Weeds as Hosts for *Colletotrichum coccodes*

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ABSTRACT

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Eighteen weed species classified within 10 families were tested under greenhouse conditions for their susceptibility to *Colletotrichum coccodes*, the causal agent of tomato anthracnose. Foliar and root inoculation of these plants has led to the identification of 10 new records of hosts for *C. coccodes*. The number of infected weed species increased with plant age; 6, 9, and 15 species were infected when the plants were inoculated at the seedling, vegetative, and senescent stages, respectively. The percentage of plants infected also increased with plant maturity. More than 50% of the infected plants were symptomless; however, when symptoms were evident, they generally appeared as inconspicuous chlorotic or necrotic flecks. Premature senescence and defoliation were also observed. Microscopic examination of infected tissue often revealed the presence of brown setae, a characteristic of *C. coccodes* acervuli and sclerotia, predominantly on senescent foliar and root tissue. These tissues supported profuse sporulation when placed in a moist chamber. Results of this investigation support the hypothesis that weeds may serve as hosts for *C. coccodes* between crop rotations. The ability of *C. coccodes* to produce acervuli and sclerotia on infected weed tissue could be important with respect to both primary and secondary inoculum levels.

Colletotrichum coccodes (Wallr.) Hughes, the causal agent of tomato anthracnose, is considered to be a weak parasite (8,11) with a very low competitive saprophytic ability (13), which limits its capability to survive as a saprobe. Blakeman and Hornby (3) reported that conidia of *C. coccodes* survive no longer than 3 wk in soil. Other investigations showed that sclerotia may survive more than 1 yr in soil but not more than 2 yr (3,11); however, longer survival periods have been suggested (9). Although results of these studies would seem to forecast total success in controlling the fungus with rotations of 3 yr or more, crop rotation has not been completely successful. Pantidou and Schroeder (21) reported instances of severe anthracnose epidemics occurring in fields that had not been planted to tomatoes for more than 5 yr. Epidemics also occurred in fields where tomatoes were the first crop after the removal of an apple orchard. These reports suggest that *C. coccodes* may survive rotations on hosts other than tomato.

Studies indicate that *C. coccodes* has a wide host range that includes at least 58 species in 17 families. Although most of these studies concerned economic crops, Chesters and Hornby (8) suggested that weed species may serve as hosts between rotations of tomatoes and between tomatoes and potatoes. Weeds serve as potential inoculum reservoirs for several plant pathogens in the absence of a susceptible economic crop (4,16,19,23). In such instances, the success of crop rotation as a means of disease control depends on the effectiveness of the weed control program (6). With a sclerotium-producing fungus such as *Verticillium dahliae*, weed control should be as close to absolute as possible (7).

Host range studies of *C. coccodes* that have examined weeds as possible hosts generally have addressed root infections (5,8), even though foliar infections by *C. coccodes* have been reported on tomato (24) and on a number of other crop species (14,21). The importance of weeds as a source of secondary inoculum has been suggested (20), and foliar lesions on weeds could provide additional secondary inoculum.

The goals of this study were to identify weeds commonly occurring in and near Pennsylvania tomato fields as possible hosts for *C. coccodes* and to relate susceptibility to plant age.

MATERIALS AND METHODS

Method of plant culture. Species of weeds selected for study are among those commonly occurring in Pennsylvania tomato fields and in crops between tomato rotations. Seeds of 18 weed species representing 10 families (Table 1) were germinated and grown in agricultural-grade vermiculite until the first true leaves began to emerge.

Seedlings were then transplanted to 7.5-cm plastic pots containing either steam-treated or *C. coccodes*-infested soil mixture (soil:peat:perlite; 1:1:1, v/v) for foliar and root inoculations, respectively. When germination was less than about 10%, procedures by Anderson (1) were performed. Plants were grown in a greenhouse at temperatures between 18 and 27 C and a 16-hr photoperiod. A 20-19-18 (NPK) water-soluble fertilizer (3.95 g/L) was applied at 10- to 14-day intervals at a rate of about 25 ml/pot.

Production of inoculum. Inoculum applied to foliage consisted of conidial suspensions containing a mixture of five

Table 1. Scientific and common names of weeds tested

Family	Scientific name	Common name[a]
Amaranthaceae	*Amaranthus albus*	Tumble pigweed
	A. retroflexus	Redroot pigweed
Chenopodiaceae	*Chenopodium album*	Common lamb's-quarters
Compositae	*Ambrosia artemisiifolia*	Common ragweed
	Cirsium arvense	Canada thistle
	Galinsoga parviflora	Galinsoga
Convolvulaceae	*Convolvulus arvensis*	Field bindweed
Cruciferae	*Capsella bursa-pastoria*	Shepherd's purse
Gramineae	*Agropyron repens*	Quackgrass
	Digitaria sanguinalis	Large crabgrass
	Echinochloa crusgalli	Barnyardgrass
	Panicum dichotomiflorum	Fall panicum
	Setaria lutescens	Yellow foxtail
Malvaceae	*Abutilon theophrasti*	Velvetleaf
Oxalidaceae	*Oxalis stricta*	Common yellow wood sorrel
Polygonaceae	*Polygonum pennsylvanicum*	Pennsylvania smartweed
Solanaceae	*Solanum dulcamara*	Bitter nightshade
	S. nigrum	Black nightshade

[a] Common names generally conform to the Weed Science Society Committee Report on Common Names.

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isolates of *C. coccodes* of proven pathogenicity to nonwounded ripe tomato fruit. The various isolates, identified by a code name, are described as to isolate source, sclerotial size, and spore dimensions in Table 2.

Inoculum was produced by sparsely seeding petri dishes containing 20 ml of potato-dextrose agar (PDA) with conidia of *C. coccodes*. Spores were harvested in 10–15 ml of sterile distilled water (SDW) from 10-day-old cultures grown at 27 C under continuous light of an intensity of 439 $\mu W/cm^2$ (2). Inoculum for leaves consisted of 8×10^4–10×10^4 propagules per milliliter of each isolate mixed in equal quantities.

Root inoculum was produced by aseptically pouring a conidial suspension over 100 g (air-dried weight) of wheat straw that had been moistened and sterilized in a 2-L culture flask. The inoculated straw was periodically remoistened with SDW and shaken to evenly distribute the inoculum. Sclerotia of *C. coccodes* formed abundantly on the straw medium after incubating at room temperature (22 C) for 60 days. Sclerotia-infested straw was air-dried and comminuted. Straw infested with each of the five isolates was mixed in equal parts, and 1-g quantities of the mixed straw were incorporated into about 220 g (dry weight) of the soil mixture to provide an inoculum density of about 50 sclerotia per gram of soil.

Inoculation procedure. A presterilized atomizer was used to apply conidial suspensions to nonwounded foliar tissue. Three plants of each species were randomized in a complete block design with six replicates in a greenhouse inoculation chamber. After inoculation, relative humidity was maintained at 100% for 48 hr at 18–27 C. Six control plants of each species were atomized with SDW and incubated under the same environmental conditions. Foliar inoculations were performed at three stages of plant development, i.e., seedling (plant emergence to about 2 wk after cotyledons fall), vegetative (from cotyledon fall until flower initiation), and senescent (after flowering to physiological maturity). Senescence was promoted by gradually reducing the photoperiod from 16 to 10 hr. Isolations were performed 2 wk after inoculation.

Roots were inoculated by transplanting three seedlings of each weed species into a 7.5-cm pot containing the infested soil mixture. The root systems of these transplants were not intentionally damaged to enhance the infection process. Pots were arranged on a greenhouse bench in a randomized complete block design with six replicates. Plants were grown for 8 wk under the cultural conditions previously described, then harvested for isolation. Six plants of each weed species were grown in a sterilized soil mixture under identical conditions to serve as controls.

Isolation procedures. Leaf and stem tissue from the top, middle, and bottom third of each plant was surface-sterilized in 0.5% sodium hypochlorite for 1 min, rinsed with SDW, and placed on acidified PDA (APDA). Root tissue was washed free of soil under running tap water. Three 1-cm root segments were surface-sterilized with 0.5% sodium hypochlorite for 1 min, rinsed with SDW, and placed on APDA. Plates were incubated at 22 C and examined after 7–10 days for growth of *C. coccodes*. Tissue was also examined microscopically for the presence of acervular setae and sclerotia. When either was present, tissue was placed in a moist chamber for 24–48 hr to promote sporulation for direct isolation.

Pathogenicity tests. Isolates of *C. coccodes* recovered from infected weeds were tested for pathogenicity on nonwounded ripe tomato fruit. Conidial suspensions created from purified cultures of each isolate were poured over

Table 2. Sources and propagule dimensions[a] of *Colletotrichum coccodes* isolates tested

Isolate	Source[b]	Sclerotial diameter (μ)	Spore dimensions (μ) (length × diameter)
RRSB	Redroot pigweed stem base	221	17.5 × 3.5
LQLP	Common lamb's-quarters leaf petiole	294	20.4 × 2.9
BW-1	Field bindweed leaf	250	21.6 × 2.9
TF-2	Tomato fruit	257	19.7 × 3.5
TF-4	Tomato fruit	200	18.3 × 2.9

[a] Sclerotial and conidial sizes in microns based on the average dimensions of 100 sclerotia and conidia produced on potato-dextrose agar. Measurements performed on propagules removed from a 10-day-old culture.
[b] All isolates were obtained from plant material within a 1-acre research plot located at The Pennsylvania State University's Agricultural Research Center at Rock Springs, Centre County.

Table 3. Number of plants infected and symptoms expressed within 14 days of inoculating weed species with *Colletotrichum coccodes* at the seedling, vegetative, and senescent stages of plant growth

	Number of plants infected[a]								
	Seedling			Vegetative			Senescent		
Weed species	Leaf	Stem	Total	Leaf	Stem	Total	Leaf	Stem	Total
Tumble pigweed	0	0	0	0	0	0	13 (0,3)[b]	2 (2)	14
Redroot pigweed	0	0	0	0	3 (0)	3	3 (0)	0	3
Common lamb's-quarters	0	4 (0)	4	0	0	0	3 (0)	0	3
Common ragweed	0	0	0	0	0	0	0	0	0
Canada thistle	0	0	0	3 (0)	3 (0)	5	5 (0,2)	0	5
Galinsoga	0	0	0	0	0	0	0	0	0
Field bindweed	2 (3)	8 (0)	8	8 (0,3)	15 (0,2)	15	12 (0,2,3)	13 (0,2)	16
Shepherd's purse	4 (0)	3 (0)	5	9 (0,1)	10 (0)	12	10 (0,2)	12 (0,2)	15
Quackgrass	0	0	0	5 (0)	6 (0)	8	5 (0)	0	5
Large crabgrass	0	0	0	0	0	0	17 (0,3)	0	17
Barnyardgrass	0	0	0	0	0	0	0	0	0
Fall panicum	0	0	0	0	0	0	1 (0)	0	1
Yellow foxtail	0	0	0	0	0	0	4 (0)	0	4
Velvetleaf	0	0	0	0	1 (2)	1	1 (2)	0	1
Common yellow wood sorrel	6 (0,2)	10 (0)	12	15 (0,1,2)	15 (0,1,2)	18	18 (1,2)	12 (1,2)	18
Pennsylvania smartweed	1 (0)	5 (0)	5	1 (0)	5 (0)	6	15 (0,3)	1 (0)	16
Bitter nightshade	0	0	0	0	0	0	0 (0,3)	0	9
Black nightshade	3 (3)	0	3	6 (0,3)	3 (0,2)	6	14 (0,3)	9 (0,2)	14
Total			37			66			141

[a] Eighteen plants per weed species were tested at each phenological stage.
[b] Symptom ratings in parentheses: 0 = no symptoms, 1 = chlorotic lesions, 2 = necrotic lesions, and 3 = premature defoliation.

double-layered, 2.5-cm squares of sterile gauze. The moist gauze was aseptically placed onto the surface of a healthy ripe tomato fruit that was surface-sterilized with 1% sodium hypochlorite. SDW was used in place of conidial suspensions as a control. Fruit were incubated in a moist chamber at 23 C for 5 days and observed for the presence of anthracnose-type lesions.

RESULTS

Foliar inoculation. Six of the 18 weed species inoculated at the seedling stage were infected by *C. coccodes* (Table 3): common lamb's-quarters, field bindweed, Pennsylvania smartweed, black nightshade, shepherd's purse, and common yellow wood sorrel. *C. coccodes* was isolated from both stem and leaf tissue of four of these six species. Only stem tissue of common lamb's-quarters and leaf tissue of black nightshade gave evidence of infection. Leaf tissue from three of the five species infected at the seedling stage and the stem tissue of all five species remained symptomless within 14 days after inoculation.

When inoculated at the vegetative stage, nine of the 18 weed species were susceptible (Table 3). In addition to the six species infected at the seedling stage, redroot pigweed, Canada thistle, quackgrass, and velvetleaf were infected at the vegetative stage. *C. coccodes* was not isolated from common lamb's-quarters, which was infected at the seedling stage. Seven of the nine species infected showed both stem and leaf infections. Redroot pigweed and velvetleaf showed only stem infections. Leaf tissue from all seven species and stem tissue from eight of the nine species infected at the vegetative stage remained symptomless.

Fifteen weed species were susceptible at the senescent stage (Table 3). In addition to those species infected at prior growth stages, tumble pigweed, fall panicum, yellow foxtail, large crabgrass, and bitter nightshade were infected at the senescent stage. Of the six species showing stem colonization, four included symptomless tissue. All 15 species revealed leaf infection, and 13 of these included symptomless tissue. *C. coccodes* was isolated from only one of the 18 inoculated plants of fall panicum and velvetleaf. Likewise, only a single velvetleaf plant was infected at the vegetative stage. Common ragweed, galinsoga, and barnyardgrass were not infected at the three phenological stages investigated.

In general, the number of infected weed species increased with plant age. *C. coccodes* was isolated from only six species at the seedling stage, whereas nine and 15 weed species were infected at the vegetative and senescent stages, respectively. The total number of plants infected within a weed species, as a rule, also increased with age. *C. coccodes* was isolated from leaves and/or stems of 37, 66, and 141 plants at the seedling, vegetative, and senescent stages, respectively.

Most infected plants were symptomless (Table 3). When symptoms were evident, they generally appeared as inconspicuous chlorotic to necrotic flecks on the foliage. Premature leaf senescence and defoliation, especially of cotyledons and aging lower leaves of more mature plants, also occurred. Microscopic examination of infected tissues often revealed the presence of brown setae, characteristic of *C. coccodes* acervuli, and sclerotia, predominantly on senescent tissue. These tissues supported profuse sporulation when placed in a moisture chamber for 24–48 hr.

Root inoculations. *C. coccodes* was isolated from root tissue of eight weed species (Table 4). Infections were observed on nonwounded root tissue. Infected roots generally showed areas of necrosis and browning; however, some root tissue from five of the eight infected roots showed no symptoms. Cortical tissue was often severely affected and, in some instances, easily sloughed off. Root systems of healthy plants appeared to be more extensive than those of infected plants.

Pathogenicity tests. All isolates of *C. coccodes* recovered from infected tissue were pathogenic on nonwounded ripe healthy tomato fruit. None of the control fruit developed anthracnose symptoms.

DISCUSSION

Results of foliar and root inoculations confirm earlier host range studies that showed *C. coccodes* can colonize a wide range of unrelated hosts (5,8,14). This study enlarges the known host range of *C. coccodes* by 10 species, with tumble pigweed, Canada thistle, shepherd's purse, quackgrass, large crabgrass, fall panicum, yellow foxtail, velvetleaf, common yellow wood sorrel, and Pennsylvania smartweed believed to be reported as hosts for the first time. In addition, two families, Malvaceae and Oxalidaceae, were added to the families previously listed as containing hosts. The fungus infected nonwounded plants at the seedling and vegetative stages; however, both the number of species infected and the total number of plants of each species infected increased with plant maturity and senescence. This supports earlier conclusions that *C. coccodes* is a weak parasite (8,11,22).

At least seven of the 18 weed species investigated in this study had been previously examined as potential hosts for *C. coccodes*. The roots of four of these species, field bindweed, redroot pigweed, bitter nightshade, and black nightshade, were infected under both natural conditions (5,8) and the artificial conditions of this study. Two species, shepherd's purse and common lamb's-quarters, previously examined by Chesters and Hornby (8) for root infection with negative results, were infected. This discrepancy probably is due to differences in inoculum density. Galinsoga was not found to be susceptible by either the current study or previous investigations (8). Five species of weeds previously recorded as hosts were not included in this experiment: common chickweed, saltwort, bermudagrass, hemp, and jimsonweed (5,8,14).

Undoubtedly, species will be added to the host list for *C. coccodes* as more are tested for susceptibility. Results of artificial inoculations performed in the greenhouse must be interpreted cautiously. Conditions necessary for successful infection that exist under artificial conditions may not be possible in nature.

With respect to environmental conditions, the temperatures and 48-hr period of high humidity that plants were exposed to after inoculation are favorable for foliar infection by *C. coccodes* on tomato and other crops (15,20). These conditions were also favorable for the infection of a number of weed species at various phenological stages. Foliar symptoms that developed on weeds were similar to those reported in the literature for studies using similar environmental conditions (15,17,24). Significantly, however, most infected plants revealed no symptoms. Appressoria formed by *C. coccodes* may survive surface sterilization and thereby result in a "false" positive isolation; however, the presence of sclerotia and acervuli on symptomless tissue revealed the tissue was colonized in

Table 4. Number of plants with root infections and symptoms expressed 8 wk after planting seedlings in soil infested with *Colletotrichum coccodes*

Weed species	Number of plants infected[a]	Symptoms[b]
Tumble pigweed	3	0,1
Redroot pigweed	5	0,1
Common lamb's-quarters	0	···
Common ragweed	0	···
Canada thistle	0	···
Galinsoga	0	···
Field bindweed	11	1,2
Shepherd's purse	4	1
Quackgrass	0	···
Large crabgrass	0	···
Barnyardgrass	0	···
Fall panicum	0	···
Yellow foxtail	0	···
Velvetleaf	0	···
Common yellow wood sorrel	8	0,1
Pennsylvania smartweed	3	0,1
Bitter nightshade	6	0,1,2
Black nightshade	12	1,2

[a] Eighteen plants per weed species were tested.
[b] Symptom ratings: 0 = no symptoms, 1 = brown necrotic lesions, and 2 = necrosis and disintegration of cortical tissue.

most cases. Garrett (10) used the term "symptomless carrier" in reference to such hosts. He also reported that weeds are more likely to serve as symptomless carriers than cultivated hosts. Races of noncultivated plant species, e.g., weeds, and their parasites tend to evolve a tolerance toward each other. Cultivated plants, on the other hand, often are selected without regard to disease resistance. The general lack of symptom development in most of the weed species examined probably indicates a lower level of susceptibility than exists in the cultivated tomato.

Ibrahimov (14) demonstrated, for several other species of *Colletotrichum*, that increasing the duration of high humidity from 48 to 75 hr after inoculation increased the number of species successfully infected. Likewise, the duration of postinoculation incubation at high humidity may also influence symptom severity (14,15,17). Longer periods of high humidity after inoculations in this study may have resulted in either larger numbers of plants showing infection or more severe symptoms. This possibility was not investigated.

An attempt was made to use the form of inoculum most likely encountered under natural conditions (conidia for foliage and sclerotia for roots). Both conidia and sclerotia of *C. coccodes* germinated and penetrated nonwounded foliage and roots, respectively. This concurs with results of other investigations on tomato and various crop species (15,20); however, it conflicts with a report (18) that *C. coccodes* is capable of only limited invasion on wounded tomato stems. A reason for this discrepancy may be the different form of inoculum used for stem tissue.

Ibrahimov (14) reported a wide variation in the ability of geographically different isolates of *C. coccodes* to infect a number of plant species. Although the isolates used in our study were tested individually for their pathogenicity on tomato fruit, they were not tested individually on the various weed species. Inoculum concentration is an important influence with respect to symptom development with other fungal pathogens (12), and high inoculum levels are an asset with regard to infection of alternate hosts (8). It is possible that greater inoculum concentrations would have increased both symptom severity and the number of plants infected.

In conclusion, results of this investigation support the hypothesis that weeds may serve as hosts of *C. coccodes* in a crop rotation system. The fact that most weed hosts are symptomless probably explains why some of them have not been previously investigated as hosts. The ability of *C. coccodes* to produce acervuli and sclerotia on infected weed tissue could be important with respect to inoculum levels. Infected weeds could serve as a potential source of secondary inoculum during the current growing season. In addition, weed tissue containing sclerotia could act as a source of primary inoculum for subsequent growing seasons. Uncontrolled weed populations could support increased inoculum levels between rotations. Further research is necessary to determine the role of weeds as hosts and inoculum sources in nature.

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