Verticicladiella wageneri Kendrick is a vascular wilt pathogen of conifers, causing a black staining of colonized sapwood of roots and lower stem. In Douglas-fir, V. wageneri is intimately associated with insects. Hylastes nigrinus, Pissodes fasciatus, and Steremnius carinatus are commonly associated with diseased hosts, carry inoculum of V. wageneri in the field, successfully transmit the pathogen to seedlings under laboratory conditions, and create suitable infection courts in susceptible hosts. Furthermore, insect-mediated transmission of V. wageneri has been documented for the first time.

Stand density management, such as precommercial thinning, results in elevated activity of H. nigrinus, P. fasciatus, and S. carinatus in disturbed stands. Insects
colonize roots and the root collar region of cut trees; these hosts are susceptible to infection by *V. wageneri*. Also, crop trees are wounded on the roots and root collar region by *H. nigrinus* for one to two years following precommercial thinning. Some of these wounds penetrate to the xylem and are, therefore, suitable infection courts for *V. wageneri*. Time of precommercial thinning can be manipulated to significantly reduce immigration of vectors, i.e., by thinning plantations during early summer after the peak flight of *H. nigrinus*.

*H. nigrinus* and *S. carinatus* are attracted to alpha-pinene, a major constituent of Douglas-fir oleoresin. Forest management activities that injure hosts, and hence cause release of alpha-pinene, may attract vectors of *V. wageneri*. *H. nigrinus* and *S. carinatus* also are attracted to ethanol. In addition, root sections infected with *V. wageneri* are more attractive to *H. nigrinus* and *S. carinatus* than uninfected roots. Aspects of injury and stress to hosts leading to the release of host attractants are discussed.

A crop production/pest management system structure is developed which links pest management activities for black-stain root disease prevention with normal intensive forest management. Pest management should be addressed at all stages of forest management: the harvest-
establishment, annual, precommercial, and commercial phases of crop production.
THE ROOT INSECT--BLACK-STAIN ROOT DISEASE
ASSOCIATION IN DOUGLAS-FIR: VECTOR
RELATIONSHIPS AND IMPLICATIONS FOR
FOREST MANAGEMENT

by

Jeffrey John Witcosky

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Verticicladiella wageneri Kendrick, causal agent of black-stain root disease of conifers, was first observed causing mortality in the late 1930's (Wagener and Mielke 1961). Now the pathogen is known to be widely distributed on Pinus spp. and Pseudotsuga menziesii (Mirb.) Franco (Smith and Graham 1975, Hunt and Morrison 1979). In 1978, Goheen and Cobb identified the sexual stage of V. wageneri, Ceratocystis wageneri Goheen and Cobb, which they found in the galleries of insects colonizing the roots of diseased ponderosa pine (Pinus ponderosa Laws.). Goheen and Cobb (1978) hypothesized that Hylastes macer LeC. is a vector of V. wageneri in ponderosa pine.

Very little is known about the role of insects in the epidemiology of black-stain root disease (Goheen and Cobb 1978, Witcosky 1981, Witcosky and Hansen 1985). This is the topic of my dissertation. The dissertation addresses four objectives: (1) to examine and document the vector relationship involving Hylastes nigrinus, Pissodes
fasciatus, and Steremnius carinatus; (2) to examine the response of these three species of insects to stand disturbance and time of disturbance by precommercially thinning plantations of Douglas-fir; (3) to examine aspects of host selection and attraction of H. nigrinus and S. carinatus to volatiles produced by stressed or injured hosts; and (4) to develop a crop production/pest management system structure for integrating pest management strategies and tactics for black-stain root disease into crop production of Douglas-fir in plantations in western Oregon.

LITERATURE REVIEW

In 1961, Wagener and Mielke reported a disease syndrome of single-leaf pinyon pine (Pinus monophylla Torr. & Frem.), ponderosa pine (Pinus ponderosa Laws.), and Jeffrey pine (Pinus jeffreyi Grev. & Balf.) characterized by a chocolate-brown to black staining of infected root and stem xylem. Microscopic examination revealed pigmented hyphae within tracheids of infected roots, and isolates from stained tissue consistently yielded a fungus in the hyphomycetous genus Verticicladiella. Kendrick (1962) described Wagener and Mielke's pinyon isolate under the binomial V. wagenerii. Reports now indicate that V. wagenerii is widely


The fungus exhibits no capacity to degrade cell walls or penetrate parenchyma cells (Hessburg 1984, Smith 1967) and must gain access to susceptible hosts via functional xylem tracheids (Hessburg 1984). Goheen (1976) reported that 79% of observed infections on ponderosa pines were observed on fine roots. Hessburg (1984), working with *V.*
wageneri on seedlings of Douglas-fir, identified the infection courts as wounds or natural openings that expose functional xylem elements to the soil environment during the production and senescence of fine roots.

V. wageneri infections in stands of conifers develop in expanding foci, with currently symptomatic trees at the periphery of foci and dead trees in the center (Landis and Helburg 1976, Wagener and Mielke 1961). Expansion of foci in stands is believed to result largely from spread across root grafts and root contacts and from fungal growth through the soil from infected to healthy roots for distances of 1-6 cm but apparently less than 15 cm (Goheen 1976, Goheen and Cobb 1978, Hessburg 1984, Hicks, Cobb, and Gersper 1980, Landis and Helburg 1976, Wagener and Mielke 1961). The soil spread hypothesis was confirmed when Hessburg (1984) obtained infection of Douglas-fir seedlings when healthy roots were adjacent to, but not in contact with, diseased roots.

The proliferation of foci of black-stain root disease has been associated with vectors, particularly insects colonizing roots of diseased trees. Goheen and Cobb (1978) observed the sexual stage of V. wageneri, Ceratocystis wageneri, associated with insect galleries and hypothesized that root insects were vectors of this fungus in ponderosa pine. They observed perithecia and conidiophores of the pathogen in the galleries of root
insects, especially galleries of *Hylastes macer*. Ceratocystis fungi are widely known to exploit bark beetles as vectors (Barras and Perry 1975).

Witcosky (1981) identified three species of beetles associated with Douglas-fir in various stages of decline due to black-stain root disease. *Hylastes nigrinus*, *Pissodes fasciatus*, and *Steremnius carinatus* were commonly associated with infected trees. Insects sequentially colonize diseased root systems as each root succumbs to infection, a process which spans two to four years (Witcosky and Hansen 1985). *S. carinatus* and *H. nigrinus* primarily colonize the roots while *Pissodes fasciatus* colonizes the lower stem and root collar. As larvae of these three species prepare to pupate, they often etch a pupal cell in the xylem. Tracheids severed during construction of the pupal chamber provide an avenue of egress for hyphae into insect galleries where conidiophores have been observed to develop (Witcosky 1981, Witcosky and Hansen 1985). Since *V. wageneri* generally remains viable within infected trees at least until tree death (Witcosky 1981), the processes of sequential colonization and engraving xylem at pupation increase the likelihood of contact and infestation of brood adults by *V. wageneri*. *H. nigrinus*, *P. fasciatus*, and *S. carinatus* have all been shown to carry inoculum in the field (Witcosky and Hansen 1985). Colonization of the
root system by root-infesting beetles precedes colonization of the stem by stem-breeding bark beetles.

The development of foci has been associated with stand disturbance. Hansen (1978) reported black-stain root disease foci associated with roadsides, Goheen and Hansen (1978) reported foci associated with road cuts, clear-cut margins, stream drainages, and plantation thinnings, and Harrington, Reinhart, Thornberg, and Cobb (1983) reported disease foci associated with precommercial thinning. Microsites with developing foci often are moist sites, with intermediate redox and aeration conditions, and cool to moderate soil temperature (Goheen, Cobb, and McKibbin 1978, Hessburg 1984, Wilks, Gersper and Cobb 1983).

Host selection by bark beetles is either a random process or a directed process influenced by host attractants (Rudinsky 1962, Wood 1982). Goheen and Cobb (1980) reported that infected pines are more likely to become infested with stem-colonizing bark beetles than healthy pines. They speculated that diseased trees were more susceptible to infestation due to decreased oleoresin exudation pressure and rate of flow as suggested by Helms, Cobb, and Whitney (1971). Further, they suggested that infected trees were more attractive due to fungal-induced production of attractive compounds. Rudinsky (1966) and Rudinsky and Zethner-Møller (1967) reported that H.
nigrinus was attracted to host material, ethanol, and various host terpenes. Condrashoff (1968) demonstrated that S. carinatus was attracted to host material. Witcosky (1981) indicated that both species could be captured readily in pitfall traps baited with 2% racemic alpha-pinene in 95% ethanol.

This dissertation consists of four components. In Chapter II, I test the vector hypothesis in the Douglas-fir ecosystem in a manner set forth by Leach (1940). I examine the relationship between time of precommercial thinning and the immigration of H. nigrinus, P. fasciatus, and S. carinatus into disturbed plantations in Chapter III. I demonstrate the occurrence of host attractants for H. nigrinus and S. carinatus and examine the response of these species to infected and healthy hosts in Chapter IV. In Chapter V, I develop a crop production/pest management system structure for management of black-stain root disease in plantations of Douglas-fir in western Oregon.
CHAPTER II

ABSTRACT

This study demonstrates that *Hylastes nigrinus*, *Pissodes fasciatus*, and *Steremnius carinatus* are vectors of *V. wageneri*, the causal agent of black-stain root disease of Douglas-fir. These insects, which have previously been associated with diseased hosts, carry inoculum in the field, transmit the pathogen to hosts under laboratory conditions, and wound and create suitable infection courts on susceptible hosts. Root systems of twelve-year-old Douglas-fir, cut during precommercial thinning, are susceptible to attack by these insects and to infection by *V. wageneri* for at least seven months. Male and female *H. nigrinus* create infection courts on roots and root collars of crop trees for one to two years following precommercial thinning. Insect-mediated transmission of *V. wageneri* to Douglas-fir by *H. nigrinus* is documented for the first time.
INTRODUCTION


Two types of spread of black-stain root disease are recognized. Local spread, or enlargement of established foci, occurs through root grafts which have continuous xylem (Goheen 1976, Hessburg 1984, Landis and Helburg 1976) and by fungal growth through the soil between diseased and healthy roots (Goheen 1976, Hessburg 1984, Hicks, Cobb, and Gersper 1980).

Above-ground spread leads to the initiation of new foci of infection either near the margin of established
foci or at some distance from such foci. In ponderosa pine, Goheen and Cobb (1978) discovered conidiophores of *V. wageneri* and the previously undescribed perithecia of the sexual stage, *Ceratocystis wageneri*, in the galleries of insects, especially *Hylastes macer* LeC. Species of *Ceratocystis* are widely reported to exploit insects as vectors (Barras and Perry 1975). Thus, Goheen and Cobb (1978) suggested that insects were vectors of *C. wageneri* in ponderosa pine. In Douglas-fir, three species of beetles, *Hylastes nigrinus* (Mann.), *Pissodes fasciatus* LeC., and *Steremnius carinatus* (Boh.), 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 1981, Witcosky, Rudinsky, and Hansen 1981, Witcosky and Hansen 1985).

Leach (1940) proposed that insects could be identified as vectors of plant diseases if: (i) they were associated with diseased hosts, (ii) they visited healthy hosts under conditions suitable for transmission of the pathogen, (iii) field-collected insects carried inoculum of the pathogen, and (iv) they successfully transmitted the pathogen to hosts under laboratory conditions. Witcosky (1981), Witcosky, Rudinsky, and Hansen (1981), and Witcosky and Hansen (1985) have confirmed (i) and indicated support for (ii), (iii), (iv) in the Douglas-fir ecosystem. In this chapter, in a manner suggested by
Leach (1940), I demonstrate that insects are vectors of *V. wageneri* and are important factors in the epidemiology of black-stain root disease of Douglas-fir.
MATERIALS AND METHODS

Insect Feeding on Uninfected 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, I attracted beetles into precommercially thinned 12-year-old plantations of Douglas-fir (which included some Tsuga heterophylla (Raf.) Sarg. and Thuja plicata Donn). Thinning and other disturbances are associated with V. wageneri occurrence and are believed to contribute to tree susceptibility (Goheen and Hansen 1978, Hansen 1978, Harrington, Reinhart, Thornburgh, and Cobb, 1983). Two 50-ha plantations, located in the Coast Range (T27S R8W and T27S R7W), Douglas County, southwest Oregon, were selected for study. The plantations were uniformly stocked and were sustaining mortality due to black-stain root disease. A 32-ha portion 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 2000-4000 to 900-1000 stems per hectare with a chain saw.

I monitored insect activity and immigration into each plot in 1983 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 consisted of five pitfall traps, one positioned within 5 m of each edge and the other three uniformly spaced at distances of approximately 1/4, 1/2, 3/4 the width of the plot. Each pitfall trap consisted of a plastic container (15.7 cm diameter, 19 cm height) buried to the soil surface and fitted with an aluminum funnel. The opening was covered by a 20.3 cm X 20.3 cm plywood board elevated 3 cm off the ground with nails. Within this container was a second plastic container (12.2 cm diameter, 8 cm height) containing the killing agent and preservative, undiluted antifreeze or water with detergent. Fresh antifreeze was added at the beginning of trapping in March and again in July. Fresh water-detergent solution was added at the beginning of each sample period in traps of one plantation throughout August, September, and October due to problems associated with resident coyotes.

Two sticky screens (surfaces facing east-west) were located in each plot, one at 5 m from one edge and one at the center of each plot, between their respective pitfall traps. The sticky traps consisted of two hardware cloth screens (2 mesh per cm) coated with Stickum Special® and stapled to opposite sides of an 80 cm long 5 cm X 5 cm
stake driven into the ground. The Stickum Special® on the screens was renewed at four to six week intervals throughout the period of trapping. No attractants were used in this study. Insects were collected at 14-day intervals from 24 March 1983 through 3 November 1983 in pitfall traps and from 7 April 1983 through 22 September 1983 on sticky traps and were identified to species.

During September 1983, populations of immature and adult insects were removed from under the bark of roots and stumps of trees felled during thinning to obtain an estimate of colonization intensity by H. nigrinus, P. fasciatus, and S. carinatus following the various thinning treatments. At randomly selected points along one edge of each plot, two stumps of thinned trees within 5 m of the edge and 2 stumps near the center of each plot were randomly selected and excavated. All insects except eggs were collected from under the bark and the number of egg galleries made by H. nigrinus were counted. The roots and root collar of the nearest crop tree were examined for any evidence of insect-induced wounds. In the unthinned plots, trees were examined for wounds or insect colonization nondestructively.

In 1984, I examined the attractiveness of trees along roads and within plots using a random sample from all plots and a roadside sample from all plots with roads. I nondestructively examined the root collar and proximal 30
cm of roots of apparently healthy crop trees (Douglas-fir only) for evidence of wounding by insects. Wounding was underestimated because the undersides of roots could not be thoroughly examined. In the random sample, each plot was divided into quarters. Each quarter was 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 quadrat, were examined for wounding. In the roadside survey, all apparently healthy Douglas-fir directly adjacent to established roads were examined for wounding as described above for the random sample.

Wounds were classified as 1983 wounds if resin had crystalized and turned white, or as 1984 wounds if resin was absent, or was uncrystalized but contained fresh frass, or if insects were actively excavating bark and phloem at the time of inspection. Wounds were classified according to causal agent based on the characteristic patterns observed for each species in laboratory experiments (described below) and described by Zethner-Møller and Rudinsky (1967) for H. nigrinus and by Condrashoff (1968) for S. carinatus or by recovery and identification of the insect from a wound at the time of inspection.

I employed the Wilcoxon signed-rank and rank sum tests (Lehmann 1975) to detect significant differences in
mean number of beetles captured per trap among treatments and mean number of wounds per tree among treatments. Means were compared at the P=0.05 level.

**Conditions Suitable for Transmission**

To determine what constituted a potentially susceptible host, I artificially inoculated the roots of Douglas-fir with *V. wageneri*. Roots of standing trees and roots of trees cut during thinning were inoculated. Inoculated trees or root systems were located at a distance of more than 15 m from known, mapped foci of *V. wageneri*. Each area was intensively examined for occurrence of infected, symptomatic trees by examining each tree and stump for symptoms of disease. In May 1983, two weeks after the May thinning, I artificially inoculated two roots of each of ten trees in an unthinned plot and two roots of each of ten felled trees in thinned plots using a technique described by Hessburg (1984). A 0.5 cm X 0.5 cm block of malt agar colonized by *V. wageneri* was introduced under the outer bark or phloem, at the cambium-xylem interface, of each root. The wound was wrapped with moistened cheese cloth and wrapped in 0.4 mil plastic; the bandage was secured at the ends with twist-ties. In September, 1983, the roots were excavated, removed, and returned to the laboratory. Each root was examined for the characteristic black-stained xylem, with
only mature tracheids colonized by ensheathed hyphae (Hessburg 1984, Smith 1967). This experiment was conducted in one plot per treatment in one of the experimental blocks during 1983 without uninoculated controls. The experiment was repeated in 1984 in one unthinned plantation, in a plantation thinned in October 1983, and in a plantation thinned in May 1984 (two weeks before inoculation), using an agar-without-*V. wageneri* control.

**Fungal Infestation of Insects**

To assay insects for transmission of *V. wageneri*, I collected insects in established foci of infection in three widely separated plantations of 14-25-year-old Douglas-fir in the Coast Range of Oregon (Benton, Lane, and Yamhill counties), using pitfall traps baited with an attractant. Attractant-baited traps were identical to those described above except the inner container was partially filled with old bark fragments (which are not colonized by *V. wageneri*) for cover. A film canister, containing a 1/4-dram glass vial containing 2% racemic alpha-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-September 1980. Few *P. fasciatus* were collected by the
traps. Therefore, adults of this species were hand-collected from stems of trees in May 1980 and collected weekly August-October 1980 from an emergence cage placed over the stump of a severely diseased tree containing abundant larvae and pupae of _P. fasciatus_, which was felled in August 1980. Beetles were collected aseptically and held individually in glass vials on ice until they were returned to the laboratory. Vials and stoppers were soaked in 95% ethanol between use.

Each insect was killed by crushing between the pro- and mesothorax, placed on an agar medium containing 200ppm cycloheximide with streptomycin added (Hicks, Cobb, and Gersper 1980) and incubated at 15 C. Insects were killed to prevent the spread of antagonistic species of fungi across the surface of the medium. Following 3 weeks of incubation, isolates believed to be _V. wageneri_ were subcultured on malt agar for verification.

In 1981 and 1982, the roots of three, two-year-old Douglas-fir seedlings were artificially inoculated with each apparent isolate of _V. wageneri_ in a manner described by Hessburg (1984) with the exceptions 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. Seedlings were planted in individual 450 ml planting containers and held in a greenhouse until
symptoms of disease appeared or until the experiment was concluded in six months. All seedlings were examined for the characteristic indicators of infection by *V. wageneri* (Hessburg 1984, Smith 1967, Wagener and Mielke 1961). Isolates from infected xylem of diseased seedlings were obtained and compared with the original isolate and with the original description provided by Kendrick (1962).

**Fungal Transmission by Insects**

To demonstrate transmission of *V. wageneri* 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 precommercially thinned plantations of Douglas-fir during 1983 and 1984. The mouthparts of individual beetles of each species were artificially infested with inoculum of 4-6 conidiophores of *V. wageneri*; artificially infested, dead beetles served as controls. Each beetle was confined to the basal portion of a single 2-year-old Douglas-fir seedling by a fine mesh plastic screen. *P. fasciatus* and *S. carinatus* were caged for five days and *H. nigrinus* was caged for 14 days.

*H. nigrinus* were captured in June 1983 and May-June 1984 and caged on seedlings as described above, except that beetles were not artificially infested with *V. wageneri*. Killed beetles were used as controls. Cages
were removed after 14 days. In all cases seedlings were
examined for wounding, for black-stained xylem, and
microscopically for the characteristic pattern of
colonization and hyphal morphology (Wagener and Mielke
RESULTS

Wounding of Susceptible Hosts by Insects Under Conditions Suitable for Transmission of V. wageneri

I observed an increased activity of beetles in thinned plots, relative to unthinned plots, as populations of *H. nigrinus*, *S. carinatus*, and *P. fasciatus* responded to disturbance within the plantations (Table II.1). Significantly more beetles of each species were captured in the thinned plots than in the unthinned plots. Significantly fewer *H. nigrinus* and *P. fasciatus* were captured in the May-thinned plots than either the September- or January-thinned plots indicating a correlation between time of thinning and trap capture for these two species. I detected no significant differences among thinning treatments for *S. carinatus*. Brood of all three species was recovered from the roots and root collar region of randomly selected stumps of thinned trees while unthinned, control trees in the unthinned plots were free of insect damage (Table II.2). More attacks by *H. nigrinus* were observed in plots thinned the previous September and January relative to the plots thinned in May. Wounds on crop trees caused by *H. nigrinus* were observed on 2 of 36 trees examined in 1983.

Based on both the random and roadside surveys, the frequency of wounds in roots and root collars of crop
trees in precommercially thinned plots was significantly greater than in unthinned plots (Table II.3). Wounds were observed primarily on the root collar and lower stem region below the surface of the litter and in the proximal 50 cm of the roots. Virtually all wounds were attributed to *H. nigrinus*. Forty-six adult *H. nigrinus* (29 females, 17 males) were observed boring into 35 of 1543 crop trees in thinned plots at the time of examination. Wounds on the lower stem and root collar were frequently superficial (within the phloem only), but beetles were recovered from tunnels, penetrating to the xylem, which were deeper than the length of the insects. Wounds on roots penetrated to the xylem more frequently, especially on small roots (<1 cm diameter) and roots with thin phloem. In the random sample, 3-16% of all crop trees in thinned plots were wounded. Significantly fewer trees in the May treatment sustained wounds relative to the January treatment. The September treatment did not differ significantly from the January and May treatments. However, the probability that crop trees in the January-thinned plots sustained more wounds than crop trees in the September plots was $P=0.92$. In the roadside survey, 8-33% of the crop trees were wounded. Significantly fewer trees in the May treatment sustained wounds relative to the September treatment. The January treatment did not differ significantly from either the September or May treatments. However, the probability
that crop trees in the January-thinned plots sustained more wounds than crop trees in the May-thinned plots was \( P=0.94 \). A larger sample probably would yield more definitive results.

Old wounds (1983), associated with immigration of *H. nigrinus* into thinned stands, were more abundant than new wounds (1984). New wounds were more frequently observed on trees which sustained wounds during 1983 than on unwounded trees. In the random sample and the roadside sample, 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*. No trees sustained wounds similar to those of *P. fasciatus* although these wounds would be difficult to detect by the examination procedure employed.

The plantation thinned in October 1983 and used in the inoculation study the following year sustained wounds by *H. nigrinus* during 1984. Wounds caused by *H. nigrinus* (13 females, 10 males) were found on 18 of 49 crop trees along one roadside, and adults were observed wounding 12 crop trees at the time of examination.

Results of the inoculation experiments indicated that the root systems of cut trees are susceptible to infection by *V. wageneri* (Table II.4). 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 seven months. Generally, the 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. Heavily stained root xylem was noted only in the roots of trees cut in May while trees cut in September, October, and January exhibited only weak, reddish stain of root xylem because few tracheids were colonized. These results suggested that vectors colonizing root systems of cut trees could have introduced *V. wageneri* into plantations via these hosts. Also, unthinned trees were susceptible to infection, suggesting that wounds to the xylem caused by *H. nigrinus* may have introduced *V. wageneri* into disturbed plantations via the crop trees.

**Recovery of *V. wageneri* from Insects**

Isolates of *V. wageneri* were obtained from seven of the 668 field-collected beetles assayed (Table II.5). Of these seven isolates, four were obtained from 173 *H. nigrinus* (two females, two males), two were obtained from 433 *S. carinatus* (two females), and one was obtained from 62 *P. fasciatus* (one female). Thus, the level of contamination detected in this study was less than 5% (Table II.5). The two *S. carinatus* determined to be infested with *V. wageneri* were captured in the same trap
during the same sample period. Therefore, one beetle may have contaminated the other beetle within the trap. None of the 41 *P. fasciatus* collected by hand during May, 1980 were infested; one of 21 *P. fasciatus* collected in the emergence cage during August-October 1980 was infested with *V. wageneri*. Beetles carrying *V. wageneri* were recovered at all three sites, indicating that contamination of beetles is a widespread phenomenon, at least in established foci.

Transmission of *V. wageneri* to Susceptible Hosts by Insects

*H. nigrinus*, *P. fasciatus*, and *S. carinatus* readily wounded Douglas-fir seedlings when confined to hosts under my laboratory conditions (Table II.6). Wounds caused by *H. nigrinus* were circular (~2mm diameter) to oval or elongate, similar to those described by Zethner-Møller and Rudinsky (1967), and occurred below the soil line. Wounds of *P. fasciatus* were small, circular punctures (~1mm diameter) and occurred above the soil line. *S. carinatus* caused gouge-like wounds above or at the soil line, similar to those described by Condrashoff (1966).

I obtained infected seedlings when beetles were artificially infested with *V. wageneri* prior to being caged on seedlings (Table II.6). Only wounded seedlings became infected. Wounds were observed on 70-80% of all
seedlings, regardless of species of beetle. Percent infection varied from a low of 25% of wounded trees for *S. carinatus* to 47% for *H. nigrinus* and 68% for *P. fasciatus*. The results suggested that the smaller, less severe but more numerous feeding wounds of *P. fasciatus* (mean=13.6 wounds per wounded seedling versus 5.1 for *S. carinatus* and 1.6 for *H. nigrinus*) were more efficacious infection courts or that an increased number of wounds increased the likelihood of transmission of the pathogen. Also, the wounds of *H. nigrinus*, which were fewer in number and below the soil line, were more efficacious infection courts than the more numerous wounds of *S. carinatus*, which generally occurred above the soil line. The control seedlings, caged with dead, artificially infested beetles, showed neither wounds nor disease (Table II.6).

Field-collected *H. nigrinus*, which were not artificially infested, transmitted *V. wageneri* to Douglas-fir seedlings in seven cases (Table II.6). In 1983, seven of 22 beetles wounded seedlings and one seedling (5%) developed black-stain root disease. In 1984, 278 of 1000 beetles wounded seedlings and six seedlings (2.2%) became infected with *V. wageneri*. 
Goheen and Cobb (1978) proposed the vector hypothesis to account for the proliferation of new V. wageneri foci in stands of ponderosa pine in the Sierra Nevada of California. They argued that because V. wageneri was related to the Ceratocystis fungi (which are intimately associated with insects, especially bark beetles), and because V. wageneri was observed to sporulate in insect galleries, root beetles would ultimately be identified as vectors of V. wageneri in ponderosa pine stands. The present study and a previous study (Witcosky and Hansen 1985) confirmed the vector hypothesis in the Douglas-fir ecosystem by demonstrating that: (1) insects are commonly associated with diseased trees (Witcosky 1981, Witcosky and Hansen 1985); (2) insects carry inoculum of V. wageneri in the field (Witcosky and Hansen 1985, Table II.5); (3) insects successfully transmit V. wageneri to seedlings under laboratory conditions (Table II.6); and (4) insects visit, colonize, and create infection courts in susceptible hosts (Tables II.1-II.4).

Furthermore, the ability of H. nigrinus to transmit V. wageneri to uninfected trees in the field was observed on two occasions during this study. One newly infected tree, which was at least 4 m from established disease foci, was excavated in June 1980 and a similar tree in
June 1983. In each of these trees, only a single, small, short root was infected and the extent of colonization by *V. wageneri* was between 15-30 cm. Each root had sustained one or two wounds identical to those made by *H. nigrinus*, penetrating to the xylem. *V. wageneri* had not colonized any other roots of these trees nor extended up the stem to the soil surface. Furthermore, no infected roots were within 4 m of these newly infected roots. Therefore, these trees could only have been infected via the vector mechanism. These results indicate that insects are important components in the epidemiology of black-stain root disease.

Two types of new *V. wageneri* foci are recognized in Douglas-fir plantations in Oregon, those appearing near but not adjacent to the margin of established disease foci, and those appearing at greater distance from established foci of *V. wageneri*. The latter strictly concerns initiation of new foci of *V. wageneri* and, at this time, can be accounted for only by the vector mechanism. The former also contributes to the enlargement of established foci, by the spread and coalescence of new foci with adjacent, established foci via the soil spread mechanism. Newly initiated foci at the margin of established foci cannot be explained only by the soil spread mechanism unless diseased roots and healthy roots are in close (6-15 cm) proximity (Goheen 1976, Goheen and
Soil spread as a mechanism of new foci formation cannot be dismissed, because some roots of Douglas-fir extend for more than 10 m before developing feeder roots (Witcosky, unpublished data). However, insect-mediated spread appears to be a more reasonable explanation for this phenomenon. This conclusion is supported by (1) the two excavations described above, in which H. nigrinus feeding wounds appeared to be the only source of inoculum, and (2) the observation that wounds on crop trees in precommercially thinned plots were more often observed on trees adjacent to established foci than on trees more distant from established foci in the random and roadside surveys. Although Hessburg (1984) concluded that the rate of expansion of disease foci in Douglas-fir (Hansen and Goheen, unpublished data) and ponderosa pine (Byler, Cobb, and Rowney 1979, Cobb, Slaughter, Rowney, and DeMars, 1982) could be explained by the soil spread mechanism alone, the expansion of established foci in Douglas-fir requires inclusion of the extent to which insects contribute to proliferation of foci at the margin of established foci. The extent to which insects contribute to the expansion of foci remains to be documented.

New foci of infection may develop when hosts are stressed by environmental and biological factors which influence the behavior of vector populations. Witcosky
excavated Douglas-fir sustaining virtually lethal infections (>60% of root system colonized) of *Phellinus weirii* (Murr.) Gilb. and infected secondarily and to a minor degree with *V. wageneri*, which was confined to the few living roots actually sustaining the declining tree at the time of excavation. Goheen and Filip (1980) also have observed *V. wageneri* in trees sustaining other root diseases. *H. nigrinus*, *S. carinatus*, and *P. fasciatus* colonized these declining trees (Witcosky 1981) and may have been responsible for introducing *V. wageneri* into these trees during feeding or oviposition.

Other factors contributing to spread include road building (Hansen 1978), compaction of soils and altered drainage, excessive soil moisture, and proximity to severely wounded trees (Goheen, Kanaskie, and Frankel 1983, Witcosky 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 (a potentially important visual cue for host-selecting beetles). Injury and stress also may result in the increased production and release of small molecular weight volatiles, such as terpenes, ethylene, and ethanol (Ayers 1984, Drew and Lynch 1980, Feldman 1984, Kozlowski 1984, Yang and Hoffman 1984) which
could potentially act, or are known to act as host attractants for host-seeking beetles (Rudinsky 1966, Rudinsky and Zethner-Møller 1967, Chapter IV).

Two alternative models of host selection may be invoked to explain this pattern of proliferation: a random wounding model superimposed on a non-random spatial distribution of stressed hosts, or a non-random model which is based on discrimination of stressed hosts by vectors. A random landing model of host selection has been proposed for the lodgepole pine-mountain pine beetle system (Hynum and Berryman 1980, but see Gara, Geiszler, and Littke 1984), the ponderosa pine-western pine beetle system (Moeck, Wood, and Lindahl 1981, Wood 1982), and the pine-southern pine beetle system (Payne 1983). A non-random model of host selection has been reported for other bark beetles (Cade, Hrutfiord, and Gara 1970, Coulson, Hennier, Flamm, Rykiel, and Hu 1983, Moeck 1970, 1971, Ryker and Oester 1982). At present, evidence supports the nonrandom model in the Douglas-fir system because alpha-pinene and ethanol are known to be host attractants for H. nigrinus and S. carinatus (Chapter IV).
Table II.1. Mean number of *Hylastes nigrinus* and *Pissodes fasciatus* caught per trap on sticky traps and *Steremnius carinatus* caught per trap in pitfall traps in unthinned and precommercially thinned 2-ha plots in two, 12-year-old plantations of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1983.

<table>
<thead>
<tr>
<th>Species</th>
<th>Unthinned Control</th>
<th>Sept. '82 Thinning</th>
<th>Jan. '83 Thinning</th>
<th>May '83 Thinning</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. nigrinus</em></td>
<td>0.003&lt;sup&gt;a&lt;/sup&gt; (0.006)</td>
<td>0.23&lt;sup&gt;c&lt;/sup&gt; (0.11)</td>
<td>0.42&lt;sup&gt;c&lt;/sup&gt; (0.45)</td>
<td>0.08&lt;sup&gt;b&lt;/sup&gt; (0.06)</td>
</tr>
<tr>
<td><em>P. fasciatus</em></td>
<td>0&lt;sup&gt;a&lt;/sup&gt; (0)</td>
<td>0.20&lt;sup&gt;c&lt;/sup&gt; (0.14)</td>
<td>0.20&lt;sup&gt;c&lt;/sup&gt; (0.17)</td>
<td>0.06&lt;sup&gt;b&lt;/sup&gt; (0.06)</td>
</tr>
<tr>
<td><em>S. carinatus</em></td>
<td>0.16&lt;sup&gt;a&lt;/sup&gt; (0.06)</td>
<td>0.53&lt;sup&gt;b&lt;/sup&gt; (0.23)</td>
<td>0.51&lt;sup&gt;b&lt;/sup&gt; (0.18)</td>
<td>0.59&lt;sup&gt;b&lt;/sup&gt; (0.20)</td>
</tr>
</tbody>
</table>

<sup>1/</sup> Different superscripts within rows indicate significantly different means at P=0.05. Wilcoxon signed-rank test (one-sided) for all paired comparisons. Values in () are standard errors. n=8 plots per treatment.
Table II.2. Recovery of *Hylastes nigrinus*, *Pissodes fasciatus* and *Steremnius carinatus* from roots, root collar, and lower stem of felled Douglas-fir four to twelve months after precommercial thinning of a 12-year-old plantation in Douglas County, Oregon, during 1983.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sept. '82 Thinning</th>
<th>Jan. '83 Thinning</th>
<th>May '83 Thinning</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. nigrinus</em></td>
<td>15/16</td>
<td>16/16</td>
<td>10/16</td>
</tr>
<tr>
<td><em>P. fasciatus</em></td>
<td>7/16</td>
<td>11/16</td>
<td>8/16</td>
</tr>
<tr>
<td><em>S. carinatus</em></td>
<td>14/16</td>
<td>12/16</td>
<td>6/16</td>
</tr>
<tr>
<td>Uninfested hosts</td>
<td>1/16</td>
<td>0/16</td>
<td>5/16</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Number of Trees Sampled</th>
<th>Number and (%) with Wounds</th>
<th>Mean Proportion Trees Wounded $^2$</th>
<th>Mean Number of Wounds per Tree $^1$</th>
<th>Mean Number of Wounds per Wounded Tree $^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Random Sample</td>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td>Total</td>
</tr>
<tr>
<td>Sept. '82 thinning</td>
<td>198</td>
<td>13 (6.6)</td>
<td>0.06 $^b,c$</td>
<td>0.14</td>
<td>0.005</td>
</tr>
<tr>
<td>Jan. '83 thinning</td>
<td>209</td>
<td>33 (15.8)</td>
<td>0.15 $^c$</td>
<td>0.48</td>
<td>0.08</td>
</tr>
<tr>
<td>May '83 thinning</td>
<td>227</td>
<td>8 (3.5)</td>
<td>0.04 $^b$</td>
<td>0.12</td>
<td>0.004</td>
</tr>
<tr>
<td>Uthinned control</td>
<td>354</td>
<td>0 (0)</td>
<td>$^a$</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Roadside Survey</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sept. '82 thinning</td>
<td>278</td>
<td>87 (31.1)</td>
<td>0.20 $^c$</td>
<td>1.85</td>
<td>0.14</td>
</tr>
<tr>
<td>Jan. '83 thinning</td>
<td>221</td>
<td>44 (19.9)</td>
<td>0.20 $^{b,c}$</td>
<td>0.89</td>
<td>0.11</td>
</tr>
<tr>
<td>May '83 thinning</td>
<td>410</td>
<td>34 (8.3)</td>
<td>0.08 $^b$</td>
<td>0.15</td>
<td>0.04</td>
</tr>
<tr>
<td>Uthinned control</td>
<td>306</td>
<td>0 (0)</td>
<td>$^a$</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

$^1$ For the random sample and the roadside survey separately, different superscripts within columns indicate significantly different means at $P=0.05$. Wilcoxon signed-rank test (one-sided) for the random sample and Wilcoxon rank sum test (one-sided) for the roadside survey for all paired comparisons.

$^2$ Per transect for the random sample and per road for the roadside survey. The random and roadside estimates are not comparable.

$^3$ $P$(Jan. $\rightarrow$ Sept.)=$0.92$.

$^4$ $P$(Jan. $\rightarrow$ May)=$0.94$. 

<table>
<thead>
<tr>
<th>Result</th>
<th>1983</th>
<th>1984</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Unthinned</td>
<td>Sept. '82</td>
</tr>
<tr>
<td>% Hosts Infected</td>
<td>Control</td>
<td>Thinning</td>
</tr>
<tr>
<td>% Roots Infected</td>
<td>90</td>
<td>40</td>
</tr>
<tr>
<td>Mean Length (cm)</td>
<td>35.8</td>
<td>6.5</td>
</tr>
<tr>
<td>Colonized</td>
<td>(26.1)</td>
<td>(3.1)</td>
</tr>
</tbody>
</table>

1/ Standard deviations are in ().

2/ Hand section and microscopic examination suggested that three roots on three cut trees were infected with *V. wageneri*. *H. nigrinus* had colonized each of these roots.

3/ Since the point of inoculation was uncertain, no value was calculated for this entry.
Table II.5. Recovery of *Verticicladiella wageneri* from *Hylastes nigrinus*, *Pissodes fasciatus*, and *Sterennium carinatus* collected at three widely separated foci of infection in 10- to 25-year-old plantations of Douglas-fir in western Oregon during 1980.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Beetles Assayed</th>
<th>Number and (%) of Beetles with <em>V. wageneri</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. nigrinus</em></td>
<td>173</td>
<td>4 (2.3)</td>
</tr>
<tr>
<td><em>P. fasciatus</em></td>
<td>62</td>
<td>1 (1.6)</td>
</tr>
<tr>
<td>hand-collected May 1980</td>
<td>41</td>
<td>0 (0)</td>
</tr>
<tr>
<td>emergence Aug.-Oct. 1980</td>
<td>21</td>
<td>1 (4.8)</td>
</tr>
<tr>
<td><em>S. carinatus</em></td>
<td>433</td>
<td>2 (0.5)</td>
</tr>
</tbody>
</table>
Table II.6. Wounds and transmission of *Verticicladiella wageneri* to 2-year-old Douglas-fir seedlings by artificially infested *Pissodes fasciatus* and *Steremnius carinatus* in 1983 and by artificially infested *Hylastes nigrinus* and *H. nigrinus* infested at field frequency in Corvallis, Oregon, during 1983 and 1984.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Number Seedlings Infested</th>
<th>Number (%) Seedlings Wounded</th>
<th>Number (%) Seedlings Infected with <em>V. wageneri</em></th>
<th>Mean Number (and Std. Dev.) of wounds per Wounded Seedling</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>P. fasciatus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>live</td>
<td>97</td>
<td>78 (80)</td>
<td>52 (68)</td>
<td>13.6 (9.7)</td>
</tr>
<tr>
<td>dead</td>
<td>13</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td><strong>S. carinatus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>live</td>
<td>128</td>
<td>93 (73)</td>
<td>23 (25)</td>
<td>5.1 (4.5)</td>
</tr>
<tr>
<td>dead</td>
<td>12</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td><strong>H. nigrinus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>artificially infested (1984)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>live</td>
<td>61</td>
<td>45 (74)</td>
<td>21 (47)</td>
<td>1.6 (1.1)</td>
</tr>
<tr>
<td>dead</td>
<td>24</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>field frequency (1983)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>live</td>
<td>22</td>
<td>7 (32)</td>
<td>1 (3)</td>
<td>1.1 (0.4)</td>
</tr>
<tr>
<td>dead</td>
<td>4</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>field frequency (1984)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>live</td>
<td>1000</td>
<td>278 (28)</td>
<td>6 (2)</td>
<td>1.5 (1.3)</td>
</tr>
<tr>
<td>dead</td>
<td>86</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
</tbody>
</table>
LITERATURE CITED


In plantations of Douglas-fir in western Oregon, stand density management through precommercial thinning results in significantly elevated activity of insects known to be vectors of black-stain root disease. *Hylastes nigrinus*, *Pissodes fasciatus*, and *Steremnius carinatus* immigrate into disturbed plantations and colonize cut trees following thinning. Within plantations, at the scale of 2-ha plots, time of thinning can be manipulated to reduce immigration of vectors. The number of *H. nigrinus* and *P. fasciatus* caught by traps was reduced when thinning occurred after peak flight activity.
INTRODUCTION

Black-stain root disease of conifers, caused by the fungus *Verticicladiella wageneri* Kendrick (sexual stage: *Ceratocystis wageneri* Goheen and Cobb) is widely distributed throughout western North America, killing principally single-leaf pinyon (*Pinus monophyla* Torr. and Frem.), ponderosa (*Pinus ponderosa* Laws.), and lodgepole (*Pinus contorta* Dougl.) pines (Wagener and Mielke 1961) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.)Franco) (Cobb and Platt 1967). *V. wageneri* spreads through the soil from diseased trees to adjacent, healthy trees via the continuous xylem of functional root grafts (Goheen 1976, Hessburg 1984) and by growth through the soil for short distances of perhaps 1-6 cm but apparently less than 15 cm (Goheen and Cobb 1978, Hessburg 1984, Hicks, Cobb, and Gersper 1980). In growth through the soil, the fungus enters healthy hosts through infection courts on fine roots (Goheen and Cobb 1978, Hessburg 1984). These infection courts are, histologically, functional xylem elements which are open and exposed to the soil environment due to the production and senescence of fine roots (Hessburg 1984).

Although the expansion of established foci of *V. wageneri*—estimated to enlarge at 0.5-6 m/yr (Byler, Cobb, and Rowney 1979, Cobb, Slaughter, Rowney, and DeMars 1982,
Hansen and Goheen unpublished)--can be explained by fungal growth alone (Hessburg 1984), new foci of disease apparently are initiated by insects (Witcosky and Hansen 1985, Chapter II).

Goheen and Cobb (1978) suggested that, in ponderosa pine, new foci of *V. wageneri* were initiated by insects, particularly the root bark beetle, *Hylastes macer* LeC. I have demonstrated that insects are vectors of *V. wageneri* in Douglas-fir and must be considered an important factor in the epidemiology of black-stain root disease in the coniferous ecosystems where this pathogen occurs (Witcosky 1981, Witcosky and Hansen 1985, Chapter II).

*Hylastes nigrinus* (Mann.), *Pissodes fasciatus* LeC., and *Stereinius carinatus* (Boh.) are vectors of *V. wageneri* in the Douglas-fir ecosystem. These species are consistently associated with diseased Douglas-fir (Witcosky 1981, Witcosky and Hansen 1985), carry inoculum of *V. wageneri* in the field (Witcosky and Hansen 1985, Chapter II), are capable of transmitting *V. wageneri* to Douglas-fir under laboratory conditions (Chapter II), and feed or oviposit in susceptible hosts under conditions suitable for transmission of *V. wageneri* (Chapter II).

Forest pathologists in the coastal Douglas-fir region of the Pacific Northwest have expressed growing concern over the reported relationship between intensive forest management practices and the development of black-stain
root disease in managed plantations. These reports have associated the development of foci of black-stain root disease with road construction (Hansen 1978), tractor logging (Goheen, Kanaskie, and Frankel 1983), and precommercial thinning (Harrington, Reinhart, Thornburgh, and Cobb 1983). This growing awareness of the association between *V. wageneri*, insects, and forest disturbance justified research aimed at providing an experimental basis for pest management strategies in young Douglas-fir plantations in this region, especially plantations sustaining black-stain root disease. In this chapter I describe the influence of time of precommercial thinning on the immigration and activity of *H. nigrinus*, *P. fasciatus*, and *S. carinatus* within plantations of Douglas-fir.
MATERIALS AND METHODS

This study was conducted in the eastern portion of the Coast Range of southern Oregon where black-stain root disease is widely distributed. Two 12-yr-old plantations (BURD, T27S R8W, and 5340, T27S R7W) were selected for study. Each plantation was uniformly stocked with 2000-4000 stems per hectare and was sustaining some mortality due to V. wageneri. In each plantation cooperators for Weyerhaeuser Company and I established four blocks, each consisting of four, 2-ha plots. The plots in each block were randomly allocated to four treatments: precommercial thinning in September 1982, January 1983, or May 1983, and unthinned. Thus, there were four replicates of each treatment per plantation. Four unthinned plots, located at a distance of >30 m from the experimental blocks in the BURD plantation, served as an external check to account for the influence of thinning on insect activity in the interspersed control plots. Stand density in the thinned plots was reduced to approximately 900-1000 stems per hectare by felling excess trees with a chainsaw.

I monitored insect activity and immigration into each plot of both plantations in 1983 and the plots in the BURD plantation in 1984. I used a series of pitfall traps to capture S. carinatus and vertical sticky traps to capture flying H. nigrinus and P. fasciatus. The pitfall traps
were placed in paired, parallel transects, 5 m apart, from edge to edge across the middle of each plot. Each transect consisted of five pitfall traps, one positioned within 5 m of both edges and the other three placed at distances of 1/4, 1/2, and 3/4 the width of the plot. A sticky screen trap was placed 5 m from one edge and in the middle of each plot, between the pitfall trap transects.

Each pitfall trap consisted of a plastic container (15.7 cm diameter, 19 cm height) buried to the soil surface and fitted with an aluminum funnel. The opening was covered by a 20.3 cm X 20.3 cm plywood board elevated ~3 cm off the ground with nails. Within this container was a second plastic container (12.2 cm diameter, 8 cm height) containing undiluted antifreeze or water with detergent. Fresh antifreeze was added at the beginning of trapping in March and again in July each year. In the 5340 plantation, coyotes removed pitfall traps and disrupted trapping (from 2 July through 13 August 1983; Julian dates 181-83 through 223-83) until the preservative was changed to water with detergent. Fresh water-detergent solution was added at the beginning of each sample period.

The sticky traps consisted of two hardware cloth screens (2 mesh per cm) coated with Stickum Special® and stapled to opposite sides of a 80 cm long, 5 cm X 5 cm stake driven into the ground. The Stickum Special® on the
screens was renewed at four to six week intervals throughout the period of trapping.

Two other nearby Douglas-fir plantations were monitored for activity of vectors following precommercial thinning. One plantation was thinned in October 1983 and the other in June 1984. Two sets of transects (pitfall traps and sticky traps) were established in each plantation and sampled during 1984.

The pitfall samples were collected at 14-day intervals from 24 March 1983 (Julian date 081-83) through 3 November 1983 (307-83) and from 14 March 1984 (074-84) through 29 August 1984 (242-84). In the plots thinned in October 1983 and June 1984, pitfall traps were collected from 25 April 1984 (116-84) through 29 August 1984 (242-84) and from 9 May 1984 (130-84) through 29 August 1984 (242-84), respectively. Sticky trap samples were collected simultaneously from 7 April 1983 (097-83) through 22 September 1983 (265-83) and from 28 March 1984 (088-84) through 1 August 1984 (214-84). In the plots thinned in October 1983 and June 1984, sticky trap samples were collected from 9 May 1984 (130-84) through 29 August 1984 (242-84).

During September 1983, populations of immature and adult insects were removed from under the bark of roots and stumps of trees cut during precommercial thinning. At randomly selected points in each plot in the BURD
plantation, two cut trees within 5 m of the edge and two cut trees near the center of each plot were randomly selected and excavated. All insects, except eggs, were collected from under the bark and the number of egg galleries made by H. nigrinus counted. In the unthinned units, trees were examined nondestructively for wounds or insects. Individuals of H. nigrinus, S. carinatus, and P. fasciatus were tallied.

During 1984, I placed emergence cages (1 m²) over randomly located stumps in the twelve thinned plots in the BURD plantation to capture emerging H. nigrinus. Four traps were placed within 10 m of the edge of each plot in groups of two traps. Emerging insects were collected up to four times daily from 28 March 1984 (088-84) through 1 July 1984 (183-84).

I employed the Wilcoxon signed-rank test (Lehmann 1975) to detect significant differences in mean number of beetles captured per trap among treatments over the entire year and at 14-day sample intervals for the 1983 data alone. Means were compared at the P=0.05 level.
RESULTS

I detected an increase in activity and immigration of insect vectors of *V. wageneri* into the disturbed plots following precommercial thinning. Significantly more beetles were caught in pitfall and sticky traps in thinned plots during 1983 than in unthinned, control plots, regardless of time of thinning (Table III.1). Fewer *H. nigrinus* and *P. fasciatus* were caught in the plots thinned in May relative to plots thinned the previous September or January.

Examination of the biweekly collections indicated that more *H. nigrinus* were caught in September and January treatments than in the May treatment during the peak flight period but that means were not significantly different at other times when captures were low (Table III.2). This trend was evident but less pronounced for *P. fasciatus* (Table III.3). These results suggested that, in the area of study and at the scale of 2-ha plots, thinning can be timed to reduce but not eliminate colonization by *H. nigrinus* and *P. fasciatus*.

I observed no significant differences in the capture of *S. carinatus* based on time of thinning (Table III.1). In general, the number of beetles captured during peak periods of activity tended to be highest in the May treatment but no consistent trend emerged over the entire
year and trap capture varied considerably among treatments (Table III.4).

*H. nigrinus* exhibited a distinct period of flight and immigration into the study sites in 1983 (Figure III.1). Although beetles were caught during the first sample period, observations during the 21 days prior to placement of the sticky traps indicated that flight had not begun because of unstable weather, rain, snow, and temperatures continuously below the 15°C threshold for flight of *H. nigrinus* (Daterman, Rudinsky, and Nagel 1965, Zethner-Møller and Rudinsky 1967). The first episode of flight, in April, was followed by a 2-week period of unstable weather, rain, snow, and low temperatures. The peak flight occurred in May over a 28-day period. Following this peak, very few beetles were caught.

Emergence and flight from the experimental area during 1984 and immigration into the plantation thinned in October 1983 indicated activity patterns similar to those observed in 1983. The flight period was protracted during 1984 due to frequent episodes of unstable weather including rain and snow. These data indicated that emergence, flight, and immigration during 1984 were concurrent processes (Figures III.2, III.3, Table III.5). More *H. nigrinus* were caught in thinned plots in the BURD plantation than in the unthinned plots during 1984. During 1984, few *H. nigrinus* were caught in the June 1984
thinned plantation, but immigration into the October 1983 thinned plantation was substantial (Figure III.3).

*P. fasciatus* was caught only in thinned plots (Figure III.4, Table III.1). The pattern of flight was similar to that observed for *H. nigrinus* although more activity was noted during July and August. Very few *P. fasciatus* were caught during 1984 in the BURD plots. Immigration into the October 1983 thinned plantation during 1984 (Figure III.5) was similar to that observed in the experimental plots in the BURD plantation during 1983 and overlapped with the apparent emigration observed in those plots in 1984 (Figure III.6). No *P. fasciatus* were caught in the June 1984 treatment, but immigration into the October 1983 thinned plantation was substantial (Figure III.5).

*S. carinatus* exhibited a broad period of activity which tended to peak during late May or June and extended through August (Figure III.7). In 1983, two peaks were observed, one at 2 June 1983 and another at 28 July 1983. There was little difference between the number of *S. carinatus* caught in the unthinned, control plots and the unthinned, check plots which were isolated from the control plots (Figure III.8). In 1984, only a single pronounced peak appeared, which was intermediate to the two peaks observed in 1983 (Figure III.9).

In 1984, unthinned plots within the blocks showed elevated activity of *S. carinatus* relative to unthinned
plots isolated from the blocks (Figure III.10). Apparently, adults emigrating from thinned plots were responsible for this increase in capture in the adjacent unthinned plots.

Activity of *S. carinatus* in the October 1983 thinned plantation during 1984 (Figure III.11) exhibited a single broad peak and is generally similar to the activity observed on the experimental plots during 1984 (Figure III.9). Fewer *S. carinatus* were caught in pitfall traps in the June 1984 thinned plantation than the October 1983 treatment (Figure III.11). This may be due, in part, to plot location and sources of dispersing adults, rather than simply to time of thinning, since dispersal is limited because adults are incapable of flight.

Results of the excavations of cut trees are presented in Table III.5. Significantly more egg galleries and individuals of *H. nigrinus* were observed in the September and January treatments than in the May treatment. Subsequent emergence of *H. nigrinus* in 1984 exhibited the same trend (Table III.5). Significantly more larvae of *P. fasciatus* were recovered from the January and May treatments than from the September treatment. Significantly more larvae of *S. carinatus* were recovered from the September and January treatments than from the May treatment. There was no evidence of insect damage on trees sampled in the unthinned plots.
DISCUSSION

A growing body of knowledge is linking insects and forest disturbance with the spread and proliferation of *V. wageneri* (Goheen and Cobb 1978, Harrington *et al.* 1983, Witcosky and Hansen 1985, Chapter II). Root bark beetles in the genus *Hylastes* and the root weevils, *Steremnius carinatus* and *Pissodes fasciatus*, are vectors of *V. wageneri* in coniferous ecosystems. In Douglas-fir, these insects are associated with diseased trees (Witcosky 1981, Witcosky and Hansen 1985), carry inoculum in the field (Witcosky and Hansen 1985, Chapter II), wound and/or oviposit in susceptible hosts under conditions suitable for transmission of the pathogen (Chapter II), and transmit the pathogen to susceptible hosts under laboratory conditions and in the field (Chapter II).

In the present study, I have demonstrated that stand density management through precommercial thinning results in elevated activity of vectors. I have demonstrated that cut trees are attractive to these root colonizing vectors. Such hosts were susceptible to infection and colonization by *V. wageneri* for at least seven months following thinning (Chapter II). In addition, crop trees were wounded throughout the roots and root collar region by *H. nigrinus* following precommercial thinning (Chapter II). Some of these wounds penetrated to the xylem (Witcosky,
personal observation) and were, therefore, suitable infection courts (Hessburg 1984). I conclude that, in areas where black-stain root disease is present and widespread, some beetles will introduce inoculum into plantations following precommercial thinning. The activity of vectors in plantations undergoing self-thinning is undocumented. The likelihood that these plantations will develop new foci of *V. wageneri* as the result of insect activity cannot be determined at this time.

I have demonstrated that time of precommercial thinning can be manipulated to reduce immigration of *H. nigrinus* and *P. fasciatus* into disturbed 2-ha plots within plantations. The capture of these two species was reduced when thinning occurred during or after the peak of flight activity. Fewer beetles were captured during the peak flight in those plots thinned in May (Table III.1). In addition, fewer attacks by *H. nigrinus* were observed on stumps of cut trees as well as on the roots and root collar of crop trees in the May treatment than in either the January or September treatments (Table III.5). These results pertain to manipulations within two plantations only. Area-wide response of vectors into plantations thinned during or shortly after peak flight remains to be documented.

Trees attractive to vectors as the result of thinning also are susceptible to infection and colonization of
roots by \textit{V. wageneri}. \textit{V. wageneri} may become established in a plantation via thinned hosts which subsequently transmit the pathogen to an adjacent crop tree through the soil spread mechanism (Chapter II). However, time of thinning can be manipulated to reduce the susceptibility of the root system of cut, 12-year-old Douglas-fir to colonization by \textit{V. wageneri}. As the time between thinning and flight increased, the susceptibility of roots to colonization decreased (Chapter II).

These results suggest that, in high-risk areas, precommercial thinning should be avoided or initiated following peak beetle flight, during the months of June and July. Plantations thinned at this time gain at least nine months of protection from colonization by \textit{H. nigrinus} and \textit{P. fasciatus} and, perhaps, a somewhat reduced level of activity of \textit{S. carinatus} (Figures III.3, III.5, III.11, Chapter II). During this period of time, the host material provided by thinning degrades, becoming less susceptible to colonization by \textit{V. wageneri} and, perhaps, less attractive to host-seeking vectors during the following flight season. Immigration of vectors into plantations during the flight season following a June or July thinning is undocumented.

Flight activity patterns of \textit{H. nigrinus} (Daterman, Rudinsky, and Nagel 1965) and \textit{Hylastes} spp. (apparently \textit{H. macer} LeC., \textit{H. nigrinus}, and \textit{H. minutus} Blkm.) (Gara and
Vité 1962) are qualitatively similar to the flight activity observed for H. nigrinus in this study. Both species exhibit peak flight early in the season. Management recommendations derived from this study may be effective in other areas, but should only be applied with a thorough knowledge of the flight of the principal vector, H. nigrinus.
Table III.1. Mean number (and standard error) of *Hylastes nigrinus* and *Pissodes fasciatus* caught per trap on sticky traps and *Sterenmus carinatus* caught per trap in pitfall traps in precommercially thinned and unthinned 2-ha plots in two, 12-year-old plantations of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1983 and 1984.

<table>
<thead>
<tr>
<th>Species</th>
<th>Unthinned Control</th>
<th>Sept. '82 Thinning</th>
<th>Jan. '83 Thinning</th>
<th>May '83 Thinning</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. nigrinus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1983</td>
<td>0.04&lt;sup&gt;a&lt;/sup&gt; (0.1)</td>
<td>3.3&lt;sup&gt;c&lt;/sup&gt; (7.2)</td>
<td>5.4&lt;sup&gt;c&lt;/sup&gt; (14.4)</td>
<td>1.1&lt;sup&gt;b&lt;/sup&gt; (2.6)</td>
</tr>
<tr>
<td>1984</td>
<td>0.1 (0.2)</td>
<td>2.0 (2.3)</td>
<td>1.0 (1.0)</td>
<td>1.3 (1.4)</td>
</tr>
<tr>
<td><em>P. fasciatus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1983</td>
<td>0&lt;sup&gt;a&lt;/sup&gt; (0)</td>
<td>0.24&lt;sup&gt;c&lt;/sup&gt; (0.29)</td>
<td>0.24&lt;sup&gt;c&lt;/sup&gt; (0.37)</td>
<td>0.07&lt;sup&gt;b&lt;/sup&gt; (0.10)</td>
</tr>
<tr>
<td>1984</td>
<td>0 (0)</td>
<td>0.1 (0.18)</td>
<td>0 (0)</td>
<td>0.11 (0.2)</td>
</tr>
<tr>
<td><em>S. carinatus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1983</td>
<td>0.16&lt;sup&gt;a&lt;/sup&gt; (0.13)</td>
<td>0.51&lt;sup&gt;b&lt;/sup&gt; (0.31)</td>
<td>0.53&lt;sup&gt;b&lt;/sup&gt; (0.36)</td>
<td>0.57&lt;sup&gt;b&lt;/sup&gt; (0.48)</td>
</tr>
<tr>
<td>1984</td>
<td>0.23 (0.17)</td>
<td>0.35 (0.20)</td>
<td>0.49 (0.28)</td>
<td>0.68 (0.49)</td>
</tr>
</tbody>
</table>

<sup>1/</sup> Different superscripts within rows indicate significantly different means at P=0.05. Wilcoxon signed-rank test (one-sided) for all paired comparisons. n=8 plots per treatment in 1983; n=4 plots per treatment in 1984.
Table III.2. Mean number (and standard error) of *Hylastes nigrinus* caught per trap on sticky traps in precommercially thinned and unthinned 2-ha plots in two, 12-year-old plantations of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1983.

<table>
<thead>
<tr>
<th>Julian Date</th>
<th>Unthinned Control</th>
<th>Sept. '82 Thinning</th>
<th>Jan. '83 Thinning</th>
<th>May '83 Thinning</th>
</tr>
</thead>
<tbody>
<tr>
<td>111-83</td>
<td>$0^a$ (0)</td>
<td>$2.3^b$ (1.3)</td>
<td>$3.7^b$ (3.8)</td>
<td>$0.3^a$ (0.3)</td>
</tr>
<tr>
<td>125-83</td>
<td>$0^a$ (0)</td>
<td>$0.5^b$ (0.5)</td>
<td>$0.4^a$ (0.7)</td>
<td>$0^a$ (0)</td>
</tr>
<tr>
<td>139-83</td>
<td>$0.06^a$ (0.2)</td>
<td>$4.4^b$ (5.3)</td>
<td>$5.3^b$ (5.9)</td>
<td>$0.06^a$ (0.2)</td>
</tr>
<tr>
<td>153-83</td>
<td>$0.4^a$ (0.07)</td>
<td>$23.5^c$ (12.4)</td>
<td>$48.5^c$ (54.0)</td>
<td>$8^b$ (9.7)</td>
</tr>
<tr>
<td>167-83</td>
<td>$0^a$ (0)</td>
<td>$1.1^b$ (0.8)</td>
<td>$0.4^a$ (0.4)</td>
<td>$0.8^a$ (1.5)</td>
</tr>
<tr>
<td>181-83</td>
<td>$0^a$ (0)</td>
<td>$0.3^a$ (0.3)</td>
<td>$0.3^a$ (0.5)</td>
<td>$0.6^b$ (0.8)</td>
</tr>
<tr>
<td>195-83</td>
<td>$0^a$ (0)</td>
<td>$0.8^b$ (0.5)</td>
<td>$0.9^b$ (0.8)</td>
<td>$0.4^a$ (0.9)</td>
</tr>
<tr>
<td>209-83</td>
<td>$0^a$ (0)</td>
<td>$0.1^a$ (0.2)</td>
<td>$0.06^a$ (0.2)</td>
<td>$0.06^a$ (0.2)</td>
</tr>
<tr>
<td>223-83</td>
<td>$0^a$ (0)</td>
<td>$0.2^a$ (0.4)</td>
<td>$0.06^a$ (0.2)</td>
<td>$0.06^a$ (0.2)</td>
</tr>
<tr>
<td>237-83</td>
<td>$0^a$ (0)</td>
<td>$0^a$ (0)</td>
<td>$0^a$ (0)</td>
<td>$0.1^a$ (0.4)</td>
</tr>
<tr>
<td>251-83</td>
<td>$0^a$ (0)</td>
<td>$0^a$ (0)</td>
<td>$0^a$ (0)</td>
<td>$0^a$ (0)</td>
</tr>
<tr>
<td>265-83</td>
<td>$0^a$ (0)</td>
<td>$0^a$ (0)</td>
<td>$0^a$ (0)</td>
<td>$0^a$ (0)</td>
</tr>
</tbody>
</table>

\[^1/\] Wilcoxon signed-rank test (one-sided) for all paired comparisons. P=0.05. n=8 plots per treatment.
Table III.3. Mean number (and standard error) of *Pissodes fasciatus* caught per trap on sticky traps in precommercially thinned and unthinned 2-ha plots in two, 12-year-old plantations of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1983.

<table>
<thead>
<tr>
<th>Julian Date</th>
<th>Unthinned</th>
<th>Sept. '82</th>
<th>Jan. '83</th>
<th>May '83</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Thinning</td>
<td>Thinning</td>
<td>Thinning</td>
</tr>
<tr>
<td>111-83</td>
<td>0 (0)</td>
<td>0.5 (0.8)</td>
<td>0.4 (0.5)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>125-83</td>
<td>0 (0)</td>
<td>0.1 (0.2)</td>
<td>0.06 (0.2)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>139-83</td>
<td>0 (0)</td>
<td>0.5 (0.7)</td>
<td>0.6 (0.9)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>153-83</td>
<td>0 (0)</td>
<td>0.9 (1.0)</td>
<td>1.1 (1.4)</td>
<td>0.3 (0.4)</td>
</tr>
<tr>
<td>167-83</td>
<td>0 (0)</td>
<td>0.06 (0.2)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>181-83</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0.1 (0.2)</td>
</tr>
<tr>
<td>195-83</td>
<td>0 (0)</td>
<td>0.1 (0.2)</td>
<td>0 (0)</td>
<td>0.06 (0.2)</td>
</tr>
<tr>
<td>209-83</td>
<td>0 (0)</td>
<td>0.3 (0.4)</td>
<td>0 (0)</td>
<td>0.1 (0.2)</td>
</tr>
<tr>
<td>223-83</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0.1 (0.2)</td>
<td>0.06 (0.2)</td>
</tr>
<tr>
<td>237-83</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0.06 (0.2)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>251-83</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>265-83</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
</tbody>
</table>

1/ Wilcoxon signed-rank test (one-sided) for all paired comparisons. P=0.05. n=8 plots per treatment.
Table 11.4. Mean number (and standard error) of *Sternatius carinatus* caught per trap in pitfall traps in precommercially thinned and unthinned 2-ha plots in two, 12-year-old plantations of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1983.

<table>
<thead>
<tr>
<th>Julian Date</th>
<th>Unthinned Control</th>
<th>Sept. '82 Thinning</th>
<th>Jan. '83 Thinning</th>
<th>May '83 Thinning</th>
</tr>
</thead>
<tbody>
<tr>
<td>097-83</td>
<td>0.06a (0.05)</td>
<td>0.16bc (0.10)</td>
<td>0.23c (0.21)</td>
<td>0.11ab (0.11)</td>
</tr>
<tr>
<td>111-83</td>
<td>0.26a (0.18)</td>
<td>0.31a (0.24)</td>
<td>0.44a (0.33)</td>
<td>0.39a (0.26)</td>
</tr>
<tr>
<td>125-83</td>
<td>0.13a (0.10)</td>
<td>0.31bc (0.24)</td>
<td>0.48c (0.50)</td>
<td>0.26b (0.16)</td>
</tr>
<tr>
<td>139-83</td>
<td>0.21a (0.17)</td>
<td>0.26b (0.32)</td>
<td>0.58b (0.35)</td>
<td>0.32a (0.26)</td>
</tr>
<tr>
<td>153-83</td>
<td>0.55a (0.26)</td>
<td>1.35b (0.72)</td>
<td>1.58bc (0.48)</td>
<td>1.94c (0.96)</td>
</tr>
<tr>
<td>167-83</td>
<td>0.10a (0.09)</td>
<td>0.43b (0.34)</td>
<td>0.53b (0.47)</td>
<td>0.91c (0.46)</td>
</tr>
<tr>
<td>181-83</td>
<td>0.23 (0.10)</td>
<td>0.68 (0.42)</td>
<td>0.40 (0.65)</td>
<td>0.65 (0.58)</td>
</tr>
<tr>
<td>195-83</td>
<td>0.10 (0.13)</td>
<td>0.68 (0.28)</td>
<td>0.60 (0.25)</td>
<td>0.75 (0.27)</td>
</tr>
<tr>
<td>209-83</td>
<td>0.03 (0.03)</td>
<td>0.75 (0.25)</td>
<td>0.48 (0.13)</td>
<td>1.05 (0.44)</td>
</tr>
<tr>
<td>223-83</td>
<td>0.08 (0.15)</td>
<td>0.95 (0.58)</td>
<td>0.43 (0.05)</td>
<td>1.03 (0.40)</td>
</tr>
<tr>
<td>237-83</td>
<td>0.13a (0.13)</td>
<td>0.74c (0.56)</td>
<td>0.34b (0.29)</td>
<td>0.70bc (0.57)</td>
</tr>
<tr>
<td>251-83</td>
<td>0.15a (0.13)</td>
<td>0.58b (0.24)</td>
<td>0.40b (0.31)</td>
<td>0.35b (0.18)</td>
</tr>
<tr>
<td>265-83</td>
<td>0.10a (0.14)</td>
<td>0.69b (0.28)</td>
<td>0.55b (0.35)</td>
<td>0.46b (0.33)</td>
</tr>
<tr>
<td>279-83</td>
<td>0.13a (0.10)</td>
<td>0.50b (0.30)</td>
<td>0.45b (0.24)</td>
<td>0.51b (0.41)</td>
</tr>
<tr>
<td>293-83</td>
<td>0.10a (0.15)</td>
<td>0.35b (0.21)</td>
<td>0.14a (0.15)</td>
<td>0.35b (0.69)</td>
</tr>
<tr>
<td>307-83</td>
<td>0.15a (0.08)</td>
<td>0.43b (0.18)</td>
<td>0.40b (0.27)</td>
<td>0.39ab (0.35)</td>
</tr>
</tbody>
</table>

1/ Wilcoxon signed-rank test (one-sided) for all paired comparisons. P<0.05. n=8 plots per treatment.
2/ n=4 plots per treatment.
Table III.5. Mean number (and standard error) of *Hylastes nigrinus*, *Pissodes fasciatus*, and *Steremnius carinatus* and egg galleries and emergence of *H. nigrinus* per tree in precommercially thinned and unthinned 2-ha plots in a 12-year-old plantation of Douglas-fir in Douglas County, Oregon, in 1983.

<table>
<thead>
<tr>
<th>Species</th>
<th>Unthinned Control 2/</th>
<th>Sept. '82 Thinning</th>
<th>Jan. '83 Thinning</th>
<th>May '83 Thinning</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. nigrinus</em></td>
<td>0a (0)</td>
<td>166.1d (155.7)</td>
<td>64.1c (88.0)</td>
<td>34.3b (69.0)</td>
</tr>
<tr>
<td>Egg galleries</td>
<td>0a (0)</td>
<td>12.9c (9.5)</td>
<td>7.8c (5.4)</td>
<td>4.1b (5.3)</td>
</tr>
<tr>
<td>Emergence</td>
<td>- (-)</td>
<td>9.9b (17.1)</td>
<td>8.6b (13.0)</td>
<td>1.2a (2.1)</td>
</tr>
<tr>
<td><em>P. fasciatus</em></td>
<td>0a (0)</td>
<td>3.4b (5.8)</td>
<td>15.6c (20.8)</td>
<td>11.9c (19.2)</td>
</tr>
<tr>
<td><em>S. carinatus</em></td>
<td>0a (0)</td>
<td>17.1c (21.1)</td>
<td>10.3c (15.2)</td>
<td>3.6b (10.9)</td>
</tr>
</tbody>
</table>

1/ Different superscripts within rows indicate significantly different means at P=0.05. Wilcoxon signed-rank test (one-sided) for all paired comparisons. n=16 trees per treatment.

2/ Nondestructively sampled.
Figure III.1. Mean number of Hylastes nigrinus caught per trap on sticky traps in precommercially thinned and unthinned 2-ha plots in two, 12-year-old plantations of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1983. Arrow indicates time of May thinning.
Figure III.2. Mean number of Hylastes nigrinus caught per trap on sticky traps in precommercially thinned and unthinned 2-ha plots in a 13-year-old plantation of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1984.
Figure III.3. Total number of Hylastes nigrinus caught in twelve m$^2$ emergence cages following precommercial thinning of a 12-year-old plantation of Douglas-fir in 1983 and mean number of H. nigrinus caught per trap on sticky traps in plantations following thinning in October 1983 and June 1984 in Douglas County, Oregon, at biweekly intervals during 1984. Arrow indicates time of June thinning.
Figure III.4. Mean number of *Pissodes fasciatus* caught per trap on sticky traps in precommercially thinned and unthinned 2-ha plots in two, 12-year-old plantations of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1983. Arrow indicates time of May thinning.
Figure III.5. Mean number of *Pissodes fasciatus* caught per trap on sticky traps following precommercial thinning of 12-year-old plantations of Douglas-fir during October 1983 and June 1984 in Douglas County, Oregon, at biweekly intervals during 1984. Arrow indicates time of June thinning.
Figure III.6. Mean number of *Pissodes fasciatus* caught per trap on sticky traps in precommercially thinned and unthinned 2-ha plots in a 13-year-old plantation of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1984.
Figure III.7. Mean number of *Steremninus carinatus* caught per trap in pitfall traps in precommercially thinned and unthinned 2-ha plots in two, 12-year-old plantations of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1983. Arrow indicates time of May thinning.
Figure 11.8. Mean number of *Stenemius carinatus* caught per trap in pitfall traps in unthinned 2-ha plots interspersed among 2-ha precommercially thinned plots and at a distance from thinned plots in Douglas County, Oregon, at biweekly intervals during 1983.
Figure III.9. Mean number of *Steremnius carinatus* caught per trap in pitfall traps in precommercially thinned and unthinned 2-ha plots in a 13-year-old plantation of Douglas-fir in Douglas County, Oregon, at biweekly intervals during 1984.
Figure III.10. Mean number of Steremnius carinatus caught per trap in pitfall traps in unthinned 2-ha plots interspersed among 2-ha precommercially thinned plots and at a distance from thinned plots in Douglas County, Oregon, at biweekly intervals during 1984.
Figure III.11. Mean number of *Stereumis carinatus* caught per trap in pitfall traps following precommercial thinning of 12-year-old plantations of Douglas-fir during October 1983 and June 1984 in Douglas County, Oregon, at biweekly intervals during 1984. Arrow indicates time of June thinning.


DEMONSTRATION OF HOST ATTRACTANTS FOR HYLASTES NIGRINUS AND STEREMNIUS CARINATUS

CHAPTER IV

ABSTRACT

The response of Hylastes nigrinus and Steremnius carinatus to alpha-pinene, ethanol, and sections of roots infected with black-stain root disease of Douglas-fir, caused by Verticicladiella wageneri, or uninfected was examined. Significantly more H. nigrinus and S. carinatus were caught in pitfall traps baited with alpha-pinene and ethanol alone and in solution than in unbaited traps, indicating that these two compounds are host attractants for these two species of insects. Root sections from diseased hosts were more attractive to H. nigrinus and S. carinatus than uninfected root sections. Injury and plant stress of hosts due to infection by V. wageneri may lead to the production and release of host attractants which are detected by vectors during the host selection process.
INTRODUCTION


Diseased trees are invaded by root-colonizing insects which are thought to serve as vectors of the pathogen (Smith and Graham 1975, Landis and Helburg 1976, Goheen and Cobb 1978, Witcosky 1981, Witcosky and Hansen 1985).

Recently, in the Douglas-fir (*Pseudotsuga menziesii* (Mirb.)Franco) ecosystem, I have demonstrated that the root bark beetle, *Hylastes nigrinus* (Mann.), and the root weevils, *Pissodes fasciatus* LeC. and *S. carinatus* (Boh.), are vectors of *V. wageneri* (Witcosky 1981, Witcosky and Hansen 1985, Chapter II). In Douglas-fir, the colonization of infected root systems is a sequential process; roots are infested by insects as they succumb to infection by *V. wageneri* (Witcosky 1981, Witcosky and Hansen 1985). Spore-bearing structures of *V. wageneri* are known to be produced in insect galleries and pupal cells on ponderosa pine (*Pinus ponderosa* Laws.) (Goheen and Cobb
1978) and Douglas-fir (Witcosky 1981). In Douglas-fir, emerging brood of *H. nigrinus*, *P. fasciatus*, and *S. carinatus* have been shown to carry inoculum of *V. wageneri* (Witcosky and Hansen 1985, Chapter II). Adults disperse, seeking feeding sites or host material suitable for oviposition and readily immigrate into Douglas-fir stands disturbed by windthrow (Zethner-Møller and Rudinsky 1967, Witcosky, unpublished data) or plantations which have been precommercially thinned (Chapter III).

The root systems of precommercially thinned trees, which are susceptible to infection by *V. wageneri* for at least seven months (Chapter II), are readily colonized by *H. nigrinus*, *P. fasciatus*, and *S. carinatus* (Chapter II). Also, the crop trees in these thinned plantations sustain wounds to the roots and root collar by *H. nigrinus* for 1-2 years following thinning (Chapter II). Earlier, Zethner-Møller and Rudinsky (1967) described the wounds made by *H. nigrinus* when caged on Douglas-fir seedlings. They observed similar wounds—which they attributed to *H. nigrinus* and called maturation feeding wounds—on the roots of trees within and adjacent to patches of windthrown Douglas-fir. Apparently, stand disturbance, tree stress, or tree injury is necessary for feeding and oviposition on susceptible hosts by the vectors of black-stain root disease. Wounding of susceptible hosts appears
to be required for the initiation of new foci of V.
wageneri.

Initiation of some types of black-stain root disease
foci can be explained by stand disturbance leading to
immigration of vectors which introduce V. wageneri into
the stand (Harrington, Reinhart, Thornburgh, and Cobb
1983, Chapters II, III). In other cases, especially those
associated with roadsides (Hansen 1978) and wet sites
(Goheen 1976, Hicks, Cobb, and Gersper 1981, Wilks,
Gersper, and Cobb 1983, Witcosky, personal observation),
the factors associated with attraction of vectors and the
initiation of new foci remain obscure. Because these new
foci arise in a predictable spatial pattern, processes and
mechanisms governing host selection by these vectors are
important to understanding the epidemiology of black-stain
root disease.

Host selection in the Scolytidae can be either a
random process or a directed process (Cade, Hrutfiord, and
Gara 1970, Coulson et al. 1983, Gara, Geiszler and Littke
1984, Hynum and Berryman 1980, Moech 1970, 1971, Moeck,
and Rudinsky and Zethner-Møller (1967) demonstrated that
either host material or a solution of alpha-pinene, a
major terpene constituent of Douglas-fir oleoresin
(Guenther 1952, Snajberk, Lee and Zavarin 1974, Snajberk
and Zavarin 1976, Von Rudloff 1972, Zavarin and Snajberk 1973), in ethanol is highly attractive to *H. nigrinus*. Condrashoff (1966) demonstrated that freshly cut disks of Douglas-fir were attractive to *S. carinatus*. Witcosky (1981) indicated that both insects could be captured readily in pitfall traps baited with 2% racemic alpha-pinene in 95% ethanol. These data support the contention that initially, host selection in these species is a directed response to volatile, host attractants, rather than the random process reported for some other bark beetles (Hynum and Berryman 1980, Moeck, Wood, and Lindahl 1981, Payne 1983, Wood 1982).

Because of the important role *H. nigrinus* and *S. carinatus* as vectors of *V. wageneri*, the host selection process of *H. nigrinus* and *S. carinatus* must be clarified to effectively manage this disease. In this chapter I examine the response of these species to alpha-pinene and ethanol alone and in solution, and to sections of roots infected with *V. wageneri* or uninfected. I will demonstrate that alpha-pinene and ethanol are host attractants for these two species of beetles and that volatiles emanating from diseased roots are more attractive to dispersing beetles than volatiles emanating from healthy roots.
MATERIALS AND METHODS

This study was conducted along the perimeter of expanding foci of *V. wageneri* in a 20-year-old plantation of Douglas-fir in the Coast Range mountains of Douglas County, Oregon. In 1983 and 1984, pitfall traps (16 cm diameter, collecting in undiluted antifreeze) were placed in groups of three. Each group of three was no closer than 15 m from another group and each trap within a group was no closer than 10 m from another trap. The three traps in each group were randomly allocated to three treatments: baited with a healthy root section, baited with a root section infected with *V. wageneri*, and unbaited (control). Each trap received the same treatment throughout the entire experiment to prevent confounding effects caused by the presence of residual odors from previous treatments. Diseased and healthy roots were matched for diameter and length. The traps were open for intervals of seven days. After a sample period, each trap was randomly reassigned to a trap location within each group and moved. After each sample period, the root sections were "freshened" by cutting ca. 1 cm from each end. This was repeated twice and then the root sections were replaced with new root sections. Only one root from any healthy or diseased tree was used so no replication of an individual tree occurred. Before discarding the used
root sections, the bark was removed to determine if, inadvertently, segments infested with insects had been placed in the traps. This was necessary to insure that results were not confounded by the production and release of pheromones or host-derived volatiles emanating from galleries and frass of root-infesting insects. Traps were sampled over 8 periods from May-July 1983 and 9 periods from May-July 1984.

In a separate plantation in 1984, four replicates of five pitfall traps, similar to those described above, were placed along transects parallel to edges of the plantation. Within each transect, traps were no less than 10 m apart; transects were no less than 15 m apart. The plantation had been precommercially thinned in October 1983 and sustained heavy colonization by H. nigrinus, P. fasciatus, and S. cariantus (Chapter III). Within a transect, each trap was randomly assigned to one of five treatments for the duration of the experiment in order to prevent confounding effects associated with residual odors from different treatments. Each trap within a transect was randomly reassigned to a trap location within the transect prior to each sample period to remove any but random effects of trap position on the capture of insects by a given treatment. The five treatments were 95% ethanol, dibutyl phthalate, 2% recemic alpha-pinene in dibutyl phthalate, or 2% racemic alpha-pinene in 95%
ethanol baits, and an unbaited control. Unlike ethanol (Rudinsky and Zethner-Møller 1967), dibutyl phthalate has been shown to be a useful, noninteractive diluent for studies on chemical communication in bark beetles (Rudinsky and Ryker 1980). An aluminum film canister containing a 1/4-dram glass vial with the particular bait was placed at the bottom of the pitfall trap, beside the collection dish. The collection dish was filled with undiluted antifreeze, the killing agent and preservative. The sample period was two days and fresh baits were added at the beginning of each period. Traps were sampled over 18 periods from April-June 1984.

Results were analyzed for treatment effects using the sign test for paired comparisons (Lehmann 1975). Treatment means were considered significantly different at P=0.05 level.
RESULTS

The numbers of *H. nigrinus* and *S. carinatus* caught in pitfall traps baited with healthy and diseased root sections are presented in Table IV.1. When the 1983 and 1984 data were combined, significantly more *H. nigrinus* were caught in traps baited with diseased roots than with healthy roots or unbaited. Too few beetles were caught in traps baited with healthy roots to confidently provide a meaningful statistical test against the unbaited traps (n=5). However, 17 *H. nigrinus* were caught in traps baited with healthy roots while only 4 *H. nigrinus* were caught in unbaited traps. In four of the five pairs of traps that caught *H. nigrinus* during 1983, those baited with healthy root sections caught more beetles than their paired, unbaited traps; the reverse was observed only once (P=0.19).

Significantly more *S. carinatus* were captured in traps baited with diseased roots than in traps baited with healthy roots or unbaited in 1983, 1984, and in the combined data. Also, significantly more *S. carinatus* were caught in traps baited with healthy roots than in unbaited traps in 1983 and in the combined years. However, no significant difference in the numbers of *S. carinatus* was noted in 1984 (P=0.08).
These results indicated that volatiles emanating from cut root sections infected with *V. wageneri* were more attractive to *H. nigrinus* and *S. cariantus* than were volatiles emanating from cut, healthy roots. Examination of these root sections prior to disposal confirmed that insects had not colonized them prior to or during their use in traps. Thus, no confounding effects were associated with the release of pheromones or attractants associated with boring of phloem by root insects. The results suggested that either infection leads to an increase in release of host attractants or that infection results in the production of a new compound or compounds by host, pathogen, or both, which enhance the attraction of *H. nigrinus* and *S. carinatus*.

I observed a pronounced response of *H. nigrinus* and *S. carinatus* to pitfall traps baited with ethanol, *alpha-pinene* in dibutyl phthalate, and *alpha-pinene* in ethanol (Table IV.2). Significantly more *H. nigrinus* and *S. carinatus* were caught in traps baited with 95% ethanol than in unbaited traps indicating that ethanol is a physiologically active attractant for these two species. Traps baited with 2% *alpha-pinene* in dibutyl phthalate also were more attractive than the unbaited controls. Because dibutyl phthalate and the control treatments were not significantly different, the increased capture of *H. nigrinus* and *S. carinatus* in traps baited with *alpha-*
pinene in dibutyl phthalate can be attributed to the addition of alpha-pinene. The capture rate in the ethanol-baited traps was significantly less than the capture rate in the traps baited with 2% alpha-pinene in dibutyl phthalate for H. nigrinus but was not significantly different for S. carinatus. Significantly more beetles were caught in traps baited with alpha-pinene in ethanol than in traps baited with either ethanol alone or alpha-pinene in dibutyl phthalate (Table IV.2). The two solvents may differ in their influence on the volatilization of alpha-pinene and therefore cannot be compared.
Factors underlying the initiation of new foci of *V. wageneri* remain one of the poorly understood aspects of the epidemiology of black-stain root disease of conifers. I have demonstrated that *H. nigrinus*, *P. fasciatus*, and *S. carinatus* are vectors of *V. wageneri* in the Douglas-fir ecosystem (Witcosky 1981, Witcosky and Hansen 1985, Chapter II). Vectors immigrate into stands following disturbance, such as windthrow, harvest, and precommercial thinning (Condrashoff 1968, Zethner-Møller and Rudinsky 1967, Chapter III) and wound or oviposit in susceptible hosts under conditions suitable for the transmission of *V. wageneri* (Chapter II).

In support of Rudinsky (1966) and Rudinsky and Zethner-Møller (1967), I have provided evidence that host selection in *H. nigrinus* and *S. carinatus* is a process governed, in part, by an olfactory response to host attractants. *Alpha*-pinene, a dominant terpene component of Douglas-fir oleoresin (Guenther, 1952, Snajberk, Lee and Zavarin 1974, Snajberk and Zavarin 1976, von Rudloff 1972, Zavarin and Snajberk 1973) is an attractant for *H. nigrinus* and *S. carianteus* when deployed in a diluent (dibutyl phthalate rather than ethanol) which does not significantly alter the behavior of these insects (Table IV.1). Forest management practices which wound trees and
hence cause a release of alpha-pinene, such as 
precommercial or commercial thinning, harvest, pruning of 
roadside trees, and girdling of trees in seed orchards, 
may lead to the immigration of vectors and the 
introduction and establishment of black-stain root disease 
in stands and plantations located in areas where the 
pathogen and its vectors are present.

Douglas-fir infected with _V. wageneri_ often develop 
resinous lesions at root branches and, occasionally, on 
the lower stem (Goheen and Hansen 1978, Hessburg 1984, 
insects orient toward volatiles emanating from these 
lesions during the host selection process. This study 
indicates that cut sections from infected roots were more 
attractive to _H. nigrinus_ and _S. carinatus_ than were 
healthy root sections. In addition to potential visual 
cues provided dispersing beetles by decline and chlorosis 
of trees in disease foci, I suggest that olfactory cues 
emanating from resinous lesions on diseased hosts 
contribute to the host selection process. Such cues would 
facilitate aggregation of _H. nigrinus_, and perhaps serve 
to retain some of the parent adults or new brood produced 
from diseased trees within established foci. Such 
aggregation would lead to injury and disease transmission 
to adjacent, healthy trees (Chapter II). Oviposition by 
insects causes additional wounds which would increase the
release of volatiles from diseased trees. Production of pheromones, if any exist, would contribute to aggregation of vectors in established foci.

Many foci arise under circumstances which remain obscure, e.g., along skid roads, in low or wet sites, and in developing drainages. Wert and Thomas (1981) indicated that Douglas-fir regenerated on the compacted soil of skid roads are less competitive and of smaller diameter than those adjacent to skid roads or on undisturbed soil. Skid roads often alter drainage patterns of plantations and may develop into drainage conduits during periods of heavy rain and surface runoff (Witcosky, personal observation). Under these conditions, hosts are probably exposed to environmental stress due to episodic or periodic anaerobiosis, of which Douglas-fir are extremely intolerant (Minore 1968, Zaerr 1983). Ethanol and ethylene are common metabolites produced by roots and soils under anaerobic conditions (Ayers 1984, Bertani, Brambilla, and Menegus 1980, Crawford 1967, Crawford, and Baines 1977, Davies 1980, Drew and Lynch 1980, Feldman 1984, Fulton and Erickson 1964, Kenefick, 1962, Kozlowski 1984, Kozlowski and Pallardy 1984, Ponnamperuma 1984, Reid and Bradford 1984, Smith and ap Rees 1979, Yang and Hoffman 1984). I have demonstrated that ethanol alone or mixed with alpha-pinene attracts H. nigrinus and S. carinatus. I suggest that stress-induced metabolites
like ethanol, produced and released to the environment during periods of anaerobiosis, act as cues for vectors during dispersal and host selection. Accordingly, vectors would tend to visit and wound trees growing on skid roads and on low, wet sites at a greater frequency relative to trees growing on better sites, thereby increasing the occurrence of new foci of *V. wageneri* on these poor sites.
Table IV.1. Mean number (and standard deviation) of *Hylastes nigrinus* and *Stereumnius carinatus* caught per trap in unbaited pitfall traps and pitfall traps baited with healthy Douglas-fir roots and Douglas-fir roots infected with *Verticicladiella wageneri* in a 20-year-old Douglas-fir plantation sustaining mortality due to black-stain root disease, Douglas County, Oregon, at weekly intervals during 1983 and 1984.

<table>
<thead>
<tr>
<th>Species</th>
<th>1983 (n=8)</th>
<th></th>
<th>1984 (n=9)</th>
<th></th>
<th>1983 + 1984</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Healthy Root</td>
<td>Infected Root</td>
<td>Unbaited Control</td>
<td>Healthy Root</td>
<td>Infected Root</td>
<td>Unbaited Control</td>
</tr>
<tr>
<td><em>H. nigrinus</em></td>
<td>0.43&lt;sup&gt;ab&lt;/sup&gt; (1.41)</td>
<td>0.65&lt;sup&gt;b&lt;/sup&gt; (1.76)</td>
<td>0.10&lt;sup&gt;a&lt;/sup&gt; (0.50)</td>
<td>0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.11&lt;sup&gt;b&lt;/sup&gt; (0.32)</td>
<td>0&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>S. carinatus</em></td>
<td>3.75&lt;sup&gt;b&lt;/sup&gt; (4.47)</td>
<td>4.73&lt;sup&gt;c&lt;/sup&gt; (3.92)</td>
<td>0.83&lt;sup&gt;a&lt;/sup&gt; (1.48)</td>
<td>0.91&lt;sup&gt;a&lt;/sup&gt; (1.33)</td>
<td>4.16&lt;sup&gt;b&lt;/sup&gt; (6.12)</td>
<td>0.53&lt;sup&gt;a&lt;/sup&gt; (0.87)</td>
</tr>
</tbody>
</table>

<sup>1/</sup> Different superscripts within rows and within individual subheadings (years) indicate significantly different means at P=0.05. Sign test (one-sided) for all paired comparisons.
Table IV.2. Mean number (and standard deviation) of *Hylastes nigrinus* and *Steremnius carinatus* caught per trap in unbaited and baited pitfall traps in a precommercially thinned plantation of Douglas-fir in Douglas County, Oregon, at two-day intervals during 1984.

Different superscripts within rows indicate significantly different means at $P=0.05$.
Sign test (one-sided) for all paired comparisons.

<table>
<thead>
<tr>
<th>Species</th>
<th>Unbaited Control</th>
<th>Dibutyl Phthalate</th>
<th>95% Ethanol</th>
<th>Alpha-pinene + Dibutyl Phthalate</th>
<th>Alpha-pinene + 95% Ethanol</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. nigrinus</em></td>
<td>0.29$^a$ (0.75)</td>
<td>0.38$^a$ (1.04)</td>
<td>0.76$^b$ (1.28)</td>
<td>1.72$^c$ (2.75)</td>
<td>4.40$^d$ (7.69)</td>
</tr>
<tr>
<td><em>S. carinatus</em></td>
<td>0.21$^a$ (0.50)</td>
<td>0.18$^a$ (0.51)</td>
<td>0.47$^b$ (0.75)</td>
<td>0.46$^b$ (0.63)</td>
<td>1.19$^c$ (1.22)</td>
</tr>
</tbody>
</table>


Pest management opportunities for control of black-stain root disease are developed for plantations of coastal Douglas-fir in western Oregon within the framework of a crop production system. Opportunities for management include harvest and plantation establishment, annual survey and inventory, precommercial density management, and commercial management. Management tactics are centered around manipulation of stand spatial structure and composition to minimize the occurrence of susceptible Douglas-fir on high-risk microsites, and manipulation of time of disturbance to minimize immigration of vectors, susceptibility of cut hosts, and incidence of wounding to crop trees. Silvicultural manipulation of community structure offers the greatest opportunity for management of black-stain root disease.
INTRODUCTION

Black-stain root disease of conifers, caused by *Verticicladiella wageneri* Kendrick (sexual stage: *Ceratocystis wageneri* Goheen and Cobb) is pathogenic on pines (*Pinus* spp.) (Wagener and Mielke 1961) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.)Franco) (Cobb and Platt 1967). Recent research has demonstrated that insects, *Hylastes nigrinus* (Mann.), *Pissodes fasciatus* LeC., and *Steremnius carinatus* (Boh.), are vectors of *V. wageneri* and are responsible for the initiation of new foci of infection (Witcosky 1981, Witcosky and Hansen 1985, Chapter II). Once established, foci of *V. wageneri* spread by growth through the soil from diseased to healthy roots of hosts through naturally occurring wounds (infection courts) on fine roots (Goheen 1976, Goheen and Cobb 1978, Hessburg 1984, Hicks, Cobb, and Gersper 1980).

In plantations of Douglas-fir, some sites, such as ridgetops and roadsides (Goheen and Hansen 1978, Hansen 1978), appear to be at greater risk of developing new foci of *V. wageneri*, and certain intensive forestry practices, such as tractor logging (Goheen, Kanaskie, and Frankel 1983) and precommercial thinning (Harrington, Reinhart, Thornburgh, and Cobb 1983) have been associated with these high-risk sites. Certain harvest activities and management techniques of intensive forestry are intimately
linked to the epidemiology of black-stain root disease through its vectors (Chapter II, III, IV). This coupling leads to an increased risk of establishing black-stain root disease in newly regenerated plantations, increased risk of spreading the pathogen throughout a plantation, and an increased risk of spreading the pathogen to adjacent plantations.

Black-stain root disease is an emerging pest problem of Douglas-fir in the Coast Range of Oregon. Although most evidence suggests that the disease is aggravated by intensive management practices, black-stain root disease may be amenable to control and management by appropriately selected silvicultural and pest management alternatives (Chapter III). In this chapter, I develop a crop production system for a long-term crop, like Douglas-fir. Opportunities for pest management are linked with the crop production system at times when pests enter the crop during forest management. This crop production/pest management scheme is designed to weaken links between intensive forest practices and the epidemiology of black-stain root disease and its vectors in the coastal Douglas-fir ecosystem of Oregon.
THE DOUGLAS-FIR CROP PRODUCTION SYSTEM

The crop production system is presented in Figure V.1. The principal component is an inventory of plantations (holdings) which contains specific data on site quality, plantation age, logging history, community structure-species composition, stand variables such as density, basal area etc., an inventory of disease foci, and dummy variables that serve as flags for certain management practices or disease problems. The inventory is coupled to a growth model, such as DFSIM (Curtis, Clendenen, and Demars 1981), which simulates growth of holdings annually. The annual plantation update from such a simulator would be separated into three classes of data: (1) growing plantations which return to update the inventory of holdings; (2) plantations slated for precommercial density management; and (3) plantations slated for commercial thinning or harvest. The decision for precommercial or commercial management would be based on age, height, density, basal area, diameter, site quality, or some combination of these parameters.

Plantation survey and inventory are important components of forest management. In the crop production scheme, these stand survey data compare and calibrate model predictions for individual units based on their specific performance. Calibrated data update the
plantation inventory data. As presented, the crop production system would be suited for coupling with a Geographic Information System (GIA) and Map Overlay Statisical System (MOSS) which could contain digitized maps of all plantations with networks of roads, skid roads, landings, log hauls, etc.

Coupled to the basic crop model are four pest management schemes, the unit harvest-establishment pest management scheme, the annual pest management scheme, the precommercial pest management scheme, and the commercial pest management scheme. Each pest management scheme is coupled to the crop production model at a time when silvicultural and management activities are being executed. The incorporation of a harvest-establishment scheme indicates that management of black-stain root disease should begin with harvest and plantation establishment practices. The annual scheme exploits the annual activities of inventory and survey to update the inventory of holdings with regard to disease spread and proliferation of foci in and among plantations. Also, it provides for annual pest management activities, such as sanitation, which may be suitably linked with other activities, such as maintenance and upkeep of road networks. The precommercial scheme would develop specific, plantation by plantation guidelines and plantation maps for density regulation, based on the
distribution of black-stain root disease regionally, locally, and within plantations. The commercial scheme would provide the same information to the user on a plantation by plantation basis for stands scheduled for commercial thinning or would direct stands scheduled for final harvest to the harvest-establishment scheme. A regional/local black-stain root disease risk map overlay would provide input from risk-rating systems for each pest management scheme.

THE HARVEST-ESTABLISHMENT PEST MANAGEMENT SCHEME

The harvest-establishment pest management scheme is presented in Figure V.2. The harvest-establishment scheme would utilize information on stands to be harvested (old growth holdings, mature plantations) and their respective unit layout to locate roads, indicate harvest method, site preparation etc. These data would be evaluated against a regional/local risk map overlay. Plantations would be divided into those with little or no regional risk, which receive standard vegetation management, and those with decided risk of developing black-stain root disease. Plantations at risk are divided into two groups based on local site risk. Low-risk plantations to be cable-logged are routed to a modified vegetation management routine and assigned default modifications in species composition and
spatial structure (pattern of planting of species) along landings and log hauls where soil disturbance is severe. Low-risk plantations to be tractor-logged are directed to a modified vegetation management routine which would evaluate the risk of developing black-stain root disease given the harvest procedure and regional and local risk. The routine would assign management guidelines ranging from the standard vegetation management to some specialized procedure, e.g., interplanting resistant species along roads and landings to planting resistant species on disturbed, high-risk microsites. High-risk microsites are separated by logging method. Each group of plantations would receive modified vegetation management recommendations, such as planting resistant species on high-risk sites, interplanting resistant and susceptible species, or block planting of resistant and susceptible species. The modified vegetation plans and plantation layouts are used in planning the vegetation management—community structure, which would determine planting density, number of seedlings of each species, and overlay the spatial pattern of planting on the plantation layout. The map and planting guidelines would be provided to the user, and the initial plantation inventory, community structure, and spatial pattern would be added to the plantation inventory and the plantation layout inventory.
Major opportunities for pest management of black-stain root disease in the harvest-establishment phase of crop production center around amelioration of impact of harvest on drainage pattern and soil compaction, reduction of immigration of vectors into harvested areas, and manipulation of species composition and spatial structure (pattern of planting of species). Observation of black-stain root disease in plantations of Douglas-fir in southwestern Oregon suggest that some foci of \textit{V. wageneri} are being initiated at the time of harvest and replanting. Initiation of foci of black-stain root disease often may occur during harvest or result from factors associated with this period of activity. For example, road building injures roots of adjacent trees prior to or following felling. These root systems may be highly susceptible to infection by \textit{V. wageneri}, especially if harvest activities occur just prior to flight of the principal vector, \textit{H. nigrinus} (Chapter III). Seedlings of Douglas-fir planted directly above injured roots of harvested trees which have become infected with \textit{V. wageneri} have been observed to become infected, apparently, from these sources of inoculum (Witcosky, personal observation).

Recommendations to plant resistant species along edges of roads in high-risk plantations would reduce establishment of foci in the newly developing stand. Douglas-fir planted on the compacted soil of skid roads are less
likely to maintain dominance in a stand than those planted on undisturbed sites (Wert and Sanders 1981). These trees may be at greater risk to mortality due to competition, or due to poor site conditions, nutrient stress, or periodic anaerobiosis (Minore 1968, Zaerr 1983). Recommendations include utilization of resistant species that are known to be tolerant of microsite characteristics associated with the development of foci of *V. wageneri*, such as western redcedar or western hemlock (Minore 1968, Forristall and Gessel 1955). Mixed species plantings should be adopted, especially in high-risk plantations, to reduce the density of susceptible hosts, which should both reduce the spread of root disease (Burdon and Chilvers 1982) and provide more options for manipulation of stand structure in subsequent entries.

**THE ANNUAL PEST MANAGEMENT SCHEME**

The annual pest management scheme (Figure V.3) exploits activities of managers in plantation survey and inventory. Since black-stain root disease foci often occur on or adjacent to roadsides, the presence, abundance, and size of foci can be readily detected in a rapid survey of the plantation along roads and skid roads. Ideally, foci would be located on a sketch map and paced to greatest length and width. The number of dead and
symptomatic trees within these foci would be counted, and the density of susceptible and resistant species estimated. These survey and inventory data, along with plantation inventory and plantation layout inventory are used in the annual pest management scheme. The principal component of this scheme would be a focus persistence, expansion, and proliferation model which predicts the outcome of focus persistence, spread, and proliferation based on probability statements derived from empirical data on size and density of susceptible and resistant hosts, stand age, estimates of spread based on size of foci, and rates of proliferation for the region. The output would be loss, in terms of trees killed and in area out of production, analogous to the model developed by Bloomberg (1980a, 1980b) for Phellinus weirii. The estimates of loss would be subjected to a decision making process which would identify appropriate remedial treatments, if any exist, based on economic evaluations and projected losses if no action is taken. If survey and inventory are performed in stands between 4-8 years of age, plantations can be sanitized while trees are still small, perhaps by hand roguing. Replanting at this time with a resistant species will reduce the area lost to production over the rotation of the crop. However, in many cases, black-stain root disease is symptomatic of poor microsite conditions (compacted soil or excess
moisture) or where trees are injured by road maintenance, brushing equipment or casting of soil at the base of the tree. In such cases, management must begin at the time of plantation establishment. The plantation inventory would be updated and flagged with appropriate dummy variables to insure that, at the time of precommercial management, the plantation is identified as a stand at risk.

THE PRECOMMERCIAL AND COMMERCIAL PEST MANAGEMENT SCHEMES

The precommercial pest management scheme (Figure V.4) exploits the opportunity provided by density management to manipulate community structure and spatial structure of plantations within the framework of normal silvicultural practices. However, this advantage is realized only when diversity of species composition and abundance has been introduced into the plantation at the establishment phase or perhaps, introduced fortuitously by seeding from neighboring stands. Without diversity in species composition and abundance, management can be based only on a thin/no-thin option and, perhaps, on a felling/chemical thinning option. The no-thin option should be considered in plantations at high risk or in plantations with modest stocking, however there is no evidence to indicate that self-thinning is to be favored in these situations.
Inputs into the precommercial scheme would utilize the inventory data of plantations slated for precommercial management, any available plantation survey and monitoring data, the regional/local risk rating map, and the layout inventory for the precommercially managed plantations. Plantations located in areas free of black-stain root disease can be managed for the desired species by standard precommercial practices. Plantations at risk from surrounding stands, but without disease, may be managed for the desired species, especially if precommercial thinning results in the removal of resistant species which do not share insect species known to be vectors of V. wageneri. Management could favor the desired species within the plantation and the resistant species along roadsides and skid roads. In plantations containing disease foci, the resistant species should be favored in and adjacent to root disease foci and along roadsides.

Low-risk areas may be thinned at any time during the season as scheduling permits, with careful regard given to community structure and risk of immigration of vectors and wounding of crop trees. In areas of high risk, however, thinning should be timed according to the vector risk, based on response of vectors and susceptibility of thinned hosts to infection (Chapter II, III). Thinning should follow flight of H. nigrinus--late June through July in southwestern Oregon. Ideally, slash should be dry and red
by fall. This minimizes immigration of the principal vector into plantations at the most susceptible period for thinned hosts and provides at least nine months of protection from colonization by *H. nigrinus*. During this period, the root systems of thinned trees should decline and be poor substrate for colonization by *V. wageneri* (Chapter II). Immigration of *H. nigrinus* into such a plantation and injury sustained by crop trees the following year is undocumented.

The presence of established foci of black-stain root disease on, or adjacent to, precommercially thinned plantations increases the risk of wounding to crop trees adjacent to foci. Precommercial thinning should capitalize on community structure to select for resistant species along edges where black-stain root disease is present and in an adjacent buffer region. Special procedures must be developed for black-stain root disease foci because cutting of diseased trees is more attractive to vectors than cutting healthy trees (Chapter IV). A modified focus proliferation and spread model for precommercially thinned plantations would evaluate the effects of treatment/no treatment on focus persistence, growth, and proliferation following precommercial thinning. These results would be evaluated against the do-nothing option of focus persistence, growth, and proliferation.
The recommendations would be coupled with the plantation layout inventory to yield maps and guidelines for treatment of each plantation. Data on density and community structure, based on precommercial management guidelines, would be returned to the plantation holdings inventory and would be updated and calibrated by survey following the precommercial treatment.

It is uncertain whether the pest management scheme associated with the commercial thinning is needed. At present, the impact of commercial thinning on stand susceptibility to black-stain root disease is unknown, the spread of *V. wageneri* in mature stands is undocumented, and few alternatives can be envisioned to minimize disturbance during this entry.
DISCUSSION

Pest management of black-stain root disease must be initiated at many points within the crop production system of Douglas-fir because foci may be initiated for a myriad of factors associated with stand disturbance, e.g., cutting, injury, soil compaction, or altered patterns of drainage. Pest management also must be coupled to normal survey and management activities to receive widespread acceptance. Control of black-stain root disease should begin in the harvest-establishment phase and be centered around harvest practices and risk-rating of units, coupled with manipulation of community and spatial structure of new stands. Cable logging should be preferred, as cost permits. Tractor logging, where practiced, should minimize site disturbance and road and skid road establishment. Rehabilitation of skid roads may be warranted, if effective, and road building should be carefully engineered to effect rapid, efficient drainage of above-slope runoff and rainfall from the road surface.

Management in the establishment phase is centered on plantation layout, risk-rating of plantations, and complex two- or three-species planting strategies which put resistant species in high-risk microsites and favored, susceptible species in other microsites. Resistant species include western redcedar, western hemlock, and
hardwoods. Western redcedar is the favored species on compacted soils of skid roads and moist, low sites because of its capacity to extend roots through severely compacted soil (Forristall 1955) and its ability to tolerate periodic flooding (Minore 1968). Due to degradation of the microsite by soil erosion and compaction, trees planted on or seeding into roads are exposed to conditions which severely limit growth and competitiveness (Wert and Thomas 1981). Both western redcedar and western hemlock are favored on these microsites because of their tolerance to low levels of light. By removing a significant portion of the high risk microsites from colonization by the susceptible species, Douglas-fir, considerable control of black-stain root disease could be effected.

Annual survey procedures should include examination and recording of developing foci of black-stain root disease in units. This is most efficiently recorded into a computer-based inventory of foci for each plantation. Young stands with developing foci may be more amenable to sanitation procedures than older stands. Since most black-stain root disease foci occur near or on road or skid road networks, roadside surveys will prove both rapid and efficient in locating disease foci in units. Annual sanitation practices may be efficiently coupled with roadside maintenance and upkeep, however it appears that these same activities increase the risk of spread through
injury of roadside trees. Sanitation of established foci by felling may not be a good choice because insects are attracted to the volatiles emanating from cut or diseased hosts, leading to greater injury of adjacent, uninfected hosts (Chapters II, IV).

At precommercial thinning, major activities in density management may inadvertently increase the proliferation of foci of black-stain root disease both within a plantation and within other plantations (Chapter II, III, IV). Area-wide or holding-wide precommercial thinning probably cannot be accomplished during the time least favorable for the spread of black-stain root disease. Therefore, a structured approach to precommercial thinning is recommended. Plantations are risk-rated, both regionally and locally, and those at greatest risk receive treatment during June-July. This should significantly reduce the susceptibility of the cut hosts to colonization by *V. wageneri*. However, a significant reduction in the response of vectors to plantations as the result of thinning at this time has not been demonstrated on an area-wide basis. The precommercial management scheme utilizes plantation mappings, black-stain root disease foci inventory, stand density and composition, spatial structure, and regional and local abundance of black-stain root disease to measure risk. Plantation maps and guidelines for thinning should
be designed to minimize the risk of disturbance and subsequent immigration of vectors. Pest management tactics applied to established foci of *V. wageneri* during the thinning process should minimize felling of diseased hosts. Sanitation by tree removal, chemical treatment, or no cutting may be favored. Buffer zones around foci, if established, should retain resistant species as crop trees. Management tactics may include trapping out of insects in established foci.

The pest management structure proposed herein identifies gaps in knowledge and areas of weakness in our understanding of the fungus-insect association within the framework of a crop production system. Future research should fill these gaps and provide additional tactics for weakening the links between the host and the epidemiology of black-stain root disease and its vectors.
Figure V.1. A crop production/pest management system for management of black-stain root disease in plantations of Douglas-fir.
Figure V.2. The harvest-establishment pest management scheme for management of black-stain root disease in plantations of Douglas-fir.
The annual pest management scheme for management of black-stain root disease in plantations of Douglas-fir.
Figure V.4. The precommercial pest management scheme for management of black-stain root disease in plantations of Douglas-fir.
LITERATURE CITED


SUMMARY

Root-colonizing insects are demonstrated to be vectors of *Verticicladiella wageneri* Kendrick, the causal agent of black-stain root disease of Douglas-fir and other conifers. *Hylastes nigrinus* Mann., *Pissodes fasciatus* LeC., and *Steremnius carinatus* (Boh.) are associated with diseased Douglas-fir, carry inoculum in the field, visit susceptible Douglas-fir under conditions suitable for transmission of the pathogen, and can inoculate and infect Douglas-fir with the pathogen. Results suggest that rates of infestation of vectors by *V. wageneri* are less than 5% (Chapter II). Besides contributing to the proliferation of new foci at a distance from established foci, vectors have a role in spread of established foci of *V. wageneri*.

The practice of precommercially thinning plantations of Douglas-fir results in the immigration of vectors into the stand. Trees cut during thinning are susceptible to infection for at least seven months. These hosts are colonized by all three vector species. In addition, crop trees are wounded throughout the roots and root collar region by *H. nigrinus* over two flight seasons; some wounds penetrate to the xylem, especially on small roots, and are therefore suitable infection courts. Within plantations, at the scale of 2-ha plots, the time of precommercial thinning can be manipulated to reduce immigration, attack
density, brood production, and emergence of vectors (Chapter III). Thinning should occur after the peak flight period of *H. nigrinus* and *P. fasciatus*. Regardless of time of thinning, immigration of vectors is stimulated by precommercial thinning.

Factors associated with host selection and host attraction of *H. nigrinus* and *S. carinatus* were explored in Chapter IV. Alpha-pinene and ethanol are attractants for these two species. Root sections infected with *V. wageneri* are more attractive to *H. nigrinus* and *S. carinatus* than are healthy root sections. Douglas-fir infected with black-stain root disease responds to infection by weak resinosus, limited generally to root branches. I propose that insects utilize these chemical cues during the host selection process. The sequential process of colonization contributes to aggregation of vectors on stressed hosts by sustained wounding of infected host tissue. Furthermore, I suggest that factors associated with soil compaction and periodic or temporary anaerobiosis lead to the production and release of host attractants by stressed Douglas-fir, such as ethanol, which serve as chemical cues for host-selecting vectors.

A crop production--pest management system structure is proposed for Douglas-fir plantations in western Oregon (Chapter V). Coupled to the crop model are four pest management schemes for black-stain root disease. These
schemes emphasize the need for pest management throughout the harvest-establishment, annual survey and inventory, precommercial density management, and commercial density management phases of crop production.
BIBLIOGRAPHY


