Hylastes nigrinus (Coleoptera: Scolytidae), *Pissodes fasciatus*, and *Steremnius carinatus* (Coleoptera: Curculionidae) as Vectors of Black-stain Root Disease of Douglas-fir

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ABSTRACT This study demonstrates that *Hylastes nigrinus* (Mannerheim), *Pissodes fasciatus* LeConte and *Steremnius carinatus* (Boheman) are vectors of *Verticicladiella wageneri* Kendrick, the causal agent of black-stain root disease of Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco. These insects, known associates of diseased hosts, wound and create suitable infection courts in susceptible hosts, carry inoculum in the field, and transmit the pathogen to hosts under laboratory conditions. Root systems of 12-year-old Douglas-fir, cut during precommercial thinning, were infested by these insects and were susceptible to *V. wageneri* infection for at least 7 months, confirming that *V. wageneri* may be introduced to thinned stands via these hosts. Male and female *H. nigrinus* created wounds suitable as infection courts on roots and root collars of crop trees for 1–2 years after precommercial thinning and may, therefore, introduce *V. wageneri* to thinned stands via these hosts. Insect-mediated transmission of *V. wageneri* to Douglas-fir by *H. nigrinus* in the field is documented.

KEY WORDS *Ceratocystis*, disturbance, forests, conifer, epidemiology

BLACK-STAIN ROOT disease of conifers, caused by the fungus *Verticicladiella wageneri* Kendrick (sexual stage: *Ceratocystis wageneri* Goheen & Cobb), kills species of *Pinus* and *Pseudotsuga*. Local spread, or enlargement of established foci of the disease, occurs through root grafts that have continuous xylem between individuals of the same species (Goheen 1976, Landis & Helburg 1976, Hessburg 1984) and by fungal growth through the soil from diseased to healthy roots (Goheen 1976, Hicks et al. 1980, Hessburg 1984). Aboveground spread may involve insects as vectors (Smith & Graham 1975, Landis & Helburg 1976, Goheen & Cobb 1978, Harrington et al. 1985, Witcosky & Hansen 1985). Species of *Ceratocystis* are widely reported to exploit insects as vectors (Barras & Perry 1975). In Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, forests, three species of beetles, *Hylastes nigrinus* (Mannerheim), *Pissodes fasciatus* LeConte, and *Steremnius carinatus* (Boheman), were consistently recovered from trees in various stages of decline due to black-stain root disease and have been implicated as vectors in this ecosystem (Witcosky & Hansen 1985).

Leach (1940) proposed that insects could be identified as vectors of plant diseases if they 1) were associated with diseased hosts, 2) visited healthy hosts under conditions suitable for transmission of the pathogen, 3) carried inoculum of the pathogen in the field, and 4) successfully transmitted the pathogen to hosts under laboratory conditions. Witcosky & Hansen (1985) have confirmed 1 and indicated support for 2, 3, and 4 in Douglas-fir forests. In this paper, we confirm 2, 3, and 4, thereby demonstrating that *H. nigrinus*, *P. fasciatus*, and *S. carinatus* are vectors of *V. wageneri* in Douglas-fir stands. We also report transmission of *V. wageneri* to Douglas-fir by *H. nigrinus* in the field for the first time.

Materials and Methods

Insect Wounding of Susceptible Hosts. To observe the feeding and colonizing behavior of *H. nigrinus*, *P. fasciatus*, and *S. carinatus* relative to periods of host susceptibility to *V. wageneri*, we precommercially thinned two 12-year-old plantations of Douglas-fir that also included some western hemlock, *Tsuga heterophylla* (Rafinesque) Sargent, and western red cedar, *Thuja plicata* Donn ex D. Don. Thinning and other disturbances are associated with *V. wageneri* occurrence and are believed to contribute to tree susceptibility to this fungus and response of potential vectors (Condrashoff 1968, Goheen & Hansen 1978, Hansen 1978, Harrington et al. 1983, 1985, Witcosky et al. 1986).

Two 50-ha plantations, located in the Coast Range (BURD, T27S R8W, and no. 5340, T27S R7W), Douglas County, southwestern Oregon, were selected for study. These uniformly stocked

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plantations were sustaining some mortality due to black-stain root disease. A portion (32 ha) of each plantation was divided into four blocks, each consisting of four 2-ha plots. Three thinning treatments, September 1982, January 1983, and May 1983, and an unthinned control treatment were randomly applied to each block; in the thinned plots, stand density was reduced from 2,000–4,000 to 900–1,000 stems per ha with a chain saw.

We monitored insect abundance in each plot using a series of pitfall traps to capture *S. carinatus* and sticky traps to capture *H. nigrinus* and *P. fasciatus*. The pitfall traps were deployed in paired, parallel transects, 5 m apart, from edge to edge across the middle and with the slope of each plot. Each transect had five pitfall traps, one positioned within 5 m of each edge and the other three uniformly spaced across the width of the plot. Each pitfall trap consisted of a plastic container (15.7 cm diam, 19 cm high) buried to the soil surface and fitted with an aluminum funnel; the opening was covered with a plywood board (20.3 by 20.3 cm) elevated ca. 3 cm aboveground with nails. Within the container was a second plastic container (12.2 cm diam, 8 cm high) containing the killing agent and preservative, undiluted antifreeze (ethylene glycol) or water with detergent. Fresh antifreeze was added at the beginning of trapping in March and again in July. However, in the no. 5430 plantation, fresh water/detergent solution was substituted for antifreeze and was replaced at the beginning of each sample period in all the traps from August to October due to trap disruption by resident coyotes.

Two sticky traps (surfaces facing east-west) were located in each plot, one 5 m from one edge, the other at the center of each plot, between the pitfall trap transects. The sticky traps consisted of two hardware cloth screens (0.25 m^2, 2 mesh per cm) coated with Stikem Special (Seabright Enterprises, Emoryville, Calif.) and stapled to opposite sides of a stake (5 by 5 cm, 80 cm long) driven into the ground such that the traps collected flying insects between 10 and 100 cm aboveground. Stikem Special was renewed at 4–6 week intervals throughout the trapping period.

No attractants were used in this study. Insects were collected at 14-day intervals from 24 March through 3 November 1983 in pitfall traps and from 7 April through 22 September 1983 on sticky traps and were identified to species.

During September 1983 in the BURD plantation only, we removed populations of immature and adult insects from under the bark of roots and stumps of felled trees to estimate colonization intensity by *H. nigrinus*, *P. fasciatus*, and *S. carinatus* after thinning. At randomly selected points along one edge of each plot, two stumps within 5 m of the edge and two stumps near the center of each plot were randomly selected and excavated. Insects, but not eggs, collected from under the bark, and egg galleries made by *H. nigrinus* were counted. The roots and root collar of the crop tree nearest the excavated root systems were examined for any evidence of insect-induced wounds. In the unthinned plots, we nondestructively examined the bark surface of the root collar and proximal 30 cm of roots of apparently healthy Douglas-fir crop trees for evidence of wounding by insects. Wounding was underestimated because the undersides of roots could not be thoroughly examined.

In June and July 1984, we examined the attractiveness of crop trees to insects along roads and within plots of the BURD plantation using a random sample from all plots and a roadside sample from all plots with roads. In the random sample, each plot was divided into quarters and each quarter traversed by a single randomly located transect. Crop trees intercepting the compass line defined point centers. These trees and the nearest four trees, one in each cardinal quadrant, were examined for wounding. In the roadside survey, all apparently healthy Douglas-fir directly adjacent to established roads were examined for wounding.

Wounds in the BURD plantation could be classified as 1983 wounds if resin had crystalized and turned white. If resin was absent or was uncrystalized but the wounds contained fresh frass, or if insects were actively excavating bark and phloem at the time of inspection, the wounds were dated 1984. Causal agent of wounds was determined on the basis of characteristic patterns observed for each species in laboratory experiments (described later) or by recovery and identification of the insect from a wound at the time of inspection.

Crop trees in the no. 5340 plantation were examined for wounding, as described above, during May and June 1985. Only three of the four plots for each treatment were examined. Wounds were counted but no attempt was made to classify them as to year of initiation.

We employed Friedman's test with the Kruskal–Wallis statistic (Lehmann 1975) to detect significant differences among treatments in mean number of beetles captured per trap and mean number of wounds per tree ($P < 0.05$).

Determining Host Susceptibility. To determine if the root systems of cut and uncut Douglas-fir were potentially susceptible to infection by *V. wageneri*, we artificially inoculated (in one experimental block) two roots of each of 10 standing Douglas-fir trees in the control plot and two roots of each of 10 felled Douglas-fir trees in each of the three thinned plots. Trees were inoculated by introducing a block (0.5 by 0.5 cm) of malt agar colonized by *V. wageneri* at the cambium/xylem interface of each root 2 weeks after the May 1983 thinning. The wound was wrapped with moistened cheese cloth and then in a plastic sheet (0.4 mil); the bandage was secured at the ends with twist ties (Hessburg 1984). In September 1983, the roots were excavated, removed, and taken to the laboratory, where each root was examined for the

characteristic black-stained xylem, with only mature tracheids colonized by ensheathed hyphae (Smith 1967, Hessburg 1984). There were no uninoculated controls in this experiment. Trees or root systems selected for inoculation were located >15 m from known foci of *V. wageneri*. The experiment was repeated in 1984 in one unthinned plot in the BURD plantation, in an adjacent plantation thinned in October 1983, and in an adjacent plot in the BURD plantation thinned in May 1984 (2 weeks before inoculation), this time with an agar medium without *V. wageneri* inoculum, as a control treatment.

Verifying Fungal Infestation of Insects in the Field. To verify transmission of *V. wageneri* by insects, we collected insects in established foci of infection in three widely separated plantations of Douglas-fir (14–25 years old) in the Oregon Coast Range (Benton, Lane, and Yamhill counties) using pitfall traps baited with an attractant. Attractant-baited traps were identical to those previously described except that the inner container was partially filled with old bark fragments (which are not colonized by *V. wageneri*) for cover. A film canister holding a glass vial (1 ml) containing the attractant, 2% racemic α-pinene in 95% ethanol (Rudinsky 1966), was placed adjacent to the inner container; the attractant was replaced weekly.

Insects were collected from traps weekly from May through September 1980. Because few *P. fasciatus* were trapped in this manner, adults of this species were collected by hand from stems of healthy and diseased trees in May 1980. Adults also were collected weekly from August to October 1980 from an emergence cage placed over the stump of a severely diseased tree, felled in August 1980, containing abundant *P. fasciatus* larvae and pupae. Beetles were collected individually with sterilized forceps and held in glass vials on ice until they were taken to the laboratory. Vials and stoppers were soaked in 95% ethanol between use.

Each insect was killed by crushing between the prothorax and mesothorax, placed on an agar medium containing 200 ppm cycloheximide with streptomycin added (Hicks et al. 1980), and incubated at 15°C. Killing was necessary to limit the spread of antagonistic fungal species across the surface of the medium. After 3 weeks of incubation, isolates believed to be *V. wageneri* were subcultured on malt agar so that morphology and pathogenicity could be verified.

In 1981 and 1982, the roots of three Douglas-fir seedlings (2 years old) were artificially inoculated with each of the apparent isolates of *V. wageneri* obtained from the beetles in a manner described by Hessburg (1984), except that the outer bark and root xylem were not intentionally wounded during the inoculation procedure and a block of inoculum was applied to each of three roots per seedling instead of to the tap root only. The seedlings were planted in individual containers (450 ml) and held in a greenhouse until symptoms of disease appeared or until the experiment was concluded after 6 months. Isolates from infected xylem of diseased seedlings were compared with the original isolate and with the original description provided by Kendrick (1962).

Demonstrating Fungal Transmission by Insects in the Laboratory. To demonstrate *V. wageneri* transmission to Douglas-fir by insects under laboratory conditions, individuals of *H. nigrinus*, *S. carinatus*, and *P. fasciatus* were collected from attractant-baited pitfall traps placed in thinned plots near the BURD plantation during 1983 and 1984. The mouthparts of individual beetles of each species were artificially infested with spores from four to six conidiophores of *V. wageneri;* artificially infested, dead beetles served as controls. Each beetle was confined to the basal portion of a single Douglas-fir seedling (2 years old) by a fine mesh (1 mm) plastic screen. *P. fasciatus* and *S. carinatus* were caged for 5 days and *H. nigrinus* for 14 days. In addition, specimens of *H. nigrinus* were captured in June 1983 and May and June 1984 and caged for 14 days on seedlings as described above, except that beetles were not artificially infested with *V. wageneri*. Killed beetles were used as controls. In all cases, seedlings were examined for wounding, for black-stained xylem, and microscopically for the characteristic pattern of colonization and hyphal morphology (Wagener & Mielke 1961, Smith 1967, Hessburg 1984).

Results

Insect Wounding of Susceptible Hosts. Significantly more beetles of each species were captured in the thinned than unthinned plots, indicating increased beetle activity in thinned plots (Table 1). Significantly fewer *H. nigrinus* and *P. fasciatus* were captured in plots thinned in May than in either the plots thinned in September or January. However, time of thinning had no apparent effect on numbers of *S. carinatus*. Brood of all three species were recovered from the roots and root collar region of randomly selected stumps of thinned trees. More *H. nigrinus* egg galleries were observed in plots thinned the previous September ($\bar{x}$ = 12.9 ± 2.4 SEM per stump) and January ($\bar{x}$ = 7.8 ± 1.4 SEM per stump) than in plots thinned in May ($\bar{x}$ = 4.1 ± 1.3 SEM per stump) (Witcosky et al. 1986). Wounds caused by *H. nigrinus* penetrated to the xylem on 2 of 36 healthy crop trees adjacent to the excavations previously described.

Significantly more trees were wounded in thinned than in unthinned plots in both the random and roadside surveys (Table 2). Virtually all the wounds were attributed to *H. nigrinus* and were found primarily on the root collar and lower stem region below the upper surface of the litter and in the proximal 50 cm of roots. Wounds on the lower stem and root collar were frequently superficial (within the phloem only), but beetles were recovered from tunnels penetrating to the

Table 1. Mean number (±1 SEM) of *H. nigrinus* and *P. fasciatus* caught per sticky trap and *S. carinatus* caught per pitfall trap at biweekly intervals in unthinned and precommercially thinned Douglas-fir plantations during 1983

Species	Unthinned control	Thinned plots		
		Sept. 1982	Jan. 1983	May 1983
H. nigrinus	0.04 (0.08)a	2.76 (1.35)c	5.06 (5.39)c	0.90 (0.77)b
P. fasciatus	0 (0)a	0.20 (0.14)c	0.20 (0.16)c	0.06 (0.06)b
S. carinatus	0.16 (0.06)a	0.53 (0.23)b	0.51 (0.18)b	0.59 (0.20)b

Means within rows followed by different letters are significantly different ($P < 0.05$; Friedman's test using the Kruskal–Wallis statistic; $n = 8$ plots per treatment).

xylem that were deeper than the lengths of the insects (≥7 mm). Wounds on roots penetrated to the xylem more frequently, especially on small roots (<1 cm diam) and roots with thin phloem. Significantly fewer trees were wounded in the May than in the September and January treatments (Table 2). The September treatment did not differ significantly from the January treatment; however, the probability that crop trees in the ~~plots thinned in~~ January ~~sustained more wounds than~~ crop trees in the September plots was 0.94 in both the random and roadside surveys (Table 2).

Old wounds (1983), associated with immigration of *H. nigrinus* into thinned stands, were more abundant than new wounds (1984) (Table 2), which were more frequently observed on trees wounded in 1983 than on previously unwounded trees. In the random sample and roadside survey, 70 and 92%, respectively, of trees sustaining wounds in 1984 had been wounded the previous year. Only two crop trees sustained wounds similar to those caused by *S. carinatus*, and no trees sustained wounds similar to those of *P. fasciatus* although these wounds would be difficult to detect by the examination procedure employed.

Host Susceptibility. The inoculation experiments indicated that the root systems of cut trees are susceptible to *V. wageneri* infection (Table 3). Inoculation success decreased as time between thinning and inoculation increased. However, root systems of these 12-year-old trees remained susceptible to infection for at least 7 months. Generally, the mean root length colonized decreased as the time between thinning and inoculation increased. The extent of colonization of root xylem appeared to follow the same pattern; root xylem of trees cut in May (2 weeks before inoculation) was heavily stained, whereas that of trees cut in September or October of the previous year or in January (4 months before inoculation) was weak and reddish because few tracheids had been colonized.

Fungal Infestation of Insects in the Field. Seven isolates of *V. wageneri* were obtained from field-collected beetles. Of these, four (2.3%) were obtained from 173 *H. nigrinus* (two females, two males); two (0.5%) were obtained from 433 *S. carinatus* (two females); and one was obtained from 21 *P. fasciatus* (one female) emerging from the diseased Douglas-fir. No isolates of *V. wageneri* were obtained from the 41 hand-collected *P. fasciatus*. The two infested *S. carinatus* were captured in the same trap during the same sample period; therefore, one beetle may have contaminated the other beetle within the trap.

Fungal Transmission by Insects in the Laboratory. *H. nigrinus*, *P. fasciatus*, and *S. carinatus* readily wounded Douglas-fir seedlings in the laboratory, frequently leading to infection with *V. wageneri* regardless of species of beetle (Table 4).

Table 2. Wounds to roots and root collars of crop trees caused by *H. nigrinus* in precommercially thinned and unthinned Douglas-fir plantations during 1983 and 1984

Treatment by sample	No. trees sampled	% proportion of trees wounded	% no. wounds per tree (BURD only)		% no. wounds per wounded tree	
			Old (1983)	New (1984)	Old (1983)	New (1984)
Random sample						
Sept. 1982 thinning	373	0.11 (0.07)c	0.14 (0.11)b	0.005 (0.01)a	2.25 (1.10)b	0.25 (0.05)a
Jan. 1983 thinning	389	0.17 (0.17)c	0.48 (0.49)b	0.08 (0.12)a	3.33 (1.31)b	1.45 (0.78)a
May 1983 thinning	442	0.05 (0.03)b	0.12 (0.14)ab	0.004 (0.01)a	4.00 (5.37)ab	0.25 (0.50)a
Unthinned control	614	0 (0)a	0 (0)a	0 (0)a	0 (0)a	0 (0)a
Roadside survey						
Sept. 1982 thinning	278	0.30 (0.17)c	1.85 (1.35)b	0.14 (0.12)a	6.11 (2.84)b	1.82 (1.07)a
Jan. 1983 thinning	221	0.20 (0.16)c	0.89 (0.93)b	0.11 (0.22)a	4.67 (1.22)b	2.08 (1.11)a
May 1983 thinning	410	0.08 (0.04)b	0.15 (0.18)b	0.04 (0.03)a	2.71 (1.83)b	2.14 (1.26)a
Unthinned control	306	0 (0)a	0 (0)a	0 (0)a	0 (0)a	0 (0)a

The random (per transect) and roadside (per road) surveys are not comparable. For the random sample and the roadside survey separately, means within columns followed by different letters are significantly different ($P < 0.05$; Friedman's test using the Kruskal–Wallis statistic; $n = 8$ per treatment for the mean proportion of trees wounded; $n = 4$ for mean number of wounds per tree and mean number of wounds per wounded tree).

Table 3. Percent infection and mean root length (±1 SEM) colonized by *V. wageneri* in artificially inoculated (Vw+) or uninoculated (Vw−) roots of standing unthinned trees and stumps of previously cut trees in a Douglas-fir plantation

Inoculated: / Examined:	May 1983 / Sept. 1983				May 1984 / Sept. 1984					
Treatment	Unthinned control	Sept. 1982 thinning	Jan. 1983 thinning	May 1983 thinning	Unthinned control		Oct. 1983 thinning		May 1984 thinning	
					Vw+	Vw−	Vw+	Vw−[a]	Vw+	Vw−
% host infected	90	40	70	80	100	0	60	30	100	0
% roots infected	80	20	50	60	65	0	40	15	90	0
ẋ length (cm) colonized	35.8 (26.1)	6.5 (3.1)	10.1 (8.3)	28.1 (18.8)	16.3 (17.8)	—	26.9 (13.1)	—	50.6 (20.1)	—

Vw+, artificially inoculated; Vw−, uninoculated.

[a] Hand section and microscopic examination suggested that three roots colonized by *H. nigrinus* on three cut trees were infected with *V. wageneri*. No value was calculated because point of inoculation was uncertain.

The control seedlings, caged with dead, artificially infested beetles, were neither wounded nor diseased (Table 4). Field-collected *H. nigrinus*, which were not artificially infested, transmitted *V. wageneri* to Douglas-fir seedlings in seven cases (Table 4). The ability of *H. nigrinus* to transmit *V. wageneri* to uninfected trees in the field was observed twice during this study. One newly infected tree, at least 4 m from established disease foci, was excavated in June 1980 and a similarly located and infected tree in June 1983. In each of these trees, only a single, small, short root was infected; the extent of *V. wageneri* colonization was between 15 and 30 cm. Each root had sustained one or two wounds identical to those made by *H. nigrinus*, penetrating to the xylem. Because *V. wageneri* had not colonized any other roots of these trees nor extended up the stem to the soil surface and because no other infected roots were within 4 m of these newly infected roots, these trees could only have been infected via the vector mechanism.

Table 4. Wounds and transmission of *V. wageneri* to 2-year-old Douglas-fir seedlings by artificially infested *P. fasciatus* and *S. carinatus* in 1983 and by artificially infested *H. nigrinus* and *H. nigrinus* infested at field frequency in a Corvallis, Oreg., laboratory during 1983 and 1984

Treatment by insect species	No. seedlings infested	No. (%) seedlings wounded	No. (%) seedlings infected with *V. wageneri*	ẋ no. (±SEM) of wounds per wounded seedling
P. fasciatus				
Live	97	78 (80)	52 (68)	13.6 (9.7)
Dead	13	0 (0)	0 (0)	0 (0)
S. carinatus				
Live	128	93 (73)	23 (25)	5.1 (4.5)
Dead	12	0 (0)	0 (0)	0 (0)
H. nigrinus				
Artificially infested (1984)				
Live	61	45 (74)	21 (47)	1.6 (1.1)
Dead	24	0 (0)	0 (0)	0 (0)
Field frequency (1983)				
Live	22	7 (32)	1 (5)	1.1 (0.4)
Dead	4	0 (0)	0 (0)	0 (0)
Field frequency (1984)				
Live	1,000	278 (28)	6 (2)	1.5 (1.3)
Dead	86	0 (0)	0 (0)	0 (0)

Discussion

The present study and a previous one (Witcosky & Hansen 1985) confirm the vector hypothesis in Douglas-fir by demonstrating that 1) three beetle species are commonly associated with diseased trees (Witcosky & Hansen 1985), 2) these insects visit, colonize, and create infection courts in susceptible hosts (Tables 1–3), 3) insects carry inoculum of *V. wageneri* in the field (Table 4), and 4) insects successfully transmit *V. wageneri* to seedlings under laboratory conditions (Table 4). Similar findings for 3 and 4 were reported by Harrington et al. (1985) for *H. nigrinus*. Although the frequency of fungus transport in this study was <5%, beetles carrying *V. wageneri* were recovered at all three sites, indicating that fungus transport by beetles was a widespread phenomenon, at least near established foci. Although this frequency of fungus transmission is low, attraction of large numbers of vectors to the vicinity of injured or stressed trees can be expected to increase substantially the risk of fungus establishment at such sites.

The proposed association between precommercial thinning and the development of *V. wageneri* infection foci (Goheen & Hansen 1978, Harrington et al. 1983, 1985, Witcosky et al. 1986) is firmly supported by our results, although the rate of stump deterioration apparently influences susceptibility to fungus establishment. Harrington et al. (1985) reported that time of precommercial thinning did not significantly affect immigration of *H. nigrinus* in northern California. However, we observed on our southern Oregon sites that the number of *H. nigrinus* caught on traps in plots thinned in May during or after the peak flight of this insect was significantly lower than in plots thinned in September or January, but significantly higher than in unthinned plots.

Other factors influencing fungus or vector activity include road building (Table 2) (Hansen 1978),

compaction of soils and altered drainage, excessive soil moisture, and proximity to severely wounded trees (Goheen & Hansen 1978; J.J.W., personal observation). Douglas-fir are highly intolerant of excessive soil moisture (Minore 1968, Zaerr 1983). Site factors such as periodic or sustained anaerobiosis reduce host growth, producing trees with thin phloem (increasing the likelihood that wounds penetrate to the xylem) and chlorotic foliage (Kozlowski 1984), a potentially important visual cue for host-selecting insects. Injury and stress increase the production and release of small molecular weight volatiles, such as terpenes, ethylene, and ethanol (Davies 1980, Drew & Lynch 1980, Ayers 1984, Feldman 1984, Kozlowski 1984, Yang & Hoffman 1984), which could or do act as host attractants for host-seeking beetles (Rudinsky 1966, Rudinsky & Zethner-Møller 1967, Witcosky 1985). We recommend that stand management or harvest activities be designed or timed to prevent attraction of large numbers of insects potentially transmitting disease organisms.

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