Frequency of *Colletotrichum* Species Causing Bitter Rot of Apple in the Southeastern United States

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ABSTRACT

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The occurrence and frequency of *Colletotrichum* spp. were determined by sampling 980 apple fruit from orchards in Arkansas, North Carolina, and Virginia in 1992 and 1993. *Colletotrichum* and *Botryosphaeria* spp. were recovered from 78.8 and 21.2% of the sampled fruit, respectively. Conidial and colony morphology, growth rate, and perithecial production were used to characterize the *Colletotrichum* spp. Based on conidial morphology, 68.6% of isolates were identified as *C. acutatum* and 31.4% as *C. gloeosporioides*. The *C. acutatum* isolates produced hyaline, elliptic-fusiform conidia tapered at one or both ends, whereas isolates of *C. gloeosporioides* produced hyaline oblong conidia with obtuse or rounded ends. Among the *C. gloeosporioides* isolates, 42.1% of monoconidial cultures produced the *Glomerella cingulata* teleomorph. None of the isolates identified as *C. acutatum* produced an ascigerous stage. All isolates of *C. acutatum* had a significantly slower growth rate on potato dextrose agar (PDA) than did isolates of *C. gloeosporioides* and *G. cingulata*. Among the isolates of *C. acutatum*, 90% were characterized as "chromogenic types" producing a distinct ruby red pigmentation on PDA. However, the ruby red colony color was not diagnostic for species identification as there were some isolates of *C. acutatum* that produced colonies orange to dark brown in color on PDA. The chromogenic isolates were only found among the isolates identified as *C. acutatum*. Of the *Botryosphaeria* spp. recovered, 84.1 and 15.9% of the isolates were identified as *B. dothidea* and *B. obtusa*, respectively. The majority of *Botryosphaeria* isolates were recovered from fruit with small (<0.5 cm in diameter), nondescript lesions. Among the bitter rot pathogens, three taxa, *C. acutatum*, *C. gloeosporioides*, and *G. cingulata*, could be distinguished. Based on this survey, there was considerable orchard-to-orchard variation in the frequency of the *Colletotrichum* spp. recovered.

Additional keyword: *Malus domestica*, vegetative compatibility

Fruit-rot diseases of apple (*Malus domestica* Borkh.) are economically important in the southeastern United States and can cause substantial yield losses during periods of warm, wet weather (27). Several fungi are involved in fruit rot diseases of apple. *Glomerella cingulata* (Stoneman) Spaulding & H. Schrenk (anamorph: *Colletotrichum gloeosporioides* (Penz.) Penz & Sacc. in Penz.) and *C. acutatum* J. H. Simmonds cause bitter rot of apples (27). Bitter rot symptoms often appear as circular lesions with the fungal reproductive structures often in concentric rings on the fruit surface. Reproductive structures of the bitter rot pathogens can include acervuli, perithecia or both. Internal "V"-shaped lesions also can be found when the fruit are cut open (27). *Botryosphaeria dothidea* (Moug.:Fr.) Ces. & De Not. causes white rot and *Botryosphaeria obtusa* (Schwein.) Shoemaker causes black rot of apple (5,15,30). White rot can be confused with black rot as the fruit symptoms often are very similar. White rot lesions appear water soaked and are soft and sunken while black rot lesions tend to be firm and dark brown. Also, when lesions are small (<0.5 cm), it is often difficult to distinguish white and black rot from bitter rot based on symptoms.

There is considerable uncertainty in the literature concerning the *Colletotrichum* spp. involved in fruit rots of apple. Most isolates examined in previous studies have been classified as *G. cingulata* (anamorph: *C. gloeosporioides*) (6,14,19,21,22,28,29). Struble and Keitt (25) originally recognized a considerable degree of diversity among the bitter rot pathogens and described seven different types of *G. cingulata* based on cultural morphology. The asexual conidial and "chromogenic" types were considered to be the most common. The conidial types were described as gray-green in color on potato dextrose agar (PDA) whereas the chromogenic types typically were pink to dark red on PDA (27). Plus and minus perithecial types also have been described based on colony color, distribution of perithecia, and relative abundance of conidia (24–27). The minus perithecial types generally produced perithecia in clusters of two to three whereas the plus perithecial types generally produced perithecia in scattered masses. More recently, both *G. cingulata* and *C. acutatum* have been recognized as apple bitter rot pathogens (3,8,9,27). In earlier studies, asexual spore shape, an important identification criterion to differentiate *C. acutatum* from *C. gloeosporioides*, was often not used. Thus, no recent studies have systematically examined the frequency of the various taxa involved in fruit-rot diseases of apple.

Accurate identification of the taxa involved in fruit diseases of apple and information on the frequency of their occurrence within orchards is crucial for improving screening methods in breeding programs as well as for developing management practices to control fruit-rot diseases of apple. For example, the various *Colletotrichum* spp. involved in fruit rot of apples, as well as other hosts, have been shown to differ in fungicide sensitivity (3,20), virulence (21), and important epidemiological parameters such as sporulation (Y. Shi et al., unpublished).

The objective of this research was to examine the occurrence and frequency of *Colletotrichum* spp. causing bitter rot of apples in several orchards in the southeastern United States. Particular attention was given to taxonomic criteria of the *Colletotrichum* spp. involved in causing bitter rot of apples. Preliminary reports of this research have been published (8,9).

MATERIALS AND METHODS

Orchards sampled. A total of 980 apples with fruit rot symptoms were collected in 1992 and 1993. Fruit with definitive bitter rot symptoms were recovered from all orchards except the two in Virginia. However, isolations were performed on some fruit with small (<0.5 cm in diameter), nondescript lesions from all orchards. Isolations were performed from such lesions to prevent introducing a bias for a particular *Colletotrichum* spp. The majority of the fruit from three orchards (Forrest City, AR, VPI Research Station, VA, and Winchester, VA) had small, nondescript lesions.

Symptomatic apples were collected from three orchards in Arkansas and one in North Carolina in 1992 and from two orchards in Arkansas, three in North Carolina, and two in Virginia in 1993. In Arkansas, North Carolina, and Virginia, one of the sample locations was a commercial

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apple orchard and the others were experimental apple orchards. Samples from Arkansas were collected by sampling one to four symptomatic fruit from one to four different locations per tree in each orchard. In Arkansas, the cultivars sampled were Idared and Spigold (Fayetteville) and Golden Delicious and AA-62 (Forrest City). Several unnamed apple selections were sampled from the Clarksville, AR, location. The fruit from North Carolina consisted of the cultivars Golden and Red Delicious. In Virginia, the apples sampled included Golden Delicious, Granny Smith, York Imperial, and Rome Beauty.

Pathogen isolation. The fruit surface of symptomatic apples was sterilized by wiping with 70% ethanol. Isolations were made under aseptic conditions by, first, removing the peel, and recovering several 3 to 5 mm^3 pieces of fruit tissue from the lesion margin. Symptomatic tissue was then placed onto PDA. PDA plates were incubated at 25°C under a 12-h light/dark cycle in which light was provided with four 40-watt cool-white fluorescent lights. Fungal colonies emerging from the tissue pieces were hyphal-tip-transferred onto new PDA plates and stored desiccated on filter paper at 4°C (7).

Pathogen identification. *Colletotrichum* spp. were distinguished by examination of conidia. The majority of the conidia from any given isolate of *C. acutatum* were hyaline and elliptic-fusiform in shape, being tapered at one or both ends, whereas conidia of *C. gloeosporioides* were hyaline and oblong in shape, being obtuse or rounded at both ends (2,11,26,27,31). All isolates were further characterized by colony color, by growing cultures on PDA for 2 to 4 weeks. Color standards from the Methuen Handbook of Colour (13) were used as references. Isolates that produced colonies with any red pigmentation (reddish orange to ruby red) when viewed from the reverse side of a PDA plate were designated chromogenic. Isolates that produced no red pigmentation were designated nonchromogenic. Isolates that produced a *C. gloeosporioides* conidial stage were further characterized by their ability to produce perithecia, asci, and ascospores of the teleomorph *G. cingulata*. Single conidia were recovered from these isolates and the isolates were grown on PDA, as previously described, for 6 weeks. Isolates that produced perithecia, asci, and ascospores under these conditions were designated *G. cingulata*.

Species of *Botryosphaeria* also were distinguished by examination of their conidia (27). *B. dothidea* produced narrow, pointed, light color conidia while *B. obtusa* had truncated, dark conidia (27).

Growth rate. Thirty-five isolates of *C. gloeosporioides*, *G. cingulata*, and *C. acutatum* were examined for growth rate. Isolates were selected to maximize diversity based on colony color, morphology, vegetative compatibility group, and mitochondrial DNA restriction fragment length polymorphisms (RFLPs) (8,9). Mycelial plugs, 0.4 cm in diameter, were cut with a cork borer from the perimeter of a colony growing on PDA. The plugs were placed in the center of a petri dish (9 cm diameter) containing PDA. All cultures were incubated as previously described at 24 ± 3°C. The colony diameter was measured after 3 and 6 days. Each isolate was grown on three replicate plates. The experiment was repeated once. The mean colony diameter after 6 days was analyzed by means of Duncan's multiple range test.

RESULTS

Pathogen isolation, identification, and distribution. A single fungal isolate was recovered from each of the 980 symptomatic fruit. The majority of the isolates recovered (78.8%, 772/980) were *Colletotrichum* spp. (Table 1). On the basis of asexual conidial morphology, 31.3% (242/772) of these isolates were identified as *C. gloeosporioides* while 68.7% (530/772) were identified as *C. acutatum*. Isolates of *C. gloeosporioides* had hyaline conidia with the majority of the conidia from a given isolate being oblong in shape, with obtuse or rounded ends (Fig. 1A and B). Isolates of *C. acutatum* produced hyaline conidia with the majority of the conidia being elliptic-fusiform in shape, tapered at one or both ends (Fig. 1C and D).

Among the isolates with a *C. gloeosporioides* conidial stage, 42.1% (102/242) of the monoconidial cultures produced abundant, fertile perithecia of *G. cingulata* (Table 1). The majority of the isolates of *C. gloeosporioides* (57.9%, 140/242) did not produce any perithecia on PDA.

A considerable range in colony color was observed among the isolates identified as *C. acutatum*. The colony color, when viewed from the reverse side of a 2- to 4-week-old PDA dish, ranged from light brown to dark brown, light orange to reddish orange to cherry red, brownish red to maroon, and ruby red to port wine (13). The majority of the isolates also had alternating concentric rings of lighter and darker shades of these colors. Due to the range in colony colors, only colonies producing reddish orange to port wine pigmentation were characterized as chromogenic. Of the isolates identified as *C. acutatum*, 79.6% (422/530) were identified as chromogenic types and more than 90% of the chromongenic isolates produced a ruby red or port wine colony color in culture. None of the isolates of *C. gloeosporioides* or *G. cingulata* examined produced any red pigmentation in culture.

The isolates of *C. gloeosporioides* generally produced white to gray mycelium with orange spore masses in concentric rings. These isolates were similar in colony morphology to some of the nonchromogenic isolates of *C. acutatum*. The isolates of *G. cingulata* produced gray to olive-

Table 1. Isolation frequency of fruit-rot pathogens recovered from apple in the southeastern United States

			Number (and %) of isolates					
			Colletotrichum acutatum		*Glomerella*	*C.*	*Botryosphaeria*	
Orchard location[w]	Sample date	Fruit sampled	C[x]	NC[x]	*cingulata*[y]	*gloeosporioides*	*dothidea*	*B. obtusa*
Clark, AR	8/24/92	89	36 (40.5)[z]	27 (30.3)	3 (3.4)	0 (0)	18 (20.2)	5 (5.6)
Clark, AR	7/26/93	108	79 (73.2)	17 (15.7)	1 (0.9)	0 (0)	9 (8.3)	2 (1.9)
Fay, AR	8/26/92	117	80 (68.4)	30 (25.6)	6 (5.1)	1 (0.9)	0 (0)	0 (0)
Fay, AR	8/30/93	242	168 (69.4)	29 (12.0)	16 (6.6)	0 (0)	11 (4.6)	18 (7.4)
SRS, NC	9/13/93	29	17 (58.6)	4 (13.8)	6 (20.7)	0 (0)	2 (6.9)	0 (0)
CCRS, NC	9/16/92	118	2 (1.7)	0 (0)	0 (0)	114 (96.6)	2 (1.7)	0 (0)
CCRS, NC	9/13/93	22	0 (0)	0 (0)	0 (0)	22 (100)	0 (0)	0 (0)
CNC, NC	9/13/93	55	0 (0)	0 (0)	53 (96.4)	0 (0)	1 (1.8)	0 (1.8)
FC, AR	9/10/92	95	21 (22.1)	1 (1.0)	17 (17.9)	3 (3.2)	49 (51.6)	4 (4.2)
VPI, VA	10/13/93	50	19 (38.0)	0 (0)	0 (0)	0 (0)	31 (62.0)	0 (0)
Farm, VA	10/13/93	55	0 (0)	0 (0)	0 (0)	0 (0)	52 (94.6)	3 (5.4)

[w] Clark = experimental orchard, Clarksville, AR; Fay = Rom commercial orchard, Fayetteville, AR; FC = commercial orchard, Forrest City, AR; SRS = SandHills Research Station, Jackson Springs, NC; CNC = Clayton commercial orchard, Jackson Springs, NC; CCRS = Central Crops Research Station, Clayton, NC; VPI = VPI Research Station, Winchester, VA; FARM = commercial farm, Winchester, VA.

[x] [b]C and NC refer to chromogenic and nonchromogenic isolates of *C. acutatum*, respectively.

[y] Monoconidial isolates of *C. gloeosporioides* that produced the ascigerous stage of *G. cingulata* on potato dextrose agar after 2 to 4 weeks.

[z] Number of isolates recovered and percentage (%) of total.

colored colonies with orange spore masses below the aerial mycelium. Macroscopically, perithecia appeared as dark granular masses embedded within or on the agar surface. None of the isolates of *C. acutatum* produced the ascigerous stage.

Colletotrichum spp. were the predominant fruit-rot pathogens recovered from five of the eight orchards sampled and from eight of the 11 samples taken (Table 1). Of the *Colletotrichum* spp. recovered, *C. acutatum* was the predominant species in two orchards in Arkansas (Fayetteville and Clarksville) in both 1992 and 1993 and in one orchard in North Carolina (Sand Hills Research Station). The majority of the isolates were chromogenic types. *C. gloeosporioides* was the predominant pathogen in one orchard in North Carolina (Central Crops Research Station), representing 96.4 and 100% of the isolates recovered in 1992 and 1993, respectively. Although isolates of *G. cingulata* were recovered from five of the eight orchards sampled, *G. cingulata* only predominated in a single orchard (Clayton commercial orchard) in North Carolina sampled in 1993.

Of the *Botryosphaeria* isolates recovered, 84.1% (175/208) were identified as *B. dothidea* and 15.9% (33/208) as *B. obtusa* (Table 1). Of the 208 isolates of *Botryosphaeria* recovered, the majority (67%) were recovered from 3 orchards, namely, Forrest City, AR, VPI Research Station, VA, and Winchester, VA. Either all, or the majority of the fruit sampled from these three locations had very small (<0.5 cm) lesions.

B. dothidea was the predominant pathogen in three orchards (Forrest City, AR, VPI Research Station, VA, and a commercial farm in VA). No *Colletotrichum* spp. were recovered from one orchard (a commercial farm in Virginia) while neither *Botryosphaeria* sp. was recovered from two locations (Fayetteville, AR, in 1992 and Central Crops Research Station, NC, in 1993).

Growth rate. A considerable range in growth rates was observed among the isolates of *G. cingulata*, *C. gloeosporioides*, and *C. acutatum* (Table 2). All *C. acutatum* isolates grew significantly ($P = 0.05$) slower than all the isolates of *G. cingulata* and *C. gloeosporioides*. After 6 days, the colony diameter of all *C. acutatum* isolates was ≤51 mm whereas all of the isolates of *G. cingulata* and *C. gloeosporioides* had colony diameters ≥54 mm. With the exception of FA173, *G. cingulata* and *C. gloeosporioides* isolates had a colony diameter ≥64 mm. FA173 was an atypical *G. cingulata* isolate in that it grew with a very irregular colony margin.

DISCUSSION

Colletotrichum spp. were recovered from 79% of the fruit sampled. Conidial morphology and colony growth rate were very useful criteria for species identification among the *Colletotrichum* isolates from apple. All isolates of *C. gloeosporioides* and *G. cingulata* from apple tested produced hyaline conidia with the majority of the conidia being oblong in shape with obtuse or rounded ends. In contrast, isolates of *C. acutatum* produced hyaline conidia with the majority of the conidia being elliptic-fusiform with tapered ends. A genetically diverse collection of apple isolates of *C. gloeosporioides* and *G. cingulata*, representing different vegetative compatibility groups and mtDNA RFLP haplotypes (8,9), also grew significantly faster than isolates of *C. acutatum* from apple (Table 2).

Table 2. Growth of apple isolates of *Colletotrichum acutatum*, *C. gloeosporioides*, and *Glomerella cingulata* on potato dextrose agar

Isolate	Species	Mean diameter (mm)[x]
A98	*G. cingulata*	74.5 a[y]
NC272	*G. cingulata*	71.3 b
NC14	*C. gloeosporioides*	70.8 bc
CL217	*G. cingulata*	69.7 bcd
FC216	*G. cingulata*	69.3 bcde
NC107	*C. gloeosporioides*	69.3 bcde
NC210	*G. cingulata*	68.3 bcdef
FC273	*C. gloeosporioides*	67.7 cdef
A45	*G. cingulata*	67.0 def
FA18	*G. cingulata*	66.5 defg
FA19	*G. cingulata*	66.2 efgh
A6	*C. gloeosporioides*	66.0 fgh
NC23	*C. gloeosporioides*	63.5 hg
NC211	*G. cingulata*	63.3 h
FA173	*G. cingulata*	54.0 i
FC139	*C. acutatum* (NC)[z]	50.8 j
A32	*C. acutatum* (NC)	50.2 j
A5	*C. acutatum* (C)	49.7 j
NC205	*C. acutatum* (NC)	49.7 j
VA184	*C. acutatum* (C)	48.8 jk
A139	*C. acutatum* (NC)	48.3 jk
A10	*C. acutatum* (C)	48.2 jk
A62	*C. acutatum*(C)	48.0 jk
VA205	*C. acutatum* (C)	47.7 jk
FC72	*C. acutatum* (C)	47.5 jk
A125	*C. acutatum* (C))	46.2 kl
A11	*C. acutatum* (NC)	44.0 lm
FC174	*C. acutatum*(C)	43.7 lmn
CL88	*C. acutatum*(C)	43.3 lmn
CL211	*C. acutatum* (NC)	42.8 mn
A110	*C. acutatum* (C)	42.0 mno
FC150	*C. acutatum* (C)	41.2 mnop
FC108	*C. acutatum* (C)	40.7 nop
FC7	*C. acutatum* (C)	39.2 op
A117	*C. acutatum* (C)	38.8 p

[x] Colony diameter was recorded after 6 days on potato dextrose agar.

[y] Numbers followed by the same letter are not significantly different based on a Duncan's multiple range test ($P = 0.05$).

[z] C and NC refer to chromogenic and nonchromogenic isolates of *C. acutatum*.

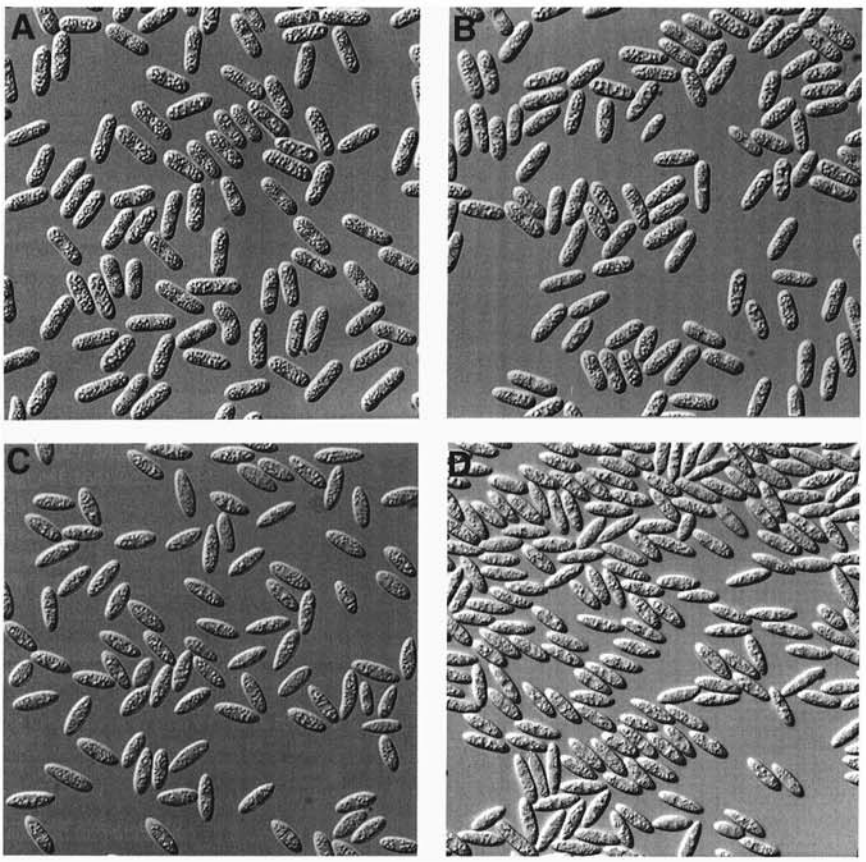

Fig. 1. Conidia of **(A)** *Glomerella cingulata* (isolate FC209); **(B)** *Colletotrichum gloeosporioides* (isolate NC82); **(C)** *Colletotrichum acutatum* (chromogenic isolate FA124); and **(D)** *Colletotrichum acutatum* (nonchromogenic isolate A32). Conidia were produced on potato dextrose agar, mounted in water after 2 weeks, and photographed using differential interference contrast microscopy. They are shown 495 times their actual size.

Colony color showed considerable variation among the isolates examined. None of the isolates identified as *C. gloeosporioides* or *G. cingulata* produced cultures with any red pigmentation. The colony color of isolates identified as *C. acutatum* ranged from dark brown through ruby red. Although the majority of the isolates of *C. acutatum* from apple produced the ruby red pigmentation in culture, some isolates produced orange to dark brown colored colonies with no red pigmentation. Thus, colony color alone cannot be used as a reliable diagnostic feature for species identification because several of the nonchromogenic isolates of *C. acutatum* were similar in colony morphology and color to some isolates of *C. gloeosporioides* and examination of conidial morphology was necessary for accurate species identification. Although not observed in this study, a chromogenic isolate of *G. cingulata* recovered from an ascospore has been reported (1). However, data from the current study, as well as others (2), indicate that chromogenic types are only associated with *C. acutatum*. Baxter et al. (2) proposed that chromogenic isolates of *C. acutatum* be designated *C. acutatum* f. sp. *chromogenum*. Although the term "chromogenic" can be informative, because of the phenotypically variable nature of colony color and the subjectivity in identification of this phenotype, the term can be difficult to interpret in the literature.

Anthracnose diseases of several agricultural crops have been shown to be caused by multiple *Colletotrichum* spp. For example, *C. gloeosporioides*, *C. acutatum*, and *C. fragariae* have all been shown to cause anthracnose of strawberry (11,24). In addition, *C. acutatum* and *C. gloeosporioides* have been shown to be involved in disease complexes on many other hosts including almond, apple, avocado, peach, pecan, blueberry, citrus, and other tropical fruit crops (3,8,9,14,16–18,20,27). In this study, three distinct taxa, *C. acutatum*, *C. gloeosporioides*, and *G. cingulata* (anamorph: *C. gloeosporioides*), were recovered from apple fruit with bitter-rot symptoms. *G. cingulata* apparently represents a homothallic component of the pathogen complex on apple, but the genetic relationship between these isolates and the nonperithecial-forming isolates of *C. gloeosporioides* is not known. Smith and Black (24) and Howard and Albregts (12) apparently observed a similar situation on strawberry and proposed that the nonteleomorphic isolates in the strawberry anthracnose complex be recognized as *C. fragariae*. Gunnell and Gubler (11) also provided evidence that *C. fragariae* was a morphologically distinct species. The *Colletotrichum* spp. pathogenic on strawberry also have been delineated by means of biochemical and molecular markers (4,10). As part of a concurrent study, examination of mitochondrial DNA RFLPs of apple isolates indicated that the teleomorphic isolates of *G. cingulata* and the nonteleomorphic isolates of *C. gloeosporioides* also represent distinct genotypes (8,9). However, detailed microscopic examination of morphological criteria was not part of this study. Such an examination may indicate that these two populations do represent two morphologically distinct species.

Very few studies have attempted to examine inter- and intra-orchard variation of the various *Colletotrichum* spp. involved in the diseases of agricultural crops. In this study, the frequency of the fruit rot pathogens varied among the orchards sampled and is likely influenced by many variables, including environmental factors, sources of initial inoculum, sample date, host cultivar, and management practices. In three orchards that were sampled in both 1992 and 1993 (Clarksville, AR, Fayetteville, AR, and Central Crops Research Station, NC), the overall fruit rot pathogen frequency did not change during the 2-year sample period. For example, *C. acutatum* was the predominant taxa recovered from Clarksville and Fayetteville, AR in both 1992 and 1993. In contrast, *C. gloeosporioides* predominated in the Central Crops Research Station, NC, sample in both 1992 and 1993. Interestingly, although *G. cingulata* was detected in five of the eight orchards sampled, it only predominated in a single orchard (commercial orchard, Clayton, NC).

B. dothidea predominated in two orchards sampled in Virginia (VPI Research Station and a commercial orchard in Winchester) and one orchard in Arkansas (Forrest City) (Table 1). The majority of the *Botryosphaeria* isolates recovered were obtained from small, nondescript lesions from these orchards. We believe it was necessary to sample small lesions to prevent introducing a bias toward a particular *Colletotrichum* spp. The data indicate that it is difficult to distinguish bitter-rot lesions from other fruit rots when lesions are very small.

Laboratory and field inoculations of apple fruit with representative isolates of *C. acutatum*, *C. gloeosporioides*, and *G. cingulata* indicate that the three taxa are pathogenic on apples and that distinct differences in virulence, sporulation capacity, and fungicide sensitivity exist among these taxa (3,20,23; and Y. Shi et al., unpublished). Further characterization of diversity within populations of the various bitter rot pathogens may help in understanding what ecological parameters and management practices influence pathogen genotype frequencies. In addition, comparisons between populations infecting different agricultural hosts also may reveal insights into the degree of host specificity that exists within these cosmopolitan taxa.

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