Etiology of Rhododendron Dieback Caused by Four Species of *Phytophthora*

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ABSTRACT

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Rhododendron dieback was present in all nine nurseries surveyed across North Carolina from 1976 to 1979. *Phytophthora* spp. isolated from plants with dieback symptoms included *P. cactorum, P. citricola, P. heveae,* and *P. nicotianae* var. *parasitica*. All species caused dieback in the greenhouse when plants with young tissue were sprayed with zoospore suspensions. Lesions on shoots developed as light to dark brown necrotic areas in 2–3 days. Mature tissue on intact plants was not infected by zoospores, but mature tissue was colonized by the fungi entering the plant through young tissue. A wedge-shaped necrosis developed in the leaf blade of mature leaves colonized through petioles from infected stems. In laboratory studies, the abaxial leaf surface was more susceptible than the adaxial surface to infection by zoospores. Infection counts did not differ between detached young leaves and detached mature leaves, although penetration of detached mature leaves was slower. Zoospores of *P. heveae* penetrated 0, 17, 67, and 100% of the detached young leaves in 6 hr at 16, 20, 25, and 30 C, respectively. Oospores were formed in infected host tissue by all species. Sporangia of *P. cactorum, P. heveae,* and *P. nicotianae* var. *parasitica* were formed in infected tissue after 12 hr when tissue was wet. Cultivar response to dieback varied. Under nursery conditions, Roseum Elegans and Roseum Pink had the least dieback (3.5% infection) and Scintillation the most (78.2% infection). Cultivars of intermediate response were Catawbiense Album, Chionoides White, Nova Zembla, Purple Splendour, and Spring Dawn.

Additional key words: *Rhododendron maximum,* shoot blight

Incidence of rhododendron dieback has increased dramatically on container-grown hybrid rhododendron in North Carolina nurseries during the past 3 yr. Typically, light to dark brown lesions develop on young leaf and stem tissue. Mature leaves may be colonized from infected young tissue, producing a wedge-shaped zone of discoloration that extends down the midrib. Colonized mature leaves abscise readily when touched. Infected 1-yr-old rhododendrons may be killed, whereas a shoot dieback or blight occurs in older plants. Several *Phytophthora* spp., including *P. heveae* Thompson, were associated consistently with dieback tissues in preliminary studies (4).

Rhododendron dieback caused by *Phytophthora cactorum* (Leb. & Cohn) Schroet. was reported on native and hybrid rhododendrons in New Jersey in 1930 (23), in the Washington, DC, area in the early 1940s (21,22), and in South Carolina in 1968 (16). Rhododendron dieback in Germany was caused by *P. citricola* Sawada (= *P. cactorum* var. *applanta* Chester) in 1959 (13) and in Denmark by *P. cambivora* (Petri) Buisman and *P. citricola* in 1971 (12). In a survey of rhododendron nurseries in the United States, Hoitink and Schmitthenner (11) found *P. cactorum* on branches and crowns, *P. citricola* on roots, crowns, and branches, and *P. citrophthora* (Smith & Smith) Leonian on branches. *P. citrophthora* was considered to be a minor dieback pathogen on rhododendron (11).

The purpose of this study was to determine the incidence, distribution, and etiology of the *Phytophthora* spp. causing rhododendron dieback as well as the effect of environmental factors on disease development.

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MATERIALS AND METHODS

Distribution and incidence. Nurseries in the coastal plain, piedmont, and mountain regions of North Carolina that specialize in producing container-grown hybrid rhododendron were inspected. Shoot samples were collected in plastic bags from rhododendron plants with symptoms of dieback. Disease incidence data were collected by counting the infected plants in randomly selected blocks of containers throughout the nursery.

Fungal identification. Isolations from hybrid rhododendron tissue with dieback symptoms were made on $P_{10}PP$, a modified medium of Eckert and Tsao (6). Fungal identification was made by using cultures grown 3–14 days on a combination of media including: 1) V-8 agar or broth (0.6 g of $CaCO_3$, 40 ml of V-8 juice per liter); 2) lima bean extract broth (50 g of frozen lima beans per liter) that was clarified by filtering through a 1-cm layer of Celite (Fisher Scientific, New Jersey); 3) Difco cornmeal agar (17 g/L); and 4) hemp seed broth (20 g/L, filtered through cheesecloth).

Greenhouse inoculations. Zoospores for inoculation were obtained by growing isolates 3–14 days on either V-8 broth, lima bean extract broth, hemp seed agar, or hemp seed broth. Cultures were rinsed three times in sterile distilled water and chilled at 4 C for 25 min to stimulate zoospore release. Zoospore inoculum was calibrated in a hemacytometer and adjusted to known concentrations.

Terminal shoots of hybrid rhododendron were wounded by removing axillary buds and inoculated by spraying zoospore inoculum to runoff or by placing cornmeal agar disks of the fungus from the margin of 5–7 day old cultures on the wound. In other studies, intact plants with young leaves and stems were inoculated by spraying the foliage with a known concentration of zoospores and placing the plants under intermittent mist (6 sec/6 min) for 24–60 hr in the greenhouse.

Root inoculations. The pathogenicity of the isolates in root inoculation was tested in the greenhouse and nursery. One-year-old hybrid rhododendrons cv. Purple Splendour growing in 15-cm-diameter pots containing a sterilized sand/soil/peat medium (1:1:1, by volume) at pH 5 were used. *Phytophthora* isolates were cultured on sterilized oat grains 2–4 wk before inoculation. Roots were inoculated by placing 30 oat grains colonized by a given isolate in each of three holes punched in the medium around the plant (3). Care was taken to cover the oat grains completely with the medium. Greenhouse test plants were placed in saucers to maintain soil moisture near saturation. Nursery test plants were placed in a lath house and irrigated daily with 0.8 cm of water, but saucers were not used. Plants were rated for root rot using a scale of: 1 = healthy roots; 2 = fine roots, necrotic; 3 = coarse roots, necrotic; 4 = crown rot; and 5 = dead plant (10).

Laboratory inoculations. Leaf disks (17-mm diameter) were cut from young and mature leaves and were placed with either the adaxial or abaxial side up on a moistened paper towel in a closed plastic container of laboratory tests. Zoospore suspensions (0.05 ml) were pipetted onto the leaf disk and incubated on the lab bench at 25 ± 2 C. There were three to

four disks per replication with two to four replications per zoospore concentration.

Leaf disks were surface-sterilized in 0.5 NaOCl for 30 sec at various times after inoculation to determine time of penetration; ie, when surface-sterilization failed to prevent infection. The effect of temperature on penetration time was studied at 16, 20, 25, and 30 C. All experiments were repeated at least twice.

RESULTS

Fungal identification. Isolations from hybrid rhododendron shoots with dieback symptoms consistently yielded one of four species of *Phytophthora*. The species were *P. cactorum, P. citricola, P. heveae*, and *P. nicotianae* Breda de Haan var. *parasitica* (Dast.) Waterh. (20, Table 1). These identifications were confirmed by G. A. Zentmyer, University of California, Riverside (except for *P. cactorum* isolate 406, which was atypical of the species).

Distribution and incidence of dieback. During 1976–1979, we found hybrid rhododendron with symptoms of dieback at the nine nurseries surveyed (Fig. 1). *P. cactorum* occurred in five nurseries, *P. nicotianae* var. *parasitica* in three, *P. citricola* in two, and *P. heveae* in one mountain nursery in 1976 and again in 1979. Usually only one *Phytophthora* sp. was isolated in each nursery, but in one, *P. cactorum, P. citricola,* and *P. nicotianae* var. *parasitica* were isolated over multiple sampling dates.

Incidence of dieback varied greatly among nurseries, but in five nurseries was estimated to average 5–10%, with up to 78% in some cultivars. In one nursery, dieback reached epidemic proportions by 15 August 1979 with an average of 23% of the 1-yr-old plants infected. In this nursery, infection counts by cultivar were Roseum Elegans, 3.4%; Roseum Pink, 3.5%; Spring Dawn, 20.3%; Nova Zembla, 22%; Catawbiense Album, 36.2%; Chionoides White, 61%; and Scintillation, 78%. In all, 638 plants were infected of 2,777 plants surveyed at the nursery. One-year-old plants infected with the dieback fungi usually died.

Greenhouse inoculations. Three-year-old hybrid rhododendrons, Catawbiense Album and Roseum Elegans, became infected by either zoospores or mycelium of *P. heveae* within 3 days after wound inoculation (Fig. 2). Lesions on young leaves and stems developed as light to dark brown, necrotic areas. Colonization of young stem tissue was rapid, progressing at a rate of 13 mm/day within 6 days after inoculation. As the fungus moved from the colonized stem into petioles of mature leaves, the brown

Table 1. *Phytophthora* spp. from hybrid rhododendron in North Carolina with dieback symptoms

Species Isolate	Location	Average size (μm)						
			Sporangia					
		Pedicel	Length	Width	Papillae	Oogonia	Oospores	Antheridial type
P. cactorum								
406[a]	Coastal plain	...[b]	...	...	...	27.4	22.6	Paragynous
407	Piedmont	2.8	37.4	28.3	+	27.8	26.6	Paragynous
411	Piedmont	+	28.3	22.7	+	28.0	24.0	Paragynous
412	Piedmont	+/−	50.4	38.0	+	27.8	23.9	Paragynous
413	Piedmont	−	38.7	31.0	+	29.8	25.0	Paragynous
P. citricola								
604	Piedmont	−	60.3	42.7	−	30.2	27.2	Paragynous
605	Mountains	−	55.7	35.8	−	30.5	26.6	Paragynous
P. heveae								
1400	Mountains	−	39.8	28.3	+	22.6	19.6	Amphigynous
P. parasitica								
316	Piedmont	3.5	44.4	37.2	+	...	...	...
317	Mountains	+	47.1	35.9	+	...	...	...
324	Piedmont	+	42.6	34.4	+	...	...	...

[a] Isolate 406 was atypical of *P. cactorum* forming noncaducous sporangia. A more precise taxonomy could not be determined.
[b] ...Not observed in single culture.

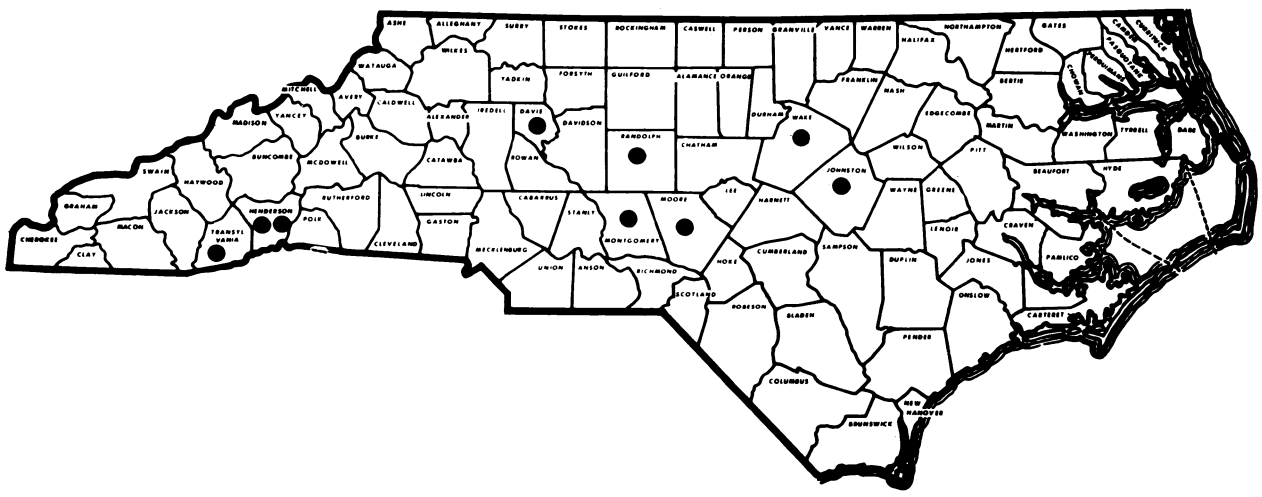

Fig. 1. Distribution of rhododendron dieback caused by *Phytophthora* spp. in North Carolina during 1976-1979. Each dot represents a rhododendron nursery where dieback was observed on container-grown hybrids.

discoloration progressed along the midrib and spread laterally toward the leaf margin, producing a wedge-shaped leaf lesion. Mature leaves infected through the petiole abscised readily. Colonization in older stems was slower, but the fungus continued down the stem to the soil line (60 cm from point of inoculation), killing the plant in 4 mo.

Nonwounded plants also were infected by zoospores of *P. heveae* when plants were incubated 48 hr in a mist chamber after inoculation. Lesions developed 3 days after inoculation on young leaves, stems, and expanding buds of plants. Lesions expanded rapidly, causing young leaves and stems to collapse within 4–5 days after inoculation. Mature tissue and nonexpanding buds were not infected. Expanding axillary buds on woody stems also were infected after inoculation. The fungus then colonized the woody stems from the infected axillary buds.

The incidence of dieback caused by *P. heveae* usually was proportional to the concentration of zoospore inoculum used. When 9–32 zoospores/ml were used for inoculation, none of the otherwise susceptible Roseum Elegans became infected. At zoospore concentrations of 337 and 364/ml, 40% of the plants were infected. When 1,875–5,491 zoospores/ml were used, infection was 100%. Shoot infection was not consistently related to zoospore concentration and ranged from 46 to 89% when zoospore concentrations ranged from 1,875 to 5,491/ml.

Shoot infection of various cultivars with young tissue inoculated with 2.8–3.0 $\times 10^3$ zoospores/ml of *P. heveae* was 50% for Purple Splendour, 55% for Nova Zembla, 72% for English Roseum, 75% for Luscombe's Red, 81% for Roseum Elegans, and 89% for Catawbiense Album. Infected 1-yr-old plants were killed 3–6 wk after inoculation. In addition to the cultivars tested, native rhododendron, *Rhododendron maximum* L., also was susceptible to *P. heveae*, but the rate of stem colonization was slower.

The other species of *Phytophthora* caused dieback when zoospores or oospores ($3–5 \times 10^3$/ml) were used as inoculum on nonwounded plants with young leaves. Shoot infection on cv. Nova Zembla was 12–42% for isolates of *P. nicotianae* var. *parasitica*, 34% for *P. cactorum* (oospore inoculum), 55% for *P. heveae*, and 89% for *P. citricola*. An isolate of *P. citrophthora* from rhododendron (supplied by H. A. J. Hoitink, Ohio State University) caused 45% shoot infection. One-year-old plants infected with *P. cactorum, P. citricola, P. heveae*, and *P. nicotianae* var. *parasitica* or *P. citrophthora* were killed in 3–6 wk.

Root inoculation studies. All species of *Phytophthora* isolated from dieback tissue, except *P. citrophthora*, caused severe root rot of 1-yr-old Purple Splendour rhododendron in the nursery. Plants developed root rot symptoms within 30 days after inoculation. Isolates and root rot rating after 45 days were: *P. cactorum*, 2.8; *P. citricola*, 3.4; *P. heveae*, 4.2; *P. parasitica*, 2.8; *P. citrophthora*, 1.0; and *P. cinnamomi*, 3.4 (used as a known root rot pathogen [3,11]). All species were recovered by plating infected root tissue on $P_{10}PP$ medium.

Fig. 2. Shoot dieback of hybrid rhododendron caused by *Phytophthora citricola*: Plant at 4 wk after zoospore inoculation in the greenhouse (left) and healthy plant not inoculated (right).

Laboratory inoculations. In humidity chambers, leaf disks developed water-soaked areas and necrotic spots on the tissue within 2 days of inoculation. The abaxial surface of leaf disks cut from Purple Splendour was more susceptible than the adaxial surface to zoospore infection by *P. heveae* (Fig. 3). Zoospore concentrations greater than 500/0.05 ml droplet per leaf disk usually were required for adaxial infection. Generally as zoospore concentration increased, abaxial infection increased. No differences in susceptibility were found between young and mature leaf disks in the laboratory.

Infection of abaxial leaf disks by *P. citricola* was similar to the results with *P. heveae*. Adaxial infection by *P. citricola* occurred in one of three experiments with mature leaf disks of Purple Splendour at 4,310 zoospores per 0.05 ml droplet per leaf disk and in none of three experiments with Roseum Elegans. In two experiments with *P. nicotianae* var. *parasitica*, no adaxial infection occurred in Purple Splendour at 2,655 zoospores per droplet per leaf disk, but abaxial infection was similar to results with *P. heveae* and *P. citricola*.

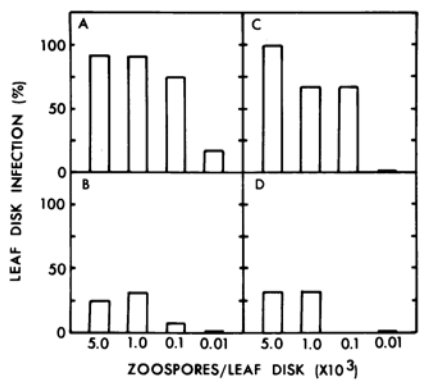

Fig. 3. Leaf disk infection of hybrid rhododendron cv. Purple Splendour caused by *Phytophthora heveae* in moist chambers. The adaxial or abaxial surface of a 17-mm-diameter leaf disk was inoculated with a range of zoospore concentrations. Leaf disks were from: **(A)** young leaves, abaxial inoculation; **(B)** young leaves, abaxial inoculation; **(C)** mature leaves, abaxial inoculation; and **(D)** mature leaves, abaxial inoculation.

Penetration of young leaf disks of

Purple Splendour by zoospore inoculum of *P. heveae* was greatest at 30 C. Lower temperatures increased the time required for penetration. For instance, at 16, 20, 25, and 30 C, penetration at 6 hr was 0, 17, 67, and 100%, respectively. At 11 hr, penetration was 0, 47, 83, and 100% at 16, 20, 25, and 30 C, respectively. On leaf disks that were not surface-sterilized, penetration was 50, 50, 100, and 100% at 16, 20, 25, and 30 C, respectively.

P. heveae penetrated young leaf disks more rapidly than mature leaf disks of Purple Splendour or Roseum Elegans. After 4 hr at 25 C, 83% and 16% of the young and mature leaf disks of Roseum Elegans, respectively, were penetrated. Mature leaf disks required 9 hr for maximum penetration.

Sporulation in host tissues. Oospores were formed in infected leaf tissue by all species including *P. nicotianae* var. *parasitica*, which is normally heterothallic in single culture. Oospores of *P. cactorum* and *P. heveae* were formed in the droplet of inoculum on the surface of the leaf disk, also.

After overnight incubation in moist chambers, sporangia developed on leaves infected with *P. cactorum, P. citrophthora, P. heveae,* and *P. nicotianae* var. *parasitica*. Sporangia were observed only on portions of infected tissue where a water film or droplet was present. Sporangia did not form on dry infected tissue in moist chambers. Leaf disks had sporangia within 42 hr of zoospore inoculation. Water content of infected tissue also affected sporangium formation Sporangia did not form on infected tissue that had dried to the brittle point.

DISCUSSION

This is the first report of *P. heveae* from rhododendron or any other host in the United States. Generally, *P. heveae* has been a pathogen of limited host range compared with other *Phytophthora* spp. Thompson (17) first described the fungus in 1929 as the cause of pod rot and black stripe on rubber (*Hevea brasiliensis* Muell.-Arg.) in Malaya. Turner (19) isolated *P. heveae* from pods of cocoa (*Theobroma cacao* L.) in Malaya, also. The fungus did not sporulate on lesions under field conditions, but oospores developed on the lesion surface in moist chambers. Occurrence of sporangia was rare. In the present study, sporangia developed overnight in water films on the lesion surface, and oospores developed on the lesion surface when wet and throughout infected host tissue.

Zentmyer et al (24) described a trunk canker of 3 to 4 year old avocado (*Persea americana* Mill.) caused by *P. heveae* in Guatemala. In New Zealand, *P. heveae* caused a canker disease on 5–30 cm diameter kauri trees (*Agathis australis* Salisb.) (7), and in Brazil, the fungus caused a blight of Brazil nut trees (*Bertholletia excelsa* Humb. & Bonp.) (1). Campbell and Gallegly (5) isolated *P. heveae* from soil samples taken from under old growth hardwoods and hemlock in two sites in eastern Tennessee and western North Carolina. No host association was made, but our results demonstrated the susceptibility of native rhododendron common in those areas. Because we found *P. heveae* in only one rhododendron nursery, the distribution of *P. heveae* in North Carolina appears to be less broad than that of other *Phytophthora* species.

Although *P. nicotianae* var. *parasitica* has not been reported from hybrid rhododendron, this fungus caused a shoot blight of forcing-type azaleas (*Rhododendron* spp.) (9). A foliage blight of Bougainvillea (*Bougainvillea* × buttiana Holttum & Standley) (2), *Pilea* Lindl. (14), and ti (*Cordyline terminalis* Kunth.) (18) was caused by *P. nicotianae* var. *parasitica* also. As with rhododendron, young tissue was more susceptible than mature tissue.

In greenhouse inoculations and in naturally infected plants, only young leaf and stem tissue was infected by the dieback pathogens. Mature tissue was not infected by spraying zoospore suspensions on plants, although it was colonized by fungi that entered the plant through young tissue. Mercier and Baxter (16) had similar results with *P. cactorum*. Infection did occur infrequently on intact mature tissue when zoospore suspensions of *P. heveae* (1,000/0.05 ml droplet) were placed on the abaxial leaf surface (Benson, *unpublished*).

The abaxial surface of leaf disks from young leaves was more susceptible than the adaxial surface. The occurrence of stomata only on the abaxial surface in rhododendron may account for this observation. Indeed, zoospores were observed to encyst around the stomata. Penetration of leaf disks by *P. heveae* was related to zoospore concentrations and temperature. At 30 C, 17% of the leaf disks were penetrated within 2 hr. Mercier (15) observed that intact leaf tissue was penetrated in 10 hr by *P. cactorum*.

All cultivars tested in greenhouse inoculations with *P. heveae* had 50% or more shoot infection. Under epidemic conditions in one nursery, however, disease incidence was 3.5% for Roseum Elegans and Roseum Pink when some cultivars had more than 70% disease incidence. Mercier (15) found Jean Marie De Montage and Madame Mason resistant to infection in greenhouse inoculations, but the rhododendron species *R. maximum* and *R. minus* Michx. were susceptible.

All four species of *Phytophthora* causing dieback also caused root rot. Dieback may be one phase of the *Phytophthora* complex that develops in rhododendron nurseries when temperature is near 30 C and rainfall or overhead irrigation is frequent. Gerlach et al (8) demonstrated the splash dispersal of *P. citrophthora* from the soil surface to the foliage of container-grown *Pieris japonica* (Thunb.) D. Don, where it caused a dieback disease similar to that on rhododendron.

Currently, nurserymen are controlling rhododendron dieback by pruning out infected tissue, avoiding late afternoon irrigations, and spraying protective fungicides.

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