Soybean Seed Decay: Prevalence of Infection and Symptom Expression Caused by Phomopsis sp., Diaporthe phaseolorum var. sojae, and D. phaseolorum var. caulivora

K. T. Kmetz, A. F. Schmitthenner, and C. W. Ellett

Former Graduate Research Associate and Professors, respectively, Department of Plant Pathology, The Ohio State University, Columbus, OH 43210 and the Ohio Agricultural Research and Development Center, Wooster, OH 44691. Present address of senior author: E. I. du Pont de Nemours & Co., Wilmington, DE 19898.

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ABSTRACT

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An undescribed *Phomopsis* sp., *Diaporthe phaseolorum* var. *sojae* (*Dps*) and *D. phaseolorum* var. *caulivora* (*Dpc*), the primary fungi associated with soybean seed decay, were isolated from immature, symptomless plants. *Phomopsis* sp. was detected more often than *Dps* at all stages of soybean growth, but *Dpc* was isolated infrequently and was first recovered shortly before plant maturity. *Phomopsis* sp. and *Dps* caused blotching and formed pycnidia on stems and pods of naturally or artificially infected mature plants. Appearance of blotching and pycnidia coincided with premature ripening on most plants in soil infested with *Phomopsis*. All three fungi were isolated infrequently from green seed but incidence increased as plants matured. *Phomopsis* was recovered significantly more often from immature and mature seed than was *Dps*, which was recovered more often than *Dpc*. All three were isolated from moldy and fissured seed. Percentage seed infected with *Phomopsis* and *Diaporthe* increased and germination decreased with harvest delay. Seed inoculated with *Phomopsis*, *Dps*, or *Dpc* or from highly-infected seed lots germinated poorly in nonsterile soil.

Additional key words: symptomless infection.

An undescribed *Phomopsis* sp. (hereafter referred to by the genus name, *Phomopsis*), *Diaporthe phaseolorum* (Cke. & Ell.) Sacc. var. *sojae* Lehman (*Dps*), and *D. phaseolorum* var. *caulivora* Athow & Caldwell (*Dpc*) caused molding and fissuring of soybean (*Glycine max* Merr.) seed in pods and reduced germination (6, 7, 12). In cases when no distinction is made between *Dps* and *Dpc* in this report, the genus name *Diaporthe* alone is used. The *Phomopsis* sp. and *Dps* also have been associated with pod and stem blight (1, 2, 5, 9, 10, 12) and *Dpc* with stem canker (1, 12). Symptomless association of *Phomopsis* sp. and *Diaporthe* with soybeans was reported recently (7) but the relative prevalence of each species at various stages of soybean development was not determined. In addition, the importance of *Phomopsis* and *Diaporthe* associated with green plants in relation to seed infection was not clarified. This paper reports: (i) further evidence for the widespread occurrence of *Phomopsis* and *Diaporthe* on immature soybeans, (ii) their association with blotching and speckling of mature plants, (iii) prevalence of immature and mature seed infection, (iv) effect of delayed harvest on seed quality, and (v) effect of the pathogens on germinating seed.

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MATERIALS AND METHODS

Plot design.—Soybean cultivars Amsoy 71, Wayne, and Calland were planted in Brookston silt loam soil near Columbus, Ohio, in a randomized block design (four replicates per cultivar) on 17 May 1973 and 10 May 1974. Each plot consisted of three rows 9.3 m long and 75 cm apart. The field had been cropped to soybeans in 1971 and 1972. In one experiment, Wayne soybeans were planted as described above but on soil previously cropped to corn. The same block also was used in the 1974 tests.

Statistical significance in all experiments was determined by analysis of variance. Significant differences were found using the LSD.

Methods for pathogen detection.—For surface disinfestation, plant material was rinsed thoroughly in tap water, soaked for 1 min in 70% ethanol, agitated in 1.3% sodium hypochlorite (NaClO) for 2 min, then air-dried on sterile paper towels. One-cm cross sections of cotyledons, hypocotyls, stems, pods, petioles, entire flowers, ovules, and seeds were plated on Difco potato-dextrose agar which was acidified to pH 4.5 with 95% lactic acid (APDA). Axils with attached pods removed from the top one-third of plants were cut in half perpendicular to the pod sutures and plated intact on APDA. Ovules and mature seeds were removed from disinfested pods and dipped in 1.3% NaClO for 5 sec before plating. Seedlings were plated on APDA amended

with 50 mg/liter ethazole (5-ethoxy-3-trichloromethyl 1,2,4-thiadiazole 30% WP) prior to pouring plates to control *Pythium* spp. (11). *Phomopsis*, *Dps*, and *Dpc* were identified on APDA as described previously (7). Plant growth stages were based on the key by Fehr et al. (4).

Phomopsis and *Diaporthe* also were detected by moist-chamber incubation (MCI). Cotyledons, pods, petioles, and 10-cm sections of hypocotyls and stems were surface disinfested and placed in plastic bags with wet paper toweling or petri dishes with moistened filter paper and incubated at 24-28 C. Numbers of plant parts with pycnidia were recorded after 14 days. Randomly selected pycnidia were plated on APDA to determine the predominant species.

Sampling method.—During 1973 and 1974, seedlings (five per replication) were sampled daily for *Phomopsis* beginning 48 hr after planting and continuing until emergence (10 days). Older plants (five per replication) were sampled weekly in 1973 and 1974 at four growth stages: (i) first trifoliate (V2); (ii) full bloom (R2); (iii) lower pod green bean (R5) and (iv) harvest maturity (R8). Percentage of plants with pod and stem blight was determined in the field (25 plants per replication) and yields were taken at maturity. In 1973, the percentage of visibly moldy seed, weight of 100 seed, percentage seed with *Phomopsis* and *Diaporthe*, and percentage germination were determined on separate 100 hand-shelled seed lots per replication harvested at: (i) maturity (R8); (ii) dry down (13-14% seed moisture, ca. 10 days after R8); (iii) 1 mo after R8, and (iv) 2 mo after R8. Also, percentage seed with *Phomopsis* was determined in seed from proximal, middle,and distal pod locules (10 pods per replication). In addition, percentage seed with *Phomopsis* from pods at each of 10 nodes per plant (five plants per replication) was recorded on plants having the following symptoms: (i) blotching, (ii) pycnida, (iii) blotching and pycnidia, and (iv) no symptoms.

Root infection.—Infection of soybean roots (cultivar Beeson) by *Phomopsis* and *Dps* was studied in infested Wooster soil mix (WSM) containing Wooster silt loam, muck, and Canadian peat (5:5:2, v/v). Inocula consisting of 10 *Phomopsis*- or *Dps*-infested pods were placed 3 cm below the surface of the soil mix in 12-cm diameter clay pots (four pots per treatment). Control plants were grown in pots with noninfested pods. Growth chambers were set at 22-24 C day and 16-18 C night temperatures and 50-60% relative humidity (RH). Roots and stems from randomly selected plants were plated biweekly on APDA. In a second experiment, *Phomopsis*, *Dps*, and *Dpc* root infection of young seedlings was examined on Wayne plants in WSM in wood flats. A 100-ml suspension of

TABLE 1. Percentage soybean plants with *Phomopsis* sp. and *Diaporthe phaseolorum* var. *sojae* (*Dps*) at different growth stages

Growth stage[a]	Stems with fungus			
	Phomopsis sp.		*Dps*	
	Lower (%)	Upper (%)	Lower (%)	Upper (%)
Emergence	1[b]	0	0[c]	0
V1	1	0	1	0
V2	9	8	1	0
V3	44	24	6	2
V5	50	35	5	2
R1	76	24	4	3
R2	78	10	3	0
R2R3	100	6	0	0
R3	70	5	3	0
R3R4	84	2	0	0
R4	92	4	3	0
R4R5	78	4	22	3
R5	100	30	3	1
R6	86	36	12	7
R7	64	32	12	12
R8	54	30	25	29

[a]Based on Fehr et al. 1971. Crop Sci. 11:929-931 in which V1 = unifoliate unrolled, R2 = full bloom, R5 = green bean stage, and R8 = maturity.

[b]Mean of four replications of five plants each of cultivars Amsoy 71, Wayne, and Calland. LSD (P=0.01) for emergence through stage V5 = 8; LSD (P=0.01) for stages R1 through R8 = 6.

[c]No significant differences between *Dps* means.

TABLE 2. Percentage of soybean plant parts with *Phomopsis*-type pycnidia after incubation in moist chambers

Plant part	Plant parts with pycnidia on plants at growth stage[a]								
	V1 (%)	V5 (%)	R2 (%)	R3 (%)	R4 (%)	R5 (%)	R6 (%)	R7 (%)	R8 (%)
Cotyledon	64[b]								
Hypocotyl	42								
Lower stem	28	33	38	21	23	58	55	53	97
Mid stem		6	32	8	8	2	31	35	77
Upper stem		1	0	2	6	2	30	25	69
Lower pod				6	8	29	62	86	94
Mid pod				0	8	17	40	73	83
Upper pod				0	0	8	37	44	75
LSD (P=0.05)	16	8	10	17	17	17	17	17	17

[a]Growth stages based on Fehr et al. 1971. Crop Sci.11:929-931 in which V1 = unifoliate unrolled, R2 = full bloom, R5 = green bean, and R8 = maturity.

[b]Mean percentage of four replications each of soybean cultivars Amsoy 71, Wayne, and Calland.

Phomopsis alpha spores or *Dps* or *Dpc* ascospores (5,000/ml) was placed in four furrows 50 cm long and 3 cm deep in each flat before the seeds were planted. Sterile water placed in furrows was used as the control. Three isolates each of *Phomopsis*, *Dps*, and *Dpc* were used. Percentage emergence was recorded and seedlings were selected and plated 1, 2, and 3 wk after planting. The experiment was repeated twice.

Seed decay.—In one experiment, Wayne seeds were surface-disinfested in 1.3% NaClO for 1 min and rinsed three times in sterile distilled water. Thirty seeds were placed at the perimeter of an actively growing colony of each of three isolates of *Phomopsis*, *Dps*, or *Dpc*. Seeds were removed after 48 and 72 hr and planted (three sets of 10 seed/6-inch pot/isolate) in a nonsterile greenhouse soil mix (GSM) containing soil, peat, and Perlite (1:1:1, v/v), in a growth chamber of 60-70% RH and a 14-hr day at 22 C and a 10-hr night at 16 C. Emergence was recorded after 8 days. Seeds that did not emerge were surface disinfested and plated. In another experiment, Amsoy 71 seeds that were naturally infected with *Phomopsis* and *Diaporthe* was studied in the same manner. Seeds from a lot with a low percentage of infection were used as a control.

RESULTS

Distribution of Phomopsis, Dps, and Dpc on immature plants.—*Phomopsis* sp. was recovered first from 12-day-old seedlings, *Dps* from 30- to 33-day-old plants, and *Dpc* as the plants approached maturity. *Phomopsis* was isolated significantly more often than *Dps* from immature plants (Table 1). The data for Amsoy 71, Wayne, and Calland were pooled because of the same isolation pattern for all three. None of the plants from which isolations were made up through stage R8 (maturity) had any visible disease symptoms. Both *Phomopsis* and *Diaporthe* were recovered more often from lower stems than from upper stems at most growth stages. The fungi were not isolated from roots of field plants. However, *Phomopsis* was recovered from symptomless roots in *Phomopsis*-infested soil in a growth-chamber study. *Phomopsis* also was readily detected on detached cotyledons, stems, and petioles using the MCI method (Table 2). Pycnidia formed after 11-21 days and were scattered or in linear rows and usually dispersed over the entire plant part. More than 90% of randomly selected pycnidia or pycnidial ooze (ca. 500 samples) plated on APDA were *Phomopsis* sp. No *Diaporthe* perithecia were found from detached vegetative parts even after 1 mo incubation.

Phomopsis was isolated from flowers relatively infrequently and first from pods at stage R2 (full bloom). *Phomopsis* incidence in young pods was low but it was isolated with greater frequency from all stages of pods as plants matured (Table 3). There were no differences in frequency of *Phomopsis* in proximal, distal, placental, or a placental pod section. *Phomopsis* was isolated as frequently from floral bracts and flower remnants as from pod walls.

Association of Phomopsis and Diaporthe with pod and stem blight symptoms on mature plants.—Pod and stem blight (PSB) symptoms (blotching and pycnidia on stems and pods) were not observed on green plants, even though *Phomopsis* and *Diaporthe* were detected. Symptoms were observed first during senescence on stems and detached petioles in the field after the leaves had fallen and stems and pods were brown.

Pycnidia of *Phomopsis*, *Dps*, *Septoria* sp., and *Phoma* sp. were observed both on and around blotched areas on stems and occasionally on pods after maturity. Other fungi associated with blotching were *Colletotrichum* sp. and *Alternaria* sp. Stem blotching and pycnidia were more common than pod symptoms.

Infection of soybeans by Phomopsis and Dps in the soil.—Pycnidia and blotching on stems occurred on Beeson soybeans after maturity in soil infested with *Phomopsis*-colonized pods but not in sterile soil or soil infested with alpha spores. Fifty-four percent of these plants ripened 14 days earlier than plants grown in sterile soil. Plants in soil infested with *Dps* (colonized pods or ascospores) did not ripen prematurely or develop characteristic blotching or pycnidia after maturity.

Phomopsis, Dps, and Dpc in green and mature seed.—*Phomopsis*, *Dps*, and *Dpc* initially were isolated from seed during the early pod stage (R3). *Phomopsis* was the predominant fungus isolated from immature and mature seed. In 1973 and 1974, 85% of the isolates from immature seed were *Phomopsis*, 14% *Dps*, and 1% *Dpc*. In 1973, 82% of mature seed isolates were *Phomopsis*, 9% *Dps*, and 9% *Dpc*. In 1974, 68%, 20%, and 12% were *Phomopsis*, *Dps*, and *Dpc*, respectively. Frequency of *Phomopsis* increased with time but yearly values differed at various stages of seed development (Table 3). Recovery of *Phomopsis* and *Diaporthe* from seed increased most dramatically between the yellow pod stage (R7) and maturity (R8). They were isolated from green and mature seed from distal pod locules as often as seed from proximal and middle pod locules.

TABLE 3. Percentage of pods and seed of Amsoy 71 soybeans infected with *Phomopsis* sp. at four stages of development

Year	Plant part	Reproductive stages R3[a]	R5	R7	R8
1972	Lower pod	20[b]	30	20	80
	Lower seed	0	10	20	52
	Upper pod	0	0	10	80
	Upper seed	0	0	0	50
	LSD (P=0.01)	NS	8	8	18
1973	Lower pod	15[c]	35	30	66
	Lower seed	5	3	10	56
	Upper pod	0	0	18	58
	Upper seed	0	0	2	55
	LSD (P=0.01)	10	10	10	10
1974	Lower pod	10	5	69	100
	Lower seed	0	0	30	45
	Upper pod	0	0	50	85
	Upper seed	0	0	15	33
	LSD (P=0.01)	NS	NS	11	17

[a]Reproductive stage based on system of Fehr et al. 1971. Crop Sci. 11:929-931 in which R3 = young pod, R5 = green bean, R7 = yellow pod, and R8 = maturity.

[b]Percentage of plants infected based on isolations from 10 plants.

[c]Percentage of plants infected based on isolations from four replications of five plants each in 1973 and 1974.

The *Diaporthe* isolation pattern was similar to that of *Phomopsis*, but much lower in magnitude. *Diaporthe phaseolorum* var. *sojae* and *Dpc* were isolated with similar frequencies from all pod nodes sampled (Table 4). *Phomopsis* was isolated more often from seed near the bottom than from the top of plants. However, *Phomopsis* and *Diaporthe* were recovered more often from seed harvested from mature (R8) plants with PSB symptoms than those without symptoms. They were recovered from 54% of seed from PSB plants and 11% of seed from symptomless plants. There was no difference in isolation frequency from pods with or without symptoms. Seed in pods with blotches at maturity usually were visibly mold-free but pods covered with pycnidia generally contained molded seed located in the distal locule. *Phomopsis* was isolated most frequently from visibly molded seed and *Dpc* was recovered occasionally. Yield and 100 seed weights were comparable in seed lots with high and low frequencies of *Phomopsis* and *Diaporthe*.

Effects of delayed harvest on plant symptoms and seed-borne fungi.—Percentage seed infected with *Phomopsis* and *Diaporthe* increased with delay in harvest (Table 5). Also, significant increase in seed infection occurred before an increase in pod or stem symptoms. *Phomopsis* was the predominant fungus isolated from seed at all harvests comprising 77% of the total *Phomopsis*-type isolates while *Dps* and *Dpc* totaled 18% and 5%, respectively. *Alternaria* sp., *Fusarium* sp, and *Cercospora Kikuchii* (Matsu & Tomo.) Chupp were detected occasionally throughout the study.

All three fungi were detected from visibly molded seed harvested 1 mo and later after maturity. Various combinations of *Phomopsis*, *Dps*, and *Dpc* were isolated frequently from seed harvested 2 mo after maturity.

Germination of Phomopsis and Diaporthe-infected seed.—Highly infected seed lots germinated poorly (Table 5). Increase in seed infection with time corresponded to a decrease in germination. A difference was noted in *in vitro* germination of diseased seed. Seed infected with *Dps* harvested up to 1 mo after maturity usually germinated on APDA but infected seed harvested later did not germinate. *Phomopsis*- or *Dpc*-infested seed rarely germinated on APDA.

Soybean seed incubated 48 hr on APDA cultures of *Phomopsis* prior to planting in nonsterile soil germinated 30%. Many seed were not visibly colonized when planted. Seed similarly incubated on cultures of *Dps* or *Dpc* germinated 53 and 50%, respectively. Germination of seed incubated on cultures 72 hr before planting were 5% for *Phomopsis*, 20% for *Dps*, and 17% for *Dpc*. Control seed incubated on APDA for 72 hr emerged 75% after planting in soil. Seed from a highly infected lot of Amsoy 71 (85% with *Phomopsis* or *Diaporthe*) germinated 55% under the same conditions. *Phomopsis*- or *Diaporthe*-inoculated seed that did not germinate disintegrated rapidly in soil. All three pathogens were capable of invading and rapidly rotting nonwounded seed during the early stages of germination.

TABLE 4. Incidence of *Phomopsis* sp., *Diaporthe phaseolorum* var. *sojae* (*Dps*), and *D. phaseolorum* var. *caulivora* (*Dpc*) in seed from pods located from the bottom to the top of plants of soybean cultivar Calland

	Mean incidence of fungal pathogens at harvest times:					
	Dry down[b]			1 mo after maturity		
Pod position[a]	*Phomopsis* (%)	*Dps* (%)	*Dpc* (%)	*Phomopsis* (%)	*Dps* (%)	*Dpc* (%)
1	44[c]	4	0	66	0	11
2	40	0	0	66	0	10
3	55	0	0	37	3	0
4	26	0	0	63	5	0
5	26	0	0	43	6	3
6	37	2	2	40	15	1
7	35	2	0	32	12	3
8	17	0	4	15	17	3
9	11	0	0	20	2	3
10	8	4	0	31	2	5

[a]Pod positions: 1 = lowest pod node, 10 = highest pod node.
[b]Approximately 7 days after maturity, seed moisture at 13-14%.
[c]Mean percentage of infected seed from 10 pods from each of four replications.

TABLE 5. Percentage of pods with symptoms, incidence of *Phomopsis* sp. and *Diaporthe* spp. in seed, and percent seed germination in soybean cultivar Wayne at four harvest times

	Pods with symptoms					
Harvest time[a]	Pycnidia (%)	Blotching (%)	Pycnidia and flotching (%)	No symptoms (%)	Seed infected (%)	Germination (%)
R8	1[b]	5	0	94	34[c]	66[d]
Dry down	1	5	0	94	44	71
1 mo	2	9	1	88	72	55
2 mo	0	62	29	9	97	10
LSD (P=0.01)	NS	14	4	10	11	10

[a]Harvest times: R8 = harvest maturity, 95% pods brown (based on Fehr et al. 1971. Crop Sci. 11:929-931). Dry down = seed at 13-14% moisture at approximately 10 days after maturity, 1 mo = 1 mo after maturity, and 2 mo = 2 mo after maturity.
[b]Mean percentage of four reps of 100 pods.
[c]Mean percentage of four reps of 100 seed plated on acidified potato-dextrose agar.
[d]Mean percentage of four reps of 100 seed using a standard germination test.

DISCUSSION

Although *Phomopsis*, *Dps*, and *Dpc* have been recognized as soybean seed pathogens for over 50 years, emphasis has been placed on their involvement with stem canker and pod and stem blight symptoms (1, 3, 5, 9, 12, 13, 15). Stem canker has been shown to cause economic loss and is a recognized disease condition (1, 5). There is no sound evidence proving that pod and stem blight per se is economically damaging to plants and is considered to be a disease associated with senescing plants (1, 5, 9). Seed infection with PSB pathogens has been tied into this disease complex but the relation between PSB and seed decay has not been established. Stem blotching can be caused by *Colletotrichum truncatum* (Schw.) Andrus & Mooret (14) and possibly by other common fungi found on mature stems (e.g., *Septoria* spp. and *Alternaria* spp.) as well as by *Phomopsis* and *Diaporthe*. In this work pycnidia of *Phomopsis*, *Septoria*, and *Phoma* all were found on mature stems. However, only *Phomopsis*, *Dps*, and *Dpc* caused seed decay.

Soybean seed decay appears to develop independently from PSB or stem canker. Studies by Prasartsee et al. (13) showed a high PSB severity index of approximately 80% with less than 10% *Phomopsis* and *Diaporthe* seed infection in the same plants. In our research, Wayne had 72% seed infection in plots with only 10% of plants having blotching and pycnidia (Table 5). Therefore, severity of stem symptoms is not indicative of the percentage of seed infected with *Phomopsis* and *Diaporthe*. However, *Phomopsis*-infected seed detected either by visible mold appearance or isolation on APDA always were found in pods with pycnidia. Pod blight symptoms probably are more indicative of seed decay than stem blight symptoms.

Phomopsis, *Dps*, and *Dpc* are all associated with soybean seed decay, but *Phomopsis* is the most prevalent. We propose that this disease be called Phomopsis seed decay because the most prevalent pathogen is a *Phomopsis* sp. and the other pathogens (*Dps* and *Dpc*) have a *Phomopsis* imperfect stage. Further evidence for taxonomic distinction between *Phomopsis*, *Dps*, and *Dpc* has been presented in a preliminary report (8) and will be subject of a future paper. Also, further work on the epidemiology and control of Phomopsis seed decay will be forthcoming.

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