Branch Dieback of Southern California Chaparral Vegetation Caused by *Botryosphaeria dothidea*

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ABSTRACT

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Branch dieback in the southern California chaparral was reported in 1985, the first year of a 5-yr drought. The pathogen was identified as a *Dothiorella*-like anamorph of *Botryosphaeria dothidea*. *B. dothidea* has been isolated from active lesions on over 50 species and cultivars of California native plants. Field inoculations during September 1990 with isolates of *B. dothidea* from four of these hosts resulted in rapid disease development. Lesions measured 60–80 mm long after 1 wk, and most of the branches were killed after 6 wk. Maximum in vitro vegetative growth occurred at 25–30 C for three isolates from southern California. Conidial germination was greatest at 30 C and declined at temperatures below 30 C. Germination at 30 C for two isolates was 98% at 12 h and 85–100% after 24 h at temperatures from 10 to 30 C. Germination and growth of the southern California isolates of *B. dothidea* tested at high temperatures were similar to those of isolates from the southeastern United States. Germination at low temperatures, however, was noticeably greater for the southern California isolates tested than the germination reported for isolates from the southeastern United States.

Additional keywords: *Botryosphaeria ribis*, canker, *Dothiorella*, drought stress.

During 1984–1985, severe branch dieback was observed in the sclerophyllous chaparral vegetation of the San Gabriel and Santa Monica mountains north of Los Angeles, CA (P. Riggan and S. Franklin, *personal communication*). The causal agent was tentatively identified as *Botryosphaeria ribis* Gross. & Duggar (J. Pronos, *personal communication*). According to von Arx and Müeller (40), the name *B. ribis* was misapplied by Grossenbacher and Duggar (14) to a species described in 1863 by de Cesate and de Notaris as *Botryosphaeria dothidea* (Moug.:Fr.) Ces. & de Not. Some mycologists and plant pathologists still list *B. ribis* and *B. dothidea* as separate species (12,22,39). The latter name, however, is most commonly used, with *B. ribis* reduced to synonomy (5,11,20,24,27,33,43). Because of the absence of the teleomorph, identification of the causal agent of branch dieback in California is usually based on its pathogenicity and the characteristics of the anamorph (11,13,21,32). In northern California, however, Worrall et al (44) reported the teleomorph of *B. dothidea* on dead and dying branches of giant sequoia (*Sequoiadendron giganteum*) and coast redwood (*Sequoia sempervirens*) planted outside their natural ranges. Most reports of branch dieback, canker disease, and fruit rot concern agricultural crops and horticultural plantings (5,7,11,18,23,28,32,37,43). This study arose from the concern of forest-fire agencies over the increase in dead biomass caused by branch dieback at the urban-chaparral interface. Branch dieback is also a threat to the success of revegetation and remediation projects throughout the state.

Reports on the biology and pathogenicity of *B. dothidea* are primarily from temperate or tropical areas where the climate is conducive to disease development during much of the year. Isolates of *B. dothidea* from the southeastern United States have been tested for pathogenicity and growth (6,43), sporulation and dissemination (26,34,36), and spore germination (35,41).

In the mediterranean climate of southern California, sufficient moisture for spore release, dispersal, and germination in native plant communities usually occurs only during the infrequent storms of late winter and early spring. This suggests a possible alteration in life strategy, the fungus remaining dormant throughout most of the year, followed by short, critical periods of activity. This could also include a change in the biological parameters of this facultative parasite.

These studies were conducted to 1) identify the anamorph of the pathogen and its relationship to *B. dothidea*, 2) describe the disease in a natural plant community, and 3) determine the pathogenicity and optimum temperatures for growth and spore germination of southern California isolates of this fungus.

MATERIALS AND METHODS

Identification and pathogenicity. From 1989 to 1992, plants in chaparral communities of the San Gabriel and San Bernardino mountains of southern California and native plants under cultivation were observed for symptoms of branch dieback. Many of these plants were growing out of their natural habitat in the native plant collection at the Rancho Santa Ana Botanic Garden in Claremont, CA, where branch dieback has been a problem for many years (19).

To identify the pathogen, five diseased branches from each of seven chaparral species were collected. These branches were surface-disinfested in 0.25% sodium hypochlorite for 3 min and placed in a moisture chamber under fluorescent light at room temperature until sporulation. A more efficient method for isolating the fungus was to excise discolored tissue from the advancing margin of the lesion and plate it on potato-dextrose agar (PDA) amended with streptomycin (0.5 g/500 ml). Hyphal tips were transferred to PDA or oatmeal agar (OA) and placed under fluorescent light (12 h/day) at room temperature until spore formation.

Fruiting bodies on infected host tissue and those formed on

PDA and OA were fixed under vacuum in FAA solution (5 ml of formalin [40% formaldehyde] and 5 ml of glacial acetic acid in 90 ml of 50% ethanol). The sporocarps were dehydrated in an ethanol series (30, 50, 75, and 95%) and infiltrated with an embedding medium of methacrylate (Historesin, Cambridge Instruments Inc., Deerfield, IL). The infiltrated samples were transferred to plastic molds containing activated embedding solution. Polymerization was enhanced by placing the molds in a desiccator with dry ice and applying a vacuum. Tangential sections 3–5 μm thick were made with a Sorvall JB-4A microtome (E. I. Du Pont De Nemours & Co., Inc., Sorvall Instruments Div., Newtown, CT) and stained with toluidine blue O. Sporocarp characteristics and sporogenesis were examined with a light microscope. Spore measurements were made on fresh squash-mounts in water with an ocular micrometer.

During September 1990, two isolates from each of four chaparral plant species were tested for pathogenicity. From this single trial, two isolates were selected for use in a 3-yr study of the effects of meterological drought on Botryosphaeria branch dieback (F. E. Brooks, *unpublished data*). The initial isolates were D-02 and D-07 from bigberry manzanita (*Arctostaphylos glauca* Lindl.), D-10 and D-14 from hoary leaf ceanothus (*Ceanothus crassifolius* Torr.), D-15 and D-16 from California silk tassle (*Garrya flavescens* S. Wats.), and D-18 and D-20 from coast live oak (*Quercus agrifolia* Neé). Inoculations were performed on the current-season growth of a single *A. glauca* in the chaparral of the San Gabriel Mountains. An oblique incision was made with a razor blade, a 5-mm-diameter plug from the margin of a 4-day-old culture of each isolate growing on PDA was applied, and the inoculation site was wrapped with Parafilm for 1 wk to prevent desiccation. Sterile PDA was applied to wounded branches as a control. Five replicated branches were inoculated with each isolate, and lesion expansion was measured weekly for 6 wk. After 6 wk, dead and dying branches from each isolate were collected. Isolation and identification of the pathogen were performed by the previously mentioned methods.

Changes in the midday plant water potential were determined with a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA). Five cuttings were taken each week, double-bagged in heavy plastic, transported to the laboratory, refrigerated, and read immediately.

Growth rate. Isolates D-07, D-10, and D-15 were grown on PDA for 4 days. A 5-mm-diameter plug taken from the colony margin was placed in the center of an 85-mm-diameter petri plate containing PDA. Three plates of each isolate were incubated at 5, 10, 15, 18, 22, 25, 27, 30, 33, 35, and 40 C. Three colony diameters per plate were measured, and the average of three plates was recorded daily for 3 days. The experiment was conducted three times.

To test for fungal survival in vitro, plates at temperatures that showed no growth during the experiments were left to incubate at those temperatures. In one experiment, the three plates of each isolate were removed from the incubators after 6 additional days (9 days total), held at 25 C for 5 days, and checked for growth. In the two other experiments, plates that showed no growth after 3 days were incubated an additional 11 days (14 days total), held at 25 C for 5 days, and checked for growth.

Spore germination. Isolates D-07 and D-10 were grown on PDA under fluorescent light (12 h/day) at room temperature for 14–16 days. Fruiting bodies were scraped from the surface of the agar, crushed in sterile water, and strained through two layers of cheesecloth. The spore concentration was adjusted to 10^4–10^5 spores per milliliter with a hemacytometer. Three 2- to 3-μl drops of spore suspension (approx. 150 spores per drop) were pipetted onto individual petri plates containing water agar (Difco Laboratories, Detroit, MI). Five plates of each isolate were placed in a heavy plastic bag and incubated at 10, 15, 20, 25, and 30 C. One plate of each isolate per temperature treatment was removed after 2, 4, 8, 12, and 24 h. Spore germination was stopped by staining with cotton blue in lactophenol. A coverslip was applied, and 50 spores per drop were counted. The average number of germinated spores per drop was calculated for each isolate at each temperature and expressed as percent germination. A spore was considered germinated if the germ tube length was at least half the length of the spore (1). The experiment was conducted three times.

RESULTS

Identification. Colonies grown on PDA were whitish and floccose, becoming greenish-gray to gray-black. Aerial hyphae remained thin (1.0–2.0 μm wide) and hyaline. The immersed mycelium became melanized and was 4.0–7.0 μm wide, forming dense mats from which the pseudoparenchymatous tissue of the pycnidia formed. Conidiomata were scattered, solitary, or in botryose clusters and were partially immersed, forming in 7–9 days, and becoming mature in 12–16 days. Single pycnidia averaged 0.5–1.0 mm in diameter, and clusters averaged 1.0–2.0 mm in diameter, with 2–9 locules.

Conidiomata on host tissue, *A. glauca*, were subperidermal on branches or beneath the epidermis and cuticle of the fruit, erumpent, solitary (0.5–1.0 mm diameter), or loosely aggregated in small superficial stromata (1.0–3.0 mm diameter), and exuded cirrhi at maturity (Fig. 1A and B). The thick outer wall was composed of dark, irregular textura angularis, the cells becoming smaller, flattened, and hyaline toward the interior of the pycnidium. Conidiophores were hyaline, occasionally branched, aseptate or septate, and lined the pycnidial cavity (Fig. 1C). Conidiogenous cells were hyaline and appeared to produce a single apical conidium. Macroconidia were holoblastic, aseptate, hyaline, fusoid to navicular, apex obtuse, with a distinctly truncate base, and measured 5.8 (4–10) × 26.3 (20–30) μm (Fig. 1D). Conidia formed one or two septations at germination, producing a germ tube from each cell. Microconidia were infrequent, hyaline, one-celled, oblong, and measured 1.0–1.5 × 2.5–4.0 μm.

Pathogenicity. *B. dothidea* was isolated from active lesions on more than 50 plant species and cultivars native to California, 22 genera, and 14 families:

- Asteraceae: *Artemesia pycnocephala*
- Cupressaceae: *Calocedrus decurrens*
- Ericaceae: *Arbutus menziesii; Arctostaphylos catalinae, A. elegans, A. glandulosa, A. g.* var. *adamsii, A. glauca, A. manzanita, A. otayensis, A. pringlei* var. *drupacea, A. pungens, A. rudis, A. viscida; Arctostaphylos* × 'Byrd Hill', 'Greensphere', 'Howard McMinn', 'Indian Hill', 'Pacific Mist', 'Palisades', 'Sandsprite', 'Sentinel', 'Trinity Ruby', 'Windswept'; *Ornithostaphylos oppositifolia; Xylococcus bicolor*
- Fabaceae: *Cercis occidentalis*
- Fagaceae: *Quercus agrifolia; Q. kelloggii*
- Garryaceae: *Garrya cogdonis; G. elliptica; G. flavescens; G. fremontii; G. veatchii*
- Lauraceae: *Umbellularia californica*
- Myricaceae: *Myrica californica*
- Pinaceae: *Pseudotsuga menziesii*
- Rhamnaceae: *Ceanothus crassifolius; C. c.* var. *planus; C. gloriosus; C. gresius* var. *horizontalis; C. oliganthus; C. rhamulosus; C. sorediatus; C. spinosus; Ceanothus* × 'Blue Buttons', 'Dark Star'; *Rhamnus californica*
- Rosaceae: *Cercocarpus ledifolius; C. betuloides; Heteromeles arbutifolia; Lyonothamnus floribundus* subsp. *asplenifolius; Prunus ilicifolia; P. lyonii*
- Saxifragaceae: *Heuchera* × 'Genevieve'; *Ribes aureum* var. *gracilimum*
- Sterculiaceae: *Fremontodendron* × 'California Glory', 'El Dorado'
- Taxodiaceae: *Sequoiadendron giganteum.*

At the Rancho Santa Ana Botanic Garden, the ericaceous shrubs were most affected, often festooned with dead and dying branches or pruned until their original form was lost. Deep decorticate cankers on older branches of *Arctostaphylos* spp. are probably the result of slow but successful wound responses to the pathogen.

The first symptoms of natural infection appear on the current

seasons growth during spring and early summer. Vegetative axillary buds and unabscised terminal panicles from the previous winter-spring are two foci of new infections on *Arctostaphylos* spp. (F. E. Brooks, *unpublished data*). An area of redness initially surrounds an infected bud, turns black, and extends along the branch and up the subtending leaf petiole. Necrosis from blighted panicles moves proximally down the stem. Symptoms of dieback appear during late summer and fall; the leaves turn a dull gray-green then reddish-brown with no evidence of wilting or abscission.

California silk tassel (*Garrya* sp.) is an example of a chaparral species that sprouts from a lignotuberous root. When disease moves down a branch to the base of the plant, the fungus becomes established in the crown and infects new branches as they emerge

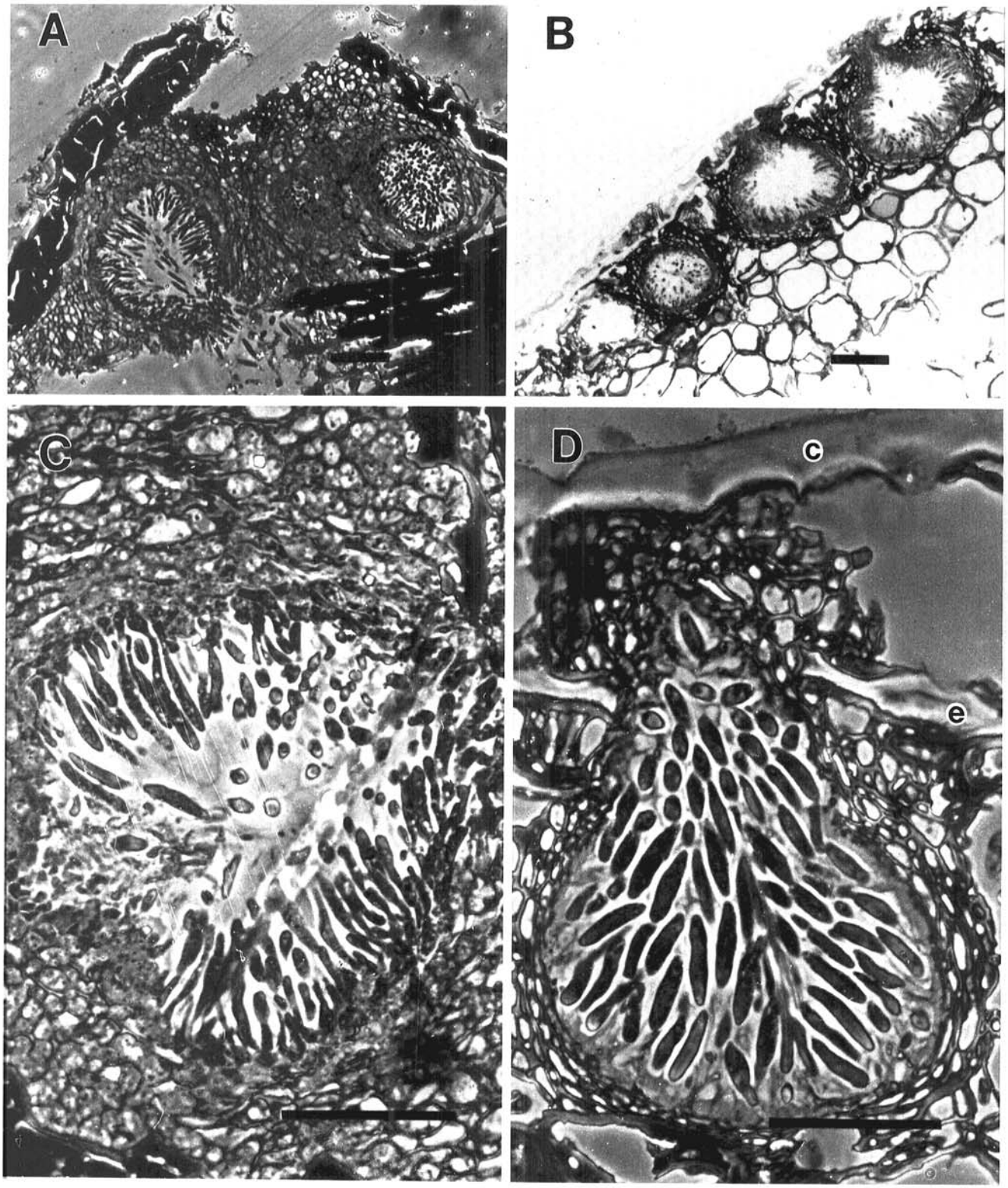

Fig. 1. Reproductive structures and conidiospores of *Botryosphaeria dothidea* on diseased branches and fruits of *Arctostaphylos glauca*. **A,** Mature pycnidia breaking through the periderm and cuticle of a diseased branch. **B,** Multiloculate stromatic tissue on fruit. **C,** Tangential section of a pycnidial wall and cavity lined with conidiophores. **D,** A single pycnidium breaking through the epidermis (e) of the fruit, separating it from the cuticle (c). Scale bars = 50 μm.

(F. E. Brooks, *personal observation*). These branches grow rapidly for several years then die back to the base of the plant. Pycnidia formed on these branches are another source of inoculum that can infect the current season's growth.

Disease development after the September 1990 inoculations was rapid. Average lesion length for all isolates was >70 mm after 1 wk (Fig. 2) and most branches were dead by 6 wk. Midday plant water-potential readings during this time were between −2.6 and −3.3 MPa. Average midday plant water potentials for winter and spring 1991–1992 were −1.2 and −1.6 MPa, respectively (F. E. Brooks, *unpublished data*). Cortical necrosis moved at variable rates above and below the wound sites. Before necrosis reached the branch tip, most branches turned grayish-black and died. Lesion expansion continued down the stem, often extending into the branches below. All visible growth of the pathogen stopped with the first rains during November and the subsequent increase in plant water potential to −1.9 MPa. Inoculations of the same plant during September 1991 and 1992 with isolates D-07 and D-10 produced similar results. *B. dothidea* was reisolated from diseased branches for all isolates.

Growth rate. The optimum temperature range of growth for all isolates was 25–30 C (Fig. 3). The maximum colony diameter of 8 cm was reached in 72 h at 27 C. There was no growth at 5 or 40 C for any isolate, and only scant mycelia was produced at 10 C. Mycelial plugs of all isolates left at 5 and 40 C for a total of 9 days survived. After a total of 14 days, however, only the isolates at 5 C had survived.

Spore germination. Spore germination was 85–100% for both isolates after 24 h at all temperatures tested (Fig. 4A and B). After 2 h, 78, 35, and 12% of the pycnidiospores of isolate D-07 germinated at 30, 25, and 20 C, respectively. However, germination of isolate D-10 after 2 h was only 13, 10, and 5% at the same temperatures. After 4 h, germination was equivalent for both isolates, except for an unexplained drop at 30 C with isolate D-07. Vigorous growth with branched germ tubes occurred by 12 h for both isolates at every temperature, except 10 C. Bipolar germination was common, with a medial germ tube produced occasionally.

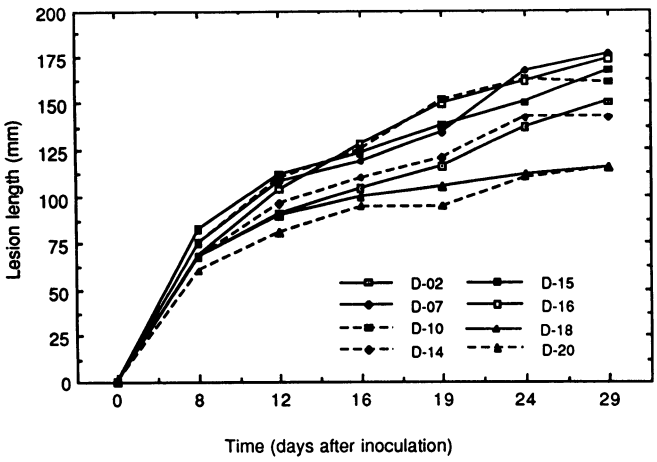

Fig. 2. Results of 17 September 1990 inoculations on a single *Arctostaphylos glauca*. The isolates tested were D-02 and D-07 from *A. glauca*, D-10 and D-14 from *Ceanothus crassifolius*, D-15 and D-16 from *Garrya flavescens*, and D-18 and D-20 from *Quercus agrifolia*. Lesion size is the mean of five replicate inoculated branches.

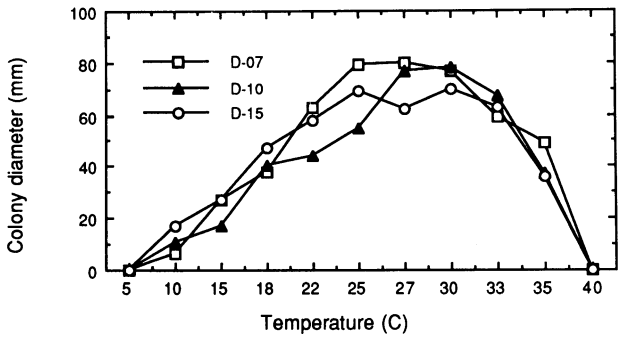

Fig. 3. Mycelial growth on potato-dextrose agar at various temperatures for isolate D-07 from *Arctostaphylos glauca*, D-10 from *Ceanothus crassifolius*, and D-15 from *Garrya flavescens*. There was no growth at 5 or 40 C for any isolate during the 3-day test. Data are based on the results of three experiments.

DISCUSSION

Based on colony characteristics and the morphology and measurements of pycnidia and pycnidiospores produced on diseased branches or on PDA and OA, we suggest that the pathogen is an anamorph of *B. dothidea*. A review of recent literature offers several alternatives in nomenclature. Sutton (33) proposed *Fusicoccum aesculi* based on his examination of Saccardo's 1863 herbarium specimen (the type specimen of Corda having never been located). Pennycook and Samuels (24) characterized the same material and suggested that it was immature, the pycnidia still immersed in host tissue. This could account for the single, holoblastic conidiogenesis reported by Sutton (33) and Morgan-Jones and White (22). Pennycook and Samuels (24), as well as Maas and Uecker (20), found that mature specimens proliferated percurrently by phialidic conidiogenesis. Barr (2) used spore formation to distinguish between *Fusicoccum* (enteroblastic phialidic) and *Dothiorella* (holoblastic). In the specimen described as *Dothiorella*, von Arx (39) stated that spores may be produced singly or in basipetal succession. Most authors avoid uncertainty by using the teleomorphic name *B. dothidea*, even in the absence of sexual structures (11,16,17,20,21,28,41,42).

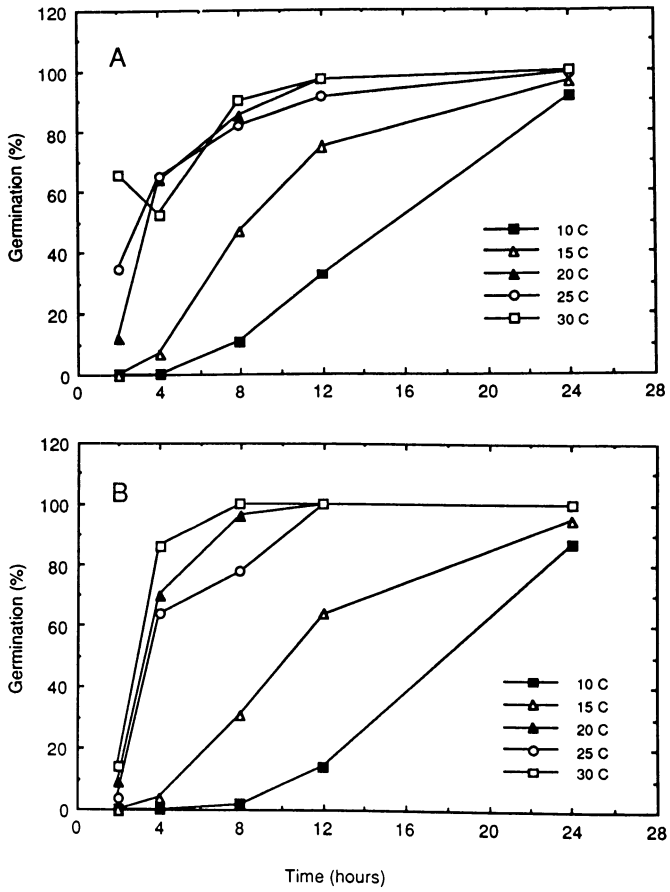

Fig. 4. The influence of temperature on conidial germination of two isolates of *Botryosphaeria dothidea*. **A,** Isolate D-07 is from *Arctostaphylos glauca*, and **B,** isolate D-10 is from *Ceanothus crassifolius*. Data are based on the results of three experiments.

The presence or absence of stromata with only the anamorph present has not proved to be diagnostic. The California hosts examined showed scattered, solitary pycnidia with scant or no stromatic tissue (Fig. 1D) or stromata 1.0–3.0 mm in length with several to numerous locules (Fig. 1B). This agrees with von Arx (38–40), Morgan-Jones and White (22), and Shear et al (31), the latter observing that the size of the stroma is host-dependent.

The host range of California native plants susceptible to *B. dothidea* (listed previously) contains many unreported species. This is due, in part, to the lack of utilitarian value placed on the species. On the other hand, disease diagnoses have been made on native plants used in horticulture, such as ceanothus and manzanita, and those known to foresters, including the coast redwood, giant sequoia, and Douglas fir. When stress-related outbreaks of Botryosphaeria branch dieback, a disease endemic to the southern California chaparral, threaten recreational areas or increase the fire danger close to human habitation, the disease gains public attention. The latter was the stimulus for this study.

The winter rains of southern California are the probable time of spore dissemination and germination. Sutton (34) found that in North Carolina apple orchards spores were produced during periods of rainfall in amounts relative to the length of the storm. The optimum temperature for spore germination of our isolates was similar to Sutton's isolates of *B. dothidea* (25–30 C) but germination at lower temperatures was not. Of the four North Carolina isolates tested previously, two did not germinate at 8 C, and 13 and 21% germination was observed for the other two isolates (35). The southern California isolates attained 87% germination within 24 h at 10 C. This would be sufficient to allow fungal penetration and establishment during the winter storms that often produce moisture and high humidity for several days at an average temperature of 10 C (10). Disease development then progresses throughout the summer, with branch death occurring from August to November, after 4–6 mo with no measurable precipitation.

Artificial inoculations conducted during late-summer 1990 caused rapid cortical necrosis, gray-black leaves and stem discoloration, and tissue collapse. These symptoms are similar to those used to describe blackstem on *Populus* spp. caused by *Cytospora chrysosperma* (4). A drought-induced dormancy common to many chaparral species (9,15), the presence of a wound (3,25), and optimal temperatures during the late summer and early fall probably favored *B. dothidea*. The incidence and severity of branch dieback in the chaparral since 1985 parallels the below-average yearly rainfall pattern (F. E. Brooks, *unpublished data*). Also, the increase in lesion length with a decreasing plant water potential indicates that water stress may predispose plants to disease. Further, Purtich and Mullick (25) and Biggs and Cline (3) demonstrated a correlation between a low level of plant hydration and a decreased host wound response. These conditions may partially explain the rapid cortical necrosis and branch death observed after the September inoculations. This concept of a predisposition to canker disease caused by *B. dothidea* was proposed by Schoeneweiss (29,30) and tested by Crist and Schoeneweiss (8) on mesophytic plants from a temperate climate. Their findings also showed a positive correlation between plant water-stress and an increase in disease severity.

The effect of temperature on colony growth for the southern California isolates was similar to that reported for *B. dothidea* isolates from the southeastern United States. Conidial germination, however, was greater at low temperatures for the former. This coincides with conditions in the chaparral during the winter, when the moisture necessary for sporulation, dissemination, and germination occurs. Morphology and pathogenicity were within the parameters described for *B. dothidea* anamorphs in other climates. Based on these results, we suggest an adaptation has occurred in the biology of this facultative parasite, as well as an increase in host susceptibility during drought conditions. Further research into the effects of plant water-deficit on branch dieback and the host response to wounding in the xeric, mediterranean-type vegetation of southern California is in progress.

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