Influence of Inoculum Density, Wetness Duration, Plant Age, Inoculation Method, and Cultivar Resistance on Infection of Pepper Plants by *Colletotrichum coccodes*

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ABSTRACT

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Effects of inoculum density, wetness duration, plant age, inoculation method, and cultivar resistance on the development of pepper anthracnose caused by *Colletotrichum coccodes* were evaluated under controlled environmental conditions. As inoculum density of *C. coccodes* increased from 10^3 to 10^6 conidia/ml, symptoms of anthracnose developed. Disease severity also increased with increasing time of wetness duration from 0 to 60 h. Wetness duration above 48 h and a high inoculum density at 10^6 conidia/ml caused severe defoliation and blight symptoms in pepper seedlings. Inoculum at 10^4 conidia/ml and 24 to 36 h of continuous wetness duration was enough to form irregular or circular brown lesions on pepper leaves. Age-related resistance was expressed as pepper plants matured. To evaluate resistance, the foliar-inoculation method was more reliable than the soil-drench method, which did not induce symptoms on older plants. The responses of 35 pepper cultivars or accessions tested to *C. coccodes* were quantitative rather than qualitative. No hypersensitive symptoms were observed in any of the cultivars inoculated with any of the two isolates. No significant differences in susceptibility to anthracnose were found among cultivars from Korea, the United States, India, and Thailand or accessions tested, irrespective of genetic or country origin of cultivars. The Korean cultivar Kwangbok was relatively less susceptible to anthracnose, compared with the other cultivars tested.

Anthracnose of pepper (*Capsicum annuum* L.) is one of the most destructive diseases in pepper-growing areas of Korea (21). The disease produces symptoms on leaves, stems, and fruits. Decay of mature red fruit caused by anthracnose can result in substantial reductions in pepper yield. Recently, Park and Kim (21) reported that five anthracnose fungi, *Colletotrichum gloeosporioides*, *C. dematium*, *C. coccodes*, *C. acutatum*, and *Glomerella cingulata*, are pathogenic to different tissues of pepper plants. Of these anthracnose fungi, *C. gloeosporioides* attacks the fruit at all stages of development, but not the leaves and stems of pepper plants (13,21).

Leaf anthracnose of pepper seedlings caused by *C. coccodes* was first found in pepper-growing fields in Chungnam province of Korea in 1988 (19). In severely infested fields, a large number of pepper seedlings were defoliated and lodged. *C.*

coccodes can infect pepper seeds, seedling leaves and stems, mature leaves, and sometimes green but not red fruits (19,21,24). Initial symptoms of the anthracnose often appear on the leaves of pepper seedlings as light brown flecks. The flecks become slightly sunken, gradually increase in size, and coalesce to form larger, irregular lesions and blights on the leaves. *C. coccodes* has a wide host range that includes at least 58 species in 17 families, primarily in Leguminosae, Solanaceae, and Cucurbitaceae (22).

Extensive studies have been conducted to examine the effects of diverse environmental variables on infection and lesion development, yield losses, and the control of *C. coccodes* in tomato and potato (1,5,7-10,15,16,20,23). The relationship, however, between environmental conditions and *C. coccodes* infection has not been established in pepper seedlings. Severe outbreaks of foliar and seedling anthracnose caused by *C. coccodes* in seedbeds under polyethylene (21) may be associated with a high relative humidity during the pepper-growing season. In general, pepper plants seem to acquire resistance to *C. coccodes* as they mature, since the anthracnose caused by *C. coccodes* does not readily occur in mature pepper plants (21). Differences in resistance to *C. coccodes*-infection have been demonstrated

among cultivars of tomato, but the expression of resistance was greatly influenced by inoculation methods (4). Although effective control of anthracnose in pepper fields can be achieved by growing resistant cultivars, few pepper cultivars or accessions from diverse genetic origins have been evaluated for resistance to *C. coccodes*.

In this study, the effect of inoculum density, wetness duration, plant age, and inoculation method on infection of pepper seedlings by *C. coccodes* was evaluated. Levels of resistance of pepper genotypes from different genetic and geographic origins were also examined using two isolates of *C. coccodes* under greenhouse conditions.

MATERIALS AND METHODS

Inoculum and plant. Isolates 2-25, 32, and 7-48 of *C. coccodes* (Wallr.) S.J. Hughes obtained from the Plant Pathology Division of the National Agricultural Sciences and Technology Institute in Korea were used in this study. Mycelial suspensions from 7-day-old cultures were spread onto oatmeal agar plates. The cultures were grown at 28°C under continuous fluorescent light. After incubation for 5 to 7 days, inoculum was prepared by gently scraping the agar surface in sterile water, then filtering the mycelial and conidial suspension through four layers of cheesecloth. The conidial suspensions were counted using a hemacytometer and adjusted from 10^3 to 10^6 conidia/ml using sterile tap water. Before inoculation, Tween 20 was added to the inoculum to give 0.05% concentration.

A total of 35 pepper cultivars or accessions were evaluated for resistance to *C. coccodes* isolates: Korean cultivars Hanbyul, Kingkun, Dabogkun, Kwangbok, and Kumtap; Korean local collections KC178, KC190, KC195, KC205, KC206, KC213, KC214, KC217, KC220, and KC243 from the Department of Horticulture, Kyungbuk National University, Korea; U.S. local collections Cayenne Cajun 1A, Cayenne Cajun 2, Cayenne Cajun 2A, Peto Seed Cayenne, Capritto Cayenne, and Tabasco (*Capsicum frutescens*) from the Department of Plant Pathology and Crop Physiology, Louisiana State University; Indian accessions KC47 (PI 244670), KC49 (PI 249434), KC53 (PI

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257048), KC55 (PI 257052), KC56 (PI 257053), KC79 (PI 271322), KC118 (PI 322718), KC126 (PI 358812), KC127 (PI 369994), and KC130 (PI 369997) from the Department of Horticulture, Kyungbuk National University, Korea; and Thai local collections KC407 (F7 nun), KC408 (F6 Malasia), KC413 (Huai Sri Then), and KC 417 (Kantoorome) from the Department of

Horticulture, Kyungbuk National University, Korea.

Seeds of each pepper cultivar or accession were sown in plastic trays (55 by 35 by 15 cm) containing a steam-sterilized soil mix of a commercial compost soil (peat moss:perlite:vermiculite, 5:3:2, vol/vol/vol), sand, and loam soil (1:1:1, vol/vol/vol). Ten seedlings at 2-leaf stage

were transplanted to plastic pots (5 by 15 by 10 cm) containing the above-described soil mix. Pepper plants were grown in a growth room at $25 \pm 2^\circ\text{C}$ with 5,000 lx illumination for 16 h/day.

Inoculation procedures. Pepper plants at various growth stages were inoculated with a conidial suspension of *C. coccodes* by foliar-spray or soil-drench methods. For foliar-spray inoculation, a conidial suspension was sprayed to runoff over both sides of leaves using an atomizer. Inoculated plants were placed in a moist chamber at 28°C for 36 h and then returned to the growth room for disease evaluation. For soil-drench inoculation, 15 ml of a suspension of conidia (10^6 conidia/ml) was uniformly poured over the soil surface in each pot. Immediately after soil-drenching, pots were placed in a large plastic tray and maintained in a growth room for disease evaluation.

To evaluate the effect of wetness duration on *C. coccodes* infection, pepper plants at the 2- and 8-leaf stages were sprayed with a conidial suspension of *C. coccodes* isolate 32 (2×10^5 conidia/ml) and incubated in a moist chamber in a growth room at 28°C for 0, 10, 24, 36, 48, and 60 h. After incubation in the moist chamber, the plastic pots, each containing 10 inoculated pepper plants, were again placed in a growth room for disease evaluation.

Disease evaluation and data analysis.

Disease development of pepper plants was recorded daily after inoculation of *C. coccodes*. To evaluate infection of *C. coccodes* on the inoculated plants, disease severity was rated based on a 0 to 5 scale, where 0 = no visible symptoms; 1 = small circular or irregular, gray-brown spots on leaves, and the plants slightly wilted; 2 = some leaves defoliated with circular or irregular gray-brown lesions with dark brown edge on leaves, damping-off in seedlings, and 30 to 50% of the plant wilted; 3 = leaves defoliated with large irregular lesions and 50 to 70% of the plant wilted; 4 = leaves defoliated or desiccated, and 70 to 90% of entire plant wilted; and 5 = plant dead. The number of lesions produced on leaves of pepper plants also were recorded at day 8 after inoculation. Disease severity ratings were used to calculate areas under disease progress curves (AUDPCs) using the formula:

$$\text{AUDPC} = \sum_{i=1}^n (X_{i+1} + X_i)(t_{i+1} - t_i)/2$$

where X_i = disease severity at the i th observation, t_i = time (days) at the i th observation, and n = total number of observations.

All data are the mean of disease ratings of 10 plants inoculated with *C. coccodes*. All experiments were repeated at least twice with similar results. Data represented are from one experiment. AUDPCs from one experiment were analyzed statistically

Fig. 1. Effect of inoculum concentration on disease development in pepper plants (cv. Hanbyul) inoculated with *Colletotrichum coccodes* isolate 32 by foliar spraying at the 2-leaf and first-branch stages. Disease severity rating based on a 0 to 5 scale, where 0 = no visible symptoms and 5 = plant dead.

Fig. 2. Effect of wetness duration on disease development in pepper plants (cv. Hanbyul) inoculated with 2×10^5 conidia/ml of *Colletotrichum coccodes* isolate 32 by foliar spraying at the 2-leaf and 8-leaf stages. Disease severity rating based on a 0 to 5 scale, where 0 = no visible symptoms and 5 = plant dead.

by the analysis of variance procedures. Linear regression analyses were used to evaluate relationships between leaf wetness duration and inoculum density for disease development. The SAS computer program (SAS Institute Inc., Cary, NC) was used for all regression analyses.

RESULTS

Effect of inoculum density on disease development. Disease severity of Hanbyul pepper plants increased as inoculum density increased from 10^3 to 10^6 conidia/ml (Fig. 1). A linear relationship was found between inoculum density and disease severity on pepper plants at the 2-leaf and first-branch stages. Conidia concentrations used for the inoculation explained 81 and 75 % of the variation in disease severity ($r^2 = 0.81$ or 0.71) at the 2-leaf and first-branch stages, respectively. Few symptoms were induced on pepper plants at the 2-leaf stage inoculated with 10^3 conidia/ml and first-branch stage inoculated at 10^3 and 10^4 conidia/ml. Disease severity was intermediate (severity ratings of 2 to 3) at 10^4 to 10^5 conidia/ml. At 10^6 conidia/ml, all juvenile plants at 2-leaf stage were killed (severity rating of 5) within 5 to 7 days after inoculation. At the first-branch stage, resistance to *C. coccodes* became more evident. After incubation for 4 days, foliar lesions coalesced on pepper leaves at the 2-leaf stage, while foliar lesions were only light brown or gray flecks on plants at first-branch stage inoculated with 10^5 and 10^6 conidia/ml.

Effect of wetness duration on disease development. Disease severity increased in pepper plants (cv. Hanbyul) as the wetness duration increased (Fig. 2). A linear relationship was observed between leaf wetness duration and disease severity on pepper plants at the 2- and 8-leaf stages. Disease did not develop on pepper leaves that were not kept wet after inoculation. After exposure to continuous wetness for 48 or 60 h, juvenile plants at 2-leaf stage were killed (severity rating of 5) 4 days after inoculation. At all wetness durations, disease developed slowly on pepper plants at the 8-leaf stage compared with the 2-leaf stage.

Effect of plant age and inoculation method. In general, as pepper plants grew older, they became more resistant to *C. coccodes* (Fig. 3). At the 2-leaf stage, there were no differences between the foliar spray and soil-drench inoculations in disease severity. All the juvenile plants at the 2-leaf stage were killed by *C. coccodes* infection. Mean disease severity was less than 1 for plants inoculated by soil drench at the 4-leaf stage. At the 8-leaf and first-branch stages, soil-drench inoculation did not cause disease. Foliar inoculation, however, produced small, circular, light-gray lesions on the pepper leaves at the 8-leaf and the first-branch stages.

Cultivar resistance to *C. coccodes* isolates. Prior to evaluating the resistance

of pepper cultivars or accessions to *C. coccodes*, levels of virulence of some *C. coccodes* isolates 7-48, 2-25, and 32 were examined in pepper plants (cv. Hanbyul) at the 2- and 6-leaf stages. Isolate 2-25 was more virulent than isolate 32 on pepper plants. Isolate 7-48 was not pathogenic to the pepper plants (*data not shown*) and was not included in further evaluations.

When inoculated by foliar spray at the 2-leaf stages with each isolate (2-25 and 32), all the cultivars or accessions tested had small, circular, light-gray lesions on the leaves, external discoloration on the stem, a sudden wilt of the entire plant, leaf defoliation, or damping-off (*data not shown*). No hypersensitive symptoms were observed in any of the cultivars tested. In general, all cultivars or accessions at the 4-leaf stage were susceptible to the two iso-

lates (2-25 and 32). AUDPCs were used to evaluate the relative resistance of the 35 pepper cultivars or accessions to the two isolates of *C. coccodes* (Table 1). Korean cultivars were quantitatively more resistant to isolate 32 than isolate 2-25. In contrast, the U.S. local peppers were more resistant to isolate 2-25. In particular, the U.S. local pepper Tabasco (*Capsicum frutescens*) showed a high level of resistance to both isolates, compared with the other pepper cultivars or accessions tested. The other Indian, Korean local, and Thai collection peppers showed similar disease severity to the two tested isolates.

The analysis of variance of the AUDPCs in this experiment (Table 2) showed significant differences among cultivars and for the cultivar $\times$ isolate interaction, but not between isolates.

Fig. 3. Effect of plant age and inoculation method on disease development in pepper plants (cv. Hanbyul) inoculated with *Colletotrichum coccodes* isolate 32. Disease severity rating based on a 0 to 5 scale, where 0 = no visible symptoms and 5 = plant dead. Bars represent standard error of the mean.

The Korean cultivars Hanbyul and Kwangbok, which were susceptible and resistant to *C. coccodes*, respectively, were reevaluated by foliar-spray inoculation with the two isolates, 2-25 and 32, on pepper plants at different growth stages using foliar spray technique (Table 3). More lesions were produced on the leaves of the cultivar Hanbyul than the cultivar Kwangbok, irrespective of plant growth stage and *C. coccodes* isolate. The total number of lesions produced per square centimeter leaf decreased as the pepper plants matured.

DISCUSSION

Inoculum density of *C. coccodes* affected anthracnose development in pepper seedlings at the two developmental stages. With a low level of inoculum density (10^3 conidia/ml), a few symptoms appeared on pepper seedlings at 2-leaf stage 4 days after inoculation. Generally, as inoculum density increased, symptom development increased. With a high level of inoculum density (10^6 conidia/ml), initial lesions appeared 3 days after inoculation, suggesting that higher inoculum densities may contribute to rapid development of anthracnose. These results agree with the observations of Dillard (9), in which anthracnose severity on tomato fruit increased as inoculum density increased from 10^1 to 10^6 conidia/ml. At the first-branch stage, inoculum above 10^5 conidia/ml was required for disease development. These results imply that mature pepper plants can effectively avoid *C. coccodes* infection compared with pepper seedlings at the 2-leaf stage. Primary inoculum density of *C. coccodes* seems to be important for producing typical anthracnose lesions on pepper plants. In an earlier study, it was demonstrated that primary inoculum density of *C. coccodes* was related to the induction and development of anthracnose of tomato fruit (9).

Available moisture was critical for infection of pepper leaves by *C. coccodes*. At the 2-leaf stage, pepper plants receiving 48 and 60 h of leaf wetness were severely blighted by *C. coccodes* infection. At least 24 to 36 h of leaf wetness seemed to be necessary for inducing naturally occurring symptoms of anthracnose under the greenhouse conditions. Moisture is known to be a very important factor for both the survival of *C. coccodes* in soil (11) and the infection in tomato fruits and potato foliage (9,15). The significance of moisture in *C. coccodes* infection on host plants such as pepper, tomato, and potato is supported by the previous findings of Pantidou and Schroeder (20), who showed that *C. phomoides* (a synonym of *C. coccodes*) could grow and sporulate abundantly on tomato leaves, depending upon the length of the postinfection humidity period. Microclimates of high temperature and high humidity in seedbeds of polyethylene film-

Table 1. Area under disease progress curves (AUDPCs)^a of 35 pepper cultivars or accessions inoculated by foliar spray at the 4-leaf stage with two *Colletotrichum coccodes* isolates 2-25 and 32

Origin, cultivar or accession	AUDPC by two isolates (mean ± SE)	
	Isolate 2-25	Isolate 32
Korean cultivar		
Hanbyul	25 ± 2.0	16 ± 4.9
Kingkun	26 ± 1.2	13 ± 1.0
Dabogkun	18 ± 4.4	17 ± 8.1
Kwangbok	11 ± 2.4	11 ± 1.5
Kumtap	19 ± 2.4	15 ± 5.5
Average	20	14
Korean local collection		
KC178	17 ± 5.5	22 ± 10.8
KC190	17 ± 3.9	13 ± 3.0
KC195	29 ± 1.7	36 ± 1.1
KC205	18 ± 5.3	17 ± 6.3
KC206	15 ± 4.4	22 ± 6.6
KC213	19 ± 3.4	21 ± 7.1
KC214	21 ± 1.1	13 ± 2.5
KC217	20 ± 2.9	23 ± 6.5
KC220	21 ± 2.1	16 ± 4.3
KC243	17 ± 1.6	22 ± 6.8
Average	19	21
U.S. local collection		
Cayenne Cajun 1A	21 ± 2.5	32 ± 6.2
Cayenne Cajun 2	17 ± 2.1	28 ± 3.0
Cayenne Cajun 2A	21 ± 5.4	26 ± 4.6
Peto Seed Cayenne	25 ± 1.9	24 ± 8.2
Capritto Cayenne	20 ± 3.4	22 ± 8.5
Tabasco(<i>Capsicum frutescens</i>)	13 ± 4.5	10 ± 0.8
Average	20	24
Indian accessions		
KC47 (PI244670)	18 ± 4.7	15 ± 2.6
KC49 (PI249434)	17 ± 1.5	21 ± 5.1
KC53 (PI257048)	24 ± 4.0	27 ± 5.6
KC55 (PI257052)	24 ± 1.9	16 ± 5.4
KC56 (PI257053)	19 ± 1.3	20 ± 4.7
KC79 (PI271322)	16 ± 2.8	19 ± 5.5
KC118 (PI322718)	21 ± 1.5	21 ± 5.8
KC126 (PI3588412)	17 ± 4.4	16 ± 3.8
KC127 (PI369994)	27 ± 1.4	16 ± 2.4
KC130 (PI369997)	13 ± 4.6	15 ± 1.8
Average	20	19
Thai collection		
KC407	16 ± 3.1	15 ± 5.8
KC408	15 ± 3.4	17 ± 5.0
KC413	27 ± 2.9	21 ± 8.0
KC417	16 ± 5.6	22 ± 7.5
Average	19	19

^a AUDPCs were calculated using a disease severity rating based on a 0 to 5 scale, where 0 = no visible symptoms and 5 = plant dead.

Table 2. Analysis of variance of the areas under disease progress curves of 35 cultivars or accessions inoculated with two isolates of *Colletotrichum coccodes*

Source of variation	df	Mean square	F value	P
Cultivar or accession	34	232.8	9.8	<0.01
Isolate	1	9.8	0.4	>0.01
Cultivar or accession × isolate	34	151.1	6.3	<0.01

Table 3. Comparison of lesion development (mean number lesions/cm² leaf) on the leaves of pepper cultivars Hanbyul (susceptible) and Kwangbok (resistant) foliar-spray inoculated with *Colletotrichum coccodes* isolates 2-25 and 32 at different growth stages

Plant growth stage	Isolate 2-25		Isolate 32	
	Hanbyul	Kwangbok	Hanbyul	Kwangbok
6-leaf	4.1 ± 0.7 ^a	3.2 ± 0.7	1.5 ± 0.6	1.1 ± 0.5
8-leaf	2.4 ± 0.4	1.7 ± 1.2	0.7 ± 0.6	0.3 ± 0.3
First-branch	1.9 ± 0.7	0.8 ± 0.3	0.2 ± 0.1	0.1 ± 0.1

^a Mean numbers evaluated 8 days after inoculation. Each value represents a mean ± standard error of seven plants.

houses may serve as favorable environmental factors for anthracnose development in pepper seedlings (21).

Inoculation method influences infection and lesion development of *C. coccodes* on pepper leaves. Foliar application of a conidial suspension produced anthracnose lesions on pepper leaves at all development stages of the plants. Root infection of *C. coccodes* by soil drench caused damping-off of pepper seedlings only at 2-leaf stage. Thus, a large number of pepper seedlings may be severely damaged by *C. coccodes* infection of roots growing in seedbeds (21). In contrast, anthracnose caused by *C. coccodes* does not result in the severe epidemics in mature leaves and fruits of pepper, possibly because of its weak parasitism (6,12) combined with a low competitive saprophytic ability (14).

All pepper cultivars became increasingly resistant to *C. coccodes* as plants aged. Expression of the age-related resistance to anthracnose was more apparent in pepper plants at late growth stages inoculated by the soil-drench method. These facts suggest that the soil-borne fungus *C. coccodes* can infect only pepper seedlings at 1- or 2-leaf stages through root tissues. In an earlier study, Kim et al. (17) demonstrated the expression of age-related resistance in pepper plants infected with the soil-borne fungus *Phytophthora capsici*.

The foliar-spray inoculation method was effective at evaluating pepper cultivars or accessions for resistance to *C. coccodes* at the 4-leaf stage of plants. Soil-drench inoculation, however, may not be appropriate for evaluating cultivar resistance on old pepper plants, because symptoms were not induced on pepper plants older than 4-leaf stage. The responses of 35 cultivars or accessions to two isolates of *C. coccodes* were evaluated by foliar-spray inoculations done under controlled environmental conditions. Hypersensitive reactions were not observed in any of the pepper cultivars of diverse genetic origins inoculated with *C. coccodes*, indicating that the difference between the susceptible and resistant responses to *C. coccodes* were more quantitative than qualitative. Significant differences in susceptibility to *C. coccodes*

isolates were not observed among the Korean, U.S. local, Indian, and Thai cultivars or accessions tested, irrespective of genetic or country origin of cultivars. The Korean cultivar, Kwangbok, and the U.S. local pepper, Tabasco (*Capsicum frutescens*), showed a high level of resistance to the *C. coccodes* isolates tested, suggesting a possible existence of resistance sources in pepper. Although inheritance of resistance to tomato anthracnose is known to be controlled by several genes (2,3,18), there is little information on sources and inheritance of resistance to *C. coccodes* in pepper. Planting cultivars such as Kwangbok, which exhibit resistance to anthracnose, may be effective in reducing outbreaks of damping-off caused by *C. coccodes* in pepper seedling plants in seedbeds.

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