

**PITYOPHTHORUS ORARIUS BRIGHT (COLEOPTERA: SCOLYTIDAE) IN A
NORTHERN CALIFORNIA DOUGLAS-FIR SEED ORCHARD: EFFECT OF CLONE,
TREE VIGOR, AND CONE CROP ON RATE OF ATTACK**

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Abstract

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The geographic range of the Douglas-fir twig beetle, *Pityophthorus orarius* Bright, was extended beyond the original provenance of southern British Columbia to northern California. A survey of 457 Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] trees in 1985 revealed that those with heavy cone crops were more likely to be infested by twig beetles than were those with a light crop. Furthermore, attack rates differed among clones. A second survey done in 1987 confirmed the importance of clone and cone crop in attack rate. In this survey, stressed trees were attacked at a higher rate than unstressed trees. Beetle distributions appeared clumped in both surveys, possibly because of semiochemicals or oviposition behavior.

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Résumé

Le scolyte des brindilles du sapin de Douglas, *Pityophthorus orarius* Bright, dont la répartition géographique était limitée au sud de la Colombie Britannique, a été récolté dans le nord de la Californie. Un relevé effectué en 1985 sur 457 sapins de Douglas, *Pseudotsuga menziesii* (Mirb.) Franco, a révélé que le taux d'attaque des cônes d'un arbre était lié à son niveau de fructification; les plus fructifères étant attaqués par plus de scolytes que ceux produisant peu de cônes. De plus, nous avons observé une corrélation positive entre les taux d'attaques et les clones de sapins. Un second relevé exécuté en 1987 a corroboré l'influence de la souche clonale et du niveau de fructification sur le taux d'attaque, en plus d'indiquer que les arbres considérés stressés étaient plus sensibles à l'attaque du scolyte que ceux sans stress. La distribution concentrée des scolytes observée lors de ces deux relevés est peut être liée au comportement de ponte ou aux substances sémio-chimiques.

Introduction

The Douglas-fir twig beetle, *Pityophthorus orarius* Bright, a scolytid that mines Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] twigs, has previously been reported only from southern British Columbia, Canada (Bright 1968; Hedlin and Ruth 1970). Hedlin and Ruth (1970) and Bright (1981) predicted that its range would eventually be found to coincide more completely with that of its host, but there have been no subsequent reports of it outside of British Columbia. The twig beetle is easy to overlook because its most noticeable symptom is flagged twigs, which often fall to the litter by late summer. For most of the year, the presence of these beetles goes largely undetected.

The genus *Pityophthorus* Eichhoff, by far the largest North American scolytid genus (S.L. Wood 1982), has nearly 400 described species worldwide (Wood 1986). Members of this and closely related genera such as *Conophthorus* Hopkins and *Pityotrichus* Wood show little morphological diversity, so generic limits have been problematic (Bright 1976; S.L. Wood 1982). Most *Pityophthorus* spp. are regarded as nonpests or even as beneficial insects, as most infest only injured or felled trees and thus enhance natural pruning and

decomposition (Bright 1981). Unlike most of its congeners, *P. orarius* mines and kills the tips of apparently healthy twigs throughout the crowns of vigorous trees. These twigs bear two generations of cones: the primordia of the subsequent season's cone crop and the currently developing conelets. Each beetle mines two twigs during its life cycle, one in which larval development is completed and one in which young adults overwinter (Hedlin and Ruth 1970). Interestingly, both attack periods are synchronized with seasonal starch maxima reported for many woody plant species (Kramer and Kozlowski 1979). Depending on the rate of attack and the size of the cone crop, then, a sizable number of both first-year and second-year cones could be destroyed by these beetles.

Here we report results of a survey in a coastal northern California Douglas-fir seed orchard that was undertaken to determine extent of twig beetle infestations, distribution patterns, and factors underlying those patterns.

Methods

In 1985, we discovered an infestation of *P. orarius* in the Louisiana-Pacific Corporation's Little River Seed Orchard, about 10 km inland from Trinidad Head in Humboldt County, CA (elevation 91 m). This orchard, located in the middle of the redwood – Douglas-fir timber type, originally had 3000 grafted clonal Douglas-fir trees (100 clones \times 30 ramets per clone) on about 6 ha. Most of the grafting was done in 1968. We first noticed flagged twigs in early August; dissections of these twigs revealed larvae, pupae, and both teneral and fully tanned adults. Beetle galleries and external appearance of twigs met the description of *P. orarius* damage (Hedlin and Ruth 1970), and species identity was confirmed by D.E. Bright. Voucher specimens have been deposited in the Canadian National Collection of Insects, Agriculture Canada, Ottawa, Ontario.

In view of the potential impact of this insect in a seed orchard, we decided to survey infestation rates on all trees within eight 100-tree plots, constituting adjacent blocks from the 305- to 610-m altitude zone, in 1985. There were 457 trees in these eight plots, the remainder having died of graft-union failure. These trees represented 39 different clones, with 4–20 ramets per clone. We assessed infestations by tallying numbers of flagged twigs per tree; each flagged twig was presumed to represent a single beetle, as only one egg is generally laid per shoot (Hedlin and Ruth 1970), and overwintering galleries had not yet been mined. Because twig pathogens can cause similar flagging, we verified the cause of damage as follows: 10 trees were randomly chosen at each of two infestation levels (1–5 flagged twigs per tree and 6–10 flagged twigs per tree), then all flagged twigs were dissected from these 20 trees and causal agents were assigned.

A separate survey had been made the previous fall to find trees with large numbers of cone buds. In this survey, reproductive buds were identified visually using the method of Allen and Owens (1972) and trees were ranked into either a "high" (more than 50 cones) or a "low" (less than 50 cones) cone crop category. This procedure allowed us to evaluate the effect of cone crop on rate of attack by twig beetles.

Two-way analysis of variance (Snedecor and Cochran 1982) was performed on numbers of beetles per tree using clone and predicted cone crop as main effects in the model. Because we anticipated an interaction between cone crop and clone (ramets from the same parent are thought to flower in synchrony), we performed the analysis both with and without the interaction term in the model so that we could determine its impact on the root mean squared error (an indicator of the predictive value of the model).

In 1987, we conducted a more intensive and extensive survey to confirm the relationship seen in 1985 between cone crop and beetle attack and to resolve potential interactions among cone crop, clone, tree vigor, and beetle attack. Many scolytids are attracted to stressed trees (D.L. Wood 1982) and such trees commonly produce "stress crops" of cones (Daniel et al. 1979), so we hypothesized that tree vigor might ultimately explain the relationship between

cone crop and beetle attack rate. Graft-union failure was common in this seed orchard, as it is in most seed orchards of its generation (Copes 1978); thus, many of the trees were stressed from graft-union insufficiency. Graft-union failure is known to have a genetic component (Copes 1970, 1978), so the chance that a tree will suffer stress from graft-union insufficiency is probably not independent of clone.

The 1987 survey was expanded to include twelve 100-tree plots (the original eight plots plus four more contiguous plots), comprising 64 clones (636 trees, with 1–29 ramets per clone). We counted beetle attacks per tree as in 1985, but instead of ranking cone crops as high or low we counted numbers of cones per tree up to 100; there were very few trees with more than 100 cones. We also ranked tree vigor according to the following index: 0 = tree apparently healthy; 1 = foliage slightly chlorotic, with internodes shorter than normal; 2 = noticeably chlorotic foliage, internodes stunted; 3 = extremely chlorotic foliage, stunted internodes, and noticeable needle-drop.

Two-way analysis of covariance was performed on the 1987 data with beetle attack rate as the response variable, cone crop as concomitant variable, and clone and tree vigor as categorical variables (Anonymous 1988).

Results and Discussion

The range of *P. orarius* is, as predicted, much greater than previously reported. We have found this insect in three central Oregon seed orchards since discovering it in northern California, and its distribution from British Columbia to California is undoubtedly continuous, given the unbroken distribution of the host type between those two locations.

Dissections showed that, of flagged twigs randomly sampled for dissection, only 4.6% (5 out of 108) were killed by agents other than twig beetles. Flagged twigs, then, were a reliable indicator of beetle infestation levels. In August of 1985, 56.0% of the seed orchard trees were infested with *P. orarius*; the average rate was 4.4 twigs per tree (SD = 8.5, range = 0–79 twigs per tree). When uninfested trees were excluded, the average infestation rate was 7.9 twigs per tree (SD = 10.0). This number is low, but the estimate may have excluded some infested twigs that had fallen off or not yet changed color.

Three-dimensional plots of attack rates for 1985 (Fig. 1) show an apparent tendency for aggregation by the beetles. This apparent aggregation could be caused by factors such as oviposition behavior, aggregation pheromones, host kairomones, microclimate, or clonal susceptibility. Although the orchard was designed to maximize the distance between ramets from the same clone, ramets were planted in repetitive sequences such that the clone of a ramet's immediate neighbors was constant throughout the orchard. Thus, if clonal susceptibility exists and susceptible clones happened to be adjacent, a contagious distribution could result as an artifact of orchard design.

Trees with "high" cone crops generally suffered more beetle attacks than trees with "low" cone crops ($P = 0.0014$), but this was obviously not true for all clones because the clone*cone crop interaction was significant ($P = 0.0008$) (Table 1). There was a significant association between attack rate and both clone ($P = 0.0014$) and cone crop ($P = 0.0001$); trees with "low" cone crops averaged 3.69 (SE 0.02) beetles per tree whereas trees with "high" cone crops averaged 7.33 (SE 0.13) beetles per tree. In general, a significant interaction term makes the interpretation of main effects difficult in analysis of variance. However, removing the interaction term from our model increased the root mean squared error by an insignificant amount (3%), so the main effects can be interpreted directly.

Mean rates of infestation ranged from 0.13 beetles per tree for clone 499 to almost 13 beetles per tree for clone 443. Given the large number of clones, the low average attack rate, and the interaction with crop level, we decided that pairwise testing for differences between clones would be pointless. A few clones (435, 438, 443, and 461), however, appeared to have high rates of attack, with averages ranging from 10 to 13 beetles per tree for those clones.

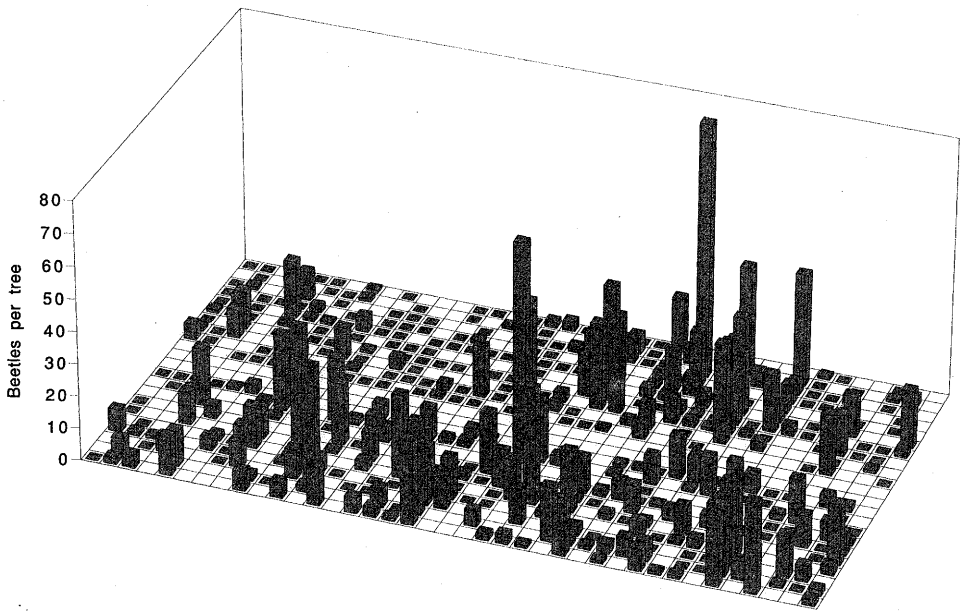


FIG. 1. Three-dimensional plot of attack rates per tree by *Pityophthorus orarius*, Little River Seed Orchard, 1985. Vertical bars represent individual trees, with bar height proportional to attack rate (range = 0–79 infested twigs per tree). Blank cells indicate absent trees; the two blank rows in the center represent the waterline.

Only two of the susceptible clones (435 and 438) were near one another and none were adjacent; thus the clustering of susceptible clones was too infrequent to explain the contagious distribution of the beetles. Because the seed orchard was remarkably homogeneous over the scale of the beetle aggregations, it does not seem likely that microclimate could explain this distribution either. Furthermore, we noted that beetle distributions appeared clumped within trees, with many attacks on a single or a few branches per tree. It seems likely, then, that this aggregation results from oviposition behavior, or semiochemicals, or both.

In 1987 beetle populations were lower than in 1985, although variability was similar (coefficients of variation for 1985 and 1987 mean attack rates were 1.9 and 2.4, respectively). The mean rate of twig beetle attacks per tree in 1987 was roughly half that in 1985 [2.5 (SD = 6.1) beetles per tree, compared with 4.4 in 1985], with attacks per tree ranging from 0 to more than 100. Mean attack rates per clone ranged from 0 to 10.0 per tree in 1987, and attacks again appeared aggregated (Fig. 2). There was only a slight association between the attack rate per tree in 1985 and that in 1987 ($r^2 = 0.17$), suggesting that clonal susceptibility to attack varies with time and that other factors affect attack rates.

TABLE 1. ANOVA table for cone beetle survey, Little River Seed Orchard, 1985

Source of variation	df	Sum of squares	F	P
Cone crop	1	966.23	15.86	0.0001
Clone	38	4402.42	1.90	0.0014
Clone*cone crop	26	2479.09	2.20	0.008

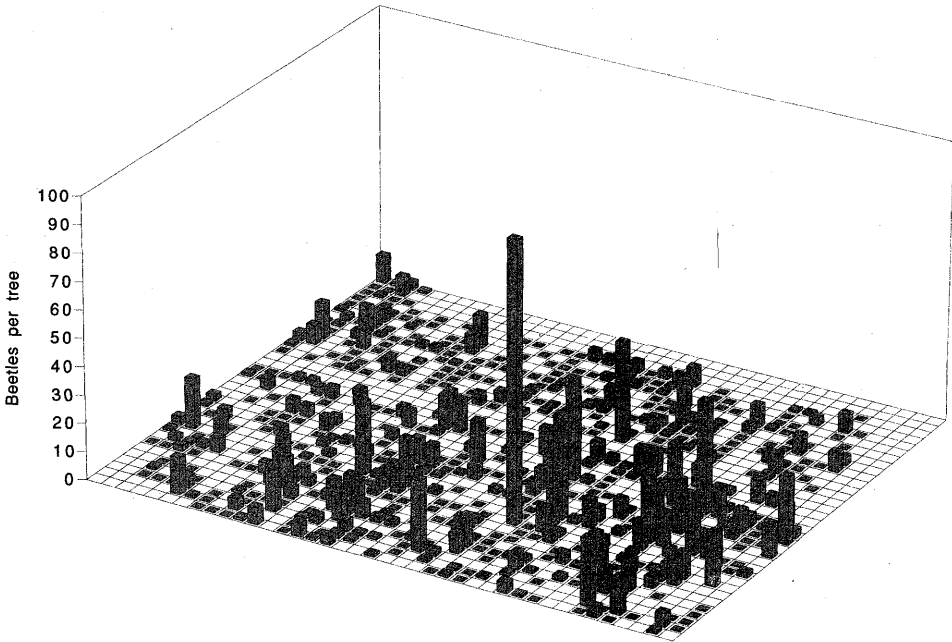


FIG. 2. Three-dimensional plot of attack rates per tree by *Pityophthorus orarius*, Little River Seed Orchard, 1987. Vertical bars represent individual trees, with bar height proportional to attack rate (range = 0–100 infested twigs per tree). Blank cells indicate absent trees; the two blank rows in the center represent the waterline.

Beetle attack rate was a linear function of cone crop in 1987 (Table 2), and attack rate was significantly different both among clones ($P < 0.01$) and among vigor classes ($P < 0.01$). Tree vigor was treated as a categorical variable in the analysis because it was not a strictly continuous variable; however, beetle attack showed a general tendency to increase with vigor class (Fig. 3). Dixon (1983) documented a similar phenomenon in a slash pine seed orchard. In Dixon's study, clones that were susceptible to attack by *Ips* and *Pityophthorus* spp. appeared healthy, but paired tree measurements revealed that beetles had selected trees with significantly poorer growth.

When means were adjusted for the effect of cone crop, both tree vigor ($P < 0.01$) and clone ($P < 0.01$) were still significant factors in beetle attack rate (Table 2). The association between cone crop and infestation rate may interest seed orchard managers because, if it remains constant over time, it may mean that the best producers are most vulnerable to attack.

TABLE 2. ANCOVA table for cone beetle survey, Little River Seed Orchard, 1987

Source of variation	df	Sum of squares	F	P
Regression (cone crop)	67	6393.87	3.11	<0.01
Error	569	17447.62		
Unadjusted means				
Vigor	3	2643.74	28.74	<0.01
Clone	63	2858.65	1.48	<0.01
Adjusted means				
Vigor	3	1845.39	20.00	<0.01
Clone	63	3164.05	1.64	<0.01

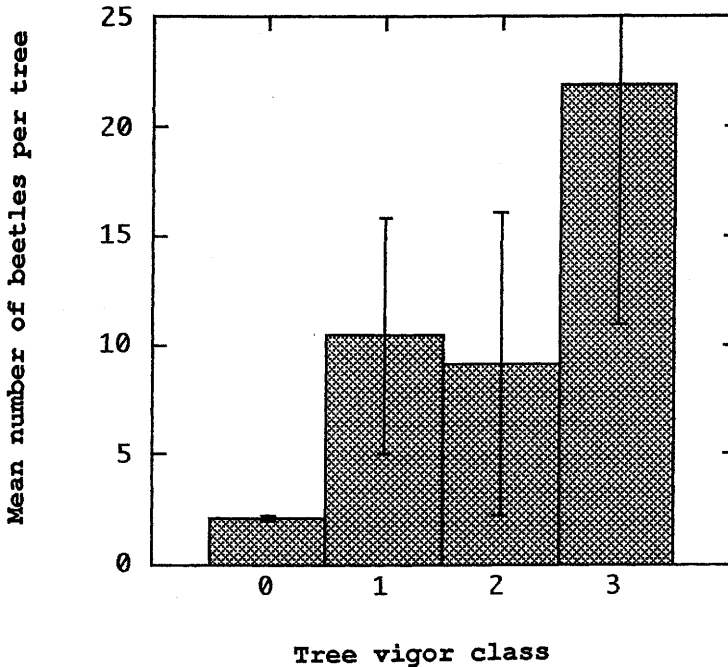


FIG. 3. Mean number of beetles per tree as a function of tree vigor class (0 = apparently healthy, 1 = slightly chlorotic, 2 = very chlorotic, 3 = very chlorotic with extensive needle-drop).

Mattson (1980) describes two classes of herbivores: those with anatomical specializations for exploiting nutrient-poor mature plant biomass, and those with behavioral adaptations for exploiting "the pulses of plant production" (fruits, seeds, and developing shoots), which have more nutrients and lower levels of fiber and toxic compounds. In Douglas-fir, carbohydrate reserves are translocated to expanding new shoots from April to early June (Kramer and Kozlowski 1979), coinciding with the twig beetle attack period (Hedlin and Ruth 1970). However, fruits and seeds compete powerfully for nutrients at the expense of vegetative growth, and reproduction uses much of the total plant carbohydrate and nitrogen reserves (Kramer and Kozlowski 1979). Thus, the selective attack of more fecund trees by twig beetles may be an adaptation to intercept nutrients being transported to expanding reproductive tissues. However, tree stress may play a role in the selective attack of trees with heavy cone crops; instances of scolytid attraction to stressed trees are common (D.L. Wood 1982; Dixon 1983). In either case, the attack pattern seen in this orchard appears doubly adaptive for *P. orarius*, because stressed trees tend both to bear heavier cone crops (Daniel et al. 1979) and to have lower levels of defense against insect attack (D.L. Wood 1982).

Hopkins (1915) split *Conophthorus* from *Pityophthorus* largely because of differences in size, feeding habit, and mating system, the cone feeders (*Conophthorus* spp.) being monogynous and larger than the twig and branch feeders (*Pityophthorus* spp.) (S.L. Wood 1982). The generic limits are obscure, however, and S.L. Wood (1982) gave only tentative status to the genus *Conophthorus*, citing intergradation with *Pityophthorus*. *Pityophthorus orarius*, in fact, shares several key behavioral attributes with *Conophthorus* spp. Like all *Conophthorus* spp., it constructs monogynous galleries in the axis of a shoot; in *P. orarius* the shoot is vegetative, and in *Conophthorus* spp. it is reproductive. Furthermore, *C. terminalis* Flores and Bright feeds exclusively on shoots (Flores and Bright 1987), and many nominally cone-feeding *Conophthorus* spp. survive in twigs when cones are scarce (Mattson

1979). *Conophthorus banksianae*, which was recently synonymized with *C. resinosae* (Wood 1989) and whose taxonomic status has been the subject of much recent study (de Groot and Ennis 1990; Page et al. 1990; de Groot and Borden 1991), also survives in shoots (McPherson et al. 1970). The selective attack by *P. orarius* on the most fecund trees elucidates further behavioral similarities between this *Pityophthorus* sp. and *Conophthorus* spp.; its ecological role in Douglas-fir, in fact, closely parallels that of *Conophthorus* spp. in pines.

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