

# Latent Infection of Soybean Plants and Seeds by Fungi

Latent infection of plants by pathogens has been recognized for many years and is often considered one of the highest levels of parasitism, since the host and the parasite coexist with minimal damage to the host. Verhoeff (33) stated that a true latent infection must involve a parasitic relationship that eventually induces symptoms. Agrios (1) defined latent infection as the state in which a host is infected with a pathogen but does not show symptoms. Latent infection persists until signs or symptoms are prompted to appear by environmental or nutritional conditions or by the stage of maturity of the host or pathogen (1). Thus, every pathogen, except necrophilic types, has a latent period in which it ramifies host tissues and begins to cause changes in the host's physiology. When biochemical changes become so severe that all or most of the local resources are diverted to the pathogen or toxic by-products are formed, the affected host tissues become symptomatic. One expects that continued conversion of host resources to those of the parasite would eventually result in stunting of the host.

Latent infection might be regarded as a type of tolerance or resistance to certain pathogens, where the parasite finds the internal environment unsuitable for growth and multiplication. Such resistance or tolerance prevents rapid multiplication of microorganisms that reach the plant interior (24). Latent infection is important in the epidemiology and control of plant diseases and also in breeding for resistance or tolerance to a pathogen. An understanding of latent

infection contributes to development of effective control measures, as does an understanding of penetration, colonization, disease expression, and yield losses.

Latent periods of infection have been described in a variety of host-pathogen interactions. A "latency period" has been defined as the time required from infection to subsequent production of inoculum (34) and as the time between lesion formation and sporulation (31). These definitions are inadequate because they apply to sporulating fungal pathogens and not to fungal mycelial growth and establishment or to nonsporulating fungi, bacteria, mycoplasma-like organisms, spiroplasmas, nematodes, viroids, and pathogens that cause symptoms before inoculum production. In this article, the latent period is considered as the interval from infection to display of macroscopic symptoms, or a "prolonged incubation period." The latent period usually ends when the plant is under stress, or begins to senesce, or is killed by any number of causes.

All who work with soybeans (*Glycine max* (L.) Merr.) in the field have observed that plants severely damaged or killed by an abiotic factor may show symptoms or signs of disease caused by a biotic agent. Such plant damage is often attributed to the pathogen inducing the most conspicuous symptom, when actually other factors may have caused plant destruction or death. For example, soybean plants killed anytime during the growing season may show symptoms of anthracnose or charcoal rot, since both fungi causing these diseases infect soybean plants early in the season and remain latent until colonized plants become stressed.

Soybean plants sprayed with benomyl in the field tend to remain green longer than unsprayed plants (25,27). This phenomenon, attributed to delay in senescence, is largely due to the fungistatic activity of benomyl on fungi causing

latent infection and delayed symptom development. Enhancement of yield and seed quality has been attributed to the use of benomyl sprays when soybean plants are stressed or harvest is delayed. These observations provide indirect evidence that latent infection by fungi does adversely affect soybeans. However, the actual effects of pathogens on infected tissues or on the plant during the latent period are virtually undetermined, especially in soybeans.

Latent infection in soybeans is the association or colonization of tissues by the pathogens for a prolonged period without visible symptoms. Soybeans have developed mechanisms, not yet understood, that arrest or delay the progress of many microorganisms reaching internal tissue during the plant's vegetative and early reproductive stages (i.e., latent infection).

Most fungal and viral pathogens of soybean seedlings, plants, pods, and seeds have an asymptomatic or latent period after infection or colonization. Less research has been done on latent infection by bacterial, viral, and nematode pathogens than by fungal pathogens of soybeans. Of more than 100 organisms known to infect soybeans, only about 35 are economically important (27). Of these, at least 10–15, including bacteria and fungi, cause disease in which an extended latent period separates pathogen introduction and symptom expression. The latent period may be several weeks. No definitive studies have been done on the effect of latent infection by any pathogen on soybean development, growth, or yield.

## Detection of Latent Infection

Bioassay and histological methods as well as serological techniques can be used to detect latent infection in soybeans. Bioassay of soybean tissues usually involves the incubation of surface-steril-

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ized tissues or seeds on moist blotters or, preferably, a selective medium. After a suitable period of incubation, usually under light, the microbial growth is examined under a dissecting microscope for the presence of characteristic fungal fruiting structures. In addition, examination of conidia or other spores under a bright-field compound microscope may be necessary. Bacteria also may be detected by incubating tissues, preferably on a selective medium, followed by examination of the characteristics of resulting colonies.

Histological studies require thin-sectioning of prepared tissues either free-hand or, for those embedded in paraffin, with a microtome. The sections are placed on a microscope slide, stained, and studied under a bright-field compound microscope. Both bacteria and fungi can be detected.

Serological methods have been developed to detect bacteria, viruses, and some

fungi in infected plant tissues. These include enzyme-linked immunosorbent assay (ELISA), radioimmunosorbent assay (RIA), solid-phase radioimmunoassay (SRIA), and serologically specific electron microscopy (SSEM).

The use of bioassay methods was enhanced by the discovery that certain desiccant herbicides induce symptoms and fruiting structures of fungi on surface-sterilized, previously asymptomatic tissues (6,7). We observed in 1977 that mature but still green (growth stage R6) soybean plants sprayed with paraquat as a defoliant in the field had significantly more symptoms and signs of infection than did unsprayed plants (Fig. 1) (3-5). Later, we found that when we immersed soybean tissues for 45-60 seconds in a paraquat solution (0.3% active ingredient, 1:40 dilution of commercial product containing 11.64% paraquat) followed by incubation for 4 days under high humidity and continuous light at 25 C, my-

celium appeared, lesions formed, and fruiting structures developed on surface-sterilized pods, leaves, and stem pieces (6). (Paraquat is extremely toxic, and label instructions must be followed carefully.) Fungal pathogens identified were *Cercospora kikuchii* (Matsumoto & Tomoyasu) M.W. Gardner, *C. sojina* K. Hara, *Colletotrichum truncatum* (Schwein) Andrus & W.D. Moore, *Fusarium* spp., and *Phomopsis* spp. (Figs. 2 and 3). Some paraquat-treated soybean tissues become overgrown with mycelia during incubation (Figs. 2 and 3). These mycelia collapse when sprayed with 70% ethanol (21), allowing the fruiting structures of the fungi colonizing the tissues to be studied.

The use of paraquat as a field spray on soybean plants induced symptoms and signs of disease about 2 weeks before symptoms appeared on unsprayed plants. However, desiccation of soybean plants 2 weeks before senescence (growth



Fig. 1. Stems from soybean plants (right) 10 days after being sprayed with paraquat, showing symptoms of anthracnose and stem blight, and (left) unsprayed, showing few or no symptoms. (Courtesy R. F. Cerkaskas)

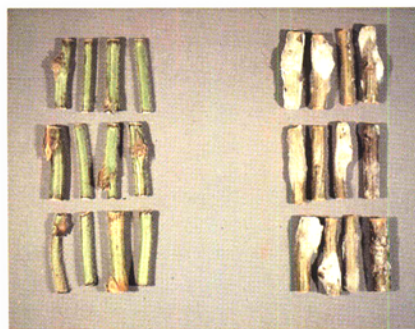


Fig. 2. Soybean stem pieces sterilized with 0.05% sodium hypochlorite (right) 5 days after being dipped in a paraquat solution, showing symptoms of anthracnose and stem blight and growth of other fungi, and (left) undipped, showing neither symptoms nor fungal growth. (Courtesy R. F. Cerkaskas)

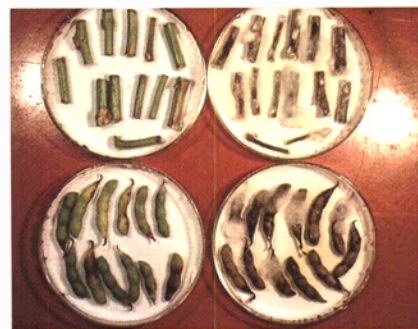


Fig. 3. Soybean stem pieces (above) and pods (below) surface-sterilized with 0.05% sodium hypochlorite (right) 5 days after being dipped in a paraquat solution, showing symptoms of anthracnose, pod and stem blight, and growth of *Alternaria* and other fungi, and (left) undipped, showing few or no symptoms and little or no fungal growth. (Courtesy R. F. Cerkaskas)

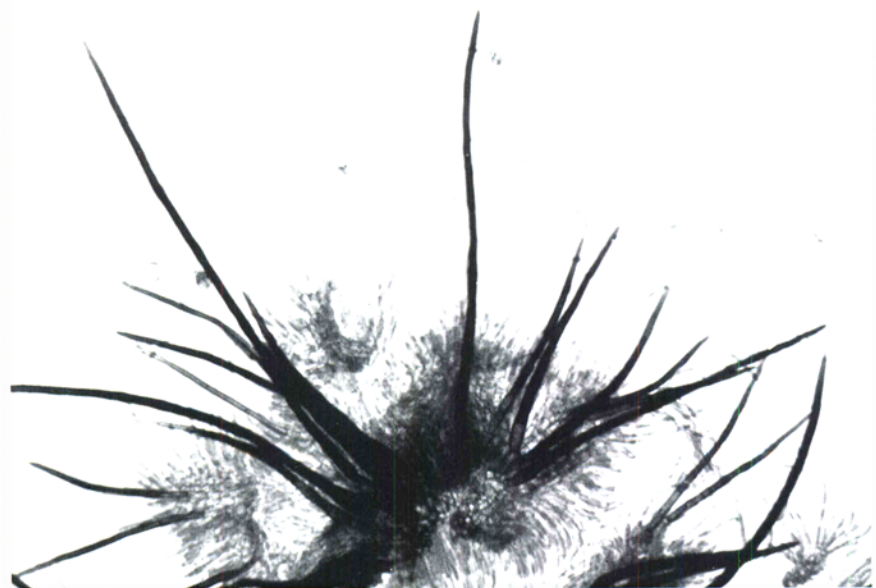


Fig. 4. Acervulus of *Colletotrichum truncatum* from a soybean stem piece surface-sterilized with 0.05% sodium hypochlorite 6 days after being dipped in a paraquat solution. (Courtesy P. R. Hepperly)

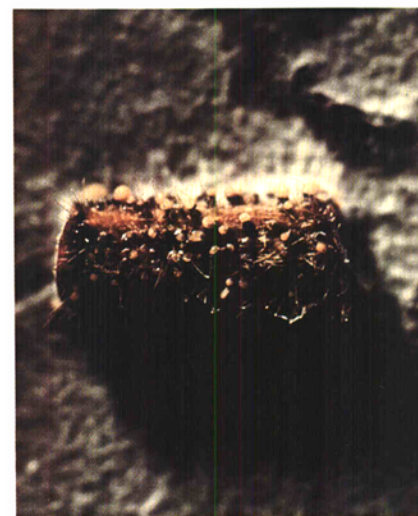


Fig. 5. Pycnidia of *Phomopsis phaseoli* on a soybean stem piece surface-sterilized with 0.05% sodium hypochlorite 6 days after being dipped in a paraquat solution. (Courtesy V. S. Bisht)



stages R6–R7) by use of a paraquat spray reduced total seed weight and percent seed germination and increased the incidence of *Alternaria* and *Phomopsis* spp. in seeds of treated plants compared with untreated plants (5). Paraquat solutions were used to detect latent infection by fungi in hosts other than soybeans. For example, a paraquat solution was used to detect *Colletotrichum* spp., including *C. truncatum*, in 17 weeds associated with soybean fields (11). Symptoms and fruiting structures of *Colletotrichum* spp. were induced on jimsonweed, lamb's-quarters, milkweed, and velvetleaf. These results suggest that other plants, as well as soybeans, have developed mechanisms that arrest or delay the progress of microorganisms in their tissues or that latent infection may not be host-specific but, rather, pathogen-specific. Further study will help resolve this uncertainty.

Glyphosate or a mixture of sodium borate plus sodium chlorate also can be used to detect latent fungal colonization or infection in soybean tissues. For example, lesions and fruiting structures of *C. truncatum*, *Phomopsis* spp., and *Macrophomina phaseolina* (Tassi) Goidanich developed 3 weeks earlier on soybean plants sprayed with glyphosate than on unsprayed plants (5).

## Latent Infection in Plants

At least 14 fungal pathogens cause latent infection in soybeans (Table 1). I will discuss five in detail: *Cercospora kikuchii*, *Colletotrichum truncatum*, *Diaporthe/Phomopsis* complex, *M. phaseolina*, and *Phytophthora megasperma* Drechs. f. sp. *glycinea*.

*C. kikuchii*, cause of Cercospora leaf blight and leaf spot, usually induces symptoms at the time of seed set (growth stages R3–R4) regardless of environmental conditions. Symptom development is associated with physiological changes in

the plant during transition from vegetative to reproductive stages. Sources of inoculum are infected seeds or infested surface debris (27). Seedlings emerging from infected seeds may become infected during emergence, whereas older plants may become infected by spores produced on crop debris throughout the growing season. Neither infected seedlings nor young plants may show symptoms. For example, symptomless pods and stems of two soybean cultivars previously inoculated with a spore suspension of *C. kikuchii* in the field developed more lesions with stromata and conidia of the fungus when tissues were treated with paraquat than when tissues were not treated (6,8), thereby implicating latent infection.

*Colletotrichum* spp., cause of anthracnose, has a latent period in soybeans and can establish latent infections in many other hosts. Soybean plants are susceptible to *Colletotrichum* spp. at all stages of development, but symptoms typically appear in the early reproductive stages (growth stages R1–R2). Severe symptoms develop after prolonged periods of high humidity, as plants senesce, or when they become stressed. The source of primary inoculum is infected soybean seeds, infested crop debris, and infected alternative hosts (27). Latent infection by *C. truncatum* in soybeans was first established when greater numbers of acervuli appeared 3 weeks earlier on field-grown plants sprayed with paraquat than on unsprayed ones (Fig. 4) (6). Latent infection was also detected in field-grown soybean leaves and freshly cut stubble dipped in paraquat but not on untreated tissues (11).

Gerdemann (10) was the first to suggest that *Diaporthe phaseolorum* (Cooke & Ellis) Sacc. var. *sojae* is latent in soybean tissues. Latent infection by members of the *Diaporthe/Phomopsis* complex in soybeans was implicated in

studies of systemic fungicides to control seedborne pathogens of soybeans (9, 25,30). Evidence for latent infection by *Phomopsis* sp. was shown when the fungus was recovered from symptomless stems and senescent cotyledons of 4-week-old soybean plants (16), and evidence for latent infection by *P. phaseoli* (Desmaz.) Sacc. was shown when this fungus was recovered from various symptomless parts of soybean plants in the vegetative stage (Fig. 5) (15,17). Additionally, *Phomopsis* sp. was isolated from 12-day-old symptomless seedlings and green pods and *D. p. sojae* was isolated from 30- to 33-day-old symptomless plants (16). When full green (growth stage R6) and yellow (growth stage R7) soybean pods were inoculated with *P. phaseoli*, lesions developed in only 5 and 26% of the pods, respectively, but the fungus was isolated from all inoculated pods (12). Bioassays of other maturing soybean tissues without symptoms recovered *D. p. caulivora*, cause of northern soybean stem canker (17). In addition, *Phomopsis* sp. was shown to colonize the vascular system of inoculated soybean plants in the mid to late vegetative stages (growth stages V6–V8) without showing symptoms (17).

Charcoal rot, caused by *M. phaseolina*, usually appears on soybean plants after midseason when plants reach senescence or after a period of drought. Symptoms appear late in the season even though 80–100% of the seedlings in the field may be infected 2–3 weeks after planting (27). Bioassay and histological methods can be used to detect the fungus in asymptomatic soybean seedlings early in the growing season and to show micro-sclerotia in the vascular system (13). Latent infection by *M. phaseolina* was established in soybeans when the number of pycnidia on soybean stems was greater after paraquat treatment than by visual rating in the field (21).

Table 1. Fungi that have a latent period in soybean plants and seeds

Fungus	Possible latent period in plants according to growth stages <sup>a</sup>	Literature citations
<i>Cercospora kikuchii</i> (Matsumoto & Tomoyasu) M. W. Gardner	V1 to R4–R5	6,8,28
<i>C. sojae</i> K. Hara	V1 to R4–R5	2
<i>Colletotrichum destructivum</i> O'Gara	V1 to R7	3,11
(teleomorph: <i>Glomerella glycines</i> F. Lehm. & F. A. Wolf)		
<i>C. gloeosporioides</i> (Penz.) Penz. & Sacc. in Penz.	Unknown	3
(teleomorph: <i>Glomerella cingulata</i> (Stoneman) Spauld. & H. Schrenk)		
<i>C. truncatum</i> (Schwein.) Andrus & W.D. Moore	V1 to R1–R7	6,7,11,20
<i>Diaporthe phaseolorum</i> (Cooke & Ellis) Sacc. var. <i>caulivora</i> K.L. Athow & R.M. Caldwell	V1 to R6–R7	16
<i>D. p. meridionales</i> Morgan-Jones	V1 to R6–R7	30
<i>D. p. sojae</i> (S.G. Lehman) Wehmeyer		
(anamorph: <i>Phomopsis phaseoli</i> (Desmaz.) Sacc.)	V1 to R6–R7	2,6,15,17
<i>Fusarium</i> spp.	Unknown	7
<i>F. oxysporum</i> Schlechtend.: Fr.	Unknown	32
<i>Macrophomina phaseolina</i> (Tassi) Goidanich	V1 to R7	4,13,19,21
<i>Phialophora gregata</i> (Allington & D.W. Chamberlain) W. Gams	V4 to R2–R3	26
<i>Phomopsis longicolla</i> T.W. Hobbs	Unknown	9,12,15,16
<i>Phytophthora megasperma</i> Drechs. f. sp. <i>glycinea</i> T. Kuan & D.C. Erwin	V2 to R5–R6	23,29

<sup>a</sup> Time of infection and environmental factors influence length of latent periods. Growth stages from Fehr et al. 1971. Crop Sci. 11:929-931.

Latent infection has been established on aboveground plant parts for several fungal pathogens and on soybean roots for *P. m. glycinea*, but for few others. Phytophthora root and stem rot, caused by *P. m. glycinea*, is usually evident only late in the growing season (27). Plant height and yield of infected plants are lower than those of uninfected plants, despite the absence of stem browning and lesion development in the greenhouse or field (23). Also, oospores were found in the roots of asymptomatic seedlings of cv. Amsoy 71, tolerant of Phytophthora root rot (29). Soybean seedlings may serve as a latent source of pathogen inoculum for the mature-plant phase of the disease over a wide temperature range (29).

### Latent Infection in Seeds

Infected or infested soybean seeds transmit pathogens and other microorganisms. The terms "infected" or "internally seedborne" and "infested" or "externally seedborne" refer to location of the microorganism in or on the seed. Soybean seeds infested with most microorganisms would appear symptomless, except when a microorganism grows extensively over the surface. An example is the encrustation of the downy mildew fungus, *Peronospora manshurica* (Nau-mov) Syd. in Gäum., on soybean seeds (Fig. 6). Generally, the expression of colonization in soybean seeds by most pathogens is exceptional.

The bioassay, histological, and serological techniques used to detect microorganisms and viruses in soybean plant tissues can be used for seeds. However, treatment with a desiccant or other herbicide does not enhance detection of latent infection of soybean seeds by microorganisms. Bioassays have recovered the following fungal genera from surface-sterilized soybean seeds (27): *Acremonium*, *Alternaria*, *Aspergillus*, *Botrytis*, *Cercospora*, *Chaetomium*, *Choanephora*, *Cladosporium*, *Diplodia*, *Fusarium*, *Penicillium*, *Pestalotia*, *Pythium*, *Rhizopus*, *Sclerotinia*, and

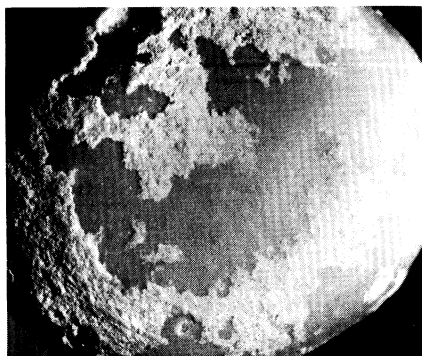


Fig. 6. Soybean seed encrusted with oospores of *Peronospora manshurica*, the downy mildew fungus. (Courtesy U.S. Department of Agriculture)

*Thielavia*. A few of these fungi induce symptoms. A complete list of characteristic fungi associated with soybeans and soybean seeds has been published (27).

Histological techniques have shown the following pathogenic fungi to colonize and infect soybean seeds: *Alternaria alternata* (Fr.:Fr.) Keissl. (18), *A. tenuissima* (Kunze:Fr.) Wiltshire (27), *Cercospora kikuchii* (28), *Colletotrichum truncatum* (20), members of the *Diaporthe/Phomopsis* complex (14,20,28), *F. oxysporum* Schlechtend.:Fr. (32), and *M. phaseolina* (19). Although these fungi may induce symptoms on seeds, they are generally latent.

### Significance and Outlook

Latent infection in soybeans, in my opinion, results from a process of coevolution between crop and pathogens that allows the ultimate accumulation of many resistance and fitness genes in the host and various parasites. Highly susceptible individual plants and highly virulent pathogens are eliminated early in the evolutionary process. The mechanisms involved in latent infection, the inheritance of such mechanisms, and the influence of the environment on the expression of these mechanisms can be important in developing tolerant cultivars.

Latent infection has been referred to as a non-race-specific or horizontal-type resistance, because such resistance is effective to some degree against most or all races of the pathogen involved (24). The degree of this type of resistance is directly correlated with the length of the latency period (24). Selecting for disease resistance among soybean cultivars and lines to one of the latent fungi can become complicated because of latent infection. Selection for resistance is based on symptom development. If symptom development by latent pathogens is triggered by plant senescence or stress, disease evaluation can be difficult. For example, in a segregating population, the development of aboveground symptoms may be related more to host susceptibility to an environmental factor or root damage than to the latent-infection fungus.

Although evidence has accumulated on latent infection by various fungal pathogens of soybeans, the role of latent infection in the epidemiology of these pathogens requires further investigation (6). An early infection that does not result in conspicuous signs or symptoms may weaken the plant, predisposing it to other stresses or diseases, or may even kill it. The epidemiology of plant diseases is partially based on the visual development and spread of disease in a plant population, on a single plant or on plant parts. The establishment of latent infection would influence the recognition of disease spread within a population. Limited stress areas within a population would result in symptom development on some plants and none on others, even though

most plants might have latent infection. Soybean anthracnose, charcoal rot, and Phytophthora root and stem rot are good examples.

Little is known about the stress placed on soybean plants by latent-infection microorganisms, either alone or in combination. Our experience has been that soybean stem pieces from field-grown plants will develop symptoms and fruiting structures of more than one fungus under laboratory conditions. These colonizing fungi require a food base during a latent period, but whether such colonization has other than a minor effect on plant growth and eventual yield is not known. This is probably not a symbiotic relationship, and I suspect there may be measurable effects. Although some information exists on the effects of various environmental factors on latent infection (5), more can be learned from continued studies.

Latent infection generally restricts host infection for a longer period and thus reduces potential inoculum production. Perhaps the ability of fungi to infect soybeans without symptoms is important for the survival of these fungi (6). By restricting its domination in host tissues, the pathogen allows for the continued growth and reproduction of the plant. As the plant becomes senescent, for whatever reason, the fungus dominates the physiology of the tissues, symptoms are induced, and sporulation occurs. Most fungi that are latent in soybeans are also seedborne, except for *Phialophora gregata* (Allington & D.W. Chamberlain) W. Gams, *P. m. glycinea*, and *M. phaseolina*. These three are soilborne in crop debris, and *M. phaseolina* is occasionally seedborne. Inoculum production on plants as seeds mature would increase the possibilities of the fungi to be established in seed tissues. Ramification in tissues and development of over-seasoning structures, such as oospores and microsclerotia, would establish the soilborne fungi in crop debris.

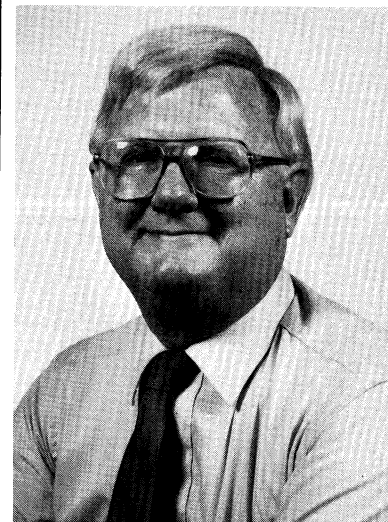
Knowledge of the latent phase of any pathogen, the length of that latency, and the mechanisms that trigger the pathogen to induce symptoms and to reproduce is important in the improvement of control measures. If pathogen infection occurs early in the season without symptoms, control measures taken later in the season could be less effective or ineffective. Control might require less effort and expenditure during the latent period of infection, when the crop plant is small and less tissue is compromised, than after symptoms appear. For example, the prediction of Phomopsis seed decay of soybeans by detection of latent infection of *P. longicolla* in pods (22) resulted in determining the need and timing for a fungicide spray to control the disease.

Many pathogenic fungi, particularly species of *Colletotrichum*, have been considered as potential mycoherbicides

to control weeds (3). Before a potential mycoherbicide is used commercially, however, latent infection by the fungus in target and nontarget plants should be ascertained to reduce the risk of early sporulation of organisms that might be found later to be pathogenic to important agricultural crops (3).

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