

Host Specificity of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* and *C. truncatum* in the Leguminosae

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Published with the approval of the Director of the Arkansas Agricultural Experiment Station.

We thank D. B. Marx and staff for statistical assistance.

Accepted for publication 23 February 1988 (submitted for electronic processing).

ABSTRACT

Weidemann, G. J., TeBeest, D. O., and Cartwright, R. D. 1988. Host specificity of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* and *C. truncatum* in the Leguminosae. *Phytopathology* 78:986-990.

The host range and virulence of *Colletotrichum gloeosporioides* f. sp. *aeschynomene*, used as the mycoherbicide Collego, and *C. truncatum* were compared on plant species within the Leguminosae. *C. g. aeschynomene* could be differentiated from *C. truncatum* on the basis of host range within the Leguminosae and on virulence within *Pisum sativum* and several other host genera. *C. g. aeschynomene* was pathogenic on species in nine host genera representing five tribes in the Papilionoideae, but was highly

virulent only on *Aeschynomene virginica* and *Lupinus arboreus*. *C. truncatum* was pathogenic on species in six genera in two tribes, but was highly virulent only on *Lathyrus odoratus*, *Vicia ervilia*, and most cultivars of *P. sativum*. Host genera common to both fungi included *Lupinus*, *Indigofera*, *Cicer*, *Lathyrus*, *Lens*, *Vicia*, and *Pisum*. Morphological studies of *C. g. aeschynomene* and *C. truncatum* suggest that *C. pisi* is synonymous with *C. truncatum* and not *C. gloeosporioides*.

Colletotrichum gloeosporioides (Penzig.) Sacc. f. sp. *aeschynomene* is utilized commercially as the mycoherbicide Collego to control the leguminous weed northern jointvetch (*Aeschynomene virginica* (L.) B.S.P.) in rice and soybean fields. Previous host range studies to ensure product safety (2) suggested a restricted host range within the Leguminosae. More recently, however, additional host range tests revealed several additional hosts within the Leguminosae, including *Pisum sativum* L. (pea) (17,25).

Several other *Colletotrichum* species have been reported to infect pea, including *C. pisi* Pat. (12), *C. truncatum* (Schw.) Andrus and Moore (1), and *C. destructivum* O'Gara (11,18). Von Arx (21) placed *C. pisi* in synonymy with *C. gloeosporioides*. However, other investigators (18,22) have suggested that *C. pisi* is synonymous with *C. truncatum*. Previous host range studies with *C. gloeosporioides*, *C. pisi*, and *C. truncatum* (8,9,10,15,18,21,25) have demonstrated numerous hosts within the Leguminosae.

Because *C. g. aeschynomene* was found to be pathogenic to pea, clarification was needed on the relationship of *C. g. aeschynomene* to the causal agent of pea anthracnose and the taxonomic

relationship of *C. pisi* to *C. truncatum* and *C. gloeosporioides*. These studies were conducted to compare *C. g. aeschynomene* to *C. truncatum* obtained from *P. sativum* on the basis of conidial morphology and host range within the Leguminosae.

MATERIALS AND METHODS

The commercial isolate of *C. g. aeschynomene* (ATCC 20358) obtained from diseased *Aeschynomene virginica* was used in all experiments. Three isolates of *Colletotrichum* spp. from pea were obtained from the following sources: isolate 240 (ATCC 64197, IMI 317934), obtained from diseased pea from Antigo, WI; isolate 167, obtained from D. J. Hagedorn; and isolate 211 (ATCC 12520), obtained from the American Type Culture Collection, Rockville, MD. Isolates 240 and 167 were identified as *C. truncatum*, sensu Sutton, and both were used for morphological comparisons. The identity of isolate 240 was confirmed as *C. truncatum* by J. E. M. Mordue (*pers. commun.*) and was used for host range studies. Isolate 167 was not used for host range studies because of low aggressiveness, even after passage through *P. sativum*. The morphology of the isolate obtained from the American Type Culture Collection (ATCC 12520) did not conform to the published description of *C. truncatum* or *C. pisi* and was

deleted from the study. All isolates were maintained in glycerol-skim milk at -80 C.

Conidial inoculum of all isolates was produced on pea juice agar plates (400 ml of canning liquid from commercial, salt-free, canned peas, 20 g of agar, and 600 ml of distilled water) seeded with conidia from 5- to 7-day-old cultures. Plates were incubated on a laboratory bench with 12 hr of supplemental, cool white fluorescent lighting at ambient air temperature (25 C). After 5-7 days, conidia were washed from the plates with distilled water, vacuum filtered through Whatman no. 4 filter paper, and resuspended in distilled water. Conidial suspensions were standardized at 2×10^6 spores per ml by using a hemacytometer.

Four replicates of three to four plants per replicate were seeded in a steam-pasteurized soil mixture in 10-cm plastic pots. An additional pot of each test plant was used as a control. Plants were maintained in the greenhouse with 15 hr of supplemental fluorescent lighting until they developed at least two fully expanded true leaves. Single pots of *A. virginica* and pea (cultivar Mammoth Melting Sugar) were inoculated in all tests as susceptible checks for *C. g. aeshynomene* and *C. truncatum*, respectively. Inoculations were repeated for all members of host genera that included species susceptible to either *C. g. aeshynomene* or *C. truncatum*.

Plants were inoculated to runoff with an atomizer and placed in a dew chamber at 28 C for 24 hr, returned to the greenhouse, and arranged in a randomized complete block design. All plants were

examined for disease symptoms weekly for 3 wk. Plants were rated as immune if no symptoms were found and susceptible if lesions were found. Also, plants were rated weekly for disease severity (D.S.) for 3 wk as follows: 0 = no disease, 1 = 1-25% of the plant tissue diseased, 2 = 26-50% diseased, 3 = 51-75% diseased, 4 = 76-100% plant diseased, and 5 = plant death.

After final ratings were obtained, three to four representative lesions were excised from each replicate, placed in moist chambers overnight, and observed for sporulation. Conidial masses, if present, were reisolated to test for cross-contamination.

Of the three subfamilies in the Leguminosae, 82 species representing 48 genera and 24 tribes were inoculated with *C. g. aeshynomene* and *C. truncatum* (Table 1). Several cultivars or accessions were tested for certain species.

Morphological comparisons were made from conidia obtained from agar cultures and mounted in distilled water. Comparisons of hyphal appressoria were made from slide cultures on potato-carrot agar (19).

Data were subjected to analysis of variance and, where appropriate, treatment means were compared by using Duncan's multiple range test at the 5% level of confidence.

RESULTS

Both fungi were pathogenic to only certain species in the subfamily Papilionoideae (Table 2). Within this subfamily, *C. g.*

TABLE 1. Taxa within the Leguminosae inoculated with *Colletotrichum gloeosporioides* f. sp. *aeshynomene* and *C. truncatum*

Subfamily	Tribe	Genus	Species ^a	Subfamily	Tribe	Genus	Species					
Caesapinoideae	Cassieae	<i>Cassia</i>	<i>fasciculata</i>			<i>Erythrina</i>	<i>coraliodendrum</i>					
			<i>obtusifolia</i>			<i>Galactia</i>	<i>jussiae</i>					
Mimosoideae	Cerceae	<i>Cercis</i>	<i>canadensis</i>			<i>Glycine</i>	<i>max</i> (7)					
	Acacieae	<i>Acacia</i>	<i>farnesiana</i>			<i>Phaseolus</i>	<i>lunatus</i> (3)					
	Ingeae	<i>Albizia</i>	<i>julibrissin</i>			Phaseoleae	<i>Psophocarpus</i>	<i>tetragonolobus</i>				
	Mimoseae	<i>Desmanthus</i>	<i>depressus</i>				<i>Pueraria</i>	<i>thunbergiana</i>				
			<i>illinoensis</i>				<i>Rhynchosia</i>	<i>minima</i>				
Papilionoideae	Aeshynomeneae	<i>Aeshynomene</i>	<i>americana</i>			<i>Vigna</i>	<i>sesquipedalis</i>					
			<i>falcata</i>			<i>cinerea</i>						
			<i>indica</i> ^b			<i>Psoralea</i>	<i>sinensis</i> (2)					
			<i>sensitiva</i> ^b			Psoraleae	<i>Robinia</i>	<i>pseudoacacia</i>				
			<i>villosa</i>				Sesbanieae	<i>Glottidium</i>	<i>vesicarium</i>			
							<i>Arachis</i>	<i>hypogaea</i> (2)	Tephrosieae		<i>Sesbania</i>	<i>exaltata</i>
								<i>Stylosanthes</i>			<i>guianensis</i>	<i>Tephrosia</i>
							<i>Zornia</i>	<i>diphyllum</i>				<i>virginiana</i>
								<i>fruticosa</i>				Thermopsidae
			Amorpheae				<i>Amorpha</i>	<i>arietinum</i> (3) ^{b,c}	Trifolieae		<i>Baptisia</i>	
	Cicereae		<i>Cicer</i>	<i>varia</i>	<i>Medicago</i>	<i>sativa</i> (3)						
	Coronilleae		<i>Coronilla</i>	<i>sativum</i>			<i>Melilotus</i>	<i>alba</i>				
	Crotalariaeae		<i>Crotalaria</i>	<i>tortuosum</i>			<i>Trifolium</i>	<i>officinale</i>				
	Desmodieae		<i>Desmodium</i>	<i>stipulacea</i>	Vicieae			<i>hirtum</i>				
				<i>arborescens</i>				<i>Lens</i>	<i>esculenta</i> (5) ^{b,c}			
				<i>Lespedeza</i>				<i>aethnensis</i>	<i>Pisum</i>	<i>sativum</i> (32) ^{b,c}		
	Galegeae		<i>Colutea</i>	<i>albus</i> ^b							<i>Vicia</i>	<i>benghalensis</i> ^{b,c}
	Genisteae		<i>Genista</i>	<i>arborescens</i> ^{b,c}							<i>regalis</i> ^{b,c}	<i>ervilia</i> ^{b,c}
				<i>nanus</i> ^{b,c}							<i>texensis</i>	<i>faba</i> (3) ^{b,c}
			<i>Lupinus</i>	<i>polyphyllus</i> ^b							<i>junceum</i>	<i>narboensis</i> ^{b,c}
				<i>regalis</i> ^{b,c}							<i>hirsuta</i> ^{b,c}	<i>pannoiae</i> ^{b,c}
				<i>regalis</i> ^{b,c}							<i>tinctoria</i> ^b	<i>sativa</i> (3) ^b
				<i>arborescens</i> ^{b,c}							Indigoferae	<i>Spartium</i>
	<i>nanus</i> ^{b,c}	<i>corniculatus</i>										
				<i>polyphyllus</i> ^b	Loteae						<i>lablab</i>	
				<i>regalis</i> ^{b,c}							<i>tetragonolobus</i> ^b	
				<i>arborescens</i> ^{b,c}				<i>ensiformis</i>				
				<i>nanus</i> ^{b,c}				<i>pubescens</i>				
				<i>polyphyllus</i> ^b				<i>ternatea</i>				
				<i>regalis</i> ^{b,c}	Phaseoleae			<i>biflorus</i>				
<i>arborescens</i> ^{b,c}				<i>Canavalia</i>								
<i>nanus</i> ^{b,c}				<i>Centrosema</i>								
<i>polyphyllus</i> ^b				<i>Clitoria</i>								
			<i>regalis</i> ^{b,c}				<i>lablab</i>					
			<i>arborescens</i> ^{b,c}				<i>Dolichos</i>					

^a The number of cultivars or accessions tested if greater than one are indicated in parentheses.

^b Includes species, cultivars, or accessions susceptible to *C. g. aeshynomene*.

^c Includes species, cultivars, or accessions susceptible to *C. truncatum*.

aeschyromene was pathogenic on species from nine genera representing five tribes; however, it was highly virulent (D.S. > 3.5) only on *A. virginica* and *Lupinus arboreus*. *C. truncatum* was pathogenic on species from six genera in two tribes, but was highly virulent (D.S. > 3.5) only on *Lathyrus odoratus*, *Vicia ervilia*, and most cultivars of *P. sativum*. *A. virginica* was killed by *C. g. aeschyromene*, but was immune to *C. truncatum*. Host genera common to both *C. g. aeschyromene* and *C. truncatum* included *Lupinus*, *Indigofera*, *Cicer*, *Lathyrus*, *Lens*, *Vicia*, and *Pisum*. All genera tested in the tribe Viciae contained species susceptible to both pathogens. However, not all species within *Lathyrus* and *Vicia* were susceptible to both pathogens and, in some cases, not all cultivars or accessions within a species were susceptible.

On pea, *C. truncatum* exhibited a mean disease rating significantly greater than *C. g. aeschyromene* for all varieties tested (Table 3). Only the cultivars Maestro and Laxton's Progress showed moderate resistance (D.S. ≤ 3) to *C. truncatum*. *C. g. aeschyromene* was virulent to 29 of 32 pea cultivars tested, but produced appreciable levels of disease (D.S. = 2.3) only on Mammoth Melting Sugar. The pea cultivars Grenadier, Little Marvel, and Oregon Sugar Pod were found to be immune to *C. g. aeschyromene*.

C. g. aeschyromene could be readily differentiated from *C. truncatum* on the basis of conidial and appressorial morphology (Fig. 1), as well as host range (Table 2). Conidia of *C. g. aeschyromene* measured 10–26 × 4–8 μm and were straight with obtuse apices. Hyphal appressoria were smooth to slightly lobed, measuring 6–12 μm in diameter. Conidia of *C. truncatum*

measured 14–20 × 4–6 μm and were falcate with obtuse to slightly truncate apices. Hyphal appressoria were smooth to slightly lobed, 4–8 × 6–16 μm, forming complex clusters of appressoria.

DISCUSSION

C. g. aeschyromene and *C. truncatum* represent distinct taxa with overlapping host ranges. *C. g. aeschyromene* was highly virulent (D.S. ≥ 3.5) only on *A. virginica* and a single species of *Lupinus*, whereas *C. truncatum* was highly virulent only on *P. sativum*, *V. ervilia*, and *L. odoratus*. Both *C. g. aeschyromene* and *C. truncatum* were pathogenic on most pea cultivars tested, but differed markedly in virulence.

The respective host ranges of each pathogen appeared unrelated to suggested phylogenetic relationships in the Papilionoideae, although susceptible taxa represented more advanced tribes within that subfamily (13). Tribes containing susceptible taxa could not be correlated with several common morphological or phytochemical features (4,5,7,14).

El-Gazzar (3) examined records of *Uromyces* incidence on legumes and correlated susceptibility to the phylogenetic groups proposed by Polhill (13). Based on host specificity of *Uromyces* spp., El-Gazzar divided the Leguminosae into two large subgroups. Both pathogens tested in this study would be placed into one of El-Gazzar's legume subgroups, with the exception of the susceptibles within the genus *Aeschynomene*. The tribe Aeschynomeneae is considered to be distantly related to the other tribes containing susceptible taxa, possibly suggesting different

TABLE 2. Mean disease severity rating of members of the Papilionoideae inoculated with *Colletotrichum gloeosporioides* f. sp. *aeschyromene* and *C. truncatum*

Genus	Species	Cultivar or accession	Disease severity rating ^{a,c}		
			<i>C. g. aeschyromene</i>	<i>C. truncatum</i>	
<i>Aeschynomene</i>	<i>indica</i>		1.2 de	0.0 k	
	<i>sensitiva</i>		1.0 defg	0.0 k	
	<i>virginica</i>		5.0 a	0.0 k	
<i>Cicer</i>	<i>arietinum</i>	Henry Field	1.0 defg	1.3 ghi	
		458870	0.8 fgh	1.1 hi	
		452611	0.8 fgh	1.0 hij	
<i>Indigofera</i>	<i>hirsuta</i>		0.7 fgh	1.0 hij	
		<i>tinctoria</i>	1.1 def	0.0 k	
<i>Lathyrus</i>	<i>odoratus</i>	Early multiflora gigantea	1.0 defg	4.9 a	
<i>Lens</i>	<i>esculenta</i>	477921	1.0 defg	2.4 cd	
		477923	1.0 defg	0.9 hij	
		477920	1.0 defg	1.4 fgh	
		477922	1.0 defg	2.0 def	
		486127	0.7 ghi	2.2 cde	
<i>Lotus</i>	<i>tetragonolobus</i>		1.0 defg	0.0 k	
<i>Lupinus</i>	<i>albus</i>	Arkansas 10	1.2 d	0.0 k	
		<i>arboreus</i>	3.5 b	1.0 hij	
		<i>nanus</i>	2.7 c	0.7 ij	
	<i>polyphyllus</i>	Russell	<i>regalis</i>	1.2 d	0.0 k
				0.9 efgh	0.4 jk
<i>Vicia</i>	<i>benghalensis</i>		1.0 defg	1.0 hij	
		<i>ervilia</i>	2.6 c	3.9 b	
	<i>faba</i>	Burpee 5083-1	0.7 fgh	1.7 efg	
		458603	1.0 defg	2.7 c	
		221517	0.5 hi	1.8 defg	
	<i>narboensis</i>	<i>pannoiae</i>		1.0 defg	2.0 def
				1.0 defg	1.0 hij
				0.4 i	0.0 k
<i>sativa</i>	205326	0.0 j	0.0 k		
	284372	0.6 hi	0.0 k		
	187012				
<i>Pisum</i>	<i>sativum</i> ^c		0.9 defg	4.7 a	

^a Disease severity rating system: 0 = no disease, 1 = 1–25% of the plant tissue diseased, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%, 5 = plant death. Final ratings were made 3 wk after inoculation. Numbers represent means of four replications.

^b Numbers in each column followed by the same letter do not differ significantly at P = 0.05 according to Duncan's multiple range test.

^c Mean of 32 cultivars.

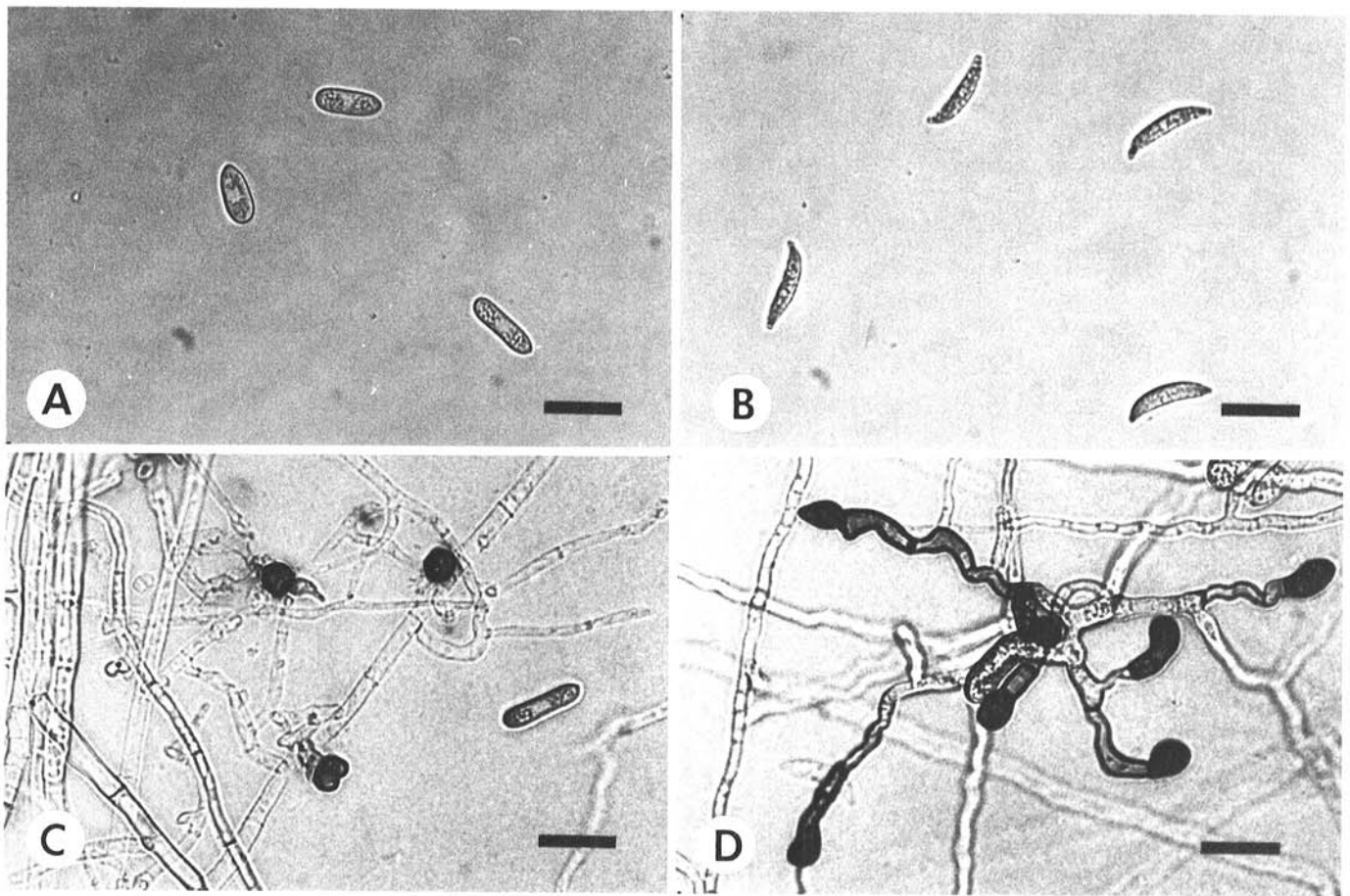


Fig. 1. Conidia and hyphal appressoria of *Colletotrichum* species infecting peas. A and C, *Colletotrichum gloeosporioides* f. sp. *aeshynomene*; B and D, *Colletotrichum truncatum* (bar = 15 μ m).

mechanisms of resistance or susceptibility, the independent development of similar mechanisms, or parallel development from a common ancestor (20).

To meet regulatory requirements and to ensure safety to nontarget hosts, current host range testing of bioherbicides generally follows the testing scheme proposed by Wapshere (23,24). The scheme is based on testing taxonomically closely related host plants first and then progressing toward more distantly related taxa, in addition to testing important cultivated plants, until the host range of the pathogen is circumscribed. The protocol generally presupposes a close phylogenetic relationship for host-parasite interactions. By using this protocol, Hasan (6) tested the ecologically obligate parasite, *Puccinia chondrillina*, on *Chondrilla juncea* and other composites, as well as numerous cultivated plants unrelated to the target weed. The scheme has also been used to test several insect pests of weeds (24). Whereas the present study suggests that phylogenetic testing is generally valid, careful consideration must be given to the potential lack of specificity of facultative parasites among phylogenetically related taxa. For instance, *C. g. aeshynomene* was pathogenic to several *Aeschynomene* species, yet the tribe Aeschynomeneae is considered distantly related to the other susceptible taxa within the subfamily (13). Care must be taken to test numerous available representatives within the highest taxonomic rank in which the pathogen is detected, particularly with cultivated plants within the group.

The taxonomic relationships of *Colletotrichum* species on pea remain unclear. At least three species of *Colletotrichum* are reported to be pathogenic to pea. Patouillard (12) originally described *C. pisi* from pea and illustrated conidia as fusiform and somewhat falcate. Jones (9) later examined the type and illustrated *C. pisi* with falcate conidia. Von Arx (21), however, included *C. pisi* as a synonym for *C. gloeosporioides*, which has straight conidia. Conidial size and morphology for *C. truncatum*

determined in the present study match those reported by Jones (9). Walker (22) considered *C. pisi* to be synonymous with *C. truncatum* as described by Andrus (1). Pending additional studies, *C. pisi* should be considered synonymous with *C. truncatum* and not *C. gloeosporioides*, as reported by von Arx (21).

The taxonomic status of *C. truncatum* and *C. dematium* on pea is also uncertain. Von Arx (21) divided *C. dematium* into three forms, with *C. dematium* f. sp. *truncatum* for isolates pathogenic to legumes. Sutton (16) retained *C. truncatum* as described by Andrus (1), but indicated that the *C. dematium* complex was in need of further revision. *C. dematium* was retained for saprophytic isolates with narrow, falcate conidia, whereas *C. capsici* (Syd.) Butl. and Bisby was retained for pathogenic isolates with wider conidia. Conidial measurements of 14–20 \times 4–6 μ m obtained in the current study are similar to those reported by Sutton (16) for *C. truncatum* but wider than those reported for *C. dematium*. Tiffany (18) differentiated several isolates of *C. truncatum* from legumes on the basis of conidial size and host preference, but did not consider the differences sufficient to delimit them as separate species. In the present study, isolates of *C. truncatum* obtained from pea could be differentiated from published descriptions of *C. dematium* on the basis of conidial size and cultural characteristics similar to that reported by Tiffany (18). Additional studies with isolates from representative legumes are needed to clarify the taxonomic status of *C. truncatum* and *C. dematium* on the Leguminosae and their relationship to *C. capsici*.

The relationship of plant parasitism to taxonomy in the genus *Colletotrichum* is uncertain because of the lack of good morphological features for comparison and the presence of numerous subspecific taxa that may vary in pathogenicity and host range. The potential of *Colletotrichum* species as bioherbicides and as model systems for studying host-parasite interactions necessitates a more thorough understanding of taxonomic and genetic relationships within the genus.

TABLE 3. Mean disease severity rating of cultivars of *Pisum sativum* inoculated with *Colletotrichum gloeosporioides* f. sp. *aeschyromene* and *C. truncatum*

Cultivar	Disease severity rating ^a	
	<i>C. g. aeschyromene</i>	<i>C. truncatum</i>
Alaska	0.9	5.0
Alderman	0.8	4.9
Blue Bantam	1.0	4.0
Burpeeana Early	0.8	4.1
Early Alaska	0.7	5.0
Early Perfection	0.8	5.0
Early Snap Sugar	1.0	4.8
Extra Early Alaska	1.0	5.0
Freezonian	1.0	5.0
Green Arrow	1.0	5.0
Grenadier	0	4.6
Laxton's Progress	1.0	2.9
Little Marvel	0	4.3
Maestro	1.0	2.4
Mannoth Melting Sugar	2.3	5.0
Mars	1.0	3.8
Miragreen	1.0	5.0
Novella II	0.9	4.7
Oregon Sugar Pod	0	5.0
Patriot	1.0	5.0
Perfection Darkseeded	0.9	5.0
Progress #9	1.0	4.9
Snowbird	1.0	5.0
Sparkle	1.0	4.9
Sugar Ann	0.8	5.0
Sugar Bon	0.9	5.0
Sugar Snap	1.0	5.0
Sweet Snap	1.2	5.0
Thomas Laxton	1.3	5.0
Venus	0.8	5.0
Victory Freezer	1.0	5.0
Wando	0.9	4.8

^aDisease severity rating system: 0 = no disease, 1 = 1–25% of the plant tissue diseased, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%, 5 = plant death. Final ratings were made 3 wk after inoculation. Numbers represent means of four replications.

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