Pathogenicity of *Leptographium* and *Verticicladiella* spp. Isolated from Roots of Western North American Conifers

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ABSTRACT

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Fourteen isolates representing seven species of *Verticicladiella* and *Leptographium* were used in greenhouse pathogenicity tests on wounded and unwounded ponderosa pine and Douglas-fir seedlings. Although each of these fungus species has been isolated from roots showing symptoms of black-stain root disease, only isolates of *V. wageneri* reproduced the unique symptomatology of the disease. Colonization by *V. wageneri* was predominantly vertical with hyphae in the tracheids, but not in xylem parenchyma. Most of the other species tested showed some degree of pathogenicity but, unlike *V. wageneri*, generally required wounds for infection counts. Also, their hyphae were found in both tracheids and parenchyma. Three of the fungi (*L. terebrantis*, *V. abietina*, and an unidentified *Verticicladiella* sp.) were isolated from common root- and stump-feeding bark beetles known to be active in roots infected by *V. wageneri*. It appears that only *V. wageneri* is capable of causing black-stain root disease, and that other fungi isolated from black-stained tissues are secondary invaders introduced into diseased roots by bark beetles.

A unique disease of pines known as black-stain root disease (29) was first discovered in the 1930s and was described by Wagener and Mielke (34) in 1961. They noted brown-to-black staining of colonized sapwood of the roots and lower bole of affected trees due to the presence of pigmented fungus hyphae in tracheids. Smith (28) noted the similarity of this disease to the vascular wilts of hardwoods in the systemic movement of the pathogen and its restriction to the tracheids. As in the vascular wilts, vertical growth of hyphae occurs more quickly than tangential or radial growth. Vascular staining tends to spread tangentially within a growth ring. Kendrick (16) named the causal agent *Verticicladiella wageneri* Kendr., and noted that it was similar to a fungus causing a root disease of pines in Montana (21). Later, Cobb and Platt (5) reported black-stain root disease on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco).

Despite the uniqueness of this disease, there is much confusion concerning its etiology and its relationship to other root diseases caused by species of *Verticicladiella*. Black-stain root disease is found only in western North America. Root-staining diseases of pines caused by species of *Verticicladiella* other than *V. wageneri* have been described in eastern North America (27,30) and elsewhere (10,25,35), but these apparently do not show the properties of vascular wilts outlined by Smith (28). In western North America, several *Verticicladiella* spp. have been isolated from roots of dead and dying conifers, including those showing symptoms of black-stain root disease, and some of these fungi have been reported to be root pathogens (14,15,17,20,23,31–33).

Inoculations with isolates of *V. wageneri* have consistently resulted in black-stain root disease (5,6,28,34). However, the pathogenicity of most of the other *Verticicladiella* spp. has not been clearly demonstrated. Mielke (23) noted limited xylem staining in roots of various conifers that he inoculated with a fungus identified as *V. penicillata* Kendr. Leaphart and Gill (22) and Hubert (13) reported lesions on roots of *Pinus monticola* Dougl. that were inoculated with isolates of a *Leptographium* (a genus similar to *Verticicladiella*) species associated with white pine pole blight. Their isolates may have been a *Verticicladiella* sp. because the latter genus was not described until after their studies. The role of these lesion-causing fungi (13,22,23) as root pathogens and their involvement in black-stain root disease have not been fully elucidated.

We have consistently isolated *V. wageneri* from freshly colonized, black-stained tissue. However, we have also isolated fungi other than *V. wageneri* from roots with black-stain root disease, especially when the roots had been attacked by root-feeding bark beetles (Coleoptera: Scolytidae) subsequent to colonization of the roots by *V. wageneri*. Thus, we hypothesized that many of the *Verticicladiella* and *Leptographium* spp. associated with black-stained roots are secondary organisms that may be introduced into diseased roots by bark beetles. Because there is confusion concerning the role of root-inhabiting *Verticicladiella* and *Leptographium* spp. as pathogens and their possible involvement in black-stain root disease, we tested the pathogenicity of isolates of these fungi obtained from our isolations and from other plant pathologists. Also, we attempted isolation of these suspected secondary fungi from root-feeding bark beetles to determine if the beetles could serve as vectors.

MATERIALS AND METHODS

Pathogenicity tests. All isolates used in inoculations were obtained from dead or dying conifer roots by plant pathologists from British Columbia, Montana, Idaho, Oregon, Colorado, and New Mexico. Isolates were placed into groups based on the morphology of conidiophores and conidia, as well as pigmentation, texture, and growth rate of mycelium. Five isolates of *V. wageneri* and one or two representative isolates of each of six other species that have been isolated frequently from the roots of conifers in western North America were used in pathogenicity tests (Table 1).

Each isolate was hyphal-tipped to ensure purity prior to colonization of inoculum blocks. Inoculum blocks were made by boiling 3-cm-long segments of ponderosa pine twigs (~1 cm in diameter) in 10% malt extract for 2 hr, placing the twigs in jars, and autoclaving them for 1 hr at 121 C. After inoculation with the appropriate isolate, each jar was incubated for 8 wk at 18 C.

Two-year-old, bare-root seedlings of Douglas-fir and ponderosa pine (*Pinus ponderosa* Laws.) were lifted and stored at 1 C until

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inoculation in December 1980. In the case of wound-inoculated seedlings, the taproot surface was cleaned with 95% ethanol, and a 1-cm-long section of the taproot representing approximately one-third of the diameter was removed at 3 cm below ground level. A 1-cm-long segment of colonized pine twig was secured over the fresh wound with masking tape. For seedlings inoculated without wounding, a 3-cm-long inoculum block was secured to the taproot 5–8 cm below the ground level. After inoculation, all seedlings were potted in a pasteurized mixture of peat and sand (1:1, v/v) in 8-cm-diameter steel cans. Ten wounded and 10 unwounded seedlings of each host were inoculated with each isolate. For controls, 40 seedlings of each host were wounded, and 40 were left unwounded and inoculated with sterile blocks. Seedlings were randomly assigned to greenhouse benches and watered heavily (2–3 times per week) until termination of the experiment.

Dead seedlings were removed weekly from the pots and examined for xylem discoloration and resinosis. Nine months after inoculation (4 wk after the last mortality was noted), the remaining live trees were examined. For each isolate used, at least three seedlings (preferably those with discolored tissue) of each host were radially sectioned near the point of inoculation and examined at ×400 for the presence of hyphae in tracheids and xylem parenchyma. In addition, isolations were attempted from at least three surviving seedlings and, if possible, from three killed seedlings of each host inoculated with each isolate. Isolations were attempted by placing three chips of xylem tissue excised from near the inoculation area onto water agar amended with 100 μg of cycloheximide and 100 μg of streptomycin per milliliter, a selective medium suitable for isolating the fungi tested in this study (11).

Isolations from insects. Potential vectors of root-inhabiting fungi were trapped by placing 6.4-mm (0.25-inch)-mesh screen coated with "Stickem-special"® (Michel and Palton, Emeryville, CA 94608) on freshly cut Douglas-fir and ponderosa pine stumps near Eureka and Georgetown, CA, respectively. Isolations were attempted from adults of five species of root- and stump-feeding bark beetles that were collected on sticky traps: *Dendroctonus valens* LeConte, *Hylastes macer* LeConte, *H. longicollis* Swaine, *H. nigrinus* (Mannerheim), and *Hylurgops porosus* LeConte. At least 10 adults of each species were individually crushed and placed on potato-dextrose agar amended with the aforementioned antibiotics. Plates were incubated at 18 C and all *Verticicladiella* species and similar fungi were subcultured and compared morphologically with the isolates used in the pathogenicity studies.

RESULTS

Verticicladiella wageneri. Only seedlings inoculated with *V. wageneri* showed symptoms characteristic of black-stain root disease. All five isolates killed both wounded and unwounded ponderosa pine and Douglas-fir seedlings (Table 2). A few surviving seedlings showed extensive colonization by *V. wageneri*, but most of the infected seedlings died. Deep amber to dark-brown hyphae were seen in the tracheids but not in the parenchyma of the stained xylem of these seedlings. The pathogen vertically colonized the vascular tissue of the roots and stems, but little radial growth was seen. Each reisolation attempt from seedlings with the typical black-staining yielded *V. wageneri*.

Other species. In contrast to *V. wageneri*, the other fungi tested (except *Leptographium terebrantis* Barras and Perry) were unable to infect unwounded pine or Douglas-fir (Table 2). However, xylem discoloration, resinosis, and some mortality was noted in wounded pine seedlings inoculated with most of the isolates tested (Table 2). Only the isolate of *Verticicladiella* sp. H caused mortality of wounded Douglas-fir. Generally, reisolation attempts from pines, but not from Douglas-fir, yielded the species inoculated into the seedlings, especially if the seedlings had been wounded. In those cases where xylem discoloration resulted, it appeared that the infection was more localized than in infections by *V. wageneri*. Vertical colonization was considerably less with the other fungus species (Table 2), and much more radial colonization was evident. Microscopic examination of seedlings colonized by these other species showed the presence of pigmented hyphae in both tracheids and ray parenchyma.

Verticicladiella abietina. Lane and Goheen (20) obtained isolate ORF-T (Table 1) from the roots of a dying *Abies grandis* (Dougl.) Lindl. They tentatively identified the fungus as *V. procera* Kendr., but the strongly curved (allantoid) conidia and other cultural characteristics of ORF-T and those of NMA-103 (Table 1) matched precisely Kendrick's (16) description of *V. abietina* (Hughes) Kendr.

Only two of 20 pines wound-inoculated with the isolates of *V. abietina* died (Table 2). Surviving seedlings of pine and Douglas-fir that were wound-inoculated with *V. abietina* showed only limited xylem discoloration in the vicinity of the wound, and the wounded pines showed some resinosis. However, this reaction was also noted in wounded controls. We were unable to reisolate ORF-T from any seedling, whereas NMA-103 was reisolated from wound-inoculated pines, but not from Douglas-firs.

Verticicladiella abietina has been frequently associated with galleries of bark beetles (16). Of the beetles from which we isolated, *Hylastes longicollis*, a root-feeding bark beetle on *Pinus* spp. (3), consistently yielded *V. abietina*. Thus, *H. longicollis* could introduce *V. abietina* into roots with black stain root disease.

Leptographium terebrantis. With the exception of *V. wageneri*, this was the species most frequently isolated from roots of pines showing symptoms of black stain root disease. Isolate IDL-101 (Table 1) was sent to us as *V. penicillata* (Grosm.) Kendr. and matches the description of the fungus Mielke (23) used in his inoculations. Mielke (23) identified his fungus as *V. penicillata*, but both IDL-101 and BCL-101 (Table 1) have conidia that are much smaller and not as curved as the European isolates of *V. penicillata* described by Kendrick (16). Our isolates do, however, fit the description of *L. terebrantis* by Barras and Perry (1).

Both isolates of *L. terebrantis* killed wounded and unwounded pine (Table 2) but did not infect Douglas-fir. Killed seedlings showed either faint discoloration or gray-to-black staining for 1–6 cm from the point of inoculation. Infected areas were commonly resinous. All surviving, wound-inoculated pine showed heavy resinosis (for up to 2–8 cm), and some showed limited gray to black staining. The surviving seedlings that were inoculated without wounding had no stain and appeared the same as unwounded controls. Hyphae were found in both tracheids and ray parenchyma, as Mielke (23) noted in his inoculations. Reisolation attempts from killed pines and from six surviving wound-inoculated pines yielded *L. terebrantis*. The fungus could not be reisolated from inoculated Douglas-fir. Although *L. terebrantis* was pathogenic to pines, it did not cause black-stain root disease.

We isolated *L. terebrantis* from two species of root and stump feeding bark beetles, *Dendroctonus valens* and *Hylurgops porosus*. It is not surprising that we isolated *L. terebrantis* from *D. valens*, a bark beetle closely related to *D. terebrans* with which the fungus was first associated (1). Mielke's (23) fungus, believed to be synonymous with *L. terebrantis*, was also associated with *H. porosus*. Perhaps the common occurrence of these two bark beetles

TABLE 1. Hosts and geographic origins of *Verticicladiella* and *Leptographium* isolates used in pathogenicity tests

Species	Isolate	Location	Host of origin
V. abietina	ORF-T	Oregon	Grand fir
	NMA-103	New Mexico	Ponderosa pine
L. terebrantis	IDL-101	Idaho	Lodgepole pine
	BCL-101	British Columbia	Lodgepole pine
Verticicladiella sp. F	COD-101	Colorado	Douglas-fir
	MOD-5	Montana	Douglas-fir
Verticicladiella sp. H	IDD-101	Idaho	Douglas-fir
Verticicladiella sp. E	NMP-103	New Mexico	Ponderosa pine
V. procera	IDD-102	Idaho	Douglas-fir
V. wageneri	COE-1	Colorado	Pinyon
	ORH-1	Oregon	Western hemlock
	IDP-1	Idaho	Ponderosa pine
	BCD-1	British Columbia	Douglas-fir
	MOD-1	Montana	Douglas-fir

TABLE 2. Results of greenhouse pathogenicity tests to ponderosa pine and Douglas-fir of isolates of *Verticicladiella* and *Leptographium* that have been associated with black-stain root disease

		Ponderosa pine seedlings[a]								Douglas-fir seedlings[a]							
		Wounded				Unwounded				Wounded				Unwounded			
Species	State of origin	Number symptomatic[b]	Number killed	Length of stain (cm)[c]	Reisolation[d]	Number symptomatic[b]	Number killed	Length of stain (cm)[c]	Reisolation[d]	Number symptomatic[b]	Number killed	Length of stain (cm)[c]	Reisolation[d]	Number symptomatic[b]	Number killed	Length of stain (cm)[c]	Reisolation[d]
V. abietina	OR	2	2	2 ± 0	−	0	0		−	0	0		−	0	0		−
V. abietina	NM	0	0		+	0	0		−	0	0		−	0	0		−
L. terebrantis	ID	10	1	2	+	2	2	5 ± 4	+	0	0		−	0	0		−
L. terebrantis	BC	10	4	3 ± 2	+	1	1	6	+	0	0		−	0	0		−
V. sp. F	CO	0	0		+	0	0		−	0	0		−	0	0		−
V. sp. F	MO	4	1	1	+	0	0		−	3	0		−	0	0		−
V. sp. H	ID	3	3	3 ± 1	+	0	0		−	6	6	4 ± 3	+	0	0		−
V. sp. E	NM	10	4	6 ± 2	+	0	0		−	10	0		−	0	0		−
V. procera	ID	0	0		+	0	0		−	0	0		+	0	0		−
V. wageneri	CO	9	9	39 ± 8	+	8	8	34 ± 9	+	9	9	16 ± 6	+	8	7	17 ± 7	+
V. wageneri	OR	10	10	25 ± 9	+	4	4	26 ± 9	+	9	8	14 ± 5	+	5	5	11 ± 5	+
V. wageneri	ID	10	10	35 ± 6	+	2	2	22 ± 9	+	10	9	16 ± 3	+	3	2	15 ± 7	+
V. wageneri	BC	10	9	38 ± 5	+	5	4	25 ± 3	+	5	5	16 ± 12	+	5	4	16 ± 6	+
V. wageneri	MO	9	8	26 ± 7	+	5	5	25 ± 6	+	7	7	18 ± 5	+	4	3	13 ± 4	+

[a] Ten, 2-yr-old seedlings of each host were inoculated with each isolate.
[b] Seedlings with xylem discoloration and/or resinosis greater than that of control seedlings.
[c] Mean and standard deviation of the extent of xylem stain above and below the inoculation point of killed seedlings.
[d] Ability to reisolate the fungus from killed or surviving seedlings.

with diseased pines (24) explains the frequent isolation of *L. terebrantis* from roots with black-stain root disease.

***Verticicladiella* sp. F.** With the exception of *V. wageneri*, this fungus was the most frequently isolated *Verticicladiella* sp. from diseased Douglas-fir roots. It appears to be morphologically distinct from those species described by Kendrick (16) and from the other species with which we are familiar. Isolate COD-101 is the unassigned *Verticicladiella* sp. isolated from black-stained Douglas-fir roots in Colorado by James and Goheen (15).

The two isolates of *Verticicladiella* sp. F that we used failed to kill either wounded or unwounded Douglas-fir seedlings, and we were unable to reisolate the fungus from them. However, one pine wound-inoculated with MOD-5 died (Table 2); it had heavy resinosis and <1 cm of gray stain. Some surviving, wound-inoculated pine and Douglas-fir seedlings also had resinosis and a small amount of staining. The fungus was recovered from the single killed seedling, but not from the other pines wound-inoculated with MOD-5. However, the fungus was recovered from pines wound-inoculated with COD-101. Although *Verticicladiella* sp. F has been frequently isolated from diseased roots of Douglas-fir, it appears to be only weakly pathogenic, if at all. Although we have been unable to identify *Verticicladiella* sp. F, it appears to be the same fungus we consistently isolated from *Hylastes nigrinus*, a root-feeding bark beetle commonly attacking black-stained roots of Douglas-fir.

***Verticicladiella* sp. H.** Isolate IDD-101 (Table 1) killed wounded seedlings of pine and Douglas-fir, but failed to infect any unwounded seedling (Table 2). The three killed pines had resinosis with some red discoloration in the xylem. The six killed Douglas-firs had only slight resinosis with light-gray discoloration. Surviving, wound-inoculated pine and Douglas-fir did not differ in appearance from wounded controls. The fungus was reisolated from killed, but not from surviving, seedlings.

This was the only species besides *V. wageneri* that caused mortality of Douglas-fir seedlings (Table 2). However, it did not infect without wounding and did not cause black-stain root disease.

***Verticicladiella* sp. E.** The third unassigned species has been isolated from roots of dead and dying ponderosa pine and Douglas-fir, but only in New Mexico. We have not isolated this species from bark beetles; however, we have not attempted isolations from New Mexico beetles.

Verticicladiella sp. E killed four wound-inoculated pines but did not infect unwounded seedlings (Table 2). All wound-inoculated pines and Douglas-firs, whether alive or dead, had 1–8 cm of blue-gray to black stain. Heavy resinosis (usually 5–6 cm) was also present in wound-inoculated pines. The fungus was reisolated only from killed seedlings.

Although *Verticicladiella* sp. E was pathogenic in this study, it did not colonize the seedlings as extensively as *V. wageneri*, and hyphae were found in both tracheids and ray parenchyma. It is not known if *Verticicladiella* sp. E can cause a root disease in nature, but it evidently is not capable of causing black-stain root disease.

***Verticicladiella procera*.** This species has been associated with lesions on roots of *Pinus strobus* L. (12,18,27,30) and *P. resinosa* Ait. (16,27). In our inoculations, isolate IDD-102 (Table 1) was unable to kill or cause any apparent disease symptoms on wounded or unwounded pine or Douglas-fir (Table 2). However, *V. procera* was readily reisolated from both wound-inoculated pine and Douglas-fir, although the xylem of wound-inoculated seedlings did not differ from that of the wounded controls.

Verticicladiella procera may not be common in western North America. We have not isolated this fungus from bark beetles or diseased roots in California. The isolate of Lane and Goheen (20), which they referred to as *V. procera*, appears to be *V. abietina*. The finding that isolate IDD-102 was not pathogenic under our test conditions, but that it still survived in inoculated seedlings suggests that this isolate is a weak pathogen or saprophyte that is able to colonize and persist in wounded tissue. However, Houston (12) did obtain annual cankers by inoculating *Pinus strobus* in New York with an isolate of *V. procera*, and Lackner and Alexander (18) demonstrated pathogenicity on seedlings of *P. strobus*.

DISCUSSION

Only isolates of *V. wageneri* caused black-stain root disease on inoculated seedlings. The fungus was able to infect without wounding, and it colonized the host in a manner similar to vascular wilt pathogens (predominantly vertical growth within an annual ring and hyphae restricted to the tracheids). Most of the isolates of the other *Verticicladiella* spp. tested infected some wounded seedlings, but they were more localized than *V. wageneri*, and their hyphae were found in both tracheids and xylem parenchyma.

When we have isolated from black-stained roots of naturally infected trees, we have most frequently isolated *V. wageneri*, but

other *Verticicladiella* spp. have been isolated, especially after the roots had been attacked by root- and stump-feeding bark beetles. Bark beetles, known to be active in trees with black-stain root disease (4,7,8,9,19,24), may vector some of these other *Verticicladiella* spp. In this study, three of the seven species used in pathogenicity tests were associated with root-feeding bark beetles, and it is likely that the other species are also associated with insects. We conclude, therefore, that black-stain root disease is caused by *V. wageneri* and that the other frequently isolated *Verticicladiella* spp. are secondary organisms probably introduced into diseased roots by bark beetles.

Although *V. wageneri* is capable of causing black-stain root disease independently, other fungi may at times contribute to the death of roots infected by *V. wageneri*. As has been demonstrated with some stem-feeding bark beetles (2,26), root-feeding bark beetles may introduce phytopathogenic fungi that kill host tissue and create a more suitable environment for insect development. Thus, when insects attack trees stressed by *V. wageneri* (4,7,8,24), pathogenic *Verticicladiella*, or *Leptographium* spp. vectored by root-feeding bark beetles may help kill the roots and hasten the death of the entire tree.

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