Field Response of *Dendroctonus valens* (Coleoptera: Scolytidae) and a Major Predator, *Temnochila chlorodia* (Coleoptera: Trogositidae), to Host Kairomones and a *Dendroctonus* spp. Pheromone Component¹

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Abstract The red turpentine beetle, Dendroctonus valens (LeConte) (Coleoptera: Scolytidae), is a common bark beetle species found throughout much of North America. Aggregation pheromones have yet to be isolated and identified for D. valens. In this study, we examined the response of D. valens and a bark beetle predator, Temnochila chlorodia (Mannerheim) (Coleoptera: Trogositidae), to host produced kairomones and to the Dendroctonus spp. pheromone component exo-brevicomin. A total of 11,604 D. valens and 586 T. chlorodia were captured in multiple-funnel traps over a 14-wk period from 27 March to 5 July 2002. There was no significant difference in trap catch related to gender. The ratio of males to females was 1.01 for D. valens and 0.97 for T. chlorodia. Dendroctonus valens showed significant attraction to $(+)-\alpha$ -pinene, (-)- β -pinene, and (+)-3-carene, but the addition of ethanol did not significantly increase trap catch. Racemic exo-brevicomin was not attractive to D. valens and significantly reduced its attraction to the monoterpene and ethanol blend. This observation, in combination with results from other authors, suggests that D. valens is not responding to the western pine beetle, D. brevicomis LeConte, pheromone or any of the individual components. Potential explanations for why D. valens is attracted to D. brevicomis infested trees are provided. There were no significant differences in the trap catch of T. chlorodia among unbaited traps or traps baited with (+)- α pinene, (-)- β -pinene, and (+)-3-carene or (+)- α -pinene, (-)-(β -pinene, and (+)-3-carene, and ethanol. The addition of exo-brevicomin significantly increased attraction. During the course of this study, a single peak in flight activity was observed during late May through early June for both species.

Key Words Dendroctonus valens, Dendroctonus brevicomis, Temnochila chlorodia, Pinus ponderosa, Scolytidae, monoterpenes, *exo*-brevicomin

The red turpentine beetle, *Dendroctonus valens* (LeConte) (Coleoptera: Scolytidae), is a common bark beetle species found throughout much of North America, exclusive of the southeastern USA. *Dendroctonus valens* colonizes all species of pine within its native range, but ponderosa pine, *Pinus ponderosa* Dougl. ex. Laws., is a preferred host throughout western North America. Attacks are usually confined to the

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basal portions of previously stressed, weakened, or dead and dying trees (Furniss and Carolin 1977), and are not considered a direct threat to the overall health of a tree (Hall 1984). *Dendroctonus valens* rarely mass attacks a tree, however, the authors have occasionally observed substantial numbers of attacks (>100 pitch tubes) along the lower bole of fire-injured trees following prescribed burning (CJF, unpubl. data) and wildfire (SLS and DRC, unpubl. data). Significant tree mortality has been attributed to *D. valens* in a 17-yr-old *P. ponderosa* plantation in northern California, and of *P. tabuliformis* Carriere in China where it was accidentally introduced (Rappaport et al. 2001). Although much uncertainty exists as to whether *D. valens* is a primary mortality agent of *P. ponderosa*, it is known to vector a rather virulent strain of the ophiostomoid fungus, *Leptographium terebrantis* Barras and Perry in California (Owen et al. 1987).

Temnochila chlorodia (Mannerheim) (Coleoptera: Trogositidae) is a common predator of many bark beetle species in western North America (Furniss and Carolin 1977). The larvae develop within the inner bark and feed on bark beetle larvae, pupae and perhaps callow adults (Miller and Keen 1960). The adults are also highly predaceous, and may be important in regulating bark beetle populations at endemic levels (Furniss and Carolin 1977).

Aggregation pheromones have not been reported for *D. valens*. Turpentine and ethanol are recognized as important host finding and recognition cues for a variety of conifer-infesting insects (Chénier and Philogéne 1989, Rieske and Raffa 1991, Byers 1992, Fettig and Salom 1998). Turpentine consists mostly of host monoterpenes and is moderately attractive to *D. valens* (Vité and Gara 1962, Chénier and Philogéne 1989, Hobson et al. 1993). The principal monoterpenes in *P. ponderosa* oleoresin are (-)- β -pinene, (+)-3-carene, (-)-limonene, myrcene, and (-)- α -pinene (Mirov 1961, Hobson et al. 1993). (-)- β -Pinene is highly attractive to both sexes of *D. valens*, and the effect increases with elevating dosage (Hobson et al. 1993). Hobson et al. (1993) also reported significant increases in *D. valens* trap catch attributable to (+)-3-carene and (+)- α -pinene. In California, (+)- α -pinene (Hobson et al. 1993). In Wisconsin, *D. valens* apparently does not exhibit a strong preference for either enantiomer of α -pinene (Erbilgin and Raffa 2000, Erbilgin et al. 2001). Limonene and myrcene are thought to have no effect on *D. valens* (Hobson et al. 1993).

Ethanol is a product of anaerobic plant and microbial metabolism (Phillips et al. 1988) and can accumulate to abnormally high levels when trees become stressed (Kimmerer and Kozlowski 1982, Kelsey and Joseph 1998) or when tissues become senescent (Kimmerer and Kozlowski 1982). Ethanol is commonly used for sampling root and stem feeding insects in forested stands (Chénier and Philogéne 1989, Rieske and Raffa 1991, Fettig and Salom 1998, Erbilgin et al. 2001). Klepzig et al. (1991) sampled the entomofauna associated with red pine decline areas in Wisconsin, and observed a 60× increase in *D. valens* trap catch when turpentine baits were replaced with a 1:1 mixture of ethanol and turpentine.

The western pine beetle, *D. brevicomis* LeConte, is a major cause of *P. ponderosa* mortality in the western USA (Furniss and Carolin 1977). *Dendroctonus valens* and *D. brevicomis* are sympatric and are commonly found in the same tree. Dendroctonus brevicomis produces two aggregation pheromone components, (+)-*exo*-brevicomin and (–)-frontalin (Wood et al. 1976, Browne et al. 1979). Hall (1983) demonstrated that *D. valens* colonized *P. ponderosa* trees baited with (+)-*exo*-brevicomin, (–)-frontalin and myrcene at significantly higher rates than unbaited trees.

The primary objectives of this study are: (1) to evaluate the response of *D. valens* and *T. chlorodia* to ethanol and *exo*-brevicomin in the presence of (+)- α -pinene, (-)- β -pinene, and (+)-3-carene, (2) to identify an effective bait for *D. valens* that minimizes capture of *T. chlorodia*, and (3) to describe the spring flight period of both species.

Materials and Methods

This study was conducted on the Lassen National Forest, Lassen Co., CA, 2002 (Swain's Hole, 40°39.96'N, 121°15.82'W, elevation 1676 m). The cover type was Ponderosa-Jeffrey (Yellowpine) Series (Smith 1994). Forest composition, in order of decreasing abundance, was *P. ponderosa*, Jeffrey pine, *Pinus jeffreyi* Grev. & Balf., white fir, *Abies concolor* (Gond. and Glend.) Hildebr., and incense cedar, *Libocedrus decurrens* Torr. The area was commercially thinned from below in 1999 and prescribed burned in October 2001.

Twenty 16-unit Lindgren[®] multiple-funnel traps (Lindgren 1983) were deployed along an existing road (FR33N18) on 27 March 2002. Trap locations were separated by >100 m to avoid interference among adjacent treatments. Traps were hung on 3-m metal poles with collection cups 5 to 8 cm above the ground, and placed >10 m from any living pine. Each trap location was randomly assigned one of four treatments: (1) (+)- α -pinene, (-)- β -pinene, and (+)-3-carene (*D. valens* lure), (2) *D. valens* lure + ethanol, (3) *D. valens* lure + ethanol + *exo*-brevicomin, and (4) untreated control (Table 1). A 3 × 3-cm time-released insecticidal Prozap Pest Strip (2,2-dichlorovinyl dimethyl phosphate (DDVP), Loveland Industries Inc., Greely, CO) was placed in the collection cup to kill arriving insects and reduce damage or loss by invertebrate predation. Baits were replaced once during the course of this study on 16 May 2002. Treatments were re-randomized weekly during each collection. Catches were immediately transported to the laboratory for storage and analysis. Final collections were made on 5 July 2002. Specimens were tallied and identified using available keys

| Semiochemical | Chemical purity | Release device | Release rate (@25°C) | |
|--------------------------|-----------------|---------------------------|-------------------------|--|
| D. valens lure* | | | | |
| (+)-α-pinene | 98% | 15 ml polyethylene bottle | 150 mg/24 h | |
| (–)-β-pinene | 98% | | | |
| (+)-3-carene | 98% | | | |
| ethanol | 98% | 150 ml polyvinyl pouch | 1-2 g/24 h** | |
| exo-brevicomin [racemic] | 97% | 400µL polyvinyl vial | 2-3 mg/24 h | |

Table 1. Description of semiochemicals and release devices used in a trapping bioassay, Lassen National Forest, (40°39.96'N, 121°15.82'W), CA, 27 March-5 July 2002

* *D. valens* lure of 1:1:1 ratio. All semiochemicals manufactured by Phero Tech Inc., Delta, BC, Canada. ** At 20°C. (Wood 1982) and voucher specimens. All *D. valens* were sexed according to Lyon (1958) based on distinguishing characteristics present on the seventh abdominal tergite. *Temnochila chlorodia* were sexed according to Struble and Carpelan (1941) based on the presence of a submental pit on the male. Voucher specimens have been deposited in the USDA Forest Service Bark Beetle and Common Associates Collection housed in Placerville, CA.

The experimental design was completely randomized with four treatments and 70 replications per treatment. We limited statistical analyses for *D. valens* to replications where \geq 8 individuals were caught in any one treatment (n = 36). Gender differences were analyzed for each of the four treatments using paired t-tests (SigmaStat Version 2.0, SPSS Inc.). A test of normality was performed, and square root transformations were used when the data deviated significantly from a normal distribution (Sokal and Rohlf 1995). We performed a one-way analysis of variance on the number of beetles caught per trap per week using $\alpha = 0.05$ (SigmaStat Version 2.0, SPSS Inc.). If a significant treatment effect was detected, the Tukey's multiple comparison test (Tukey's HSD) was used for separation of treatment means.

Results and Discussion

A total of 11,604 *D. valens* and 586 *T. chlorodia* were captured in funnel traps over a 14-week period from 27 March through 5 July 2002. The ratio of males to females was 1.01 and 0.97 for *D. valens* and *T. chlorodia*, respectively. There were no significant differences in trap catch related to gender (P > 0.5; all cases), and therefore, the data for each species were pooled, and results pertain to both male and female responses. The equivalent responses observed between genders suggest that these kairomones may function as both host finding and ovipositional (mating) cues in *D. valens* (Fettig and Salom 1998). Mating pairs are commonly observed at the base of host trees, and unlike many congenerics, an aggregation or sex pheromone has not been identified for this species.

Dendroctonus valens. During this study, a single peak in flight activity occurred in late May through early June (Julian dates 136 to 164; Fig. 1). *Dendroctonus valens* overwinters as an adult and there is often a period in early spring when a large number of adults are captured (Smith 1971). It is at this time that *D. valens* is likely searching for viable hosts. *Dendroctonus valens* is univoltine throughout most of the northern USA, but may have 2 to 3 generations per year in warmer climates (Furniss and Carolin 1977). In the Sierra Nevada, the usual length of development from egg to adult is approximately 12 wks (Smith 1971), and it is, therefore, possible that a second peak in flight activity may occur in fall.

A significant treatment effect was observed (P < 0.001). The kairomonal blend of (+)- α -pinene, (-)- β -pinene, and (+)-3-carene (*D. valens* lure) and ethanol, and the *D. valens* lure alone accounted for 5,432 and 4,687 *D. valens*, respectively, representing 87.2% of the total trap catch. The addition of ethanol slightly increased attraction, but the effect was not statistically significant (Table 2). Joseph et al. (2001) sampled the response of some scolytids, including *D. valens*, to ethanol and 4-allylanisole in combination with (+)- α -pinene and (-)- β -pinene in ponderosa pine forests of central Oregon. *Dendroctonus valens* was captured 4× more frequently in traps baited with high release rates (986 mg/24 hr) of ethanol than low release rates (108 mg/24 h). Similarly, in Wisconsin, Klepzig et al. (1991) observed a 60× increase in *D. valens* trap catch associated with the use of ethanol, but the release rate was not reported in that

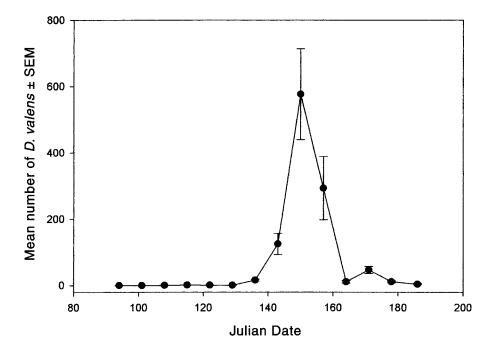


Fig. 1. The flight periodicity of *Dendroctonus valens* LeConte at Lassen National Forest (40°39.96'N, 121°15.82'W), California, 27 March-5 July 2002.

| Table 2. | 2. Mean number (±SEM) of <i>D. valens</i> caught per trap per week in multiple- | | | |
|--|---|--|--|--|
| | funnel traps baited with kairomones and a bark beetle pheromone | | | |
| component, Lassen National Forest, California 2002 | | | | |

| Treatment | Mean ± SEM |
|--|----------------|
| Control | 2.4 ± 1.0 a* |
| <i>D. valens</i> lure | 129.7 ± 33.2 c |
| D. valens lure + ETOH | 149.8 ± 39.4 c |
| D. valens lure + ETOH + exo-brevicomin | 38.4 ± 10.8 b |

* Means followed by the same letter are not significantly different (P > 0.05 all cases; Tukey's HSD).

study. Our ethanol release rates were slightly higher (1-2 g/24h) than those reported by Joseph et al. (2001); yet, we only observed a 1.2× increase in attraction when presented in combination with (+)- α -pinene, (-)- β -pinene, and (+)-3-carene.

The *D. valens* lure plus ethanol and *exo*-brevicomin accounted for 1,397 *D. valens*, representing 12% of the total trap catch. The addition of *exo*-brevicomin to the *D. valens* lure plus ethanol significantly reduced trap catch by approximately 3.8× (Table 2). *exo*-Brevicomin is an aggregation pheromone component produced by at least

three economically important bark beetle species, including the roundheaded pine beetle, D. adjunctus Blanford, the mountain pine beetle, D. ponderosae Hopkins, and D. brevicomis (Skillen et al. 1997). The release of exo-brevicomin by female D. brevicomis induces an aggregation response (Wood et al. 1976, Browne et al. 1979), which is further enhanced by the release of small quantities of frontalin by males (Browne et al. 1979). Originally, we hypothesized that exo-brevicomin would increase attraction because D. valens attacks commonly follow D. brevicomis attacks, and D. valens is attracted to D. brevicomis-infested logs (Vité and Gara 1962), and standing trees (Hall 1983). The trees in Hall's (1983) study were baited with exo-brevicomin, frontalin and myrcene to induce D. brevicomis attack, and unfortunately the confounding effects of the two treatments (pheromone/kairomone bait and beetle-induced tree responses) are problematic. For example, it is not possible to determine if the response of D. valens was mediated by attraction to the bait or its individual components; to host volatiles released in response to severing of the resin canals by boring beetles; to other host compounds released in response to D. brevicomis attack; or other beetle-produced compounds.

Hall (1983) suggested that compounds released from trees under attack by D. brevicomis play a role in the attraction of D. valens to them. Our data show that three of the major monoterpenes found in the oleoresin of P. ponderosa (and ethanol) are attractive to D. valens when presented in combination. The observation that exobrevicomin is not attractive to D. valens, in combination with results from Furniss and Schmitz (1971) and Hobson et al. (1993) regarding frontalin and host monoterpenes, suggests that D. valens is not responding to the D. brevicomis aggregation pheromone or any of the individual components. Our results support the suggestion by Hall (1983) that D. valens must be responding to the monoterpenes released from host trees upon attack by D. brevicomis. The most probable source of these monoterpenes is the oleoresin present in pitch tubes. Dendroctonus valens is commonly attracted to wounded trees (Furniss and Schmitz 1971, Smith 1971), and D. brevicomis is one of many potential mechanisms that cause wounding to occur. Similarly, we have observed high levels of D. valens attacks on trees that have been wounded following prescribed fire and wildfire. exo-brevicomin may function as an allomone in this system thereby reducing interspecific competition through partitioning of a limiting resource between congenerics.

Temnochila chlorodia. The flight period of *T. chlorodia* closely agreed with that reported for *D. valens* in this study (Fig. 1, 2). A single peak occurred during late May to early June (Julian dates 136 to 164; Fig. 2), but a second smaller peak also was observed in mid-June (Fig. 2). *Temnochila chlorodia* is likely univoltine in this region (Struble 1942).

A significant treatment effect was observed (P < 0.001). The addition of *exo*brevicomin to the monoterpene blend plus ethanol significantly increased trap catch and accounted for 505 *T. chlorodia*, representing 86.2% of the total trap catch (Table 3). There were no significant differences among the remaining treatments suggesting that *T. chlorodia* is not attracted to monoterpenes and ethanol emitted from the primary host of their bark beetle prey (Table 3). *Temnochila chlorodia* is usually attracted to *P. ponderosa* that are recently attacked by *D. brevicomis* (Stephen and Dahlsten 1976), and the components of several bark beetle aggregation pheromones, including *exo*-brevicomin (Pitman and Vité 1971, Bedard et al. 1980, Seybold et al. 1992). Our results confirm this observation.

Conclusion. Several recent attempts at trapping D. valens with host kairomones

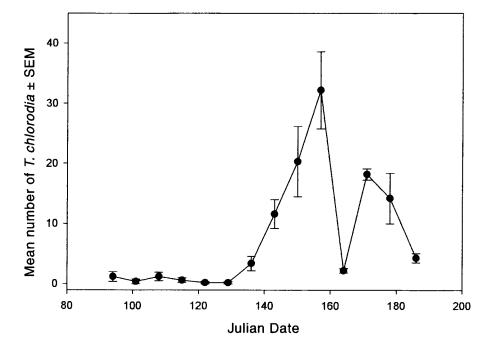


Fig. 2. The flight periodicity of *Temnochila chlorodia* (Mannerheim) at Lassen National Forest (40°39.96'N, 121°15.82'W), California, 27 March-5 July 2002.

| Table 3. | Mean number (±SEM) of <i>T. chloridia</i> caught per trap per week in mul- | | | |
|----------|--|--|--|--|
| | tiple-funnel traps baited with kairomones and a bark beetle phero- | | | |
| | mone component, Lassen National Forest, California 2002 | | | |

| Treatment | Mean ± SEM |
|--|---------------------|
| Control | $0.02 \pm 0.02 a^*$ |
| D. valens lure | 0.64 ± 0.14 a |
| D. valens lure + ETOH | 0.51 ± 0.12 a |
| D. valens lure + ETOH + exo-brevicomin | 7.49 ± 1.30 b |

* Means followed by the same letter are not significantly different (P > 0.05 all cases; Tukey's HSD).

have resulted in the collection of relatively few individuals per unit time (Klepzig et al. 1991, Peck et al. 1997, Erbilgin and Raffa 2000, Erbilgin et al. 2001, Rappaport et al. 2001) which we suggest would be insufficient to induce attack on apparently-healthy trees (<30 *D. valens* per trap per week; all cases). Our data show that the combination of (+)- α -pinene, (-)- β -pinene, and (+)-3-carene (*D. valens* lure) is highly attractive to *D. valens* during peak flight activity (Table 2; Fig. 1). The addition of ethanol increases attraction, but the effect was not significant (Table 2). The addition of *exo*-brevicomin

significantly reduces attraction and, therefore, may be functioning as an allomone in this system. *Temnochila chlorodia* is not attracted to host monoterpenes or the addition of ethanol. *exo*-brevicomin is highly attractive (Table 3) and, therefore, likely functions as a kairomone signaling prey location.

In recent years, *D. valens* infestations appear to be increasing throughout the Pacific Northwest, and with a greater emphasis on the use of prescribed fire as a management tool this trend will likely increase for some time (Ferrell 1996). Future studies are required to determine if *D. valens* is capable of causing direct tree mortality in the absence of other scolytids. We intend to use the combination of host kairomones identified in this study to explore the possibility of this phenomenon in mature *P. ponderosa* forests.

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References Cited

- Bedard, W. D., D. L. Wood, P. E. Tilden, K. Q. Lindahl Jr., R. M. Silverstein and J. O. Rodin. 1980. Field responses of the western pine beetle and one of its predators to host and beetle-produced compounds. J. Chem. Ecol. 6: 625-641.
- Browne, L. E., D. L. Wood, W. D. Bedard, R. M. Silverstein and J. R. West. 1979. Quantitative estimates of the western pine beetle attractive pheromone components, *exo*-brevicomin, frontalin, and myrcene in nature. J. Chem. Ecol. 5: 397-414.
- **Byers, J. A. 1992.** Attraction of bark beetles, *Tomicus piniperda, Hylurgops palliatus* and *Try-podendron domesticum* and other insects to short-chain alcohols and monoterpenes. J. Chem. Ecol. 18: 2385-2402.
- Chénier, J. V. and J. R. Philogéne. 1989. Field responses of certain forest coleoptera to conifer monoterpenes and ethanol. J. Chem. Ecol. 15: 1729-1745.
- Erbilgin, N. and K. F. Raffa. 2000. Opposing effects of host monoterpenes on responses by two sympatric species of bark beetles to their aggregation pheromones. J. Chem. Ecol. 26: 2527-2548.
- **Erbilgin, N., A. Szele, K. D. Klepzig and K. F. Raffa. 2001.** Trap type, chirality of α-pinene, and geographic region affect sampling efficiency of root and lower stem insects in pine. J. Econ. Entomol. 94: 1113-1121.
- Ferrell, G. T. 1996. The influence of insect pests and pathogens on Sierra forests. In Sierra Nevada Ecosystem Project, Final Report to Congress, Vol II., Assessments and Scientific Basis for Management Options. Davis: University of California, Centers for Water and Wildland Resources, pp. 1177-1192.
- Fettig, C. J. and S. M. Salom. 1998. Comparisons of two trapping methods for *Hylobius pales* (Coleoptera: Curculionidae) in Virginia. Environ. Entomol. 27: 572-577.
- Furniss, M. M. and R. F. Schmitz. 1971. Comparative attraction of Douglas fir beetles to frontalin and tree volatiles. U.S. Dept. of Agric. For. Serv. Res. Pap. INT-96. 16 p.
- Furniss, R. L. and V. M. Carolin. 1977. Western forest insects. U.S. Dept. of Agric. For. Serv. Misc. Publ. 1339. 654 p.
- Hall, R. W. 1983. Attraction of *Dendroctonus valens* (Coleoptera: Scolytidae) to ponderosa pines baited with *Dendroctonus brevicomis* (Coleoptera: Scolytidae) pheromone. Environ. Entomol. 12: 718-719.

- **1984.** Effectiveness of insecticides for protecting ponderosa pines from attack by the red turpentine beetle (Coleoptera: Scolytidae). J. Econ. Entomol. 77: 446-448.
- Hobson, K. R., D. L. Wood, L. C. Cool, P. R. White, T. Ohtsuka, I. Kubo and E. Zavarin. 1993. Chiral specificity in responses by the bark beetle *Dendroctonus valens* to host kairomones. J. Chem. Ecol. 19: 1837-1846.
- Joseph, G., R. G. Kelsey, R. W. Peck and C. G. Niwa. 2001. Response of some scolytids and their predators to ethanol and 4-allylanisole in pine forests of central Oregon. J. Chem. Ecol. 27: 697-713.
- Kelsey, R. G. and G. Joseph. 1998. Ethanol in Douglas-fir with black stain root disease (*Leptographium wagnerii*). Can. J. For. Res. 28: 1207-1212.
- Kimmerer, T. W. and T. T. Kozlowski. 1982. Ethylene, ethane, acetaldehyde, and ethanol production by plants under stress. Plant Physiol. 69: 840-847.
- Klepzig, K. D., K. F. Raffa and E. B. Smalley. 1991. Association of insect-fungal complexes with red pine decline in Wisconsin. For. Sci. 37: 1119-1139.
- Lindgren, B. S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). Can. Entomol. 115: 299-302.
- Lyon, R. L. 1958. A useful secondary sex character in *Dendroctonus* bark beetles. Can. Entomol. 10: 382-384.
- Miller, J. M. and F. P. Keen. 1960. Biology and control of the western pine beetle. U.S. Dept. of Agric. Misc. Pub. 800.
- Mirov, N. T. 1961. Composition of gum turpentines of pines. U.S. Dept. of Agric. For. Serv. Tech. Bull. 1239. 158 p.
- Owen, D. R., K. Q. Lindahl Jr., D. L. Wood and J. R. Parmeter, Jr. 1987. Pathogenicity from fungi isolated from *Dendroctnus valens*, *D. brevicomis*, and *D. ponderosae* to ponderosa pine seedlings. Phytopathology 77: 631-636.
- Peck, R. W., A. Equihua-Martinez and D. W. Ross. 1997. Seasonal flight patterns of bark and ambrosia beetles (Coleoptera: Scolytidae) in northeastern Oregon. Pan-Pacific Entomol. 73: 204-212.
- Phillips, T. W., A. J. Wilkening, T. H. Atkinson, J. L. Nation, R. C. Wilkinson and J. L. Foltz. 1988. Synergism of turpentine and ethanol as attractants for certain pine-infesting beetles (Coleoptera). Environ. Entomol. 17: 456-462.
- Pitman, G. B. and J. P. Vité. 1971. Predator-prey response to western pine beetle attractants. J. Econ. Entomol. 64: 402-404.
- Rappaport, N. G., D. R. Owen and J. D. Stein. 2001. Interruption of semiochemical-mediated attraction of *Dendroctonus valens* (Coleoptera: Scolytidae) and selected nontarget insects by verbenone. Environ. Entomol. 30: 837-841.
- Rieske, L. K. and K. F. Raffa. 1991. Effect of varying ethanol and turpentine levels on attraction of two pine root weevil species, *Hylobius pales* and *Pachylobius picivorus* (Coleoptera: Curculionidae). Environ. Entomol. 20: 48-52.
- Seybold, S. J., S. A. Teale, D. L. Wood, A. Zhang, F. X. Webster, K. Q. Lindahl, Jr. and I. Kubo. 1992. The role of lanierone in the chemical ecology of *lps pini* (Coleoptera: Scolytidae) in California. J. Chem. Ecol. 18: 2305-2329.
- Skillen, E. L., C. W. Berisford, M. A. Camann and R. C. Reardon. 1997. Semiochemicals of forest and shade tree insects in North America and management implications. Morgantown, WV: U.S. Dept. of Agric. For. Serv. FHTET-96-15. 182 pp.
- Smith, R. H. 1971. Red turpentine beetle. U.S. Dept. of Agric. For. Serv. Forest Pest Leaflet. 7 p.
- Smith, S. 1994. Ecological guide to eastside pine plant associations. Northeastern California: Modoc, Lassen, Klamath, Shasta-Trinity, Plumas, and Tahoe National Forests. R5-ECOL-TP-004. Albany, CA: U.S. Dept. of Agric. For. Serv. Pacific Southwest Region. 174 p.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry, 3rd ed. W. H. Freeman & Co., New York. 887 p. Stephen, F. M. and D. L. Dahlsten. 1976. The arrival sequence of the arthropod complex

following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine. Can. Entomol. 108: 283-304.

- Struble, G. R. 1942. Biology of two native predators of the mountain pine beetle in sugar pine. Pan-Pacific Entomol. 18: 97-107.
- Struble, G. R. and L. H. Carpelan. 1941. External sex characters of two important native predators of the mountain pine beetle in sugar pine. Pan-Pacific Entomol. 17: 153-156.
- Vité, J. P. and R. I. Gara. 1962. Volatile attractants from ponderosa pine attacked by bark beetles (Coleoptera: Scolytidae). Contrib. Boyce Thompson. Inst. 21: 251-274.
- Wood, D. L., L. E. Browne, B. Ewing, K. Q. Lindahl, W. D. Bedard, P. E. Tilden, K. Mori, G. B. Pitman and P. R. Hughes. 1976. Western pine beetle: specificity among enantiomers of male and female components and attractant pheromone. Science 192: 896-898.
- Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America. (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin. Nat. Mem. No. 6.