Prediction of Phomopsis Seed Decay by Measuring Soybean Pod Infection

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ABSTRACT

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The epidemiological basis for predicting the incidence of soybean seed infection by *Phomopsis longicolla, Diaporthe phaseolorum* var. *sojae*, and *D. phaseolorum* var. *caulivora* (collectively referred to as PD) by measuring pod infection at the R6 (full seed) growth stage was elucidated. Extensive seed infection by PD could not be induced in pods exposed to 100% relative humidity for 7 days in the laboratory when they were detached from plants before the R7 growth stage (beginning maturity). Pod infection therefore can be measured and a fungicide applied during R6 without risk of seed infection already having occurred. Pods artificially inoculated at various growth stages between R3 (beginning pod) and R8 (full maturity) by an isolate of *P. longicolla* were susceptible to infection only before R7 under field conditions and in growth chambers held at 50–70% relative humidity. They were susceptible, however, after inoculation at R7 and R8 in growth chambers at 86–97% relative humidity. Periodic measurements of pod infection between R4 (full pod) and R8 in four soybean fields showed low levels of infection until R7, then they increased markedly. This was attributed to further colonization of pods by inoculum already present and not to new inoculum that might have reached pods since R6. It was concluded that under environmental conditions likely to occur in the Midwest, a predictive measurement at R6 would not be invalidated by inoculum that later reached pods. Pod infection was measured by a quick, inexpensive test that could be done by seed company personnel. The predictive capability of the test was demonstrated by clear relationships between inoculum artificially applied to pods and incidences of pod infection at R6 and seed infection at harvest maturity. Also, a correlation of 0.67 was obtained between natural pod and seed infection in 23 soybean fields in Iowa in 1982. Benomyl, applied during R6, reduced seed infection by PD in plots with 71% pod infection but was of no benefit in plots with 27% pod infection where seed quality was not impaired by infection by PD.

Phomopsis seed decay of soybeans (*Glycine max* L.) can be controlled by applying benzimidazole fungicides to the growing seed crop at the R6 (full seed) growth stage (11). The disease is caused by a complex of fungi, including *Phomopsis longicolla* Hobbs sp. nov. (4), *Diaporthe phaseolorum* (Cke. & Ell.) Sacc. var. *sojae* Lehman and *D. phaseolorum* var. *caulivora* Athow & Caldwell (collectively referred to as PD). In the northern United States, Phomopsis seed decay often is not severe enough to justify treatment. Disease prediction methods to identify fields that would benefit from spraying are therefore needed. One approach developed in Kentucky (11) is based on the assumption that disease incidence is related to the additive effects of cultural and environmental factors that have separately been associated with increased severity of the disease. Another method uses the knowledge that pods are a pathway for infection of seeds (6,7) to predict seed infection by measuring pod infection at growth stage R6. Preliminary descriptions (9,10) of the latter method have not adequately described its epidemiological basis. In particular, a more precise definition is needed of the growth stage at which seed infection can occur to determine the latest growth stage at which pod infection can be measured. This is necessary because fungicides are ineffective after PD has infected seeds (7). It also is necessary to know whether the predictive measurement could be invalidated by inoculum that subsequently reached pods and caused seed infection. This paper provides additional epidemiological data to establish the feasibility of the method, validates it in the field in Iowa, and demonstrates its practical application in soybean seed production.

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MATERIALS AND METHODS

Measurements of infection of soybean pods and seeds by PD. Infection of pods by PD was measured either in a plate test or a pod test. For the plate test, whole pods were surface-sterilized in 1.3% sodium hypochlorite for either 3 min (in field experiments) or 1 min (in growth chamber experiments), rinsed in sterile water, and plated on potato-dextrose agar adjusted to pH 4.5 with lactic acid (APDA). After incubation for 7 days at 25 C in the dark, the number of pods from which colonies of PD grew was recorded. For the pod test, pods were surface-sterilized in 1.3% sodium hypochlorite for 1 min, immersed for 5 sec in an 11.9-mg/ml solution of paraquat (Ortho Paraquat CL), then incubated on moist blotters in plastic boxes for 7 days at 25 C under continuous light. The pods on which fruiting bodies of PD were detected were counted. Seed infection was measured by surface-sterilizing in 1.3% sodium hypochlorite for 5 sec (for seeds sampled before harvest maturity) or in 0.5% sodium hypochlorite for 1 min (for seeds sampled at harvest maturity), rinsing in sterile water, and plating on APDA. The milder surface-sterilization technique was used before harvest maturity, because it was assumed that the pathogen would not be well established within the seeds. In some experiments, seed infection was induced by placing detached pods on wire racks over free water in sealed plastic boxes. After incubation in the dark for 7 days at 25 C, seeds were removed and tested for PD infection as described for harvest-mature seeds.

Epidemiological experiments. Soybean growth stages were described according to the system of Fehr and Caviness (3). Those used in this study were R3 (beginning pod), R4 (full pod), R5 (beginning seed), R6 (full seed), R7 (beginning maturity), and R8 (full maturity). Harvest maturity was indicated when seed moisture was less than 15%. An experimental plot, or field, was considered to reach a particular growth stage when 50% of the plants were at that stage of development.

Susceptibility of soybean pods and seeds to infection by *P. longicolla* at various growth stages was examined at different relative humidities in growth chambers. In one experiment, four groups of eight pots, each containing three Amsoy 71 plants, were planted at different times and held in a growth chamber maintained on a cycle of 14 hr of light and 50% relative humidity at 28 C and 10 hr of darkness and 70% relative humidity at 20 C. When the growth stages in the groups were simultaneously R3, R5, R7, and R8, all pods in four pots of each group were sprayed with a suspension of 1.5×10^8 conidia per milliliter of a *P. longicolla* isolate originally obtained from a soybean seed. The remaining four pots in each group were not inoculated. Pots were arranged in four randomized blocks with growth stages as the main plots and inoculated and uninoculated pots as the subplots. Five pods were detached from each

subplot 2 wk after inoculation and pods and seeds (except for R3 detachments) were tested for infection by *P. longicolla* in plate tests. This procedure was repeated for all treatments when the last group planted reached harvest maturity. A second experiment was done in the same way, except relative humidities were increased to 86% in the light cycle and 97% in the dark, inoculations were made only at the R5 and R8, and treatments were replicated three instead of four times. Each experiment was repeated once.

The susceptibility of pods and seeds to infection by *P. longicolla* also was examined in a field near Ames in 1979 and 1980. Plots of Amsoy 71 soybeans consisting of four rows 4.5 m long and 0.8 m wide were inoculated at the R3, R4, R5, and R8 growth stages with a culture of *P. longicolla*. Inoculum was sprayed in a suspension of 1.5×10^7 conidia per milliliter to 600 pods in the middle two rows in one half of the plot; the other half was used to measure natural infection. Treatments were arranged in four randomized blocks with inoculation times as the main plot and artificial or natural infection as the subplot. For each growth stage treatment, 50 pods were detached 2 wk after inoculation from both inoculated and uninoculated plots and seeds were removed immediately. All 50 pods and 100 seeds then were tested for infection in plate tests. In 1979, an additional 50 pods were detached from each plot at harvest maturity and 100 seeds were removed and tested for infection by PD. In 1980, 20 pods were detached from each subplot at harvest maturity and 50 seeds were tested.

In 1980, the plots in which pods were inoculated on 21 August (at R5) also were used to determine the growth stage at which PD could grow from pod to seeds. At weekly intervals from 28 August to 25 September, 40 pods were detached from both the inoculated and uninoculated plots of this treatment. Seeds were immediately removed from 20 pods, then pods and seeds were tested for infection by PD in the plate test. The other 20 pods were placed in a moisture chamber to induce seed infection before the seeds were removed and tested. These plots also were used to determine the effect of a fungicide on seed infection by PD and seed germination in relation to the level of pod infection. Pod infection was measured at R6 in inoculated and uninoculated plots by pod tests. The fungicide benomyl was applied at 4 g/L on 25 August and 2 and 9 September to 1-m sections of row in inoculated and uninoculated plots. Care was taken to ensure that the fungicide did not drift to other parts of the plots. On 10 October, 20 pods per plant were detached and the seeds tested for PD infection by plating. Seed germination was estimated on the culture plates by counting those that produced radicles at least two and one-half times the length of the cotyledons.

The progression of PD infection of pods between R3 and R8 was examined in two commercial soybean fields in Ames with cultivars Corsoy (maturity group II) and Wayne (group III) in 1981 and Corsoy 79 (group II) and Wayne (group III) in 1982. A section in each field was divided into four contiguous blocks of 20 rows 50 m long. Samples of pods were taken from different rows within each block at 3- or 4-day intervals between the R3 and R7 growth stages in 1981. In 1982, the sampling interval was extended to 7 days. At each sampling, 50 pods were obtained by removing one pod from the middle part of the main stem of single plants 1 m apart along the row. Pods were then tested for PD infection in plate tests. Rainfall was measured throughout the experiment at each location.

The relationship between the amount of inoculum of *P. longicolla* applied to pods and subsequent pod and seed infection was examined. An isolate of *P. longicolla* that originated on a soybean seed was applied at concentrations of 0, 1.5×10^3, 1.5×10^6, and 1.5×10^8 conidia per milliliter to pods on Amsoy 71 plants at R5 in the field near Ames in 1982 and 1983. Inoculum at each concentration was applied in the center two rows of separate plots consisting of four rows 4.5 m long and 0.8 m wide. Treatments were replicated in each of four randomized blocks. At R6, 25 pods from each plot were tested for infection by PD in pod tests. At harvest maturity, an additional 25 pods per plot were sampled and the seeds tested for infection by PD.

Cooperative experiments with seed companies. The practical application of pod infection and rainfall as predictors of seed infection was examined in a cooperative experiment with 20 seed companies from various parts of Iowa in 1981, 1982, and 1983. Each year, personnel from these companies attended a half-day training session in Ames on the methodology of the pod test, then selected a soybean seed production field at their seed farm that would not be sprayed with a fungicide. At the R6 growth stage, they sampled 50 pods by walking 25 m into the field and detaching one pod from the middle section of the main stem of one plant every 2 m for 100 m and tested them for infection by PD in a pod test. I visited the seed farm within 3 days of completion of the test to confirm their results. In 1982, I sampled an additional 100 pods during my visit by detaching one pod from plants 1 m apart for 100 m (in the same row sampled by the cooperator). These pods were immediately returned to Ames and tested for PD infection in plate tests. Another 100-pod sample was taken in each field the same way at harvest maturity (in all three years), and the seeds were tested for PD infection. Correlation coefficients were calculated to compare pod test and plate test measurements of PD infection in 1982 and to compare pod test values at R6 with seed infection at harvest maturity for each year. Rainfall was measured

Table 1. Infection of soybean pods and seeds by *Phomopsis longicolla* and *Diaporthe phaseolorum* vars. *sojae* and *caulivora* after inoculation of pods with *P. longicolla* at different growth stages in the field near Ames, IA

Year	Growth stage when inoculated[a]	Pod infection 2 wk after inoculation[b,c] (%)		Seed infection[b]			
				2 wk After inoculation[d] (%)		Harvest maturity[c] (%)	
		Inoculated	Uninoculated	Inoculated	Uninoculated	Inoculated	Uninoculated
1979	R3	...[e]	...	...	...	5.5	1.5
	R4	86.0	4.3	0.0	0.0	13.0	6.5
	R5	100.0	84.0	3.3	0.8	13.2	4.0
	R8	98.0	94.0	0.6	3.4	1.5	5.0
1980	R3	55.9	0.5	...	...	8.5	2.2
	R4	93.0	4.2	2.0	0.0	28.5	4.1
	R5	80.5	27.0	8.0	0.5	22.5	3.4
	R8	27.2	34.0	2.3	1.6	0.8	0.9

[a] Pods inoculated with a conidial suspension of *P. longicolla*.
[b] Infection is expressed as the percentage of pods or seeds from which *P. longicolla* and *Diaporthe phaseolorum* vars. *sojae* and *caulivora* grew on APDA. Values are the mean of four replicates.
[c] The *F*-test in analysis of variance indicated a significant ($P = 0.001$) interaction between main treatments in both years.
[d] The *F*-test in analysis of variance indicated no significant interaction between main treatments in either year.
[e] Data not taken.

daily from R4 until harvest maturity at each location. Correlation coefficients were calculated to compare rainfall during the 2 wk before the sampling time for the pod test with seed infection at harvest maturity in each year. These also were calculated to compare rainfall between sampling times for the two pod infection tests in 1982 and the difference in values between the tests.

RESULTS

Pod infection by PD was increased by inoculation at R3, R4, or R5 but not at R8 (Table 1). Little effect of pod inoculation on seed infection was detected 2 wk after inoculation for any treatment. At harvest maturity, however, there was more seed infection in pods inoculated at R4 and R5 than at R8 (Table 1). Similar results were obtained when plants were grown in growth chambers maintained at a low relative humidity range (50–70%) as indicated by greater pod infection after inoculation at R3 than at R8 and greater seed infection at harvest maturity after inoculation at R3 and R5 than at R7 and R8 (Table 2). Unlike results in the field or low-humidity growth chamber, extensive pod and seed infection occurred at a higher humidity range (86–97%) after inoculation at R8.

The seed infection induced in pods detached in the field at R6 and placed in moisture chambers for 1 wk was minimal (Fig. 1). A progressive increase in seed infection was detected, however, during subsequent weekly detachments of pods. This increase continued until the R8 growth stage, when infection was comparable to that at harvest maturity. Trends were similar for both artificially inoculated and naturally infected pods, although seed infection was generally greater in the artificially inoculated treatment.

The percentage of pods naturally infected by PD in soybean seed production fields in Ames in 1981 and 1982 remained below 30% until the R7 growth stage, when a distinct increase occurred (Fig. 2). No consistent relationships could be detected between changes in pod infection and rainfall between sampling times.

Pod test values in 1982 and 1983 were

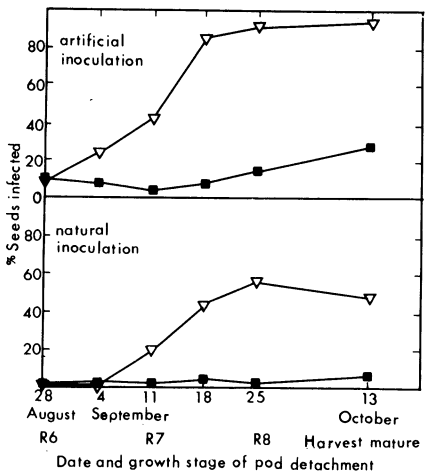

Fig. 1. Seed infection by *Phomopsis longicolla* and *Diaporthe phaseolorum* vars. *sojae* and *caulivora* induced by high humidity in soybean pods either artificially or naturally inoculated with *P. longicolla*. Pods were detached from plants in the field at different growth stages and either tested for seed infection directly (solid squares) or placed in moisture chambers for 7 days to induce seed infection before testing (open triangles).

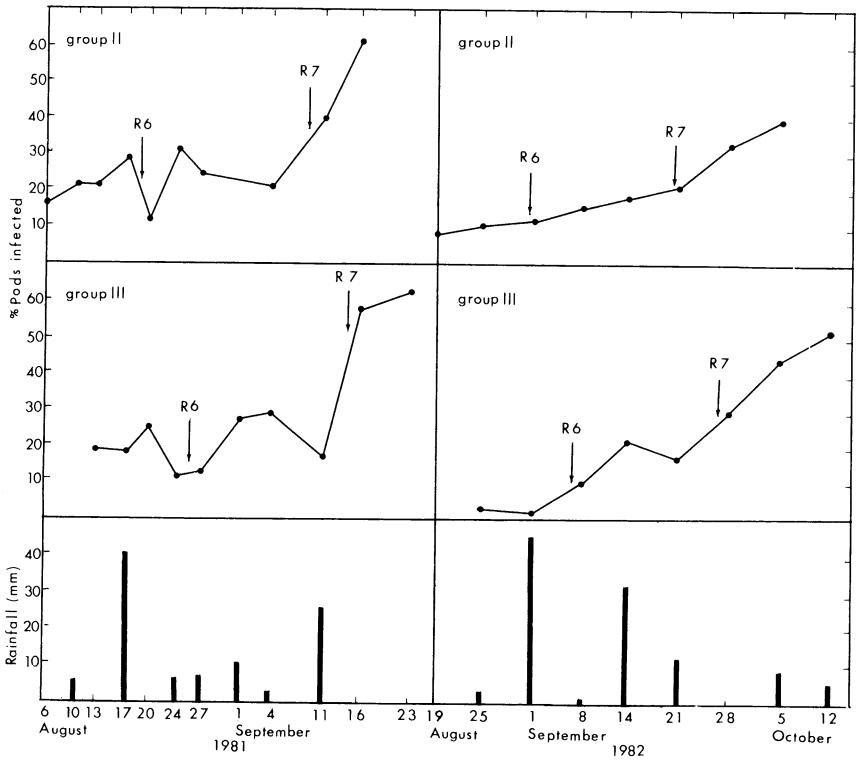

Fig. 2. Seasonal progression of infection by *Phomopsis longicolla* and *Diaporthe phaseolorum* vars. *sojae* and *caulivora* of soybean pods in relation to rainfall for cultivars of maturity groups II and III grown in the field in Ames, IA, in 1981 and 1982. The beginnings of the R6 and R7 growth stages are indicated. Rainfall is expressed as the amount since the previous date.

Table 2. Infection of soybean pods and seeds by *Phomopsis longicolla* after inoculation of pods at different growth stages in growth chambers maintained at two humidity regimes

	Relative humidity range (%)[b]					
	50–70			86–97		
	Pod infection	Seed infection[c,e]		Pod infection	Seed infection[e]	
Growth stage when inoculated[a]	2 wk after inoculation[c,d] (%)	2 wk After inoculation (%)	Harvest maturity (%)	2 wk after inoculation[d] (%)	2 wk After inoculation (%)	Harvest maturity (%)
R3	50	12	22			
R5	24	12	17	80	26	80
R7	10	2	0			
R8	0	0	0	100	90	96

[a] Pods inoculated with a conidial suspension of *P. longicolla*. Infection values for uninoculated pods were 0 for all growth stage treatments at each sampling time.
[b] Growth chambers were maintained on a 14-hr light and 10-hr dark cycle, at temperatures of 28 and 22 C, respectively. For each relative humidity range, the high and low numbers are those for the light and dark cycles, respectively.
[c] Infection is expressed as the percentage of pods or seeds from which *P. longicolla* grew on APDA. Values are the mean of four replicates.
[d] The *F*-test in analysis of variance indicated significant differences ($P = 0.001$) between growth stage treatments.
[e] The *F*-test in analysis of variance indicated significant differences ($P = 0.001$) for interactions between main treatments.

greater for pods inoculated at R5 with 1.5×10^8 and 1.5×10^6 spores per milliliter of *P. longicolla* than on those inoculated with 1.5×10^3 spores per milliliter or not inoculated (Table 3). Seed infection measured at harvest maturity was similarly related to the initial amounts of inoculum. Although the level of seed infection was much lower in 1982 than in 1983, pod and seed infection values were well correlated in both years.

In 1982, pod test values obtained by cooperators at seed farms correlated well with those for pods sampled 2 wk later and tested in plate tests (Fig. 3). Rainfall between sampling times for each test did not correlate ($r = 0.13$) with differences between test results. A significant correlation ($r = 0.67$, $P = 0.001$) was obtained in 1982 between results of pod infection tests made by cooperators and seed infection at harvest maturity (Fig. 4). Rainfall measurements, however, in the 2-wk period before sampling did not correlate ($r = 0.07$) with seed infection.

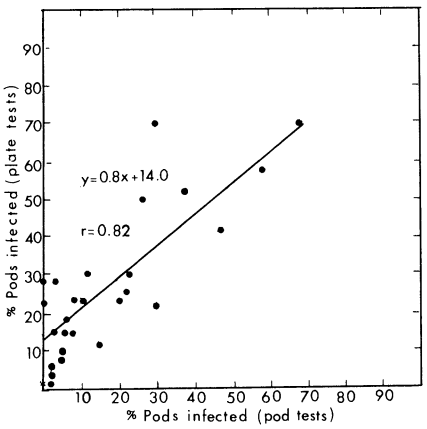

Fig. 3. Relationship between estimates of soybean pod infection by *Phomopsis longicolla* and *Diaporthe phaseolorum* vars. *sojae* and *caulivora* in pod tests at the R6 growth stage and in plate tests made 2 wk later in soybean fields in Iowa in 1982.

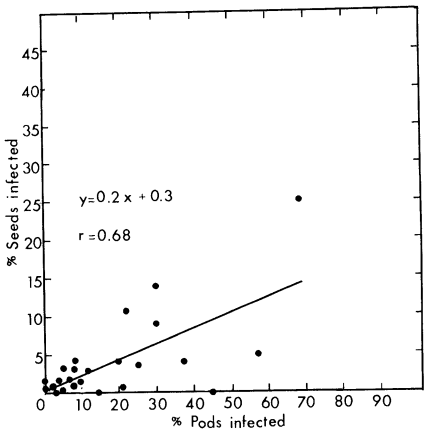

Fig. 4. Relationship between soybean pod infection by *Phomopsis longicolla* and *Diaporthe phaseolorum* vars. *sojae* and *caulivora* measured in pod tests at the R6 growth stage and seed infection in plate tests at harvest maturity in commercial soybean fields in Iowa in 1982.

Table 3. Pod and seed infection by *Phomopsis longicolla* and *Diaporthe phaseolorum* vars. *sojae* and *caulivora* in soybean pods inoculated at the R5 growth stage with different concentrations of conidia of *Phomopsis longicolla*

Inoculum concentration (conidia/ml)	1982 Pod infection[a] (%)	1982 Seed infection[b] (%)	1983 Pod infection (%)	1983 Seed infection (%)
0	9.0	2.0	13.8	1.0
1.5×10^3	14.0	1.5	12.0	1.5
1.5×10^6	96.0	26.0	73.0	5.0
1.5×10^8	100.0	52.0	88.0	10.5
r[c]	0.91		0.93	

[a] Pod infection measured in pod tests made at R6 growth stage. Values are the mean of four replicates.
[b] Seed infection measured at harvest maturity in plate tests. Values are the mean of four replicates.
[c] Correlation coefficient between pod and seed infection values for each year.

Table 4. Seed infection by *Phomopsis longicolla* and *Diaporthe phaseolorum* vars. *sojae* and *caulivora* and seed germination in soybeans with different levels of pod infection by the fungi treated with benomyl at different times

Date benomyl applied[a]	Pod infection[b] 71% Seed infection[c]	71% Germination[d]	27% Seed infection	27% Germination
25 August	0	97	0	97
2 September	0	92	0	90
9 September	7	89	0	92
No fungicide applied	29	51	4	92

[a] Benomyl applied at 6 g/L to 1-m sections of row in field plots.
[b] Pod infection was measured at R6 in pod tests.
[c] Infection is expressed as the percentage of seeds for which *Phomopsis longicolla* and *Diaporthe phaseolorum* vars. *sojae* and *caulivora* grew on APDA. Values are the mean of four replicates.
[d] Germination is expressed as the percentage of seeds in which the radicle was 2.5 times the length of the cotyledon on APDA plates. Values are the mean of four replicates.

In 1981 and 1983, pod test values were 0–24 and 0–28%, respectively, but seed infection values were 0–1.7 and 0–6.5%, respectively. These seed infection values were too low to test the predictability of pod infection or rainfall measurements.

Benomyl applied during the R6 growth stage reduced seed infection by PD and improved germination in plots with 71% pod infection (Table 4). For plots with 27% pod infection, little seed infection occurred in untreated plots and germination was unaffected. Fungicide applications were of no benefit in improving seed quality.

DISCUSSION

The pattern of pod and seed infection by PD elucidated in this study meets the criteria needed for using pod infection at R6 as a predictive measurement of seed infection. Extensive seed infection can occur from R7 onward; therefore, pod infection must be measured and a fungicide applied during the R6 growth stage. According to Fehr and Caviness (3), there are 9–30 days between R6 and R7, which is adequate time to accomplish this. The marked increase in pod infection detected at R7 could be interpreted as the result of new inoculum reaching pods. Artificial inoculation of pods in the field and at low relative humidity (50–70%) in growth chambers, however, indicated that pods were not susceptible to infection at R7 and R8. A more likely explanation for increased pod infection is that it reflected further colonization of pods by inoculum already present. Tomes et al (14) showed that this does occur at R7. There is no question that at R8, pods exposed to high relative humidity (86–97%) were susceptible to infection by new inoculum. In Iowa, however, plants normally are at R7 and R8 in September, when the average daytime relative humidity is 60% (1). Balducchi and McGee (2) used overhead irrigation to simulate relative humidity conditions greater than 85% for 5-day periods in September and showed that extensive seed infection by PD occurred only if the temperature averaged 19 C or higher during the irrigation period. It would be extremely unusual for prolonged wet periods to be accompanied by these temperatures in Iowa; therefore, there seems to be little risk of a predictive measurement at R6 being invalidated by inoculum of PD that might subsequently reach pods and cause seed infection.

The pod test proved to be an effective method of measuring pod infection. Equipment and materials are inexpensive and readily obtainable. Seed company personnel also were able to do the test with minimal training. The herbicide treatment is necessary to induce production of pycnidia of PD. Glyphosate (Roundup) was used in the original test (8) but required an incubation time of 10 days, which is too long for the test to be

practical. Paraquat reduced this period to 7 days but was undesirable because of its toxicity to humans. Further investigations (D. C. McGee, *unpublished*) showed that the test could be carried out within 7 days with the less toxic bentazon (Basagran), which has now been recommended for use in the pod test (9). The possibility that, because of the incubation time, test values might not accurately indicate pod infection at the time fungicides would be applied was dispelled by the good correlation between values in pod tests and plate tests made on pods sampled 2 wk later. Rainfall measurements did not offer an alternative method for predicting seed infection. Rainfall between R4 and R6 could not be correlated with seed infection nor could it be related to the natural progression of pod infection in the field. TeKrony et al (12) also found a poor correlation between rainfall from R5 to R7 and seed infection. Rainfall probably is the major cause of dissemination of PD and undoubtedly has an important effect on the incidence of pod and seed infection, but until more is known about its relationship to other factors that influence this disease, its value as a predictive measurement is questionable.

The predictive capability of the pod test was clearly shown in artificial inoculation experiments in the field. The method also could identify soybean field plots that would benefit from fungicide application by reduced seed infection by PD and improved germination. It was more difficult to correlate pod and seed infection under conditions of natural infection in soybean fields. In only one year of three was a significant correlation obtained. This is because prolonged periods of warm, wet weather are needed for seed infection to occur within pods (2,5,12) and, unless these occur, seed infection will not take place regardless of the amount of pod infection. Good evidence to validate the method under conditions of natural infection has been reported from Kentucky, where pod infection by PD correlated well ($r = 0.86$) with seed infection for 13 fields in 1982, with pod infection values well distributed over a range of 10–98% and seed infection of 0–47% (13). These authors (13) also reported a similar relationship ($r = 0.73$) for 38 soybean fields over a 4-yr period. The effect of weather after R6 on seed infection limits the predictive capability of this and other (11) methods. The pod test can, however, identify fields with low levels of pod infection in which there would be very little risk of severe seed infection regardless of subsequent weather conditions. These fields, therefore, would not need to be sprayed. This information alone can greatly improve management systems for use of foliar fungicides on soybean seed crops.

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