, planting dates, and cultivars provided a wide range in levels of soybean seed infection by *Phomopsis* sp. Previous analysis of cultivar and planting date effects suggested that the five cultivars exhibited no genetically controlled differences in resistance or tolerance to seed infection by *Phomopsis* sp. (1). Differences in seed infection by *Phomopsis* sp. among cultivars and planting dates seemed to be related to environmental conditions during seed development or maturation or both periods. Inoculum levels are also important (8), although these were not quantified in this study. The experiments in 1977 through 1979 were located in fields where soybeans had been grown previously, and in the experiment with cultivar Williams in 1978 and 1979, infested plant residue had been spread on the soil surface. Thus, it is unlikely that low inoculum levels limited *Phomopsis* sp. seed infection from 1977 through 1979. Because soybeans had not been grown in the experimental area before 1976, the influence of inoculum availability on the development of pod and stem blight disease in 1976 was examined. The relationships between the weather variables and the levels of seed infection by *Phomopsis* sp. showed no bias associated with the 1976 data and suggested that weather factors predominantly determined the level of seed infection by *Phomopsis* sp. Consequently, the 1976 data were included with those for the other years in analyses of weather relationships.

The levels of soybean seed infection were significantly correlated with temperature and minimum RH but not with precipitation. The correlation between temperature and seed infection by *Phomopsis* sp. was similar for both developmental periods (Table

TABLE 3. Relationship of environmental variables to levels of soybean seed infection by *Phomopsis* sp. at harvest maturity, 1976 through 1979

	Correlation coefficients[a]	
Environmental variable	Seed development[b]	Seed maturation[c]
Temperature		
Maximum	0.29*	0.33*
Minimum	0.49**	0.43**
Average	0.39**	0.38**
Minimum relative humidity	0.62**	0.45**
Precipitation		
Total	0.21	0.02
Per day	0.28	0.14

[a] * and ** indicate statistical significance at $\alpha = 0.05$ and 0.01, respectively. Sample size was 52.
[b] Growth stage R5 to physiological maturity.
[c] Physiological maturity to harvest maturity.

TABLE 4. Regression model relating environmental conditions during seed development and maturation to percentage of seed infection by *Phomopsis* sp. at harvest maturity (HM), 1976, 1978, and 1979 at Lexington, KY

Source	Coefficient[a]	Partial sum of squares
Intercept	232.26191	...
Linear		
Precipitation per day (R5 to PM)	−16.66113	97.9769
Minimum relative humidity (PM to HM)	−10.41683**	438.4049
Quadratic		
Minimum temperature (R5 to PM)	−0.15041	60.4755
Minimum relative humidity (PM to HM)	0.08913*	302.5997
Interactions		
Minimum temperature (R5 to PM) × precipitation per day (R5 to PM)	−1.07536**	644.8849
Minimum relative humidity (R5 to PM) × precipitation per day (R5 to PM)	0.41317*	349.2127
Minimum temperature (PM to HM) × minimum relative humidity (PM to HM)	−0.11812**	493.2707
Minimum temperature (R5 to PM) × minimum relative humidity (PM to HM)	0.22164*	251.1948
Precipitation per day (R5 to PM) × minimum temperature (PM to HM)	1.18562**	530.3165

[a] * and ** indicate statistical significance at $\alpha = 0.01$ and 0.01, respectively. Sample size was 37.

3). This suggests that temperatures during both periods may have been important in determining the level of seed infection. However, temperatures during seed development were significantly correlated with temperatures during seed maturation ($r = 0.58$ or greater), making it difficult to estimate temperature effects for a specific developmental period. The correlation of minimum RH with seed infection was higher than that for temperature in both developmental periods, which is in agreement with the results of Spilker et al (13). However, all of the correlation coefficients were relatively low, suggesting that neither temperature nor minimum RH was the dominant factor in either developmental period.

Neither precipitation variable was significantly correlated with seed infection by *Phomopsis* sp. for either developmental period. However, they were both significantly correlated with minimum RH although the correlation coefficients were higher during seed development (r = 0.93 and 0.66 for total precipitation and precipitation per day, respectively) than during seed maturation ($r = 0.34$ for both total precipitation and precipitation per day). The poor correlation of the precipitation variables with seed infection may result from using total precipitation or precipitation per day over a long period, which ignores variations in the distribution of precipitation or variation in the number of precipitation events. In view of the results of Shortt et al (11) and Ross (10), the lack of a significant correlation of seed infection with precipitation is somewhat surprising, especially since precipitation per day and minimum RH were significantly correlated.

The movement of the fungus from the carpel to the seed occurs near PM (yellow and brown pods), which may be a crucial period in the seed infection process (5,8). This suggests that environmental conditions at PM (growth stage R7) may be more important than conditions during other developmental periods. However, the correlations of seed infection by *Phomopsis* sp. with the weather conditions from 5 days before to 5 days after PM were no better than those from the other developmental periods. Thus, with the data used in this study, the weather conditions at PM were not more important in determining the level of seed infection by *Phomopsis* sp. than those during seed development or seed maturation.

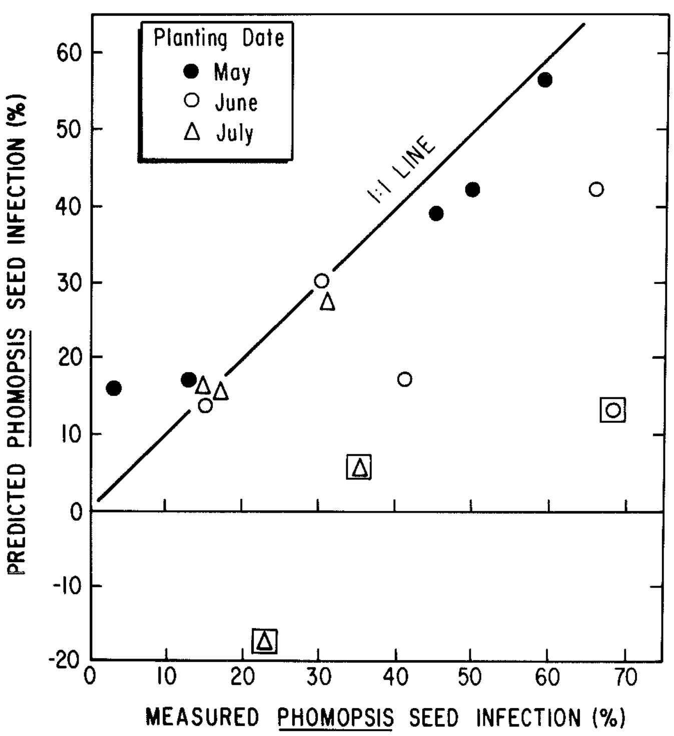

Fig. 1. Relationship between the levels of seed infection by *Phomopsis* sp. predicted by the regression model and the levels measured at harvest maturity in 1977. The boxed data points were considered to be outliers and were therefore excluded from the correlation analysis.

Temperature and minimum RH levels during seed development were significantly correlated with the levels during seed maturation; however, there was no significant correlation between precipitation during seed development and seed maturation. There were also significant correlations between weather variables. The intercorrelations among the weather variables and the correlations for individual weather variables between developmental periods makes it difficult to clearly separate the effects of the individual variables or to distinguish the effects on seed infection by *Phomopsis* sp. during each development period. However, the data, in general, agree with previous reports (7,10,11,15) suggesting that temperature and moisture conditions during seed development and maturation are important determinants of the level of seed infection by *Phomopsis* sp.

The nine-term regression model satisfactorily predicted the levels of seed infection by *Phomopsis* sp. occurring in 1977 in 12 of the 15 planting date × cultivar combinations, suggesting that the model accurately described the relationship between the environmental conditions during seed development and maturation and the levels of seed infection by *Phomopsis* sp. It was not possible to develop a satisfactory model by using only weather variables that occurred during either the seed development or seed maturation period, suggesting that pod and stem blight development was influenced by weather conditions during both periods. Examination of the residuals from the data used to develop the nine-term model indicated that there was no bias associated with any of the cultivars, which is consistent with the suggestion that differences in seed infection by *Phomopsis* sp. among cultivars and planting dates in these experiments were related primarily to environmental differences during seed development and maturation (1). There was also no bias shown for any of the years, suggesting that inoculum levels were not limiting seed infection by *Phomopsis* in these experiments. There were three data points that the model failed completely to predict (Fig. 1). The cultivar York planted in July (measured level of seed infection by *Phomopsis* of 23%, predicted level of −18%) reached harvest maturity later (22 November) than any of the other cultivars. The lack of predictive ability for the July planting of cultivar York may result from using weather data outside the range of the data used to derive the model. Thus, the model may not be useful for late cultivars that are planted late and mature late in the fall. The weather data for cultivar Cutler 71 from the June planting and cultivar Kent from the July planting were within the range of the data used to develop the model; however, the predictive ability of the model was also poor for these two points (Fig. 1). The weather data included in the model were averaged over the seed development or maturation periods, and this averaging may obscure the effect of a particular weather variable at a crucial developmental stage of the disease. The weather data used were collected at a standard weather station near the plots and may not adequately represent the conditions in the plant canopy, which would be the conditions that directly affect pod and stem blight development. Both of these factors may have contributed to the poor predictive ability of these two data points. More complete epidemiological information on the disease and detailed information on the canopy environment are needed to develop a more detailed model with improved predictive ability.

The model was used to estimate the level of seed infection by *Phomopsis* sp. that would be expected during exposure to a range of environmental conditions. Long-term average weather data (26 yr for temperature and precipitation, 14 yr for minimum RH) for Lexington for the average dates of the two developmental periods for cultivar Williams planted in mid-May were used. The predicted level of seed infection by *Phomopsis* sp. using the average long-term weather conditions was 3%; however, when the temperature, precipitation per day, and minimum RH were increased by 20%, the predicted level increased to 39%. If temperature was held at the average and the moisture variables were increased by 20%, the predicted seed infection by *Phomopsis* sp. was 34% compared with a predicted level of 4% when moisture was held at the average level and temperature was increased by 20%. Under the environmental conditions normally encountered at Lexington, moisture conditions (precipitation and minimum RH) appear much more important than temperature in determining the levels of seed infection by *Phomopsis* sp. This is consistent with the report of Shortt et al (11) that the incidence of seed decay by *Phomopsis* sp. was closely associated with precipitation during August, September, and October in Illinois and also with the results of Spilker et al (13) that suggest that RH is more important than temperature in controlling the disease. Balles (1) reported that levels of seed infection by *Phomopsis* sp. are frequently lower for late maturing cultivars or early maturing cultivars planted late at Lexington. In both situations, the seed development and maturation periods would occur later in the growing season when average precipitation is less. Thus, Balles' observations (1) are in agreement with the suggestion from the model that drier conditions during seed development and desiccation result in lower levels of seed infection by *Phomopsis* sp.

Chemical control of pod and stem blight disease in soybean seed has been practiced only on a limited basis. Reductions in the incidence of seedborne infection have been reported following application of foliar fungicides (3,9,10), but the fungicides must be applied before disease symptoms are visible. Thus, fungicide applications must be made before it is known if economically significant levels of pod and stem blight will develop. Several predictive systems have been developed to determine when to use a foliar fungicide (12). The regression model presented here could be used to develop improved predictive systems or (more directly) to evaluate current weather conditions as a basis for scheduling fungicide applications.

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