

Botryosphaeria dothidea Cane Canker of Thornless Blackberry

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ABSTRACT

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A new stem (cane) canker of the cultivated thornless blackberry is described. The anamorph of *Botryosphaeria dothidea* is shown to be the causal agent and the fungus is characterized morphologically to distinguish it from several other fungi that cause similar-appearing cane diseases. Disease evaluation of several commercial cultivars indicates that cultivars vary in degree of field resistance to the disease.

Thornless blackberry cultivars (*Rubus* spp. hybrids, subgenus *Eubatus*) are subject to diseases having similar symptoms commonly described as cane canker. Causal organisms of cankers include *Leptosphaeria coniothyrium* (Fckl.) Sacc., *Didymella applanata* (Niessl.) Sacc., *Glomerella cingulata* (Stonem.) Spauld. & Schrenk, *Gnomonia rubi* (Rehm) Winter, and *Botryosphaeria obtusa* (Schw.) Shoemaker (3,5,15). In addition to these organisms, the anamorph of *B. dothidea* (Moug.:Fr.) Ces. & de Not. (= *B. ribis* Grossenb. & Dug.) also causes a cane canker of thornless blackberry. We have not observed the teleomorphic state of this fungus on blackberry or in our cultures.

Taxonomically, *B. dothidea* and *B. ribis* are now generally treated as synonyms (3,16,18), with *B. dothidea* having priority; however, some workers (7,10) still consider them separate. There is no general agreement on the identity of the anamorph. Wiehe (17) considered the anamorph to be *Dothiorella gregaria* Sacc. Shaw (10) listed the anamorph as *D. ribis* (Fckl.) Sacc. Shahin and Clafin (9) used the name *D. dothidea* without author citation, but the description of *D. dothidea* was not published in Latin and no type specimen was designated. Therefore, the name *D. dothidea* is not validly published. *Dothiorella* itself is used in more than one sense (1), and we prefer to avoid the use of any name for the anamorph until the status of *Dothiorella* is clarified.

Reports of *Botryosphaeria* spp. occurring on cultivated *Rubus* spp. are

scarce: *B. quercuum* (Schw.) Sacc. (as *B. fuliginosa*) was reported from *Rubus* sp. in New York in 1921 (4); *B. ribis* f. *chromogena* Shear, Stevens, & Wilcox was reported on cultivated raspberries (*Rubus* sp., subgenus *Idaeobatus*) in Florida in 1926 (13); and in a general listing, *B. dothidea* (as *B. ribis*) has been reported from blackberry in Alabama (15), but no confirming literature could be located on this report. One investigator (12) artificially inoculated the blackberry Mammoth with *B. dothidea* (as *B. ribis*) isolates from walnut (*Juglans regia* L.) and avocado (*Persea americana* Mill.) but not in relation to an occurrence of a blackberry disease. *B. obtusa* has recently been reported to cause a serious cane canker disease in Ohio (5).

This cane canker disease is highly destructive, reducing fruit yields to uneconomic levels and forcing abandonment of plantings in some instances. It is far more important than the other cane canker diseases, with the possible exception of that caused by *B. obtusa*. The disease and pathogen are characterized in this paper.

MATERIALS AND METHODS

Pathogen. The organism was isolated from naturally occurring cankers on thornless blackberry plants at Beltsville, MD. Isolates were grown on potato-dextrose agar (PDA, Difco) and water agar (WA, Difco). Alfalfa stem pieces were colonized by placing them on WA around a centrally located inoculum plug of *B. dothidea* grown on PDA. Stems were prepared by cutting 2-cm-long pieces and sterilizing them briefly at 120 C with 15 psi in an autoclave. All cultures were incubated at 24 C under continuous cool-white fluorescent light. Pycnidia on alfalfa and blackberry stems were sectioned, fixed in FAA, dehydrated in tert-butyl alcohol, imbedded in paraffin containing plastic polymers, sectioned 7 μ m thick, and stained with Harris' hematoxylin (14). Pycnidia that developed on PDA were fixed in 1:3 acetic acid-

alcohol and stained with ferric-propionic-hematoxylin (FPH) (14). Ungerminated conidia and conidia germinated in 1% sucrose were allowed to dry on a slide, then fixed in acetic acid:alcohol (1:3) and stained with FPH.

Induction of perithecial production was attempted by pairing 12 blackberry isolates of *B. dothidea* obtained from several localities. Isolates were paired in all combinations on PDA and incubated at 24 C under continuous fluorescent light.

Pathogenicity. Greenhouse-grown plants of Hull Thornless, Dirksen Thornless, Smoothstem, Thornfree, Black Satin, and SIUS-68-6-17 were inoculated with blackberry isolates of *B. dothidea*. Young stems (5-10 mm in diameter) were wound-inoculated by drilling 2-mm holes through stems or by cutting into the vascular system and inserting a plug of mycelial inoculum from PDA culture or colonized alfalfa stem pieces into the hole or appressing an inoculum disk (3 mm in diameter) to the wounded area. Unwounded stems were inoculated by appressing an inoculum disk or colonized alfalfa stem piece to the stem. All inoculated and control stems were wrapped with Parafilm to secure the inoculum in place and to prevent desiccation. Treatments were replicated five times. Leaves were inoculated with an inoculum disk appressed to the upper lamina, covered with a glass microscope slide, and held in place with a small clamp. Plants were kept on a greenhouse bench at ambient temperatures (20-26 C). Parafilm was removed from stems after 2 wk and plants were examined for symptoms 5 wk after inoculation. Lesions were measured lengthwise on each stem and the stem diameter recorded.

Fruits of Delicious, Golden Delicious, and Spuree Rome apple cultivars were inoculated with *B. dothidea* and *B. obtusa* (Ohio isolate) to determine if blackberry isolates produce typical symptoms of white rot and black rot, respectively. Apples were wounded by cutting a small flap of tissue (2.5-3 cm in diameter) from each fruit and placing an inoculum disk (3 mm in diameter) of *B. dothidea* or *B. obtusa* from PDA under the flap and securing the flap in place with Parafilm. Fruits were examined after 5 and 7 days of incubation at 24 C.

Cultivar resistance. Blackberry cultivars and an advanced selection were evaluated for resistance to *B. dothidea*. Field plots were established in 1979 on sandy loam

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soil with Dirksen Thornless, Black Satin, Thornfree, Hull Thornless, and Smoothstem and the selection SIUS 68-6-17. Plots were arranged in a randomized complete-block design with four plants per plot and with six replicates per cultivar or selection. Planting distance between rows and plants was 4 × 2 m. No fungicides were applied to established plants. Plants were trained onto a three-wire vertical trellis. Overhead irrigation was applied when necessary. No artificial inoculations were made; all cankers resulted from natural infection.

Field resistance or susceptibility of thornless blackberry cultivars were evaluated by subjective and objective methods. Subjective evaluations were obtained by visually estimating the severity of disease effects on plant vigor, cane survival, leaf color, leaf abscission, and canker prevalence. A single (10-point) rating score was assigned to each experimental unit on the basis of these parameters. The subjective rating scale

consisted of the following categories: 1 = 100% of canes dead; 2 = 75% of canes dead, plants low in vigor; 3 = 75% of canes with cankers, some dead, much chlorosis, canes low in vigor; 4 = 50% of canes with cankers, some dead, much chlorosis, canes low in vigor; 5 = 33% of canes with cankers, some dead, 20–30% chlorosis, canes low in vigor; 6 = 25% of canes with cankers, frequent chlorosis, moderate plant vigor; 7 = 10–25% of canes with cankers, some chlorosis evident, most plants vigorous; 8 = 5–10% of canes with cankers, no chlorosis evident, plants vigorous; 9 = 1–5% of canes with cankers, no chlorosis, all plants vigorous; 10 = 100% of canes apparently healthy and exceptionally vigorous. Objective evaluations of disease effects were obtained by recording the numbers of canes with *Botryosphaeria* cankers and the total number of canes in each experimental unit. Both types of evaluations were recorded once during July.

RESULTS

Disease description. The cane canker symptoms caused by *B. dothidea* are similar to those of raspberry spur blight caused by *Didymella applanata* (3). Cankers generally develop at one or more lateral buds on the main stem of the second-year (fruiting year) cane and were evident as reddish brown to dark reddish brown discoloration below or to one side of the subtending leaf petiole (Fig. 1A). The lateral bud or branch at the infected node was usually killed. Occasional cankers developed along internodes but only at wound sites. Lesions developed around and beneath the node and later spread above the node, resulting in girdling of the cane (Fig. 2). The disease usually is not evident until fruit ripen; leaves on the entire cane or only on portions above the canker wilt, turn yellow, then desiccate and fruit development ceases. Developing cankers often have a zonate pattern of dark and lighter coloration (Fig. 2A) and old

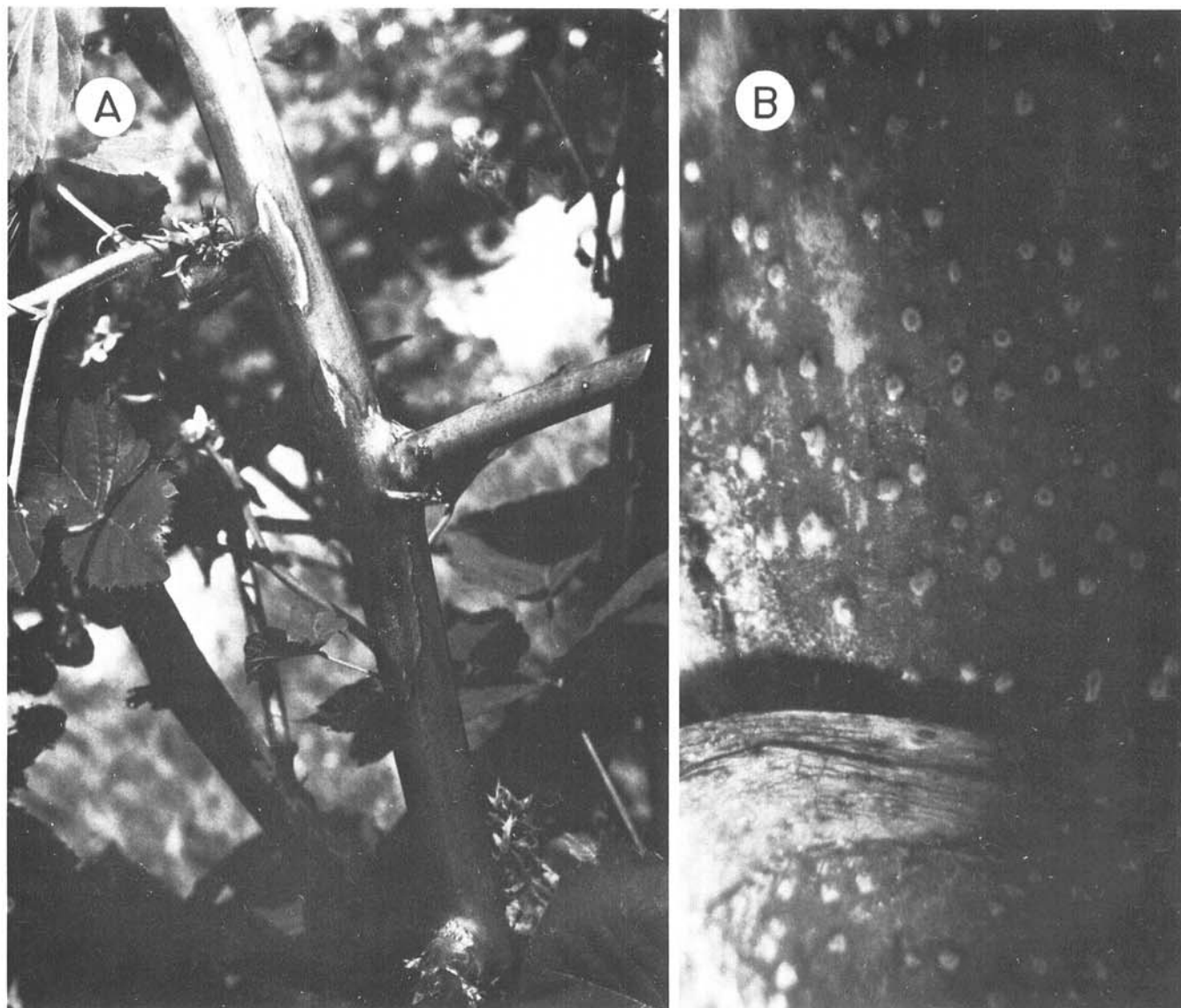


Fig. 1. (A) *Botryosphaeria dothidea* cane canker of thornless blackberry and enlargement (B) of a portion of a canker showing the presence of numerous, scattered pycnidia of the pathogen.

cankers become lightly colored (to silvery gray) on dead canes (Fig. 2B). Well-developed cankers often split open longitudinally exposing the pith of the cane (Fig. 2C). Conidiomata (pycnidia)

of the fungus are scattered subepidermally throughout the canker, becoming erumpent and exposing their ostioles (Fig. 1B).

Pathogen. The fungus has been

identified as the conidial anamorph of *B. dothidea*, the causal agent of Botryosphaeria fruit rot and canker of apple as well as diseases of many other woody plants. The teleomorph (sexual)

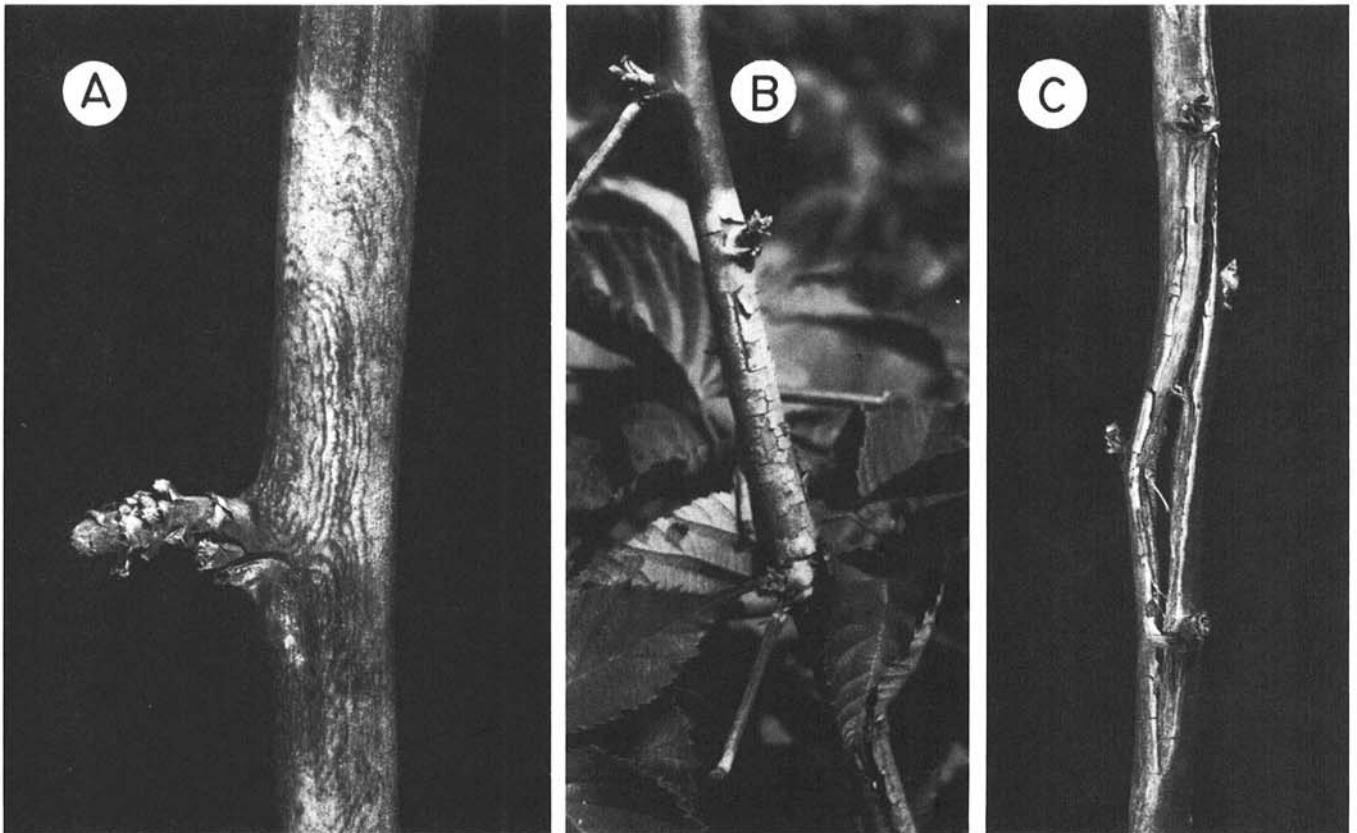


Fig. 2. *Botryosphaeria dothidea* cane cankers on thornless blackberry showing (A) the characteristic zonate pattern of development and killed lateral branch, (B) old cankers showing sloughing of epidermal tissues of canes, and (C) deep, longitudinal fissuring of the cane.

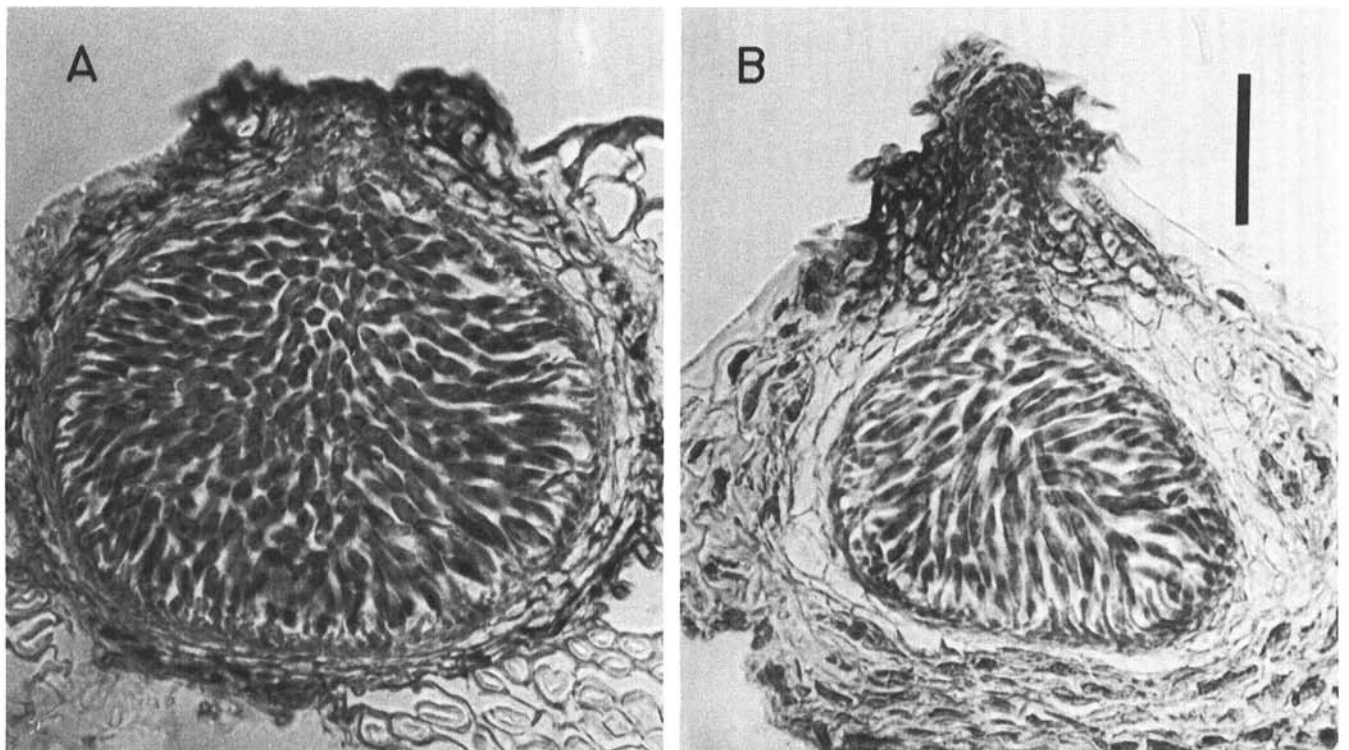


Fig. 3. Pycnidia of *Botryosphaeria dothidea* from (A) colonized alfalfa stem piece and (B) naturally infected blackberry cane. Note differences in size and submersion in host substrate. Tissues stained with Harris' hematoxylin. Scale bar = 20 μ m.

state has not been observed on blackberry or in our cultures. This is the first report of *B. dothidea* causing a serious disease of blackberry.

Colonies of the anamorph of *B. dothidea* on PDA grew rapidly, covering the entire surface of the medium in a 10-cm petri plate within 4 days. Initial colonies were white and cottony and turned dark gray and floccose after 3–5 days. Numerous solitary black conidiomata (200–350 μm in diameter) developed on the medium surface. No color was imparted to the growth medium by the fungus.

The fungus rapidly colonized sterilized alfalfa stems and produced numerous pycnidia. Pycnidia in alfalfa stems were generally suberumpent, globose, black, 75–95 μm in diameter (mean = 85 μm), with well-defined ostioles and short necks (10–20 μm long (mean = 15 μm) (Fig. 3A). Pycnidia in blackberry stems were immersed to erumpent, globose to irregularly globose, black, 52–65 μm in diameter (mean = 60 μm), and had well-defined ostioles and elongate necks 35–37 μm long (mean = 36 μm) (Fig. 3B). Conidiogenous cells in pycnidia from either substrate lined the cavity of the pycnidium (Fig. 3). Conidiophores were short, hyaline, unbranched, and arose from the cell layer lining the interior of the pycnidium. Conidiophores were holoblastic phialides (Fig. 4A), and portions of the outer conidiophore wall were observed at the truncate ends of conidia (Fig. 5A). Conidia were hyaline, single-celled, ellipsoid to fusoid, distinctly basally truncate, multinucleate (as many as eight to 10 nuclei per conidium), and measured 6.3–8 \times 16.5–20 μm (mean = 6.9 \times 18.4 μm) (Fig. 5). Conidia often became 2-septate (occasionally 1- or 3-septate) with the middle cell often darker than the others (Fig. 5E). Conidia germinated within 12 hr in 1% sucrose. Long, sparingly branched germ tubes grew from one or more of the individual cells (Fig. 6). Conidial initials were devoid of nuclear material (Fig. 4B). A nucleus from the conidiophore migrated to the abscission area of the conidium and entered the developing conidium (Fig. 4B). Nuclear divisions occurred in the conidium until as many as eight to 10 nuclei were present (Fig. 5B). Upon germination, nuclei from the conidial cell migrated into the germ tube (Fig. 6). Attempts to induce production of perithecia by pairing *B. dothidea* isolates from blackberry were unsuccessful.

Disease etiology. Blackberry stems developed elongate, dark brown lesions 2 wk after inoculation with *B. dothidea* (Fig. 7). No differences were apparent between colonized alfalfa stem pieces or mycelium from agar culture as inoculum sources. Differences between wounded (mean = 29.8 mm) and unwounded (mean = 14.4 mm) treatments were apparent (Table 1), but statistical comparisons were not made because of the unequal

numbers of lesions that developed among the treatments. Lesions developed equally well at inoculation points at nodes and along internode sections of stems (Fig. 7). Differences in the development of lesions were apparent among the cultivars inoculated. Lesions were longer on wound-inoculated stems of Dirksen Thornless, SIUS 68-6-17, and

Hull Thornless than on Black Satin and Thornfree. Lesion development among unwounded stems was greatest on Dirksen Thornless. No lesions formed on unwounded stems of Black Satin, Thornfree, or Smoothstem. All leaves inoculated with *B. dothidea* failed to develop lesions except one on which the brown lesion enlarged to 1.5 cm diameter

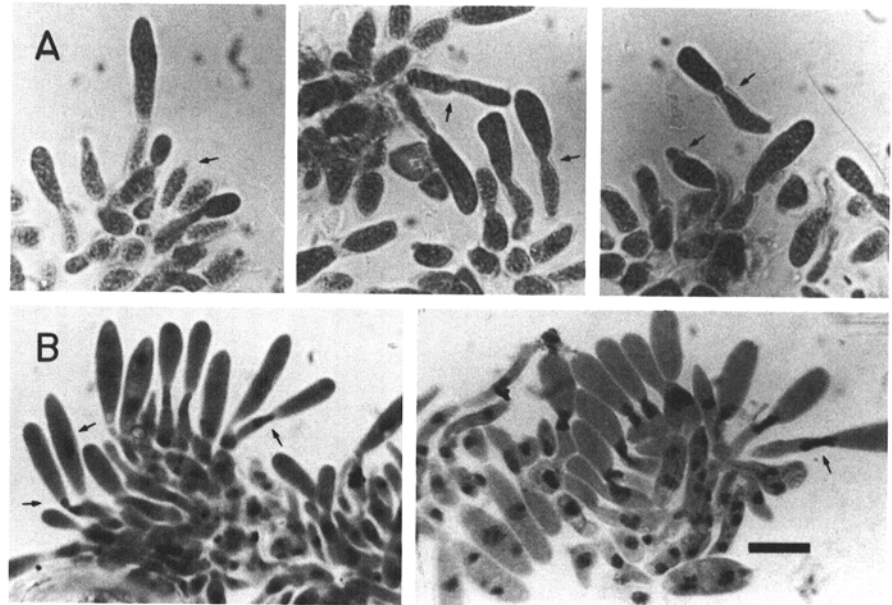


Fig. 4. Conidiogenesis in *Botryosphaeria dothidea*. Scale bar = 10 μm . (A) Conidia are formed by extrusion of the inner phialide cell wall. Various stages of development are indicated by the arrows. Tissues stained with erythrosin in ammonium hydroxide. (B) Nuclear migration from conidiophores into developing conidia. Various stages of migration are shown (arrows) and individual chromosomes can be seen in conidium at lower right. Conidia and conidiophores stained with FPH.

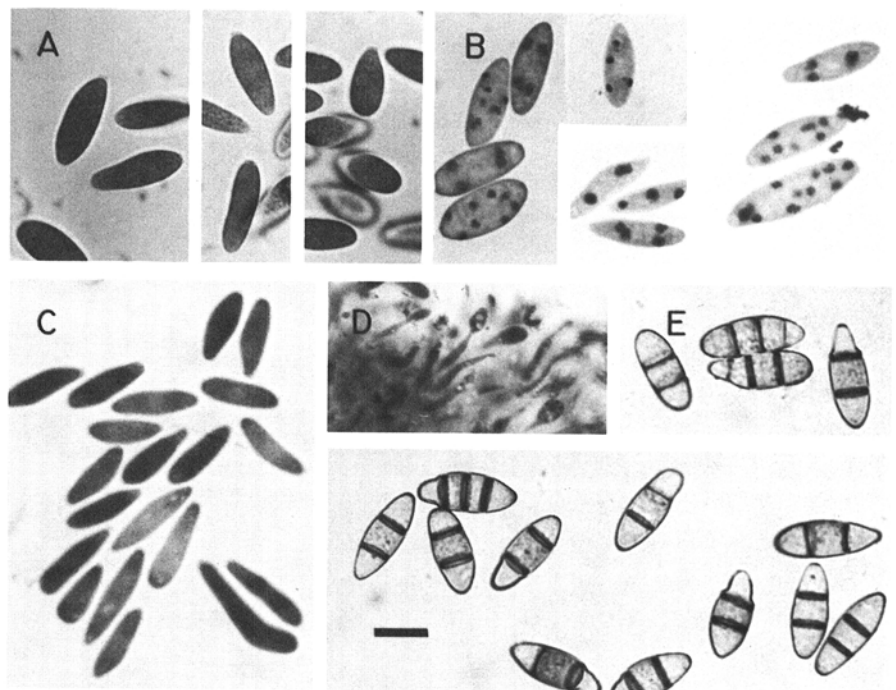


Fig. 5. Conidia of *Botryosphaeria dothidea* showing variations in size, shape, septation, and numbers of nuclei. Scale bar = 10 μm . (A) Conidia clearly showing basal truncation, stained with erythrosin in ammonium hydroxide. (B) Multinucleate conidia stained with FPH. Fresh mounts of (C) conidia and (D) interior of pycnidium stained with cotton blue in lactic acid. (E) Multiple septations formed in conidia before germination, water mount.

and ceased development. Pure cultures of *B. dothidea* were isolated from all lesions sampled. No lesions developed on uninoculated stems.

Apple fruits inoculated with *B. obtusa* and *B. dothidea* developed lesions within 5 days after inoculation. Lesions produced by *B. obtusa* were dark brown with well-defined borders, but smaller than those produced by *B. dothidea* (Fig. 7E). Lesions caused by *B. dothidea* developed faint, concentric, zonate, dark and light brown color patterns, and the red color of Delicious and Spuree Rome fruits was bleached in advance of the expanding lesions. Conidiomata of *B. dothidea* were produced only after fruits

were completely rotted; ascomata were not found.

Cultivar field resistance. Five cultivars and one advanced selection were rated for susceptibility to *B. dothidea* cane canker under field conditions with natural infections using two methods of plot evaluation (Table 2). Variations in disease reaction were demonstrated by both methods, with similar results from each. SIUS 68-6-17 and Dirksen Thornless were rated most resistant and Smoothstem most susceptible to the disease. Black Satin, Thornfree, and Hull Thornless were intermediate in disease reaction. Thornfree had fewer canes per plot than the other cultivars, but this did

not appear to affect the results of the evaluation. The subjective method of estimating plant infection and overall vigor of plants was surprisingly less variable (coefficient of variation = 21.5% and standard error of treatment means = 0.5416) than the objective method of counting infected canes (coefficient of variation = 57.6%, standard error of treatment means = 7.6634). There were no significant differences among replicates ($P = 0.05$) for either method.

DISCUSSION

During this investigation, we isolated several fungi from thornless blackberry cane cankers: *Leptosphaeria coniothyrium*, *Glomerella cingulata*, *Gnomonia rubi*, *Apioportha vepris* (Lacroix) Wehm., *Macrophoma* sp., and *Cytospora* sp. These isolates and an isolate of *B. obtusa* from blackberry cane cankers in Ohio (courtesy of M. Ellis) were compared with the morphology and symptomatology of *B. dothidea* to confirm that the disease caused by *B. dothidea* is an important new disease of thornless blackberry. The characteristics of our isolates of *B. dothidea* from thornless blackberry agree with published descriptions of *B. dothidea* (3,7,18). The pathogen's identity was also confirmed by specialists at the Commonwealth Mycological Institute, Kew, England. Inoculation of apple fruits showed that the blackberry isolates of *B. dothidea* cause typical Botryosphaeria white rot symptoms in contrast to the blackberry isolate of *B. obtusa*, which caused typical black rot symptoms.

Cankers on blackberry canes caused by several fungi are similar in appearance, and identification in the field may be difficult. In addition, two or more of these pathogens may occur on the same stems or cause confluent cankers. *B. dothidea*, however, can be distinguished microscopically from *L. coniothyrium* (3), *D. applanata* (3), *Glomerella cingulata* (16), *Gnomonia rubi* (2), and *B. obtusa* (8).

Formation of septations in germinating conidia has been reported for *B. dothidea* (18), but little is known concerning the factors that stimulate this process. Not all conidia formed septations and became darkened; aseptate, hyaline conidia were able to germinate. No attempt was made to compare pathogenicities of subspecies derived from single-cell or multicellular conidia.

The epidemiology of this disease has not been determined fully, but lateral buds with persistent leaf petioles are apparently the primary locus of infection. However, artificial inoculation of wounded and unwounded node and internode portions of stems and the observation of natural infections around wounds in internodal areas indicate that wounds are also important points of entry for the fungus. *B. dothidea* is considered a wound-invading pathogen.

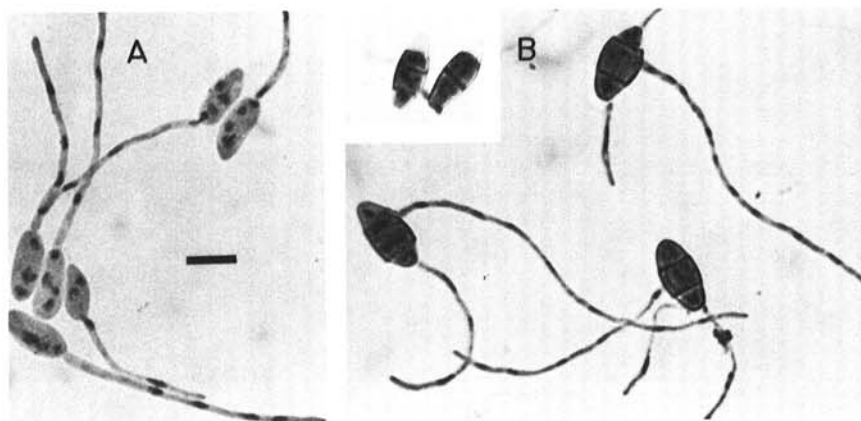


Fig. 6. Germinating single-celled (A) and 3-celled (B) conidia of *Botryosphaeria dothidea*; note the multinucleate state of the unbranched germ tubes and conidia. Conidia stained with FPH. Abnormal germinating conidia with apical cells devoid of contents are shown in the inset. Scale bar = 10 μ m.

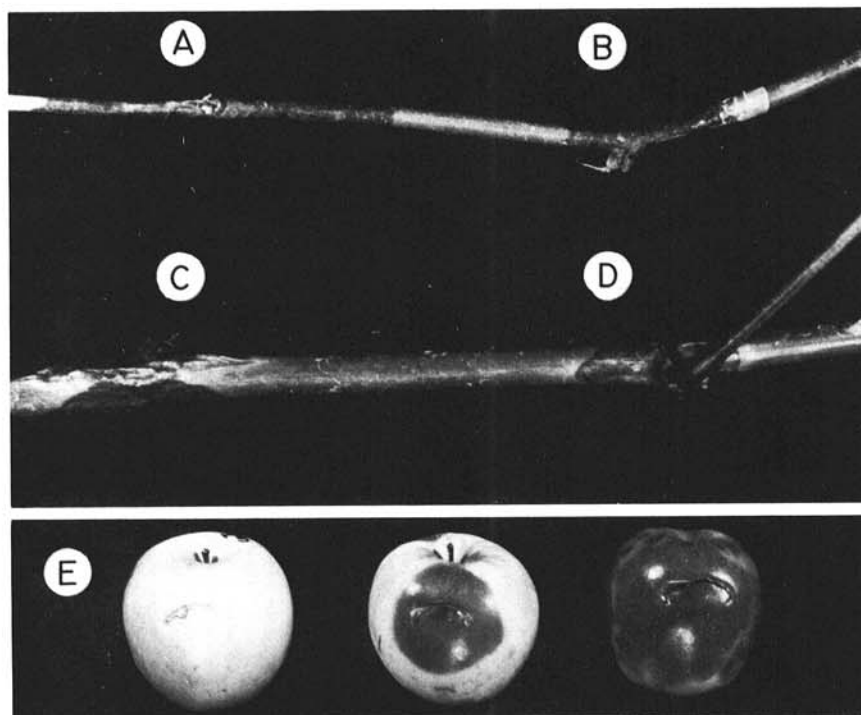


Fig. 7. (A-D) Artificial inoculation of thornless blackberry stems with *Botryosphaeria dothidea*. Lesions developed from (A) wound and (B) no-wound inoculation of stems with colonized alfalfa stem pieces and lesions developed from (C) wound and (D) no-wound inoculation with mycelial disks from culture. (E) Golden Delicious apples inoculated with a thornless blackberry isolate of (center) *B. obtusa* and (right) *B. dothidea*; (left) uninoculated control.

Blackberry canes wounded by pruning in the summer or winter are often sites of colonization by several fungi. We have observed, however, that these areas are most often invaded by *L. coniothyrium* and only infrequently by *B. dothidea*. It is not clear if wounding of lateral buds or damage from winter injury are essential for natural infection of canes or if healthy tissues may be attacked directly. Conidial inoculation of wounded and unwounded blueberry stems has shown that germinating conidia can penetrate stomata but cannot penetrate stem tissues directly (6). Involvement of leaf tissue infection does not appear to be important in the development of the blackberry cane canker disease as it is with spur blight of raspberry caused by *Didymella applanata*. Inoculation of leaf blades was successful on only one occasion and the resultant lesion failed to develop to any extent. Young lesions (less than 2 cm in diameter) on canes have been found throughout the growing season, indicating infection may take place anytime from early spring (April–May) to fall (September–October).

In blueberry, once the fungus enters the vascular system of the stem, it moves rapidly down the stem, but lateral movement is slow (6). This may explain why blackberry cane cankers often extend below the point of infection at the node with relatively little upward or lateral extension of the canker. Death of the portion of cane above the canker may result from occlusion of xylem vessels by tyloses and mycelium as has been shown to occur in blueberry infections (6). Although this has not been determined for blackberry cane canker, by analogy, it could help explain the sudden decline of canes during fruit development, when demand for water by the plant is great.

The fungus may overwinter in cankers in dead canes and probably also in cankers on living primocanes (1-yr-old canes). In many areas, inoculum presumably is produced from cankers on other hosts, such as apple or other woody plants. The original source of inoculum is academic once *B. dothidea* becomes established in a blackberry planting, because the biennial growth habit of

blackberry plants accommodates perennation of the fungus.

Resistance, or differential susceptibility, of thornless blackberry cultivars to *B. dothidea* cane canker was assessed because this is potentially a very serious disease and because reliable methods are needed to assess germ plasm for possible sources of resistance. Greenhouse inoculation tests showed that none of the cultivars were immune to infection by *B. dothidea*. Both the subjective and objective evaluation methods were successful, however, in determining relative resistance in the field under natural inoculum pressures. Counting infected canes was the more variable method of evaluation. Canker measurements or numbers of cankers per cane were not recorded; variability in disease susceptibility ratings might have been reduced if they had included such observations. The subjective method of rating disease severity has the inherent problems of interpretation and of being subject to annual and observer variation. Although variation in both methods was high, this is neither unusual nor unacceptable for assessments made for other fruit crops under similar conditions. Both are relatively rapid methods, but each requires a completely randomized planting design of sufficiently replicated plots.

Table 1. Lesion development on wounded and unwounded stems of several thornless blackberry cultivars 5 wk after inoculation

Cultivar or selection	Wounded			Unwounded		
	Stem diameter (mm)	Lesions (no.)	Lesion length (mm)	Stem diameter (mm)	Lesions (no.)	Lesion length (mm)
Dirksen Thornless	3.6 ^a	3.0	37.0	2.2	2.0	21.0
Black Satin	3.0	5.0	21.0	3.2	0.0	0.0
Hull Thornless	3.8	5.0	36.0	3.0	1.0	1.5
Thornfree	5.0	4.0	21.0	5.0	0.0	0.0
SIUS 68-6-17	5.8	5.0	36.0	3.0	2.0	7.5
Smoothstem	3.6	3.0	28.0	2.6	0.0	0.0
Mean	4.1	4.2	29.8	3.3	0.8	14.4

^a Means of five replicates per treatment.

Table 2. Subjective and objective ratings of thornless blackberry cultivars for resistance to infection by *Botryosphaeria dothidea*^a

Cultivar or selection	Canes per plot (mean)	Method of evaluation			
		Subjective (plot rating)		Objective (percent canes diseased)	
		Range	Mean	Range	Mean
SIUS 68-6-17	12.0 a ^x	6–10	8.0 a	0–25	8.6 a
Dirksen Thornless	11.0 a	6–9	7.0 a	0–29	14.5 a
Black Satin	10.7 a	4–9	6.3 b	0–50	26.4 ab
Thornfree	8.7 b	5–8	6.3 b	0–60	28.3 ab
Hull Thornless	11.8 a	4–6	5.0 bc	39–56	48.4 bc
Smoothstem	10.5 a	3–6	4.3 c	20–100	69.4 c
Mean	10.8		6.2		32.6
SE ^y			0.5416		7.6634
C.V. (%) ^z			21.5		57.6

^a Randomized plot design, four plants per plot with six replicates. Subjective = plots rated on a scale of 1–10, where 1 = 100% of canes dead; 2 = 75% of canes dead, plants low in vigor; 3 = 75% of canes with cankers, some dead, much chlorosis, canes low in vigor; 4 = 50% of canes with cankers, some dead, much chlorosis, canes low in vigor; 5 = 33% of canes with cankers, some dead, 20–30% chlorosis, canes low in vigor; 6 = 25% of canes with cankers, frequent chlorosis, moderate plant vigor; 7 = 10–25% of canes with cankers, some chlorosis evident, most plants vigorous; 8 = 5–10% of canes with cankers, no chlorosis evident, plants vigorous; 9 = 1–5% of canes with cankers, no chlorosis, all plants vigorous; and 10 = 100% of canes apparently healthy and exceptionally vigorous.

^x Means in the same column followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

^y SE = standard error of the treatment means.

^z C.V. (%) = coefficient of variation.

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