Root-Colonizing Insects Recovered from Douglas-Fir in Various Stages of Decline Due to Black-Stain Root Disease

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ABSTRACT

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Douglas-fir (*Pseudotsuga menziesii*) trees infected with *Verticicladiella wageneri* were assigned to one of five symptom classes by crown color and terminal growth characteristics at three widely separated sites in the Coast Range of Oregon. Root systems of trees in each symptom class were excavated, and the insects beneath the bark were collected. Two weevils, *Steremnius carinatus* and *Pissodes fasciatus*, and the root bark beetle *Hylastes nigrinus* were commonly associated with diseased trees. Insects sequentially colonized roots of diseased trees as each root succumbed to infection; the colonization period generally lasted from 2 to 4 yr. The occurrence of these root-colonizing insects throughout the decline of the host suggests that *S. carinatus, P. fasciatus*, and *H. nigrinus* may act as vectors of *V. wageneri* in this ecosystem.

Additional key words: *Ceratocystis*, Curculionidae, Scolytidae.

Verticicladiella wageneri Kendrick (sexual stage *Ceratocystis wageneri* Goheen and Cobb), the fungal cause of black-stain root disease, kills principally Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and species of *Pinus* (17). *V. wageneri* colonizes the tracheids of the roots, root collar, and lower stem, causing a black, ringlike stain of infected sapwood rather than the wedge-like stain characteristic of most sapstain fungi (27). Most research on this disease has involved *V. wageneri* on ponderosa pine (*Pinus ponderosa* Laws.) in California. Currently, the hypotheses proposed for its spread are transmission from diseased trees to healthy trees by contact of major roots (8,20,27) or hyphal growth through the soil (8,14), and transmission by vectors (8–10,20,26).

V. wageneri can successfully colonize a root of a healthy tree that is grafted to, and thereby has tracheid continuity with, an infected root of an adjacent diseased tree (8,13,20). Simple contact of major roots is reported as a possible pathway for tree-to-tree transmission (8,20,27). Goheen (8) found that these two mechanisms account for a relatively small percentage of the infection in ponderosa pine and that 92% of diseased trees showed evidence of infection courts on fine rootlets. In 79% of these, the fine rootlets were the only observable means of entry of the pathogen. Hicks et al (14) demonstrated that *V. wageneri* is capable of limited hyphal growth (up to 6 cm) through the soil from infected roots, which supports the observation that fine roots need not be in contact for transmission of the pathogen (8). Recently, Hessburg (13) demonstrated the validity of this mechanism of transmission.

The vector hypothesis is supported by two lines of evidence: Landis and Helburg (20) observed insect galleries adjacent to stain margins of *V. wageneri*, and Goheen and Cobb (9) found conidiophores of *V. wageneri* and perithecia of the sexual stage, *Ceratocystis wageneri*, only in insect galleries in diseased roots; insects serve as vectors of several other *Ceratocystis* species that are pathogenic on woody plants (2,15,18,24). Both perithecia and conidiophores of *Ceratocystis* fungi produce spores borne in a viscous matrix well suited for contact contamination of surfaces but ill suited for wind or water-splash dispersal. Vectors may contact inoculum of these pathogens on diseased brood trees and then disperse to feed on healthy, wounded, or stressed trees.

Although *V. wageneri* is widely distributed on Douglas-fir throughout the Coast Range and the west side of the Cascade Mountains of Washington, Oregon, and northern California (5,10), little is known about the host-pathogen-insect interaction in this community. The lack of information, the increased incidence of *V. wageneri* associated with forest management activities (11,12), and the implication of insects as vectors, have prompted us to examine the relationship between insects and diseased and healthy Douglas-fir (29). This paper describes the insect guild within the roots, root collars, and lower stems of healthy and infected trees. We tested the prediction that the number of insects in diseased trees is significantly greater than the number of insects in healthy trees. Such a test should confirm or deny the first of four postulates set forth by Leach (21) for identifying vectors of pathogenic organisms: a strong association of insects and diseased trees.

MATERIALS AND METHODS

Root systems of *V. wageneri*-infected and healthy Douglas-fir trees were excavated in 1979–1980 in one plantation in each of three locations in the Oregon Coast Range: Alsea (Benton County), Ball Bearing Hill (Yamhill County), and Velvet Creek (Lane County). The plantations were 10–15, 14, and 24 yr old, respectively. *V. wageneri* was identified in the vicinity of each plot by the characteristic stain in dying trees (27).

In August 1979, diseased trees at four separate sites of infection in each plantation were assigned to one of five symptom classes based on crown color and terminal growth. Trees were classified as follows: presymptomatic (normal green foliage with normal growth of the terminal shoot), symptomatic (normal green foliage with conspicuously reduced growth of the terminal shoot), yellow (chlorotic foliage with reduced growth of the terminal shoot), red (red foliage, with little or no current growth), and dead (recently

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dead, defoliated, with no current growth). A sixth class of healthy control trees was located at least 10 m from the visibly affected diseased trees at each site. Trees appearing long dead or having exfoliating bark, broken branch tips, or fruiting bodies of *Polyporus* spp. were excluded. Also, trees wounded with an axe during inspection for site selection were excluded because wounding of diseased trees has been shown to influence the aggregation of insects (8). Each sample site contained one or more trees in each symptom class. One randomly selected tree from each symptom class was excavated and removed by hand from a single, randomly assigned site in each plantation during the sampling periods August–September 1979, November–December 1979, March–April 1980, and June–July 1980. Each site was sampled only once.

Nearly all roots ⩾0.3 cm in diameter were removed; only a few that were beneath old stumps, rocks, or nonsample trees were irretrievable. Length of the last 10 internodes of the leader was measured on all trees except those sampled in August–September 1979, which were measured for only five internodes.

Bark was removed from the roots and the lower 1 m of stem in the laboratory. All subcortical insects within each root and within the lower stem were collected and preserved separately. Stem-colonizing bark beetles were collected but not tallied because the species associated with diseased Douglas-fir have been reported previously (10). We used several generally accepted publications (1,3,6,16,23) to identify the insects.

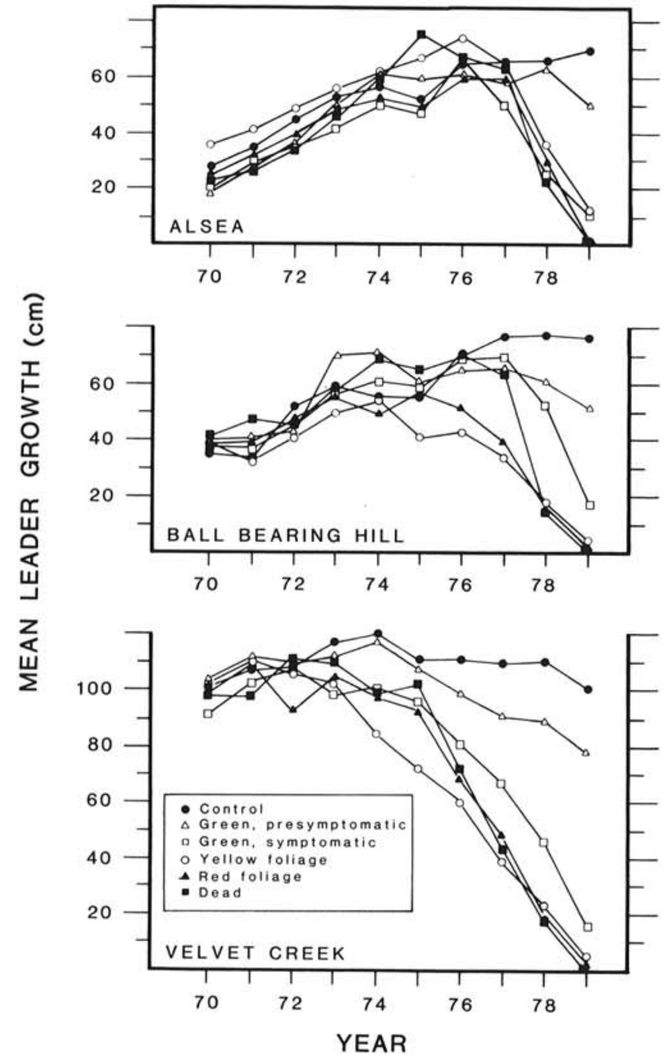

Fig. 1. Mean internode length of healthy Douglas-fir and Douglas-fir showing crown symptoms (see text for symptom classes) resulting from infection with *Verticicladiella wageneri* in the Oregon Coast Range, 1979–1980 (n = four trees per symptom class).

To index the extent of colonization of the host xylem by the pathogen, we compared the circumference of black-stained xylem of each excavated tree with the total circumference of roots at the root-collar juncture and with the circumference of the stem at the soil line. An isolate from a single diseased tree excavated at each plantation was tested for pathogenicity to Douglas-fir seedlings according to Koch's postulates. We isolated from stained root xylem on a selective medium (14) and inoculated 2-yr-old seedlings by means of a technique developed by Hessburg (13). A 0.5-cm-square block of agar colonized by the test fungus was applied to an unwounded root of each of three seedlings. The inoculum and root were wrapped with a small square of moistened cheesecloth, then bandaged with a square of 0.4-mil polyethylene. The ends of the bandage were secured with twist-ties. Planted seedlings were held in a greenhouse for 6 mo, or until severe disease symptoms developed. Each seedling was examined for the characteristic black-stain of colonized xylem and microscopically examined for the typical tracheid colonization pattern (13,25,27). Conidiophores of the isolates taken from diseased seedlings were compared with Kendrick's (19) description of *V. wageneri.*

Distribution of the abundance of insects was strongly bimodal; therefore, nonparametric techniques (the Wilcoxon rank sum test and signed rank test [22]) were used to detect significant differences between treatments (symptom classes). All tests for significant differences were calculated at $P = 0.05$.

RESULTS

Disease symptoms. Douglas-fir infected with *V. wageneri* exhibited reduced leader and branch growth, chlorosis, reduced needle length, reduced needle retention, a distress cone crop, and, on occasion, resinous lesions on the lower stem. Reduced leader length was the first aboveground indicator of fungal colonization, and in most instances this change was abrupt from one season to the next (Fig. 1). Trees usually died in two seasons or occasionally in a single season after severe leader reduction. Only a few trees survived three or more seasons. Survival of diseased trees with red foliage (i.e., trees that died in 1979) averaged 4 yr at Velvet Creek, 3 yr at Ball Bearing Hill, and 2 yr at Alsea (Fig. 1).

Black-stained xylem was present in all infected trees but in no control trees. Mean circumference of roots and lower stems with black-stained xylem increased from 24% in presymptomatic trees to 63% in symptomatic trees (Table 1). Trees classified red and dead were black-stained on almost the entire circumference. As black-stain of the xylem increased, leader growth decreased (Table 1).

The fine-root system of Douglas-fir heavily colonized by *V. wageneri* was invariably destroyed as a result of infection by the pathogen; the rootlets were brittle and dry or resin-soaked. Heavy resinosis of diseased, woody roots was only occasionally observed. However, root junctions frequently had dead cambium and resin-impregnated bark (28).

The isolates of *V. wageneri* from all three plantations were pathogenic to inoculated seedlings. Infected seedlings died within 12 wk of inoculation. Microscopic examination revealed hyphae in tracheids only, which is typical of *V. wageneri* (13,25,27).

Root-inhabiting insects. Three species of beetle were consistently recovered from diseased trees, *Hylastes nigrinus* (Mann.) (Scolytidae), *Steremnius carinatus* (Boh.) (Curculionidae), and *Pissodes fasciatus* LeC. (Curculionidae) (Table 2). These species constituted 97% of the insects recovered. Associated insects were beetles in the families Elateridae (three insects), Cleridae (four insects), and Cerambycidae (27 insects); other Scolytidae (two insects); flies in the Dolichopodidae (11 insects); and wasps in the Braconidae (28 insects). Because there were so few of these associated insects, the analysis was confined to *H. nigrinus, S. carinatus*, and *P. fasciatus*.

When *H. nigrinus, S. carinatus*, and *P. fasciatus* are considered collectively, presymptomatic trees contributed 4% (88 insects); green, symptomatic trees 24% (526 insects); trees with yellow foliage 9% (196 insects); trees with red foliage 45% (1,017 insects);

and dead trees 18% (421 insects). Of diseased, symptomatic trees, 83–100% (10–12 trees) in each symptom class were infested with insects at the time of excavation (Table 2). In infected, presymptomatic trees, 50% (six trees) were infested and 67% (eight trees) had evidence of damage by insects at the time of excavation. In this symptom class, *P. fasciatus* was recovered from only a single tree (Table 2) in which the root collar directly above a heavily stained root was infested.

Taken collectively, significantly more *H. nigrinus, S. carinatus*, and *P. fasciatus* were recovered from diseased trees than from control trees that were free of insects or insect damage (Table 2), and significantly more insects were recovered from roots than from the root collar and lower stem of diseased trees (Table 3). Sample date had no significant effect on numbers of insects collected, but site was an important factor. The older trees at Velvet Creek yielded significantly more insects than those at either Alsea or Ball Bearing Hill which did not differ significantly. The difference can be wholly attributed to the abundance of *S. carinatus* in the Velvet Creek trees.

Steremnius carinatus. *S. carinatus* was the most abundant insect collected, contributing 48% of all beetles recovered. Its occurrence, or evidence of its prior occupation, was observed in eight (67%) of the infected, presymptomatic trees. Six of twelve trees were infested at the time of sampling. Trees in all diseased symptom classes had significantly more *S. carinatus* than the control trees (Table 2). *S. carinatus* preferred the root portion of diseased trees to the lower stem (Table 3). *S. carinatus* discovered and invaded diseased trees throughout the decline of the host and preceded invasion of the stem by bark beetles.

Site had a significant effect on abundance. The mean number of beetles per sample replicate (one tree from each diseased symptom class from a single sample location on a single sample date) at the 24-yr-old Velvet Creek plantation was greater than the mean number at either the 15-yr-old Alsea or the 14-yr-old Ball Bearing Hill plantations (218 versus 31 and 25, respectively).

Hylastes nigrinus. The Douglas-fir root bark beetle, *H. nigrinus*, occurred most frequently in red (50%) and dead (67%) trees (Table 2). If evidence of prior occupation is considered, 92% of red and dead trees were infested by this beetle. *H. nigrinus* was collected from trees in all stages of decline, even from 33% of the infected, presymptomatic trees. Analysis of the abundance of *H. nigrinus* indicated significantly more insects in yellow, red, and dead trees than in control trees (Table 2).

H. nigrinus preferred roots to the lower stem and root collar of diseased trees (Table 3), never colonizing the lower stem but often the underside of the root collar, an area infrequently colonized by *S. carinatus* or *P. fasciatus*. *H. nigrinus* was frequently observed with *S. carinatus* in roots of diseased trees but was usually the only beetle recovered from tap roots and lateral, buttress roots.

Pissodes faciatus. At the time of sampling, 67, 75, and 92% of symptomatic trees with green, yellow, and red foliage, respectively, were infested with brood of *P. fasciatus* (Table 2). This species was found most often in trees dying at the time of the survey or in symptomatic trees that succumbed in the following 9 mo. All red and dead trees had once contained brood of *P. fasciatus*. Significantly more *P. fasciatus* occurred in symptomatic trees with green, yellow, or red foliage, and in dead trees than in the control trees, but numbers in presymptomatic trees were not significantly different from those in control trees (Table 2). Consistently more *P. fasciatus* were recovered from the root collar and lower stem than from the roots, in contrast to recovery of *H. nigrinus* and *S. carinatus* (Table 3). As eggs are oviposited at or above the soil line (7), the data indicate that a substantial portion (34%) of the larvae mined into the roots after egg eclosion. However, larvae of *P. fasciatus* occupied only the proximal 10–20 cm of invaded roots, a fact supporting earlier observations by Condrashoff (4).

In most cases, *P. fasciatus* colonized diseased trees the season before bark beetles colonized the stem, but sometimes these events were simultaneous. Patches of stem phloem and cambium were killed by *P. fasciatus* in some older trees at Velvet Creek, but only in

TABLE 1. Mean percentage of the circumference of Douglas-fir root xylem at the root-collar juncture and of stem xylem at ground level that is stained by *Verticicladiella wageneri*, and the terminal growth ratio of sampled 10- to 24-yr-old trees from the Oregon Coast Range, 1979–1980

	Symptom class ($n = 12$ trees)					
Measurement	Control	Green foliage, presymptomatic	Green foliage, symptomatic	Yellow foliage	Red foliage	Dead
Root xylem, percent stained[x]	0 a (0)	24 b (21)	64 c (18)	68 c (23)	86 d (16)	92 d (10)
Stem xylem, percent stained[x]	0 a (0)	20 b (19)	63 c (25)	70 c (23)	87 d (18)	94 d (9)
Terminal growth ratio[y]	92 a (7)	74 b (10)	20 c (09)	10 d (8)	0 e (0)	0 e (0)

[x] Different superscripts within rows indicate significantly different means at $P = 0.05$. Wilcoxon rank sum test (one-sided) for all paired comparisons. Numbers in parentheses are standard deviations.

[y] Terminal growth ratio = leader growth (cm) in 1979 divided by leader growth (cm) of the single longest internode of the previous five internodes. Numbers in parentheses are standard deviations.

TABLE 2. Percentage of occurrence of insects (I) or their damage (D) and the mean number of insects per tree ($\overline{X}$) in 10- to 24-yr-old control Douglas-fir and Douglas-fir infected with *Verticicladiella wageneri* in the Oregon Coast Range, 1979–1980[y]

	Symptom class ($n = 12$ trees)																	
	Control			Green foliage, presymptomatic			Green foliage, symptomatic			Yellow foliage			Red foliage			Dead		
Species	I	D	$\overline{X}$	I	D	$\overline{X}$	I	D	$\overline{X}$	I	D	$\overline{X}$	I	D	$\overline{X}$	I	D	$\overline{X}$
All insects	0	0	0 a (0)[z]	50	67	7.3 b (15.0)	83	92	43.8 c (81.0)	100	100	16.3 c (12.4)	100	100	84.8 d (100.2)	92	100	35.1 cd (30.2)
Steremnius carinatus	0	0	0 a (0)	50	67	5.2 b (11.5)	67	92	16.6 bc (44.9)	67	100	4.4 bc (4.9)	92	100	48.4 d (78.4)	75	100	14.8 cd (12.4)
Hylastes nigrinus	0	0	0 a (0)	33	33	1.7 ab (3.4)	33	58	3.8 abc (9.3)	42	67	4.3 bcd (10.3)	50	92	15.6 bcd (28.4)	67	92	17.0 d (24.0)
Pissodes fasciatus	0	0	0 a (0)	8	8	0.3 a (0.9)	58	67	23.4 b (62.4)	75	75	7.7 bc (6.6)	92	100	20.8 c (32.2)	50	100	3.3 b (8.2)

[x] Different superscripts within rows indicate significantly different means at $P = 0.05$. Wilcoxon rank sum test (one-sided) for all paired comparisons. Numbers in parentheses are standard deviations.

TABLE 3. Mean number of insects taken from roots and from lower stems and root-collars in each replicate of Douglas-fir trees infected with *Verticicladiella wageneri* in the Oregon Coast Range, 1979–1980[x]

Species	Number of insects		
	Roots	Lower stem	*P*-value[y]
All insects	133.8 (117.1)	54.3 (55.5)	0.0171
Steremnius carinatus	78.9 (98.8)	10.6 (28.4)	0.0005
Hylastes nigrinus	34.9 (41.0)	7.0 (11.0)	0.0415
Pissodes fasciatus	19.9 (20.0)	36.8 (44.2)	0.0105

[x] A replicate is one tree from each disease symptom class (5) removed from a single location on the same sample date. Numbers in parentheses are standard deviations.

[y] Wilcoxon signed rank test. *P* values indicate the probability that the means are not significantly different.

tissue of the root collar and stem-phloem that was adjacent to black-stained xylem. Such trees were typically colonized by *P. fasciatus* and bark beetles the following year, and rapidly died.

DISCUSSION

The hypothesis that insects are vectors of black-stain root disease of conifers was first set forth by Goheen and Cobb (9), who observed that conidiophores and perithecia of *C. wageneri* occurred only in insect galleries in roots of infected ponderosa pine, particularly in the galleries of the bark beetle *H. macer*. We extend the list of insects colonizing roots of conifers infected with black-stain root disease, adding *H. nigrinus, S. carinatus*, and *P. fasciatus*; and we extend the insect-pathogen association by demonstrating that these insects consistently colonized diseased Douglas-fir in all stages of decline. This process spans 1–4 yr and frequently begins before symptoms develop in the crowns of infected trees.

The pattern of insect colonization of an infected root system follows the pattern of colonization by the pathogen; as *V. wageneri* spreads through the root system, heavily infected roots become suitable for oviposition and brood production (28). *S. carinatus* and *H. nigrinus* initially infest the distal portions of these same roots and then other roots as the pathogen colonizes the root system. Beetles infest a root system sequentially rather than by the mass attack characteristic of stem-colonizing bark beetles and thus increase the opportunity for contact between emerging beetles and viable inoculum of *V. wageneri*.

During gallery construction and pupation, particularly beneath the thin bark of the root system, the three species remove overlying cambial parenchyma and expose, or sever, tracheids of the outermost annual ring (or rings) (28), the region of root and stem xylem most commonly colonized by *V. wageneri* (28). Colonized tracheids must be exposed before *V. wageneri* can invade insect galleries because hyphae cannot penetrate tracheid cell walls or parenchyma cells directly (13,25).

Support for the vector hypothesis is provided by three other lines of evidence. First, beetles collected in areas of diseased Douglas-fir have been found to carry inoculum of *V. wageneri*: four of 173 *H. nigrinus*, two of 433 *S. carinatus*, and one of 62 *P. fasciatus* (J. J. Witcosky, *unpublished*). Second, beetles may feed or oviposit on susceptible hosts. *H. nigrinus* is known to wound roots of standing trees both within and surrounding patches of windthrown Douglas-fir (30) and has been observed to wound crop trees to the xylem after precommercial thinning (J. J. Witcosky, *unpublished*). All three species oviposit in the roots and root collar area of trees cut during precommercial thinning. These hosts are known to be susceptible to infection by *V. wageneri* (J. J. Witcosky, *unpublished*). *S. carinatus* is known to wound recently planted seedlings after brood emergence from root systems of harvested trees (4). Third, individuals of all three species, artificially infested with *V. wageneri*, are capable of transmitting *V. wageneri* to seedlings under laboratory conditions (J. J. Witcosky, *unpublished*). Our study of the *V. wageneri*-associated insect guild on Douglas-fir provides more evidence in support of the vector hypothesis of Goheen and Cobb (9) by demonstrating that beetles are consistently and closely associated with trees sustaining infection by *V. wageneri* throughout the decline of the host.

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