

Variability in Virulence of *Calonectria ilicicola* Isolates on Soybean

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콩에 대한 *Calonectria ilicicola* 균주의 병원성 변이

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ABSTRACT: Variability in virulence of *Calonectria ilicicola* isolates from different hosts and geographic origin provides important information for breeding cultivars resistant to red crown rot. A wide range in virulence for 25 isolates of *C. ilicicola* from soybean and peanut was observed on six soybean cultivars. Soybean isolates were pathogenic on soybean although some were less virulent. Virulence of isolates was not affected greatly by cultivar and relatively consistent regardless of virulence level. Soybean isolates were more virulent on soybean than were peanut isolates. When virulence of two soybean and two peanut isolates was compared between laboratory and greenhouse tests, it was stable across a range of cultivars. Mycelial growth of isolates from either soybean or peanut was reduced significantly on potato dextrose chlorate when compared with potato dextrose agar. Isolates from soybean on potato dextrose chlorate showed significant reduction of fungal growth than isolates from peanut did although their growth on potato dextrose agar was not significantly different. Evidence for physiologic specialization was not recognized in this system. However, the findings that soybean isolates of *C. ilicicola* were more virulent on soybean and reduction of fungal growth on potato dextrose chlorate than were peanut isolates suggest that host specialization may exist in this fungus.

Key words: *Calonectria crotalariae*, *Cylindrocladium parasiticum*, host specialization, *Glycine max*, red crown rot, virulence variability.

The soilborne fungus *Calonectria ilicicola* Boediu and Reitsma [anamorph: *Cylindrocladium parasiticum* Crous, Wingf. and Alfenas (10), syn. *C. crotalariae* (Loos) Bell and Sobers (2)] causes red crown rot (3, 4, 5, 6) on soybean [*Glycine max* (L.) Merr.]. Since its description on peanut (*Arachis hypogaea* L.) in 1966 (2), *C. ilicicola* has been reported as pathogenic on koa in 1972 (1), soybean in 1973 (24), papaya in 1973 (17), blueberry in 1974 (16), lea in 1981 (15), alfalfa in 1982 (18), indigo in 1988 (6), and palm in 1992 (28). In a host range study, tobacco and cotton were good hosts but corn, wheat, and rye were poor hosts for *C. ilicicola* (22). Nevertheless, the pathogen infected leaves of barley, oats, rye, and wheat in artificial inoculations, and it has been suggested that these small grains can be infected

naturally (27).

Use of resistant cultivars and delayed planting are recommended measures for managing red crown rot in Louisiana (5); however, delayed planting sometimes results in yield reduction. Planting resistant cultivars is more desirable. Choices are limited due to a lack of identified resistant germplasms. Whether physiologic races exist in a pathogen population is important information for breeding disease resistant cultivars because developing resistant genotypes may depend on physiologic or host specialization. For example, soybean cultivar Tracy M is resistant to Mississippi isolates of *Diaporthe phaseolorum* var. *caulivora* but very susceptible to an isolate from Iowa (12).

Nishijima and Aragaki (17) observed that an isolate of *C. ilicicola* from papaya caused severe collar rot disease on three commercial papaya varieties but not on variety

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Kapoho Solo, which was known to be susceptible to this pathogen. This may indicate that physiologic specialization of *C. ilicicola* on papaya already occurred although they did not account for this specialization in the system. However, the existence of races in *C. ilicicola* has been proposed in several reports (7, 11, 23), primarily because of variability in disease severity (24), prevalence of the sexual stage (2), a multinucleate hypha (13), and hyphal anastomosis (7) known to occur in this fungus. Since Bell and Sobers (2) suggested the possibility of physiologic specialization in *C. ilicicola*, there have been several attempts to identify races (8, 11, 23) but clear evidence has not been obtained. Pathogenic variability of this fungus on soybean has not been evaluated. It is important to identify pathogenic variability in the *C. ilicicola*-soybean system so that breeding efforts can be conducted appropriately.

Morphological phenotypes using chlorate-amended media have been used for characterizing variability in virulence (19, 20) because chlorate affects the nitrate reductase pathway, consequently, production of restricted growth of fungi. Pearson *et al.* (19, 20) found differential growth pattern on a medium containing chlorate between *Macrophomina phaseolina*, the causal agent of charcoal rot, from soybean and corn. The morphology of this fungus on the chlorate-amended medium can be used for a indicator of host specialization. The objectives of this study were to identify variability in virulence among *C. ilicicola* isolates, to compare in virulence in selected isolates between laboratory and greenhouse tests, and to differentiate fungal growth between isolates from soybean and peanut on a medium containing chlorate.

MATERIALS AND METHODS

Variability in virulence of *C. ilicicola* isolates from soybean and peanut. Twenty-five isolates of *C. ilicicola* from different hosts and geographic origins were tested for variability of virulence in the laboratory (Table 1). Soybean isolates were obtained from ascospores produced by perithecia on diseased stems or from microsclerotia in soil. For isolation from soil, microsclerotia were extracted by passing through nested sieves with pore sizes of 250 μm and 45 μm . Microsclerotia on the 45 μm sieve were collected, plated on the semiselective medium described by Phipps *et al.* (21), and incubated 4-7 days at room temperature (ca. 25°C) under continuous fluorescent light to promote production of conidia. Isolation of single conidia produced by these cultures was conducted on 2% water agar. The isolates were cultured and preserved at

Table 1. Geographic origin, host, date collected, and provider/collector of *Calonectria ilicicola* isolates included in this study

Isolate	Geographic origin	Original host	Date collected	Provider/collector
BH1	Louisiana	<i>Glycine max</i>	1991	1 ^a
BH2	Louisiana	<i>G. max</i>	1991	1
BSD	Louisiana	<i>G. max</i>	...	2
SG911	Louisiana	<i>G. max</i>	1991	1
SG912	Louisiana	<i>G. max</i>	1991	1
SG913	Louisiana	<i>G. max</i>	1991	1
SG914	Louisiana	<i>G. max</i>	1991	1
SG915	Louisiana	<i>G. max</i>	1991	1
SG916	Louisiana	<i>G. max</i>	1991	1
SG917	Louisiana	<i>G. max</i>	1991	1
SGD	Louisiana	<i>G. max</i>	...	2
323	North Carolina	<i>Arachis hypogaea</i>	...	3
417	North Carolina	<i>A. hypogaea</i>	...	3
447	North Carolina	<i>A. hypogaea</i>	...	3
48	North Carolina	<i>A. hypogaea</i>	...	3
1PN	North Carolina	<i>A. hypogaea</i>	1986	3
2PN	North Carolina	<i>A. hypogaea</i>	1986	3
3PN	North Carolina	<i>A. hypogaea</i>	1986	3
4PN	North Carolina	<i>A. hypogaea</i>	1986	3
C31	North Carolina	<i>A. hypogaea</i>	1973	3
J1	North Carolina	<i>A. hypogaea</i>	1985	3
J2	North Carolina	<i>A. hypogaea</i>	1985	3
J3	North Carolina	<i>A. hypogaea</i>	1985	3
S38	North Carolina	<i>A. hypogaea</i>	...	3
S44	North Carolina	<i>A. hypogaea</i>	...	3

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^bUnknown.

4°C on potato dextrose agar (PDA, Difco Laboratories, Detroit, Michigan).

Six soybean cultivars (Table 2) were tested for reaction to *C. ilicicola*. These soybean plants were grown in a greenhouse in 72-cell (5×5×7 cm) plastic trays (67×35×7 cm) filled with a commercial potting mixture (Peat-lite mix, Conrad Fafard Inc., Springfield, Massachusetts) for 10 days. Seedlings were removed from the plastic trays, washed with tap water to remove soil, then placed on wet paper towels. Seedlings were inoculated in the crown region with mycelium of *C. ilicicola* in PDA discs (5 mm in diameter) cut from margins of actively growing cultures (10 days old). Inoculated seedlings were kept in a dark chamber (90×70×190 cm) at 25°C. Control plants were inoculated with PDA discs without mycelium and incubated as described. Disease severity was evaluated 9 days after inoculation based on a 0-5 scale as follows: 0=no visible symptoms; 1=reddish necrotic stem lesions <10 mm in length; 2=stem lesions

Table 2. Severity of disease^a caused by isolates of *Calonectria ilicicola* on six soybean cultivars in laboratory tests

Isolate	Cultivar						Mean	LSD _{0.05}
	Asgrow 7986	Braxton	Cajun	Centennial	Forrest	Hartz 7126		
SG914	3.5	3.9	3.9	3.3	3.1	3.0	3.5	0.7
SG917	4.0	3.3	3.9	2.7	3.2	3.3	3.4	0.8
SG915	3.6	3.6	3.7	3.6	2.7	3.1	3.4	0.9
BH2	2.9	3.4	3.5	3.5	3.4	3.0	3.3	ns ^b
SG916	3.7	3.0	3.7	2.7	2.9	3.0	3.2	0.9
SG913	3.6	3.0	3.5	2.9	2.6	2.5	3.0	1.0
2PN	3.4	2.8	3.5	2.3	2.7	2.2	2.8	1.2
SG911	2.0	3.4	2.7	3.3	3.0	2.2	2.8	1.2
SG912	3.3	2.0	2.9	2.4	2.4	2.4	2.6	ns
1PN	2.6	2.9	2.7	2.5	2.1	2.4	2.5	ns
48	2.0	1.7	2.5	2.0	2.0	1.5	2.0	ns
J3	1.9	2.9	1.9	2.3	1.7	1.1	1.9	1.0
4PN	3.1	2.3	2.4	0.9	1.5	0.8	1.8	1.2
447	2.1	1.8	1.0	1.0	1.4	1.2	1.5	ns
323	2.1	1.2	1.4	0.8	1.0	1.3	1.3	1.2
SGD	1.9	1.8	1.4	0.6	1.2	0.8	1.3	ns
BH1	1.3	0.8	1.5	0.5	1.0	0.8	1.0	ns
C31	1.3	1.0	0.1	0.2	0.7	0.2	0.6	0.8
3PN	0.4	1.1	1.0	0.4	0.3	0.1	0.6	0.9
BSD	0.6	0.3	0.5	0.3	0.9	0.2	0.5	ns
S38	0.5	0.4	0	0.4	0.3	0	0.3	0.5
J1	0.3	0	0.1	0.4	0	0	0.1	ns
J2	0	0.1	0.2	0	0.2	0	0.1	ns
417	0	0	0	0.2	0.3	0	0.1	ns
S44	0	0.5	0	0	0	0	0.1	ns
Mean	2.0	1.9	2.1	1.6	1.6	1.5		0.3
LSD _{0.05}	1.0	1.1	0.9	1.0	0.8	0.9	0.5	

^aDisease severity was rated using a scale of 0 (no visible symptoms) to 5 (dead plants) 9 days after inoculation of 10-day-old plants.

^bns indicates no significant difference across soybean cultivars.

10~40 mm; 3=stem lesions extending up to cotyledon (40~50 mm), and slight leaf yellowing; 4=stem lesions \geq 40 mm with water-soaking of stem above cotyledon, loss of cotyledons, severe leaf yellowing; and 5=seedlings dead. This experiment was conducted twice in a completely randomized design with five and six replicates.

Comparison in virulence of *C. ilicicola* isolates from soybean and peanut between laboratory and greenhouse tests. Laboratory and greenhouse tests were conducted using two virulent (SG915 and 2PN) and two less virulent (BH1 and 48) isolates which were selected based on results from laboratory inoculations (Table 2). Eleven soybean cultivars (Table 3), including six cultivars used previously, were utilized in this study. The number of cultivars was increased to allow examination of virulence in these isolates across a range of cultivars.

In the laboratory test, procedures for production of plants and inoculum, fungal inoculation, and disease evaluation were as described previously. For the greenhouse test, plants were grown in 22-cm-diameter plastic pots filled a mixture of methyl bromide-treated loamy soil (80% sand, 5% silt, 15% clay), peat moss, and perlite (3:2:1, v/v/v) for 10 days. Soil was removed gently from a small (1×1 cm) area near the crown of the plants. Discs (10 mm in diameter) of mycelium in PDA from 10-day-old cultures of the fungus were placed in direct contact with crowns of plants at the soil-line, then covered with soil. Control plants were treated with PDA discs without mycelium. Inoculated plants were watered carefully to prevent dislodging inoculum discs from stems. Lesion length was measured directly on diseased stems as the extent of necrotic lesions above the soil line 35 days after inoculation. This experiment was conducted in a

Table 3. Severity of disease^a and stem length^b (mm) caused by two soybean and two peanut isolates of *Calonectria ilicicola* on 11 soybean cultivars in laboratory and greenhouse tests

Cultivar	Isolate				Mean	LSD _{0.05}
	Soybean		Peanut			
	SG915	BH1	2PN	48		
Laboratory test						
Deltapine 726	4.7	1.4	4.7	2.1	3.2	0.6
Hartz 6200	4.6	1.6	4.3	1.9	3.1	0.7
Bedford	4.4	1.8	4.8	1.3	3.1	0.8
Centennial	4.2	1.6	4.7	1.4	3.0	0.7
Hartz 7126	4.4	0.7	4.8	1.7	2.9	0.5
Forrest	4.3	1.3	4.7	1.2	2.9	0.6
Riverside 699	4.2	1.2	3.9	1.2	2.6	0.6
Asgrow 7986	3.6	1.2	4.0	1.5	2.6	0.7
Riverside 677	4.1	1.2	3.3	1.4	2.5	0.7
Cajun	3.1	1.1	2.8	1.2	2.1	0.8
Braxton	2.9	0.9	2.6	0.9	1.8	0.9
Mean	4.0	1.3	4.1	1.4		0.2
LSD _{0.05}	0.8	0.7	0.6	0.6	0.3	
Greenhouse test						
Bedford	20.1	13.9	17.1	16.3	16.7	4.4
Riverside 699	19.5	13.0	16.8	12.7	15.5	3.9
Riverside 677	16.2	12.4	20.0	11.1	14.9	3.3
Centennial	14.3	17.1	15.0	12.8	14.7	2.8
Hartz 712	17.5	15.9	16.9	7.8	14.5	2.0
Hartz 6200	12.1	12.3	16.3	15.3	14.0	ns ^c
Deltapine 726	16.8	12.4	11.0	11.5	13.2	3.7
Forrest	12.1	6.6	10.5	10.8	10.0	2.9
Asgrow 7986	8.3	7.8	12.0	9.6	9.6	2.8
Braxton	9.5	7.9	6.8	9.2	8.6	ns
Cajun	7.8	7.8	10.8	5.5	8.0	2.3
Mean	13.8	11.6	14.3	11.2		1.0
LSD _{0.05}	3.4	3.3	4.2	3.0	1.7	

^aDisease severity was rated using a scale of 0 (no visible symptoms) to 5 (dead plants) 9 days after inoculation of 10-day-old plants.

^bLesion length was determined 35 days after inoculation of 10-day-old plants.

^cns indicates no significant difference across isolates of *C. ilicicola*.

completely randomized design with 10 and 12 replicates in laboratory and greenhouse tests, respectively.

Mycelial growth of *C. ilicicola* isolates from soybean and peanut on a medium containing chlorate. Isolates of *C. ilicicola* tested in the laboratory tests except SG911 and SG914, which were not available at this experiment, were precultured on PDA and potato dextrose chlorate (PDC) which contains 1.5% KClO₃ for 5 days. One disc (4 mm in diameter) of mycelium in PDA or PDC from margins of actively growing precultures was inoculated onto the center of a PDA or a PDC plate (90 mm in diameter). These were incubated in darkness at 25°C. Mycelial growth pattern was observed and colony diameters were measured 7 days after inoculation. This

test was conducted twice with four replicates each.

Analysis of data. Statistical analyses were conducted with pooled data from repeated experiments using Statistical Analysis System (25). Analysis of variance was determined using the General Linear Model and means were separated using Least Significant Difference test.

RESULTS

Variability in virulence of *C. ilicicola* isolates from soybean and peanut. A wide range in virulence for *C. ilicicola* isolates was observed in the laboratory test (Table 2). All soybean isolates were pathogenic on soybean in laboratory inoculations although some (i.e.,

BSD, BH1, and SGD) consistently were less virulent than others (Table 2). Isolates with less virulence were pathogenic on some but not all cultivars. Virulence of isolates was not affected greatly by cultivars and severity of disease produced by isolates was relatively consistent regardless of virulence level (Table 2). Control plants inoculated with PDA discs without mycelium produced no disease symptoms.

When virulence between isolates from soybean and peanut was compared, virulence (mean disease severity =2.5) of isolates from soybean was significantly ($P \leq 0.0001$) higher on soybean than that (mean disease severity=1.1) of isolates from peanut.

Comparison in virulence of *C. ilicicola* isolates from soybean and peanut between laboratory and greenhouse tests. Severity of disease caused by SG 915, a virulent isolate from soybean, was comparable to that caused by 2PN, a virulent isolate from peanut, on all soybean cultivars tested in the laboratory (Table 3). Severity of disease caused by less virulent BH1 and 48 from soybean and peanut, respectively, also was similar (Table 3). Disease induced by SG915 and 48 was most severe on Deltapine 726 whereas that by BH1 and 2PN was greatest on Bedford. No difference in virulence between soybean and peanut isolates was observed, however, virulent isolates SG915 and 2PN produced greater disease on soybean than did less virulent isolates BH1 and 48.

Results from the greenhouse test were similar to those obtained in laboratory inoculations. Virulent isolates SG 915 and 2PN induced longer lesions than did less virulent isolates BH1 and 48 (Table 3). A wide range of susceptibility of soybean cultivars was observed. Cajun and Braxton were the least susceptible in the greenhouse as well as the laboratory test (Table 3). Disease induced by SG915 and 48 was most severe on Bedford whereas that by BH1 and 2PN was most severe on Centennial and Riverside 677, respectively. Relative levels of virulence among isolates of *C. ilicicola* were similar to those observed in the laboratory test. No difference in virulence between soybean and peanut isolates was detected but virulent isolates produced more disease on soybean than did less virulent isolates, as seen in laboratory test. Control plants inoculated with PDA discs without mycelium produced no disease symptoms in laboratory and greenhouse tests.

Mycelial growth of *C. ilicicola* isolates from soybean and peanut on a medium containing chlorate. When mycelial growth between isolates from soybean and

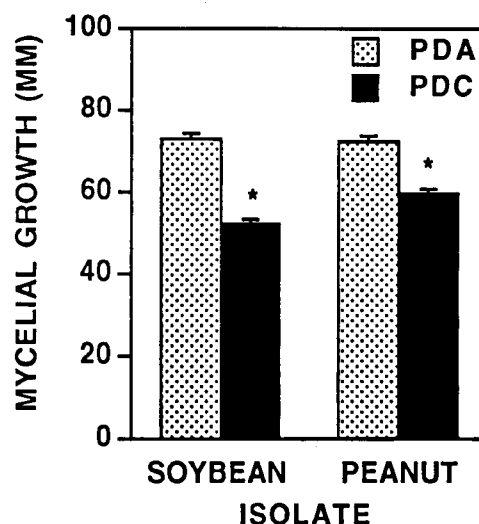


Fig. 1. Mycelial growth of *Calonectria ilicicola* isolates from soybean and peanut on potato dextrose agar with (PDC) or without (PDA) potassium chlorate 7 days after inoculation. Bars indicate standard errors of the means. Within isolates, an asterisk indicate a significant difference ($P \leq 0.05$).

peanut was compared on PDA and PDC media, mycelial growth of isolates either soybean or peanut was reduced significantly on PDC when compared with PDA (Fig. 1). Isolates from soybean on PDC showed significant reduction of fungal growth than isolates from peanut did ($P \leq 0.001$) although their growth on PDA was not significantly different ($P=0.786$). However, no distinct growth pattern among isolates was observed between PDA and PDC media although certain isolates regardless of host origin produced lack of aerial mycelia.

DISCUSSION

There have been several attempts to identify physiologic specialization, i.e., races, in *C. ilicicola* (8, 11, 23). Rowe and Beute (23) reported a wide range of virulence in isolates of *C. ilicicola* but found no relationship between virulence and growth rate in culture or geographic isolates of the fungus. These authors suggested physiologic races within *C. ilicicola* still may exist at undetectable levels in fields and pointed out that the absence of resistant cultivars probably has provided no selection pressure for these races to become predominant. However, later reports (8, 11) suggested that race development had occurred in this fungus. Hadley *et al.* (11) found that virulence specific for a resistant peanut cultivar increased greatly due to continual cropping of this cultivar.

On soybean, changes in relative rankings among cultivars with regard to red crown rot reaction have been reported in field trials (4). From these changes, the possible existence of races within this fungus on soybean has been implied (4). Results from the present study do not support this hypothesis. A wide range in virulence among *C. ilicicola* isolates from soybean was found; similar results were reported by Rowe and Beute (23) for peanut isolates. However, the tested cultivars did not show differential responses to individual isolates in laboratory and greenhouse tests, suggesting no evidence for physiologic specialization in this fungus on soybean. Moreover, current results show that virulence in *C. ilicicola* is stable across a range of cultivars. Isolates from soybean and peanut that exhibited high and low levels of virulence maintained their virulence when inoculated to cultivars that ranged from more to less susceptible to red crown rot.

Shifts in relative rankings among soybean cultivars reported by Berner (4) may be explained by several other factors, including differences in levels of virulence in fungal isolates, levels of the fungus inoculum in soil, and uneven distribution of the fungus within the field, all of which may contribute to disease escape. Because soybean cultivars resistant to red crown rot are not available, it may be premature to speculate about race development in this system. Instead, results from the present study suggest some degree of adaptation within isolates of *C. ilicicola* to their original hosts. Using a large number of isolates from both soybean and peanut, virulence on soybean and reduction of fungal growth on PDC of isolates from soybean were significantly higher than that from isolates from peanut. In our preliminary tests (14), soybean isolates produced more perithecia in culture than did peanut isolates, and perithecia production was correlated positively with virulence. These increased virulence and perithecia production of isolates from soybean compared to those from peanut (14) have been considered to be signs of host specialization. A similar phenomenon was documented by Cloud and Rupe (9) who observed that isolates of *M. phaseolina* from soybean, causal agent of charcoal rot on numerous hosts, colonized soybean roots to a greater extent than did isolates from sorghum. Thus they suggest that host specialization was detected only in soybean isolates (9).

Rowe *et al.* (22) inoculated isolates of *C. ilicicola* from soybean and peanut to both hosts and found that they were virulent on both. Later, Hadley *et al.* (11) compared virulence between isolates from the resistant

peanut cultivar NC 3033 and susceptible cultivar Florigiant, mean virulence between isolates from the resistant cultivar and from susceptible hosts was not different. After one cropping cycle, however, isolates from the resistant cultivar NC 3033 showed increased virulence specific to the resistant cultivar whereas this was not detected when isolates from the susceptible hosts were inoculated to the susceptible Florigiant. Therefore, they suggested that host adaptation occurred in this fungus and that this should be considered in developing cultivars resistant to *C. ilicicola* because resistance of a cultivar or its lines may be no longer effective against new isolates with adapted virulence.

Evidence of physiologic specialization was not recognized in this *C. ilicicola*-soybean system, which may result from no selection pressure by cultivars resistant to red crown rot. Wynne *et al.* (29) stated that polygenic, additive genes are involved in resistance of peanut against soilborne fungal pathogens; therefore, appearance of races in the soilborne fungi on peanut may not be possible. This also may explain why physiologic specialization was not detected in our *C. ilicicola*-soybean system. However, greater ability in soybean than peanut isolates to induce disease on soybean suggests that host specialization on soybean may occur in *C. ilicicola*. Therefore, efforts to develop cultivars resistant to red crown rot as described in peanut (26, 29) would be preferable to utilize only virulent isolates from soybean.

요 약

상이한 기주와 지역에서 유래한 *Calonectria ilicicola*에서 병원성 변이 연구는 red crown rot 병 저항성 품종을 육종하는데 유용한 기초자료를 제공하는데 있다. 6개의 콩 품종에 대한 다양한 병원성 변이가 콩과 땅콩에서 각각 분리된 25개의 균주에서 관찰되었다. 콩 균주들은 콩에 대부분 병원성을 나타내었고 이러한 병원성 수준은 품종에 영향을 받지 않고 비교적 안정하였다. 콩에서 분리된 균주들은 땅콩에서 분리된 균주보다 콩에 더 강한 병원성을 나타내었다. 2개의 콩 균주와 2개의 땅콩 균주를 이용하여 실험실과 온실에서 각각 병원성 정도를 비교하여 본 결과, 시험된 모든 콩 품종에서 일정한 병원성을 보여 주었다. 또한 *C. ilicicola* 균주들은 potato dextrose agar(PDA) 배지와 비교하여 볼 때 potato dextrose chlorate (PDC) 배지에서 생장이 감소하였고, 이러한 생장 감소는 땅콩 균주보다 콩 균주에서 더욱 심하게 나타났다. 그러나 PDA에서는 콩 균주와 땅콩 균주

간의 생장의 차이는 관찰되지 않았다. 본 콩-*C. ilicicola* 시스템에서 균의 생리적 분화는 관찰되지 않았으나 콩 균주가 땅콩 균주보다 병원성이 강하고 PDC 배지상의 생장이 느린점 등은 본 균에서 기주 특이성의 존재 가능성을 보여주고 있다.

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