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VISITATION FREQUENCIES OF SOME INSECT SPECIES ON *CERATOCYSTIS WAGENERI* INFECTED AND APPARENTLY HEALTHY PONDEROSA PINES

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Abstract

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To test the hypothesis that bark beetles and some associated insect species are attracted to ponderosa pines infected by *Ceratocystis wageneri*, insect visitations on 11 severely diseased, 9 moderately diseased, and 10 apparently healthy trees were monitored from 1 August to 15 October 1972. Larger numbers of *Dendroctonus brevicomis*, *D. ponderosae*, *Temnochila chlorodia*, and buprestids were captured on diseased trees uninfested by bark beetles than on apparently healthy ones, thus possibly indicating attraction to diseased trees. There was strong evidence that *D. valens* and *Spondylis upiformis* were attracted more frequently to wounds on diseased than on healthy trees. Arrival patterns of beetles were recorded for trees that became infested during the study. Predators became abundant on traps as bark beetle catches increased.

Résumé

On a surveillé l'arrivée d'insectes sur 11 arbres sévèrement malades, 9 moyennement malades et 10 apparamment sains, du 1 août au 15 octobre 1972, afin de tester l'hypothèse voulant que les scolytes et certains insectes qui leur sont associés soient attirés par le pin ponderosa infecté du *Ceratocystis wageneri*. On a capturé des nombres plus élevés de *Dendroctonus brevicomis*, *D. ponderosae*, *Temnochila chlorodia* et de buprestes sur des arbres malades non infestés de scolytes, que sur des arbres apparamment sains, indiquant une attraction possible vers les arbres malades. Il est apparu très évident que *D. valens* et *Spondylis upiformis* étaient attirés plus fréquemment aux blessures sur des arbres malades que sur des arbres sains. On a noté l'évolution de l'arrivée des insectes sur des arbres qui sont devenus infestés au cours de l'étude. L'abondance des prédateurs sur les pièges a augmenté avec l'augmentation du nombre de coléoptères de l'écorce capturés.

Introduction

The fungus *Ceratocystis wageneri* Goheen and Cobb (= *Verticicladiella wageneri* Kendrick) causes black stain root disease of several western conifers, including ponderosa pine (*Pinus ponderosa* Laws.) in California. Diagnostic evidence of infection by *C. wageneri* is a brown to black stain in the sapwood of host roots and lower stems. The darkly pigmented hyphae grow through the xylem tracheids, pass from cell to cell through bordered pit pairs, and interfere with water uptake (Smith 1967). The health of most infected trees declines rapidly, and the trees die within a few years. However, ponderosa pines rarely die from the effects of *C. wageneri* infection alone. Instead, most are infested by bark beetles before they are killed.

In areas where the fungus is active, a high proportion of all trees killed by bark beetles shows evidence of infection by *C. wageneri*. Based on these observations, it has been suggested that *C. wageneri* plays an important role in maintaining endemic bark beetle populations by predisposing trees to infestation (Cobb *et al.* 1974). The mechanism by which bark beetles locate and kill disease-weakened trees preferentially has been a matter for conjecture (Cobb *et al.* 1968; Moeck *et al.* 1981; Wood 1972). Bark beetles may land on trees at random, successfully infesting only those trees that are weakened, or alternatively, they may be attracted to such trees. The objective of the present investigation was to determine if there is an increase in visitation rates prior to infestation that might indicate attraction to *C. wageneri* infected trees.

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Materials and Methods

The study was made from mid-July to mid-October 1972, along the margin of a 30-ha area of dead and dying ponderosa pines situated at an elevation of 1400 m on the University of California Blodgett Research Forest, El Dorado County, California (38°54′ N, 120°40′ W). *Ceratocystis wageneri* and 2 species of bark beetles, *Dendroctonus brevicomis* LeC. and *D. ponderosae* Hopkins (Coleoptera: Scolytidae), were associated with the mortality.

On the basis of the proportion of root crown circumference colonized by *C. wageneri*, 3 categories of trees were chosen for study: (*a*) apparently healthy — no evidence of colonization at the root crown; (*b*) moderately diseased — 1–49% of the root crown colonized; and (*c*) severely diseased — 50–100% of the root crown colonized. Some of the apparently healthy trees might have had root infection, but previous studies (unpublished) have shown that *C. wageneri* usually causes substantial effects on host physiology only after the fungus has reached the root crown.

Foliage symptoms, proximity to areas with trees infected by *C. wageneri*, and presence of the red turpentine beetle, *D. valens* LeC., in the lower boles were aids in finding diseased trees. Information on attacks by *D. valens* was used because observations had indicated that the beetle occurred more frequently on *C. wageneri* infected trees than on healthy ones. The proportion of root-crown colonization was determined by driving a 6-mm arch-punch into the sapwood at 15-cm intervals around the base of each tree, removing the sapwood cores, and computing a percentage on the basis of the proportion of cores with characteristic stain (Goheen and Cobb 1980).

Thirty codominant (crowns in the overstory) ponderosa pines 30–50 cm in diameter at 1.4 m above ground (d.b.h., diameter breast height) which showed no evidence of prior bark beetle attacks were chosen for study. Ten trees were apparently healthy, 9 were moderately diseased, and 11 were severely diseased. All trees were in the same area along the margin of the infection center, where infection of many trees was current, and all trees, including healthy ones, were chosen relative to spacing and location to minimize differences in exposure to insects. Percentage circumference stained by *C. wageneri*, d.b.h., crown class, height, and foliage symptoms such as yellowing of needles and reduction in quantity of foliage were recorded for each tree.

Six 15 × 30 cm traps made from rigid, 6-mm-mesh hardware screen coated with Stickem Special®[2] were mounted, 2 each at heights of 2, 7, and 11 m to monitor insects landing in each tree. Traps were attached to nylon twine, and all trees were rigged so that traps could be lowered and examined on the ground. The traps covered approximately 1% of the stem below the live crown of each tree. *Dendroctonus brevicomis*, *D. ponderosae*, *Ips* spp., buprestids, and the important bark beetle predators *Enoclerus* spp. (Coleoptera: Cleridae) and *Temnochila chlorodia* Mannerheim (Coleoptera: Trogositidae) were removed from the traps and counted daily or every other day from 1 August until sample trees became infested, or until 15 October, whichever occurred first.

The frequent examination of traps was made to determine when visitation rates increased prior to bark beetle infestation (i.e. successful attack) and whether visitation rates differed between healthy and diseased trees. Based on the data collected, trees were divided into 2 groups, those with no beetle trapped on them and those with 1 beetle or more. A contingency table was prepared and Chi-square and Fisher's exact test were used to test for differences between the apparently healthy and the diseased-tree categories.

Results

Between 1 August and 15 October 1972, 7 of the severely diseased trees became infested by bark beetles. Six of the infested trees had exhibited foliage symptoms of disease

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[2] Michel and Pelton Co., Emeryville, CA, USA 94608.

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at the beginning of the study, and mean stem circumference colonized by *C. wageneri* was 70%. Four trees were infested by *D. brevicomis* alone, 1 by *D. ponderosae* alone, and 2 by both species. Determination of beetle species infesting each tree was made by examining galleries under the bark after tree death. In 2 cases (Fig. 1 A and B) where *D. brevicomis* infested alone, beetles appeared suddenly in large numbers following periods during which no *D. brevicomis* were trapped. The other 2 trees that became infested by *D. brevicomis* alone (Fig. 2 A and B) had only a small number of *D. brevicomis* on traps prior to infestation. Also, a small number of *D. ponderosae* was trapped at the time of infestation by *D. brevicomis*. Numbers of *D. brevicomis* trapped were smaller and spread over a longer period on trees infested by both *D. brevicomis* and *D. ponderosae* (Fig. 1C and 2C) when compared with trees infested with *D. brevicomis* alone. Trees infested by *D. ponderosae* alone or in combination with *D. brevicomis* exhibited a less precipitous increase and fewer beetles than was observed for those with *D. brevicomis* alone. All but 1 of the infested trees were killed in August. One (Fig. 3) was killed in late September. On this tree, *D. brevicomis* and *D. ponderosae* were trapped in small numbers beginning in mid-August. During the next 6 weeks, the tree exuded copious amounts of resin, resulting in formation of pitch tubes at attack sites. When the tree finally was killed, bark removal showed that only *D. ponderosae* had constructed galleries.

Predators became abundant on traps as bark beetle catches increased (Fig. 1–3). *Enoclerus lecontei* Wolcott was captured on trees infested by both *D. brevicomis* and *D. ponderosae*, and *E. sphegeus* (F.) was captured on trees infested by *D. brevicomis* alone. *Enoclerus lecontei* often appeared 1 or 2 days before *D. brevicomis* was trapped.

Buprestid galleries and larvae were found under the bark of 5 infested trees at the time bark beetles were captured in large numbers. Most of these were identified tentatively as *Melanophila californica* Van Dyke. Evidence indicated that buprestids attacked diseased trees well in advance of *Dendroctonus* spp. *Ips paraconfusus* Lanier was found constructing galleries in the top of 1 tree infested by *D. ponderosae* alone and 1 tree infested by both *D. ponderosae* and *D. brevicomis*, but it was captured infrequently on traps.

Before comparing disease categories relative to incidence of captured insects, 2 severely diseased trees were excluded because they became infested immediately after trap installation, and 1 healthy tree was excluded because a diseased tree 2 m away became infested, resulting in increased insect visitation on that tree as well. With these exclusions, numbers of *D. brevicomis* and *D. ponderosae* captured on traps were consistently higher on diseased trees than on healthy ones (Table 1). Only *E. lecontei* showed an opposite trend. However, numbers of captured insects were small in all cases.

The test for possible primary attraction was based on comparisons of numbers of diseased versus healthy trees that had *D. brevicomis*, *D. ponderosae*, and/or buprestids captured on them but did not become infested during the study, plus those that became infested but had insects captured on them at least 8 days prior to infestation (mass attack). On these infested trees, we concluded that the small numbers of insects captured 8 or more days before mass attack were probably not attracted to the tree by bark beetle pheromones. Every 2–3 days a Swedish climbing ladder was used to examine critically these trees for any evidence of beetle boring activity. Time of beetle infestation was considered and was also confirmed through use of the ladders and critical examination to detect evidence of attack such as oleoresin oozing from entry galleries, boring dust, and early development of pitch tubes.

Both *D. brevicomis* and *D. ponderosae* were trapped on a larger proportion of diseased trees than of healthy trees (Table 2). In the case of *D. ponderosae*, the differences between severely diseased or total diseased and healthy trees were statistically significant at $P<0.05$. The differences with *D. brevicomis* were not significant at $P<0.05$; however, the comparison between diseased and healthy trees yielded a probability (0.16) that points

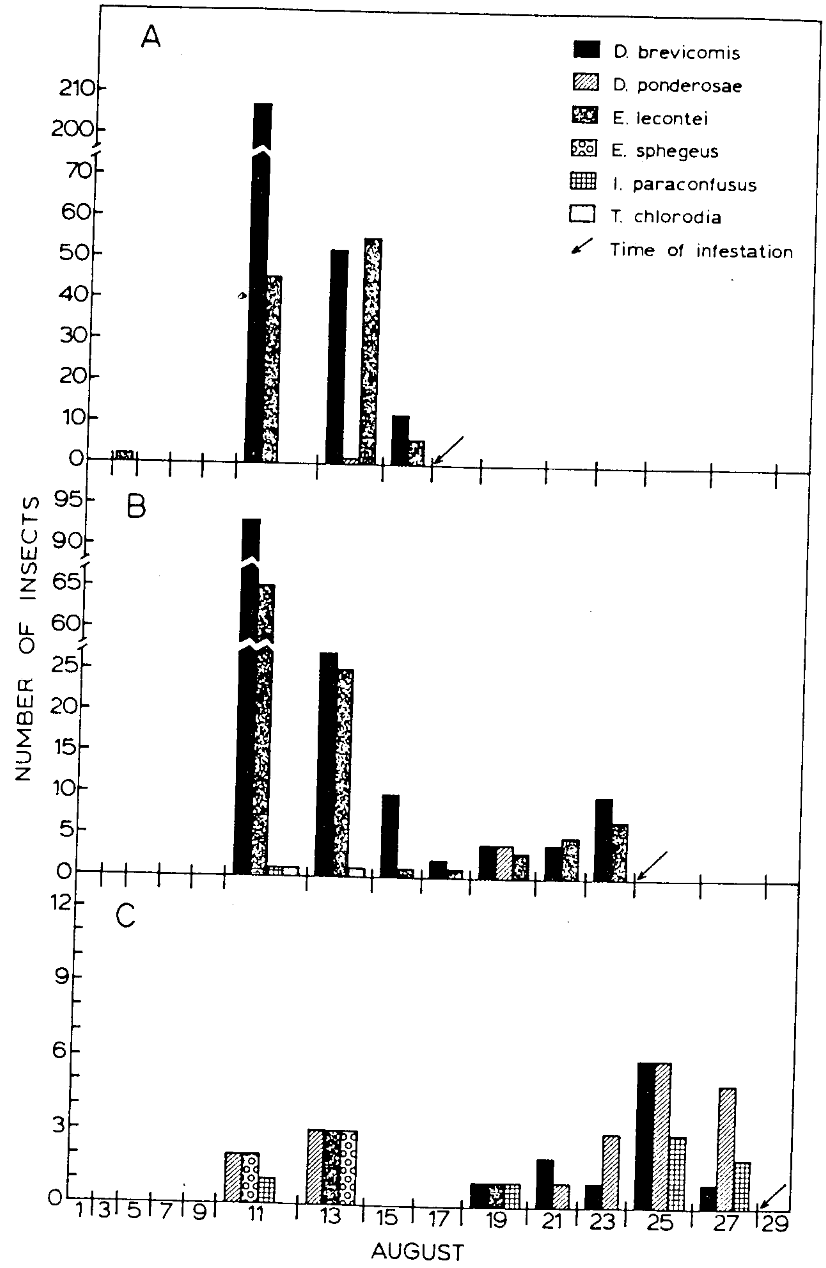

FIG. 1. Numbers of bark beetles and predators trapped over time on *Ceratocystis wageneri* infected ponderosa pines prior to evidence of initial beetle infestation. Trees A and B became infested by *Dendroctonus brevicomis* alone while C became infested by both *D. brevicomis* and *D. ponderosae*.

to potential significance with a larger sample size. There were no significant differences in proportions of trees with buprestids. Numbers of predators (*E. lecontei* and *T. chlorodia*) were so small that no statistical analyses were made.

Dendroctonus valens often attacked trees at wounds made with the arch-punch. When trees were examined 1 week after wounding, *D. valens* attacks occurred in wounds on 1

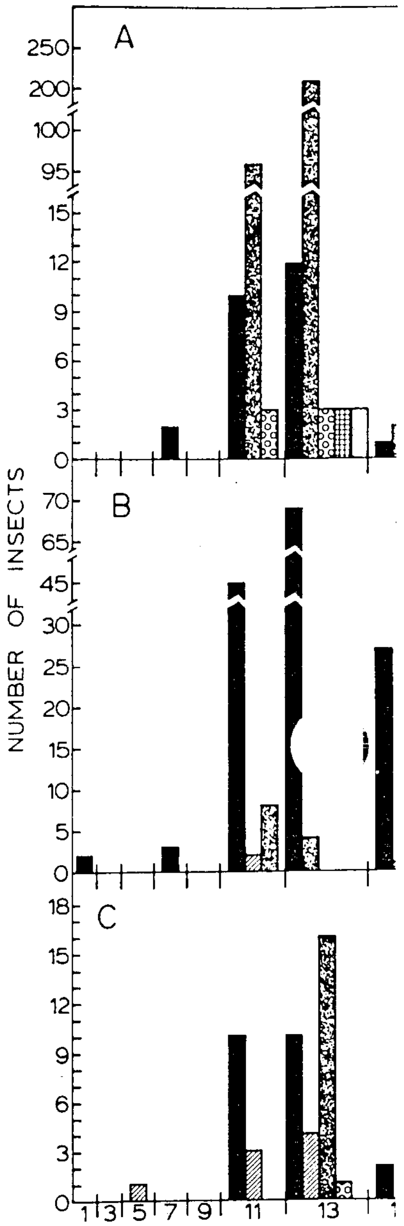

FIG. 2. Numbers of bark beetles and predators trapp
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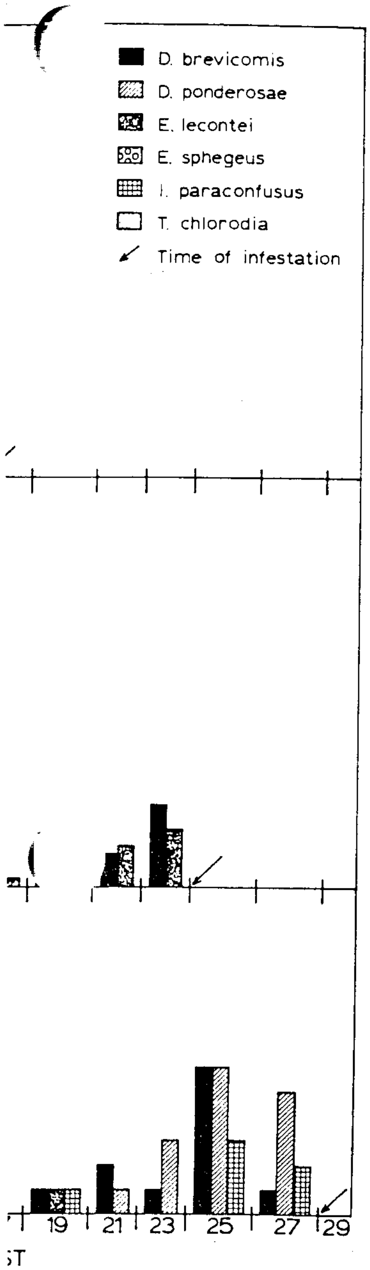

time on *Ceratocystis wageneri* infected ponderosa id B became infested by *Dendroctonus brevicomis* *brevicomis* and *D. ponderosae*.

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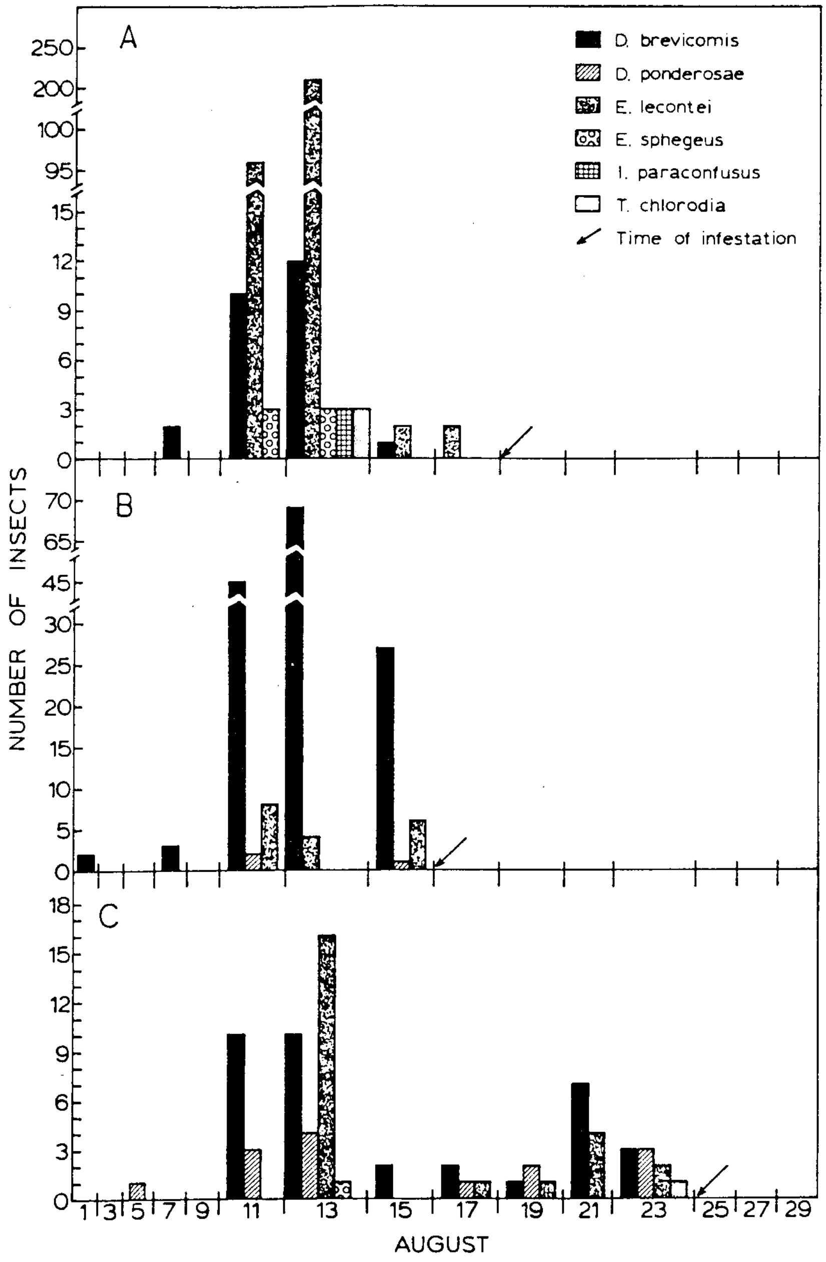

FIG. 2. Numbers of bark beetles and predators trapped over time on *Ceratocystis wageneri* infected ponderosa pines prior to evidence of initial beetle infestation. Trees A and B became infested by *Dendroctonus brevicomis* alone while C became infested by both *D. brevicomis* and *D. ponderosae*.

healthy tree (10%), 3 moderately diseased trees (33%), and 6 severely diseased trees (55%). Average numbers of attacks per attacked tree were 1.0 for healthy trees, 2.6 for moderately diseased trees, and 3.7 for severely diseased trees. In a sample of 256 trees that subsequently were monitored for disease increase at 3- to 12-month intervals over a

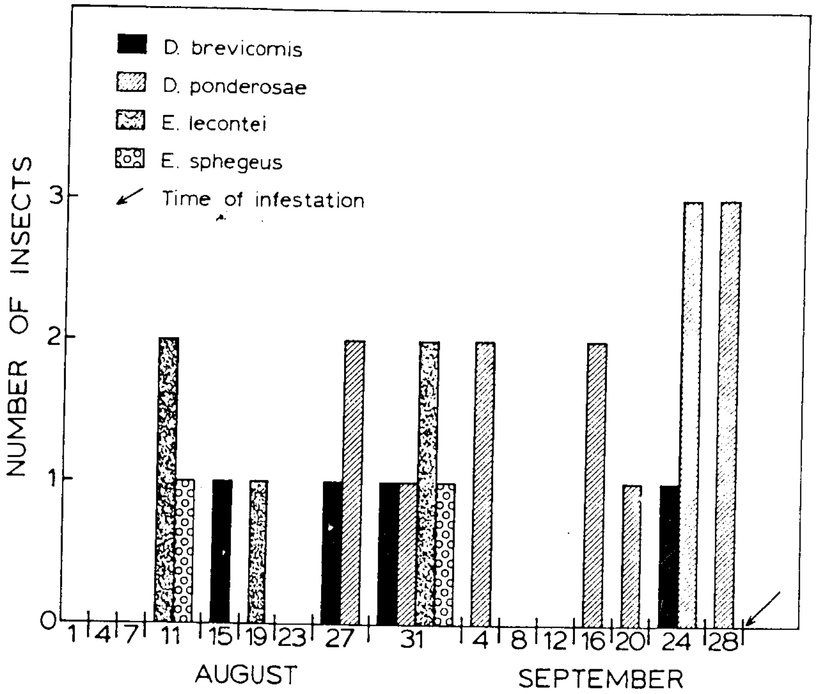

FIG. 3. Numbers of bark beetles and predators trapped over time on a *Ceratocystis wageneri* infected ponderosa pine prior to infestation by *Dendroctonus ponderosae*.

4-year period, similar patterns of attack by *D. valens* were observed (Table 3). The proportion of trees exhibiting *D. valens* attacks in wounds 1 week after wounding was 7–8 times greater for infected than for healthy trees. Among attacked trees, those infected by *C. wageneri* had 2–3 times as many attacks as healthy trees. Differences between healthy and diseased trees in numbers of trees attacked by *D. valens* and in numbers of attacks per tree were significant ($P<0.05$).

A cerambycid, *Spondylis upiformis* Mannerheim, was also observed at wounds at bases of trees. In June 1975, a sample of 6 *C. wageneri* infected and 6 uninfected ponderosa pines were injured by chopping with an axe to the sapwood on at least 2 sides of each tree. Healthy and diseased trees were in the same areas around margins of 2 infection centers of *C. wageneri*. Beetles began ar
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rates were significant ($P<0.05$, *T*-test
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Table 1. Mean numbers of insects trapped per tree on apparently healthy and *Ceratocystis wageneri* infected ponderosa pines at Blodgett Forest, California, from 1 August to 16 October 1972

		Mean no. of insects trapped per tree				
Disease class	No. trees	*Dendroctonus brevicomis*	*Dendroctonus ponderosae*	Buprestidae	*Enoclerus lecontei*	*Temnochila chlorodia*
Moderately diseased	9	3.6	0.8	0.8	0.3	0.4
Severely diseased	9*	2.0	1.7	0.2	1.3	0.3
Total diseased	18	2.8	1.2	0.5	0.8	0.4
Healthy	9†	1.3	0.1	0.4	1.0	0

*Reduced from 11 to 9 because 2 trees were mass attacked at the beginning of the study.
†Reduced from 10 to 9 because 1 tree was adjacent to a mass-attacked tree.

Table 2. Proportion of healthy and *Ceratocystis wa*
were captured at Blodgett Resear

Disease class	Total no. trees	*D*
Severely diseased	9	
Moderately diseased	9	
Total diseased	18	
Healthy	9	

*Includes non-attacked trees and attacked trees with insec
†Ratios followed by the same letter are not significantly c

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Table 3. Proportion of trees attacked by
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healthy

Disease category	No. trees
Healthy	136
Moderately diseased	90
Severely diseased	

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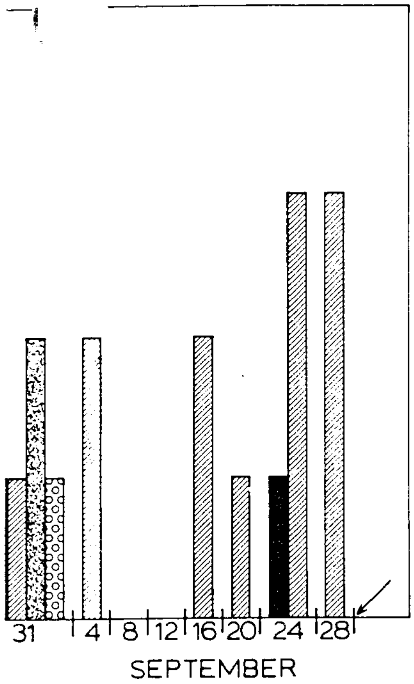

over time on a *Ceratocystis wageneri* infected ponderosa ' *Dendroctonus ponderosae.*

D 's were observed (Table 3). The pro- s nds 1 week after wounding was 7–8 'ees. Among attacked trees, those infected by as healthy trees. Differences between healthy :ked by *D. valens* and in numbers of attacks

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apparently healthy and *Ceratocystis wageneri* infected fornia, from 1 August to 16 October 1972

ean no. of insects trapped per tree			
droctonus *ıderosae*	Buprestidae	*Enoclerus lecontei*	*Temnochila chlorodia*
0.8	0.8	0.3	0.4
1.7	0.2	1.3	0.3
1.2	0.5	0.8	0.4
0.1	0.4	1.0	0

the beginning of the study.
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Table 2. Proportion of healthy and *Ceratocystis wageneri* infected ponderosa pines* on which tree-killing insects were captured at Blodgett Research Forest from 1 August to 16 October 1972

Disease class	Total no. trees	Percentage of trees with 1 or more insects†		
		D. brevicomis	*D. ponderosae*	Buprestidae
Severely diseased	9	67A	89A	33A
Moderately diseased	9	78A	44AB	44A
Total diseased	18	72A	67A	39A
Healthy	9	44A	22B	33A

*Includes non-attacked trees and attacked trees with insects of the attacking species present at least 8 days prior to mass attack.
†Ratios followed by the same letter are not significantly different at $P>0.05$ (Fisher's Exact Test).

centers of *C. wageneri*. Beetles began arriving 15–40 min after wounding. Mean numbers of beetles captured on healthy and diseased trees within 2 h of wounding were 3.0 and 9.7, respectively. *Spondylis upiformis* did not land on any of the 12 unwounded healthy and diseased trees monitored during the study. Differences between *S. upiformis* landing rates were significant ($P<0.05$, T-test for paired comparisons) between wounded and unwounded trees and between wounded diseased and wounded healthy trees.

Discussion

Many investigators have observed that bark beetles normally infest trees that have been injured by drought, flood, intense cold or heat, lightning, or fire. Pathogens also have been implicated in predisposing forest trees to attack by bark beetles (Miller and Keen 1960; Rudinsky 1962; Norris 1964; Nourteva and Laine 1968; Felix *et al.* 1971; Kangas 1971; Cobb *et al.* 1974; Ferrell 1974; Hertert *et al.* 1975; Ferrell and Smith 1976). Results of the present investigation confirm earlier work (Wagener and Mielke 1961; Cobb *et al.* 1974; Goheen and Cobb 1980; Moeck *et al.* 1981) indicating that bark beetles preferentially infest *C. wageneri* infected trees.

The selectivity exhibited by bark beetles in infesting often widely scattered, weakened trees has led investigators to postulate that physiological changes associated with injury or weakening may result in production of primary attractants, i.e. odors detectable by bark beetles (see review by Moeck *et al.* 1981). The fact that many bark beetles produce aggregation pheromones makes confirmation of primary attraction in living trees difficult. However, primary attraction has been demonstrated for many species of scolytids, e.g. ambrosia beetles (Cade *et al.* 1970; Chapman 1962; Graham 1968; Moeck 1970) and bark beetles

Table 3. Proportion of trees attacked by *Dendroctonus valens* within 1 week of wounding and mean number of attacks per tree on *Ceratocystis wageneri* infected and apparently healthy ponderosa pines

Disease category	No. trees	Percentage trees attacked*	Mean no. of attacks*,† per tree
Healthy	136	6A	1.2A
Moderately diseased	90	41B	2.5B
Severely diseased	80	53B	3.3C

*Proportions and means followed by the same letter are not significantly different at $P>0.05$ (Cochran and Cox test for comparing sample means with unpaired observations and unequal variances).
†Based on attacked trees only, not on total number of trees.

(Jantz and Rudinsky 1966; Rudinsky *et al.* 1971; Moeck 1978). Attempts to demonstrate primary attraction in living trees have failed for many species, including *D. brevicomis* and *D. ponderosae* (Moeck *et al.* 1981).

The present study covered only a short time period and was made with a small number of trees. Nevertheless, the data showed that *D. brevicomis* and especially *D. ponderosae* tended to be present more often on diseased than on healthy trees. These differences may be due to primary attraction, but the possibility that they are due to pheromones rather than primary attraction cannot be excluded. In spite of intensive efforts to monitor any bark beetle attack, an isolated attack that conceivably could result in low level pheromone production might have gone undetected. Moeck *et al.* (1981) found no evidence of primary attraction of *D. brevicomis* or *D. ponderosae* by *C. wageneri* infected trees in similar stands when attempts were made to exclude beetle access with screens. In our study there is little doubt that *S. upiformis* is attracted preferentially to wounds at the bases of infected trees. The higher incidence of *D. valens* on diseased trees than on symptomless trees is a result of higher attraction to and/or arrestment at diseased trees (see also Goheen and Cobb 1980; Moeck *et al.* 1981).

The mass-attack phenomenon involving attraction of large numbers of bark beetles to trees in response to pheromones produced by the earliest arrivals is now a well understood aspect of bark beetle biology (Borden 1982; Wood 1982). However, documentation of mass attack is based on only a few field studies. Wood and Vité (1961) presented data on arrival sequence of *I. paraconfusus* on naturally infested trees, but to date, studies of sequential arrival of *Dendroctonus* spp. and their associates have been done primarily on artificially baited trees (Camors and Payne 1973), although Stephen and Dahlsten (1976*a*, 1976*b*) included several naturally infested trees in their studies. Data obtained in the present study show that the arrival pattern of *D. brevicomis* on naturally infested trees is similar to the mass attack pattern observed on baited trees. The bark beetle predators *E. lecontei* and *T. chlorodia* often arrive at the same time (Stephen and Dahlsten 1976*a*, 1976*b*) or shortly before the main body of bark beetles, indicating efficient detection of, and rapid response to, bark beetle pheromones. Because of the predictability of bark beetle attack, *C. wageneri* infected trees constitute an excellent natural system for the study of arrival patterns of bark beetles and their associates.

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