# Field Bioassays of Synthetic Pheromones and Host Monoterpenes for *Conophthorus coniperda* (Coleoptera: Scolytidae)

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**ABSTRACT** Four major monoterpenes, (±)-α-pinene, 1 (S)-(−)-β-pinene, (*R*)-(+)-limonene, and myrcene are found in the cones of eastern white pines, *Pinus strobus* L. Mixtures of these, as well as. u-pinene or β-pinene alone. increased catches of male white pine cone beetles, *Conophthorus* coniperda (Schwartz). in traps baited with the female sex pheromone, (±)-*trans*-pityol. The monoterpenes by themselves as mistures or individually (a-pinene, β-pinene) were not attractants for males or females. Traps baited with (±)-*trans*-pityol and α-pinene caught as many, or significantly more beetles than those baited with pityol and a four monoterpene mixture (1:1:1:1) used in seed orchards in North Carolina, Ohio. and Virginia. Three beetle-produced compounds, conophthorin, *trans*-pinocarveol. and myrtenol did not enhance catches of males or females in (±)-*trans*-pityol-baited traps. Racemic E-(k)- conophthorin. E-( -)- conophthorin, and *E*-( +)- conophthorin significantly reduced catches of males in traps baited with (±)-*trans*-pityol alone. Female *C.* coniperda were not attracted to any of the host- or beetle-produced compounds tested. The study demonstrated that traps with baits releasing (±)-*trans*-pityol at about 1 mg/wk with (±)-α-pinene (98% pure) are potentially valuable tools for C *coniperda* pest management. Baited traps can be used to monitor *C. coniperda* populations or possibly to reduce seed losses in a beetle trap-out control strategy.

**KEY WORDS** *Conophthorus coniperda*, pheromone. monoterpenes

EASTERN WHITE PINE. *Pinus strobus* L.. is highly desirable as lumber. To produce genetically improved planting stock. forestry organizations have established seed orchards. The most destructive cone pest in these orchards is the white pine cone beetle. *Conophthorus coniperda* (Hedlin et al. 1980: DeBarr et al. 1982: de Groot 1986. 1990: Turgeon and de Groot 1992), which occurs throughout the range of eastern white pine (Wood 1982) Current control options for C. *coniperda* in seed orchards are severely limited. The Environmental Protection Agency (EPA) registration for carbofuran, the only insecticide with demonstrated efficacy for C. *coniperda* control (DeBarr et al. 1982), was recently canceled. Adult beetles overwintering in old cones on the forest floor can be killed by prescribed fire. but this technique requires adequate fuel and ideal burning conditions to be successful (Wade et al. 1989). Development of effective semiochemical-based pest management techniques to monitor and control C. *coniperda* in seed orchards is highly desirable.

In early spring. female C. *coniperda* fly to the crowns of trees to initiate cone attacks. The females nrejoined by males (Godwin and Odell 1965) once they begin to construct galleries. Evidence for a female-produced pheromone for *Conophthorus resinosae* Hopkins and C. *coniperda* was presented by de Groot et al. (1991). In laboratory bioassays with walking beetles. male C. *coniperda* showed strong responses to volatiles from cones infested with female beetles or pairs of beetles. while females reacted strongly to volatiles from pairs of beetles in cones and to cones with male beetles. In the related species. *Conophthorus ponderosae* Hopkins. males responded to odors from female-infested cones ofponderosapine. ***Pinusponderosa*** Laws. in laboratory bioassavs, while females reacted to odors from male beetlesin cones (Kinzer et al. 1972. Kinzer and Reeves 1976).

Pheromones from male and female C. *coniperda* and C. *resinosae* and volatiles from their host cones have been identified (Birgersson et al. 1995; Pierce et al. 1995). The principal compound produced by female C. *coniperda* is (+)-*trans*-pityol, (2*R*,5*S*)-2-(1-hydroxy-1-methylethyl)-5-methyltetrahydrofuran (Birgersson et al. 1995). The major compound produced by C. *coniperda* males is the spiroacetal, (5*S*,7*S*)-7-methyl-1,6-dioxaspiro[4.5]-decane hereafter called conophthorin (de Croot 1992). Conophthorin is also produced by the females. Both pityol and conophthorin have 2 geometric and two optical isomers. Both sexes also produce lesser amounts Of *trans*-pinocarveol, (−)-myrtenol, *trans*-verbenol and perilla alcohol (unpublished data). The major host volatiles released by beetle-infested *P. strobus* cones included the monoterpene hydrocarbons, a-pinene. β-pinene. myrcene, limonene and a monoterpene ester. bornyl

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acetate. For other scolytids, particularly bark beetles. host monoterpenes such as a-pinene and **myrcene** are known to enhance the capture of beetles in traps baited with pheromones (Borden 1985. Borden et al. 1987. Byers et al. 1988).

We report the results of field experiments designed to examine the response of *C. coniperda* to traps baited with various combinations of the beetle-produced compounds (±)-*E*-conophthorin, (+)-*E*-conophthorin. (−) -E-conophthorin. (±)-*cis*-pityol, (±)-*trans*-pityol, *trans*-pinocarveol, and myrtenol: the host-produced compound borynl acetate; extracted white pine cone oils. and the synthetic monoterpenes, α-pinene. β-pinene. myrcene. and limonene.

## Materials and Methods

Treatments. Nine experiments were conducted to test the effects of various compounds. alone or in combination. on the attractiveness of pityol in traps. Experiment 1 compared beetle catches for (±)-*E*-conophthorin. (±)-*trans*-pityol (hereafter referred to as conophthorin and pityol, respectively) and white pine cone oils alone or in combination. The (+ ), (−) isomers of -E-conophthorin and (± )-E-conophthorin. combined with pityol were examined in experiment 2. and in experiment 3. three ratios of *trans:cis* pityol were compared. Experiment 4 was a subtractive bioassay where trap catches were compared for single component deletions from treatments containing (+)-*trans*-pityol, truns-pinocarveol, myrtenol, bornyl acetate and a mixture of (±)-α-pinene, (1*S*)-(−)-β-pinene. *(R)* - *(±)* -limonene, and myrcene (tech.) in a 1:1:1:1 mis. Different release rates of pityol and host monoterpenes were studied in experiment 5. In experiment 6. pityol and single deletions of monoterpenes from a mixture of α-pinene, β-pinene, limonene, and myrcene were compared. Experiments 7, 8, and 9 compared catches for pityol alone or pityol combined with α-pinene or β-pinene. Experiments contained the same unbaited traps as their controls, except experiments 4 and 5 where vials containing only n-octane were used.

Study sites. The experiments were conducted from April to June 1990-1993, in the Beech Creek Seed Orchard. 10 km south of Murphy, NC (experiments 1, 4), and in ON, Canada, at the Orono Seed Orchard, Orono (experiments 7–9), and Pancake Bay Provincial Park, 80 km north of Sault Ste. Marie (experiments 2, 3, 6). In 1991, 3 eastern white pine seed orchards at Morganton, NC; Gifford, OH: and Buckingham, VA were used for experiment 5.

Chemicals. The synthetic pheromones, (±)-*E*-conophthorin, (+)-E-conophthorin, (−)-*E*-conophthorin, (± )-*cis*-pityol, (±)-*trans*-pityol, and (+)-*trans*-pityol were made by H. Pierce, Jr. (Pierce et al. 1995). The (±)-*trans*-pityol used in the experiments was 95.4% pure, contained 1.2% of the *cis* isomer and was prepared from (±) sulcatol (97% optically pure, Phero Tech, Delta, British Columbia) by the method described in Pierce et al. **(1995).** The purities and synthesis of the other isomers of pityol and the isomers of conophthorin are reported in Pierce et al. (1995). The *trans*-pinocarveol was a gift from W. Francke and was prepared from β-pinene (Aldrich, Milwaukee, WI) according to Joshi et al. (1968). Myrtenol, bornyl acetate and the monoterpene hydrocarbons. (±)-α-pinene (98% pure). (1S)-(−)-β-pinene (99%), (R)-(±)-limonene (97% pure). and myrcene (technical grade) were purchased from Aldrich. and n-octane (>99% pure) was purchased from Sigma, St. Louis, MO.

In experiment 1, cone oil was extracted from eastern white pine cones with pentane. The extract was filtered through a column of silica gel to exclude resin acids. using pentane as the mobile phase. The purified pine oil fraction was concentrated prior to use. In experiment 2. cone oil was obtained by steam distillation (Pierce et al. 1995).

Chemical Release Devices. Releasers for volatiles in experiments 4 and 5 consisted of 5-cm lengths of 1.6-mm i.d. nonstick tubing, with cotton wicks, inserted through a hole cut in the screw-top of 2-ml glass vials (Birgersson et al. 1995). A spring clip was used to attach the vial to one of the plastic rods between funnels 6 and 7 on each trap. Each vial contained volatiles formulated in a final volume of 2 ml of *n*-octane. with a release rate of 0.3 ml/24 h at 25°C. in the laboratory. All baits for experiments 4 and 5 contained synthetic pheromones or host monoterpenes formulated in n-octane, and released at rates from 10–1,000 cone-equivalents, or beetle-equivalents per hour, where 1 cone-equivalent or beetle-equivalent is the quantity of volatiles collected during aerations of one cone or beetle-infested cone for one h (unpublished data). For experiment 4, the baits contained 66.7 μg (+)-*trans*-pityol diluted in n-octane to achieve a release rate of 10 female-equivalents/h. Treatments with monoterpenes contained cu-pinene, β-pinene, myrcene and limonene (1:1:1:1) or various combinations of three of the four monoterpenes (1:1:1). For each bait, 10 μ liter of monoterpenes were diluted in *n*-octane to achieve a release rate of 1.4 mg/d. For experiment 5, (±)-*trans*-pityol was released at 10 female-equivalents/h (0.01 mg/d), 100 female-equivalents/h (0.1 mg/d) and 1,000 female-equivalents/h (1.0 mg/d). For experiment 6, baits released (±)-*trans*-pityol at 100 female-equivalents/h (0.1 mg/ d) and monoterpenes at 14.3 mg/d. The monoterpenes were released at 1.4, 14.3, and 142.8 mg/d.

For all other experiments, capillary tubes 1.04mm i.d. sealed at one end, were used to dispense 2-3 μ liter neat pityol or conophthorin. The white pine cone oils or monoterpenes were dispensed from 2-ml polyethylene Eppendorf tubes (Brinkman Instruments, Rexdall, ON, Canada). For experiment 6, monoterpenes were released from vials with wicks and capillary tubes containing pityol were placed in 400 μ liter polypropylene, Eppendorf tubes with four 0.5-mm holes equally spaced just below the top. The release rate was 0.61 mg of pityol per day at 24°C in the laboratory.

Traps. Yellow Japanese beetle trap-tops (Trécé, Salinas, CA) fitted with plastic jar bottoms were used in all experiments except in experiments 4 and 5 in

**Table 1. Reponse of male *C. coniperda* to traps baited with pityol, conophthorin and white pine cone oils at Beech Creek Seed Orchard, NC (experiment 1) and Pancake Bay Provincial Park, Ontario (experiments 2, 3)**

| Experiment | Treatment | Males caught mean ± SE[b] |
|---|---|---|
| 1 | (±)-*trans*-pityol + *E*-(±)-conophthorin + white pine cone oils | 4.0 ± 1.7a |
| | (±)-*trans*-pityol + *E*-(±)-conophthorin | 1.0 ± 0.7b |
| | (±)-*trans*-pityol | 0.3 ± 0.2b |
| | *E*-(±)-conophthorin | 0.0 ± 0.0b |
| | White pine cone oils | 0.5 ± 0.3b |
| | Unbaited trap | 0.0 ± 0.0b |
| 2 | (±)-*trans*-pityol + *E*-(±)-conophthorin | 0.4 ± 0.3b |
| | (±)-*trans*-pityol + *E*-(±)-conophthorin | 1.2 ± 0.6b |
| | (±)-*trans*-pityol + *E*-(−)-conophthorin | 0.2 ± 0.1b |
| | (±)-*trans*-pityol | 8.2 ± 3.7a |
| | unbaited trap | 0.0 ± 0.0b |
| 3 | pityol (*trans:cis* 19:1) + white pine cone oils | 1.8 ± 1.0ab |
| | pityol (*trans:cis* 66:1) + white pine cone oils | 2.2 ± 0.7a |
| | pityol (*trans:cis* 364:1) + white pine cone oils | 1.2 ± 0.4ab |
| | unbaited trap | 0.3 ± 0.2b |

[a] Experiment 1.93 April-10 Ma!. 1990.6 traps per treatment; experiment 2. 11–25 June 1990. 7 traps per treatment: experiment 2. 1-8 July 1990. 10 traps per treatment.
[b] Means followed by different letters within an experiment are significantly different at $P < 0.05$. Tukey test.

which black. 12-unit Lindgren multiple-funnel traps (Phero Tech. Vancouver. British Columbia, Canada) were used. Traps were hung ≈10–15 m high in the upper third of the crown. 1 trap per tree, and were spaced 12-30 m apart. For each experiment, traps were deployed in complete randomized blocks (spatially distinct lines of traps) with at least 6 blocks, except experiment 5 where 2 blocks were used at each of the 3 sites. Beetles were removed from the traps weekly, treatment locations reassigned randomly and the traps supplied with new baits. Each trap location and trapping interval (1 wk) was considered as a replicate. Captured beetles were preserved in 70% alcohol, identified. counted. and the sex determined by examination of the abdominal terpites (Herdy 1959).

Data Analysis. Trap catches of males were transformed by log $(x + 1)$ to meet the assumptions of analysis of variance (ANOVA) and analyzed using the general linear model for randomized block designs of SYSTAT 6.0 (SPSS, 1996). followed by the Tukey test at a = 0.05. Counts of captured females in traps were at or near zero and therefore were not analyzed.

## Results and Discussion

In all experiments. traps baited with pityol caught male white pine cone beetles (Tables 1-4). Traps baited with E-(±)-conophthorin alone failed to catch males (experiment 1: Table 1). Addition of *E-(-C)*-conophthorin and the (+) and (−) enantiomers of E-conophthorin to traps baited with (±)-*trans*-pityol (hereafter referred as pityol) . significantly reduced ($F$ = 17.9: df = 4. 58: $P < 0.001$) the trap catch in Ontario when compared to pityol alone (experiment 2: Table 1). The effectiveness of *E*-(±)-conophthorin as a *Conophthorus* spp. inhibitor has practical importance because it will be easy and inexpensive to make the racemic mixture for pest management use. The pattern of inhibition is consistent with previous work on *C. coniperda* in North Carolina and C. *resinosae* in Ontario (Birgersson et al. 1993. Pierce et al. 1995). However. in experiment 1. conophthorin did not inhibit the male response to pityol. When white pine cone oils were present. trap catch was significantly greater ($F$ = 6.6: df = 3. 25: $P < 0.001$) than for pityol

**Table 2. Response of male *C. coniperda* to traps baited with pityol. *trans*-pinocarveol. myrtenol. bornyl acetate. and α-pinene, β-pinene. limonene and myrcene at Beech Creek Seed Orchard, NC (experiment 4)**

| Treatment[a] | Males caught mean ± sE[b] |
|---|---|
| (+)-*trans*-pityol + *trans*-pinocarveol − myrtenol + monoterpenes[c] + bornyl acetate | 1.6 ± 0.4a |
| (+)-*trans*-pityol + *trans*-pinocarveol − myrtenol + monoterpenes | 1.4 ± 0.3a |
| (+)-*trans*-pityol + *trans*-pinocarveol − monoterpenes + bornyl acetate | 1.4 ± 0.3a |
| (+)-*trans*-pityol + myrtenol + monoterpenes + bornyl acetate | 0.9 ± 0.2ab |
| (+)-*trans*-pityol + *trans*-pinocarveol − myrtenol + bornyl acetate | 0.3 ± 0.1bc |
| *trans*-pinocarveol + myrtenol + monoterpenes + bornyl acetate | 0.1 ± 0.1c |
| octane control | 0.0 ± 0.0c |

[a] 26 April–31 May 1990. 8 traps per treatment.
[b] Means followed by different letters are significantly different at $P < 0.05$. Tukey test.
[c] Monoterpenes consisted of a 1:1:1:1 mixture of (±)-α-pinene (98% pure). (IS)-(-)-β-pinene (99%). (R)-(±)-limonene (97%). and myrcene (tech.) (Aldrich).

**Table 3. Response of male *C. coniperda* to traps baited with Pityol, α-pinene, β-pinene, limonene and myrcene (experiment 5)**

| Treatment[a] | Males caught (mean ± SE)[b] | | |
|---|---|---|---|
| | Morganton North Carolina | Buckingham Virginia | Gifford Ohio |
| 100 FE (±)-*trans*-pityol + 100 mg α-pinene | 13.3 ± 4.4a | 3.6 ± 1.1a | 12.6 ± 4.7a |
| 1000 FE (±)-*trans*-pityol + 1000 mg monoterpenes[c] | 6.0 ± 1.6b | 1.8 ± 0.6ab | 21.8 ± 6.4a |
| 100 FE (±)-*trans*-pityol + 100 mg monoterpenes[c] | 3.3 ± 2.1c | 1.2 ± 0.4ab | 5.8 ± 2.4b |
| 10 FE (±)-*trans*-pityol + 10 mg monoterpenes[c] | 1.3 ± 0.4c | 0.9 ± 0.4b | 1.8 ± 0.7b |
| octane control | 0.5 ± 0.3c | 0.2 ± 0.1b | 0.2 ± 0.2b |

[a] April-24 May, 1991. Morganton; 17 April–29 May 1991. Buckingham; 25 April-7 June 1991, Gifford; 2 traps per treatment.
[b] Means followed by different letters within a column are significantly different at $P < 0.05$, Tukey test.
[c] Monoterpenes consisted of a 1:1:1:1 mixture of (±)-α-pinene (98% pore), (IS)-(−)-β-pinene (99%). (R)-(±)-limonene (97%), and myrcene (technical grade) (Aldrich).

alone or the 2-component misture (Table 1). This suggests that white pine cone oil may have acted as a powerful enough synergist for pityol to overcome the inhibitory effect of conophthorin.

Baits with the geometric isomers. (±)-*trans*-pityol and (±)-*cis*-pityol, mixed at ratios of 19:1. 66:1. and 364:1 were similarly attractive (experiment 3: Table 1). A combination of *trans*-pinocarveol, myrtenol, bornyl acetate and the 4 monoterpenes-a-pinene, β-pinene. limonene. and myrcene (mixture 1)—attracted no more male beetles than unbaited traps (experiment 4: Table 2). Addition of (−)-*trans*-pityol to mixture 1. resulted in capture of significantly more beetles ($F = 12.5$: df = 6. 266: $P < 0.001$) than the mixture alone. Addition of the 4 monoterpenes to the (+)-*trans*-pityol, *trans*-pinocarveol, myrtenol and bornyl acetate mixture increased trap catch significantly ($F = 12.5$: df = 6. 266: $P < 0.001$). Deletion of the 2 beetle-produced compounds. *trans*-pinocarveol and myrtenol. as well as bornyl acetate from mixture 1 with (+)-*trans*-pityol did not affect trap catch. confirming that male beetles have little response to these compounds. These results are similar to responses to *trans*-pinocarveol, myrtenol. host monoterpenes and pityol observed for male C. *coniperda* in laboratory bioassays (Birgersson et al. 1995).

Traps baited with α-pinene and pityol were as effective or better than traps baited with mixture 1 and pityol (experiment 5; Table 3). Traps baited with 100 female equivalents of pityol and 100 mg α-pinene per week. were consistently better than the traps with 10 female equivalents and 10 mg of the 4 monoterpenes. More beetles were captured as the weekly release rates of pityol and monoterpenes were increased.

The effects of the 4 monoterpenes. particularly α-pinene and β-pinene, were examined in the remaining 4 experiments (experiments 6-9: Table 4). In experiment 6, single deletions of one of the four mono-

Table 4. Response of male C. *coniperda* to traps baited with **Pityol** and **host** monoterpenes at Pancake Bay **Provincial Park.** Ontario (experiment **6**), and **Orono.** Ontario (**experiments 7–9**)

| Experiment | Treatment[a] | Males caught mean ± SE[b] |
|---|---|---|
| 6 | (I )-*trans*-pityol + α & β-pinene + limonene + myrcene | 11.3 I 4.0a |
| | (±)-*trans*-pityol + a-pinene + β-pinene + limonene | 4.5 ± 1.9a |
| | (±)-*trans*-pityol + a-pinene + β-pinene + myrcene | 11.4 ± 5.3a |
| | (±)-*trans*-pityol + a-pinene + limonene + myrcene | 11.3 ± 5.3a |
| | (±)-*trans*-pityol + β-pinene + limonene + myrcene | 8.6 ± 3.9a |
| | (±)-*trans*-pityol | 3.0 ± 2.2a |
| | unbaited trap | 0.1 ± O.lb |
| 7 | (±)-*trans*-pityol + a-pinene + β-pinene | 14.0 ± 3.1a |
| | (±)-*trans*-pityol + a-pinene | 10.3 ± 2.7a |
| | (±)-*trans*-pityol + β-pinene | 11.2 ± 2.6a |
| | (±)-*trans*-pityol | 6.0 ± 1.8a |
| | unbaited trap | 0.0 ± 0.0b |
| 8 | (±)-*trans*-pityol + Pa-pinene | 26.5 ± 6.0a |
| | (I )-*trans*-pityol + 1 a-pinene | 30.3 ± 6.5a |
| | (±)-*trans*-pityol | 15.9 ± 3.2a |
| | 2 a-pinene | 1.4 ± 0.6b |
| | 1 a-pinene | 2.4 ± 1.1b |
| | unbaited trap | 3.3 ± 1.4b |
| 9 | (±)-*trans*-pityol + 3 a-pinene | 25.3 ± 4.7a |
| | (±)-*trans*-pityol + 2 a-pinene | 22.4 ± 3.6a |
| | (±)-*trans*-pityol + 1 a-pinene | 14.8 ± 3.1a |
| | (±)-*trans*-pityol | 4.8 ± 1.7b |
| | unbaited trap | 0.0 ± 0.0c |

[a] Experiment 6.30 May-13 June, 1991: experiment 7, 21 May–4 June 1992: experiment 8.26 May-9 June 1993; experiment 9, 4–8 June 1992. all experiments 6 traps per treatment.
[b] Means followed by different letters within an experiment are significantly different at $P < 0.05$, Tukey test.

terpenes from traps baited with pityol did not affect the number of males caught. There were no significant differences between a-pinene and β-pinene alone or in combination when added to pityol baits (experiment 7), and doubling *or* tripling the number of α-pinene baits did not increase trap catch significantly (experiments 8 and 9). Alpha-Pinene by itself was not attractive to males (experiment 8). Although traps baited with one or more of the monoterpenes always caught more beetles, and often twice as many beetles as traps baited with pityol alone, the results were only statistically significant in experiment 9. The enhanced response of male C. *coniperda* to pityol released with host volatiles is in contrast to the lack of such a response by C. *resinosae* males (de Groot and Zylstra 1995, Pierce et al. 1995). As noted previously, the capture of females in traps was at or near zero, including those that contained only host volatiles. This provides added support for the conclusion of Mattson and Strauss (1986) that terpene volatiles are too pervasive and variable for use in host finding by *Conophthorus* spp.

Our studies have demonstrated that traps with baits releasing (±)-*trans*-pityol at ≈1 mg/wk with (±)-α-pinene (98% pure) are potentially valuable tools for C. ***coniperda*** pest management. Baited traps can be used to monitor C. ***coniperda*** populations or possibly to reduce seed losses in a beetle trap-out control strategy.

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## References Cited

Birgersson, G., G. **L. DeBarr. P. de Groot, M. J. Dalusky**, H. D. **Pierce,** Jr., J. H. Borden. H. **Meyer,** W. Francke, K. **Espelie,** and C. **W. Berisford.** 1995. Pheromones in white pine cone beetle *Conophthorus coniperda* (Schwarz) (Coleoptera: Scolytidae). J. Chem. Ecol. 21: 1-13-167.

Borden, J. H. **1985.** Aggregation pheromones. pp. 275-285. In G. A. Kerkut and L. I. Gilbert [eds.]. Behaviour Vol. 9, Comprehensive Insect Physiology. Biochemistry. and Pharmacology. Pergamon. Oxford. England.

Borden, **J.** H., L. C. **Ryker**. L. **J.** Chong. H. D. Pierce, Jr.. B. D. Johnston. and **A.** C. **Oehlschlager.** 1987. Response of the mountain pine beetle. *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). to five semiochemicals in British Columbia lodgepole pine forests. Can. J. For. Res. 17: 118-128.

**Byers,** J. A., G. Birgersson, J. **Löfqvist,** and G. **Bergström.** 1988. Synergistic pheromones and monoterpenes enable aggregation and host recognition by a bark beetle. Naturwissenschaften 75: 153-155.

**DeBarr,** G. L., L. R. Barber, and A. H. Maxwell. 1982. Use of carbofuran for control of eastern white pine cone and seed insects. For. Ecol. Manage. 4: 1-8.

de Groot, P. 1986. Cone and twig beetles (Coleoptera: Scolytidae) of the genus *Conophthorus:* **an** annotated bibliography. Can. For. Serv. Sault Ste. Marie Ont. Inf. Rep. FPM-X-76.

**1990.** The taxonomy, life history and control of *Conophthorus* (Coleoptera: Scolytidae) in eastern North America. pp. 37-46. In R. J. West [ ed.] Proceedings Cone and Seed Pest Workshop, 4 October 1989, St. Johns, Newfoundland, Canada. For. Can. Inf. Rep. N-X-274.

1992. Biosystematics of *Conophthorus* Hopkins (Coleoptera: Scolytidae) in eastern North America. Ph.D. dissertation, Department of Biological Sciences, Simon Fraser University, Bumaby, British Columbia, Canada

de **Groot,** P., and B. F. Zylstra. 1995. Factors affecting capture of male red pine cone beetles, *Conophthorus resinosae* Hopkins (Coleoptera: Scolytidae), in pheromone traps. Can. Entomol. 127: 851-858.

de Groot, P., G. L. DeBarr, G. 0. Birgersson. H. D. Pierce. J. H. Borden, Y. C. **Berisford.** and C. **W. Berisford.** 1991. Evidence for a female-produced pheromone in white pine cone beetle, *Conophthorus coniperda* (Schwarz). and in the red pine cone beetle, C. *resinosae* Hopkins (Coleoptera: Scolytidae). Can. Entomol. 123: 1037-1061.

**Godwin, P.** A., and T. M. **Odell. 1965.** The life history of the white pine cone beetle, *Conophthorus* ***coniperda.*** Ann. Entomol. Soc. Am. 58: 213-219.

**Hedlin, A. F., H. 0. Yates III, D. C. Tovar, B. H. Ebel, T. W. Koeber, and E. P. hlerkel. 1980.** Cone and seed insects on North American conifers. Can. For. Serv.. U.S. Dep. Agric. For. Serv., Secr. Acric. Recur. Hidrual. Mexico.

Herdy, H. 1959. A method of determining the sex of adult bark beetles of the genus *Conophthorus*. Can. Dep. Agric.. For. Biol. Div., Bi-Mon. Prog. Rep. 15: 1-2.

**Joshi,** V. S., N. P. **Damodaran,** and S. **Dev**. 1968. Organic reactions in a solid matrix-alumina induced oxiranes rearrangements. Tetrahedran 24: 5817-5830.

**Kinzer,** H. G., B. J. **Ridgill,** and J. **M.** Reeves. 1952. Response of walking *Conophthorus ponderosae* to volatile attractants. J. Econ. Entomol. 65: 726-729.

**Kinzer,** H. G., and J. M. Reeves. 1976. Biology and behavior of cone beetles of ponderosa pine and southwestern white **pine** in New Mexico. New Mexico State Univ. Agric. Expt. Stn. Bull. 641.

Mattson, W. **J.,** and S. H. Strauss. 1986. Are cone volatiles involved in cone finding by the red pine cone beetle. *Conophthorus resinosae* (Colsoptera: Scolytidae). pp. 185-204. *In* A. Roques [ed.], Proceedings Cone and Seed Insects Conference, 3-5 September 1986. International Union of Forestry Research Organizations (IUFRO) Working Party S2.07-01. INRA. Ardon. France.

Pierce, H. D., Jr., P. de Groot, J. H. Borden. S. **Ramaswamy, and A. C. Oehlschager. 1995.** Pheromones in the red pine cone beetle, *Conophthorus resinosae* Hopkins. and its synonym, *C. banksianae* McPherson (Coleoptera: Scolytidae). J. Chem. Ecol. 21: 169-185.

SPSS. 1996. SYSTAT 6.0 for Windows. SPPS Inc. Chicago. IL.

**Turgeon,** J. **J., and** P. de **Groot. 1992.** Management of insect pests of cones in seed orchards in eastern Canada. Forestry Canada. Sault Ste. Marie. Ontario.

**Wade, D. D., G. L. DeBarr, L. R. Barber, and E. Manchester. 1989.** Prescribed fire: a cost effective control for the white pine cone beetle. pp. 117–121. *In* Proceedings 10th Conference on fire and forest meterology. 17–21 April 1989. Environment Canada, Ottawa, Canada.

**Wood, S. L. 1982.** The bark and ambrosia beetles in North and Central America (Coleoptera: Scolytidae). A taxonomic monograph. Great Basin Nat. Mem. 6:1359.

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