

Effects of resin flow and monoterpene composition on susceptibility of lodgepole pine to attack by the Douglas-fir pitch moth, *Synanthedon novaroensis* (Lep., Sesiidae)

L. A. Rocchini, B. S. Lindgren and R. G. Bennett

College of Science and Management, University of Northern British Columbia, Prince George, BC, Canada

Abstract: Resin flow differed significantly among three of six clones of lodgepole pine seed orchard trees, but did not differ among the clones categorized as susceptible or resistant to attack by the Douglas-fir pitch moth. A stepwise regression analysis identified δ -3-carene, cyclohexene, and α -terpinolene as significant compounds, explaining 49.9% of the variation in the number of attacks per tree. δ -3-Carene alone explained 41.8% of the variation in the regression, and analysis of variance showed that resistant clones consistently had high relative amounts ($>17.9\%$) of this compound, whereas susceptible clones had low amounts ($<10\%$). The significant effect by cyclohexene and α -terpinolene in the stepwise regression appeared to be due to a correlation between α -terpinolene and δ -3-carene in several clones, and that cyclohexene was only present in one clone, rather than any discernable biological relationship. Limonene co-eluted with β -phellandrene, so its role must be determined by additional study.

1 Introduction

An important defence mechanism of conifers against the majority of wood- and phloem-feeding insects is the secretion of resinous materials (CHRISTIANSEN, 1989). In pines, this secretion consists of primary resinosis, where resin exudes from existing, severed resin canals, and secondary or induced resinosis, where, in reaction to injury, resin is produced in living parenchyma cells of the phloem and sapwood (REID et al., 1967). Both primary and secondary resinosis have been strongly associated with lodgepole pine defence mechanisms against the phloem-feeding bark beetle, mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (REID et al., 1967; RAFFA and BERRYMAN, 1982).

Pinus spp. have preformed vertical and horizontal resin ducts in the needles, shoots, buds, and stem, and oleoresin flow rate and amount has been correlated with oleoresin exudation pressure (the force with which resin is expelled into the resin ducts from damaged conifer tissues), and with the size and number of resin ducts and viscosity of resin (VITÉ, 1961; HODGES and LORIO, 1971). There is evidence that resin-canal frequency in lodgepole pine is under genetic control, indicating that resin flow may vary among clones (WHITE and NILSSON, 1984).

Qualitative as well as a quantitative attributes of resin may influence susceptibility of trees to attack or suitability for larval development. Differences in relative amounts of monoterpenes in resin were found to correlate with Maritime pine, *Pinus pinaster* Ait, susceptibility to the pitch moth *Dioryctria sylvestrella* Ratz. (JACTEL et al., 1996; JACTEL and KLEINHENTZ, 1997).

The Douglas-fir pitch moth, *Synanthedon novaroensis* (Hy. Edwards), like other pitch moths, utilizes tree resin

as a protective habitat. Therefore, the amount, as well as the chemical composition, of oleoresin present in a tree may be highly relevant to its susceptibility to pitch moth attack, as well as its suitability for pitch moth larval development.

In four lodgepole pine seed orchards at the Prince George Tree Improvement Station (PGTIS), tree genotype significantly affected the probability of a tree being attacked by Douglas-fir pitch moth (ROCCHINI, 1997). Most of the trees in one of these orchards, Omineca-Pinchi No.201, were topped in 1994, and this resulted in copious amounts of pitch running down the stem of some trees, whereas in other topped trees very little resin flow resulted. The apparent variation in pitch flow among trees, the important role that resin plays in the life cycle of the Douglas-fir pitch moth and the demonstrated clonal susceptibility of trees to pitch moth attack led us to test the following null hypotheses: (1) resin flow does not differ between susceptible and resistant clones of lodgepole pine; (2) resin flow does not differ among clones; and (3) relative monoterpene composition does not correlate with pitch moth attack.

2 Methods

2.1 Tree selection

The PGTIS contains four lodgepole pine seed orchards that are infested with Douglas-fir pitch moth. Trees were sampled in one of these four orchards in order to minimize variance due to environmental factors. The Omineca-Pinchi No. 201 orchard was chosen for sampling, because this orchard has the highest levels of pitch moth attack (30.8% of trees attacked, ROCCHINI, 1997). Clones for this study were selected on the basis of their relative susceptibilities to pitch moth attack as determined by regression analysis (ROCCHINI, 1997). Two

Table 1. Number of trees attacked by Douglas-fir pitch moth, mean number of attacks per tree (± 1 SD), and mean pitch flow (ml/24 h ± 1 SD) collected in 24 h for each of six clones of lodgepole pine. Prince George Tree Improvement Station, Prince George, BC, 24–25 June 1997

Clone	<i>n</i>	No. trees attacked	Mean no. attacks/tree ± 1 SD	Mean pitch flow ¹ (ml/24 h) ± 1 SD
Resistant clones				
130	19	3	0.16 \pm 0.375	0.38 \pm 0.252 b
133	18	2	0.17 \pm 0.514	0.50 \pm 0.314 ab
140	18	1	0.11 \pm 0.471	0.36 \pm 0.141 b
Susceptible clones				
103	17	13	1.30 \pm 1.047	0.43 \pm 0.192 b
105	18	13	1.50 \pm 1.150	0.59 \pm 0.396 ab
200	19	18	2.58 \pm 2.009	0.80 \pm 0.707 a

¹ Means followed by the same letter not significantly different, analysis of variance ($\alpha = 0.05$) followed by Tukey's test for mean separation.

categories, 'resistant' and 'susceptible' to pitch moth attack, of three clones each were chosen for sampling. Another selection criterion was that each clone must contain a minimum of 20 ramets propagated in 1972. The resistant clones selected were 130, 133, and 140, and susceptible clones 103, 105, and 200. The number of trees attacked, and mean attacks per tree for each clone are listed in table 1. In each clone, 20 trees were randomly selected for sampling, and three samples were taken from each tree, for a total of 360 samples from 120 trees. Thus, each susceptibility category was replicated three times by way of clone, and each clone was replicated 20 times by way of tree.

2.2 Resin flow collection

Measurement of the relative rate of resin flow was measured 24–25 June 1997. A 1 cm diameter hole was cut in the bark and phloem to the sapwood surface using a bark punch (Arch Punch®; C.S. Osborne and Co., Harrison, NJ, USA) and hammer. All wounds were made at approximately breast height, as this was a convenient height to sample, and is within the area of the tree normally attacked by Douglas-fir pitch moth. To ensure that the side of the tree sampled did not affect quantity of resin collected, samples were collected from the north-, south-, and arbitrarily from either the east- or west-facing sides.

The exuding resin was collected over 24 h in devices fashioned from 1 mm aluminium sheeting and 15 ml conical graduated polystyrene centrifuge tubes (Oxford Labware, St. Louis, MO, USA). The aluminium sheeting was cut into approximately 4 cm \times 4 cm square sections, and the bottom half of the sheet was bent into the shape of a funnel. Each funnel was stapled to the chosen spot on the tree, and a hole was created with the bark punch immediately above each funnel, so that the top 2 mm of the funnel were pushed into the hole. This prevented resin from flowing between the tree bark and the underside of the funnel. A centrifuge tube was then placed at the bottom of each funnel so that the funnel was inside the tube, and attached with a piece of duct tape.

After 24 h, all tubes were collected. Resin that had run down the outside of the centrifuge tubes or funnels was scraped off with a knife and placed inside the tube. The volume of resin was calculated by subtracting the volume of water displaced by resin in each tube from the total volume.

2.3 Monoterpene analyses

The phloem removed by the bark punch was carefully placed in a paper envelope, which was immediately labelled and

placed in liquid nitrogen. The bark punch was cleaned with hexane between samples to minimize contamination. All samples were transferred to a -40°C freezer until analysed. One sample from each tree was cut into small pieces, and the pieces extracted for 24 h at room temperature in hexane containing 0.01% undecane as an internal standard. The raw extract was shaken for 15 s, and then transferred to a 10 cc sterile single use syringe (Beckon Dickinson, Singapore) and filtered into a sample vial through a Gelman (Gelman Sciences, Ann Arbor, MI, USA) nylon Acrodisc 13, 0.2 μm fitted onto the syringe. The filtered extract was analysed by coupled gas chromatography – mass spectrometry (GC–MS), using a Hewlett-Packard (Palo Alto, CA, USA) HP 5890 Series 11 GC fitted with a 30 m \times 0.25 mm \times 0.25 μm DB 5 capillary column, and connected to a HP 5989B MS. One microlitre of each sample were injected splitless using a HP6890 Series Injector auto-sampler. Helium was used as a carrier gas at a flow rate of 1 ml/min. The injection temperature of 60°C was maintained for 6 min, and the temperature was then ramped at $5^{\circ}\text{C}/\text{min}$ to 90°C , at $10^{\circ}\text{C}/\text{min}$ to 150°C , and finally at $20^{\circ}\text{C}/\text{min}$ to 250°C , where it was held for 10 min. The injector needle was triple-washed in methylene chloride and hexanes between sample injections. Approximately every 10th sample analysed was a solvent control.

Compounds eluting before 12 min were tentatively identified using a Wiley MS library, and their identity confirmed by comparison with authentic samples by R. Gries (Simon Fraser University, Burnaby, BC, Canada) using DB 5 and DB 23 capillary columns. Relative content was estimated for each monoterpene as the percentage area count of the sum of monoterpene area counts.

2.4 Statistical analyses

Paired *t*-tests on the resin flow data obtained from the samples taken on north- and south-facing sides of the tree were carried out to determine if aspect was significantly affecting resin flow within a tree (ZAR, 1984). A separate test was performed for each clone, so that differences among clones did not affect the outcome of this test.

For all subsequent analyses, an average of the three measurements on each tree was used as the dependent variable, based on the assumption that resin flow was not significantly affected by the side of tree that was sampled. These data were also subjected to a logarithmic transformation after Lévene's test indicated that the data violated the assumption of homogeneity of variances (WILKINSON et al., 1996).

Visual examination of scatterplots revealed that resin flow

was positively correlated with time of sampling. Analysis of covariance confirmed this correlation, and was used to remove variance due to sample time, using sample number as a surrogate for actual sample time.

A nested analysis of covariance was performed on the data from all trees, with the categorical variable 'clone' with six levels nested within the categorical variable 'susceptibility' with two levels. To test the second null hypothesis of no variation between clones, independent of tree category, a one-way analysis of covariance followed by a Tukey multiple comparisons test to detect clonal differences in pitch volumes in the absence of susceptible or resistant categories (ZAR, 1984) was performed.

A stepwise multiple regression, with numbers of pitch moth attacks as the dependent variable, and percentage monoterpenes and pitch volume as independent variables was used to test the third null hypothesis. A nested analysis of variance, followed by a Tukey multiple comparisons test for mean separation, was then performed on the independent variables that contributed significantly to the regression, in order to determine whether or not their relative amounts differed among susceptible and resistant categories. A one-way analysis of variance, followed by a Tukey test for mean separation, was performed to detect clonal differences in relative monoterpene amounts in the absence of susceptible or resistant categories (ZAR, 1984).

All statistical analyses were performed at $\alpha = 0.05$ using Systat[®] 7.0 for Windows[®] (SPSS INC. 1996).

3 Results

The six paired *t*-tests indicated that there were no consistent patterns relating resin flow to tree aspect. Resin flow was higher on the north-facing side than on the south-facing side in clone 103 ($P < 0.05$). In clone 140, mean flow approached significance ($P = 0.07$) in favour of the south-facing side. In the four other clones, there were no significant differences in the volume of resin collected in 24 h between the north- and south-facing aspects ($P > 0.1$). Thus, resin measurements were averaged for each tree for the subsequent analyses.

The results from the nested analysis of covariance with logarithmic-transformed data indicated that when clones were nested within the two treatments, the amount of resin collected in 24 h was significantly different among the six clones ($P = 0.021$). Resin volumes from susceptible (0.57 ± 0.05 ml/24 h) and resistant (0.42 ± 0.03 ml/24 h) categories were not significantly different ($P = 0.131$). The results from the one-way analysis of covariance of clones in the absence of nesting in susceptibility categories indicated that there were significant differences between the clones ($P = 0.001$, table 1). The Tukey multiple comparison test indicated that clone 200 (a susceptible clone) exuded significantly more resin in a 24 h period than clones 130 and 140 (both resistant clones ($P = 0.001$ and 0.003 , respectively) and the susceptible clone 103 ($P = 0.046$). No other significant differences occurred between clones.

Table 2 shows the relative amount of monoterpenes by clone. The presence of limonene was not detected since it co-elutes with β -phellandrene on the DB 5 column. The stepwise regression analysis using the relative monoterpene amount and pitch flow data as independent variables, and the logarithm of the number of

attacks per tree as the dependent variable yielded a highly significant regression, where δ -3-carene, terpinolene, and cyclohexene explained 49.9% of the variation. δ -3-Carene alone explained 41.8% of the variation when all these variables were considered.

Analysis of covariance indicated that only the relative amounts of δ -3-carene differed significantly among resistance categories ($P = 0.009$), unlike α -terpinolene ($P = 0.594$) and cyclohexene ($P = 0.374$) (fig.). The analysis of variance showed significant differences of relative amounts among clones for many of the compounds analysed (table 2), but only δ -3-carene was consistent between susceptibility category, with resistant clones having more than 17.9% and susceptible clones having less than 10% of this monoterpene.

4 Discussion

The hypothesis of no difference in resin flow between susceptible and resistant clones was accepted, whereas the second hypothesis was rejected, since clonal differences were evident. The clonal differences in mean resin flow did not explain susceptibility to pitch moth attacks, but may be a factor in some clones. The clone with highest resin flow was susceptible, whereas the two clones with lowest flow were resistant. However, other factors are evidently more important.

Resin flow was not affected consistently by the side of the tree sampled (south- versus north-facing). This is consistent with a study by REID and WATSON (1966), who found that in 30-year-old lodgepole pine trees vertical resin duct length varied with growth ring, but not with aspect. Resin duct length in their study ranged from 1.2 to 12.0 cm within a single tree, and mean resin duct density was $40.5/\text{cm}^2$ (REID and WATSON, 1966). Thus, the within-tree variation in resin flow in our study was likely the result of variation in the size of resin ducts that were severed, and their density at the sample location, and independent of environmental factors that can vary with aspect, such as temperature.

The significant differences in resin flow among some clones indicate that resin canal characteristics are genetically controlled. Needles of lodgepole pine trees from coastal Washington had significant differences in frequency of resin canals among clones, indicating the number of resin canals is under genetic control (WHITE and NILSSON, 1984).

In addition to resin canal frequency, other factors which may cause variation in resin flow, and thus affect pitch moth performance, include oleoresin exudation pressure, resin viscosity and resin-crystallization rate. In a study of ponderosa pine (*Pinus ponderosa* Dougl.), oleoresin exudation pressure positively influenced oleoresin exudation flow (VITÉ, 1961). In another study on loblolly pine (*Pinus taeda* L.), oleoresin flow was more strongly related to the size and number of resin ducts and viscosity of resin than exudation pressure (HODGES and LORIO, 1971). Therefore, the influence of oleoresin exudation pressure appears to be species-specific, and its effects on the resin flow of lodgepole pine are not known. Diurnal variation in resin flow was evident in this study by the positive correlation between resin vol-

Table 2. Relative amounts of phloem monoterpenes in susceptible and resistant clones of lodgepole pine. Prince George Tree Improvement Station, Prince George, June 1997¹

Monoterpene	Resistant clones			Susceptible clones		
	130	133	140	103	105	200
Thujene ³	0.0	0.0	0.1	0.0	0.0	0.1
α -Pinene	4.0a	5.1a	5.1a	6.3b	5.2a	7.9b
Camphene	0.3c	0.3c	0.4b	0.8ab	0.3c	1.0a
β -Pinene	3.5f	15.9bc	16.3ab	13.2cd	6.3e	19.0a
β -Myrcene ²	2.3	2.5	2.6	2.3	2.5	2.8
α -Phellandrene	1.2a	1.1a	0.7b	1.1a	1.5a	1.4a
δ -3-Carene	23.4b	17.9c	28.1a	8.0de	10.0d	4.6e
β -Phellandrene ⁴	61.7b	54.7c	39.8d	67.9a	72.1a	57.6bc
Cyclohexene ³	0.0	0.8	0.0	0.0	0.0	0.0
γ -Terpinene ³	0.1	0.03	0.4	0.01	0.0	0.2
α -Terpinolene	3.5b	1.7c	5.9a	0.6d	2.1c	5.3a

¹ Means within rows followed by the same letters are not significantly different, analysis of variance ($\alpha = 0.05$) followed by Tukey's mean separation test.
² Means not significantly different, analysis of variance ($\alpha = 0.05$).
³ Not analysed.
⁴ Includes limonene.

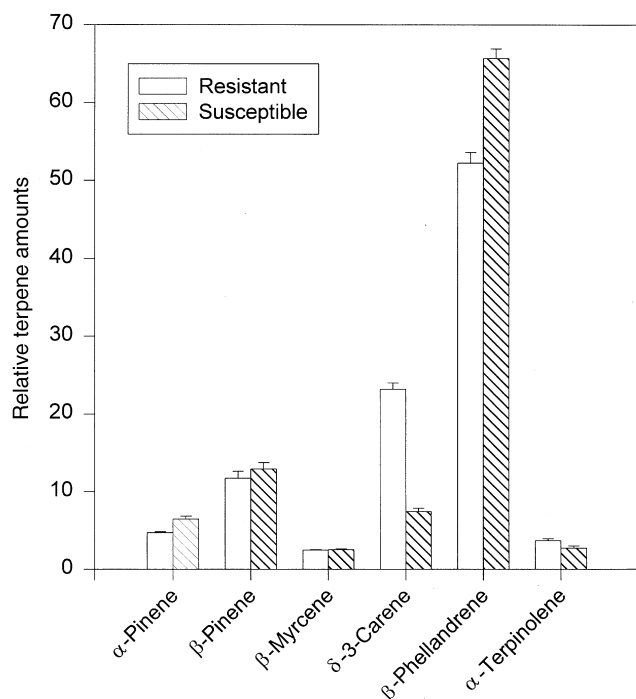


Figure. Histogram showing mean (\pm SE) percentage of the five most common monoterpenes in lodgepole pine clones resistant and susceptible to attack by the Douglas-fir pitch moth. Prince George Tree Improvement Station, Prince George, BC, 24–25 June 1997

ume collected and time of sampling, with samples collected late in the day generally yielding higher volumes.

Resin viscosity is dependent on the amount and chemical composition of turpentine in the resin, and is probably an important factor in resin flow rate (HODGES and LORIO, 1971; BARBOSA and WAGNER, 1989). If a resin duct is severed, resin that is less viscous would have a higher rate of downward flow due to gravitational forces, and volume collected per hour would be greater. Crystallization rate of resin is also

important, and we observed some variation in relative stages of crystallization among samples after 24 h. For most invading insects, rapid crystallization is beneficial, because it is physiologically easier for them to dispose of crystallized resin, and some insects are capable of inducing resin crystallization, e.g. the white pine weevil, *Pissodes strobi* Peck (WILKINSON, 1979). Douglas-fir pitch moth, however, does not appear to induce crystallization, since trees continually produce resin at larval feeding sites, and active pitch masses always contain flowing pitch.

The third null hypothesis was rejected, since the relative amount of δ -3-carene in the phloem explained over 40% of the variation in the number of pitch moth attacks per tree in the stepwise regression, and resistant category clones had significantly higher relative amounts of this compound than susceptible categories. δ -3-Carene has been shown in numerous studies to be toxic to phloeophagous insects (COOK and HAIN, 1988; WERNER, 1995), so it can be assumed that it affects larval survival, if not host selection by the female. A detailed look at the data indicated general support for δ -3-carene as the monoterpene that determines susceptibility of lodgepole pine to Douglas-fir pitch moth, but some inconsistencies were evident. For example, only one tree in the 'resistant' clone 140 was attacked by pitch moths. This tree was either an outlier within the clone, or it was mislabelled, because it contained only 2% δ -3-carene, significantly departing from the mean (\pm SD) of 28.1 (\pm 6.53)% of that clone. On the other hand, attacked trees in resistant clones 130 and 133 did not have low δ -3-carene levels, indicating that some other factor also plays a significant role in resistance or susceptibility of trees. It is possible that limonene is important, since it has been shown to be toxic and/or repellent to several bark beetle species (COOK and HAIN, 1988; WERNER, 1995), and has shown repellency and toxicity to a pine weevil (NORLANDER, 1990; LINDGREN et al., 1996). The effect by limonene on pitch moth attack could not be analysed in this study, so additional sampling and analyses are required.

The contribution to the model by α -terpinolene and cyclohexene could not be readily explained, e.g. cyclohexene was only present in resistant clone 133, but absent in all other clones. JACTEL et al. (1996) and JACTEL and KLEINHENTZ (1997) found that high amounts of α -terpinolene in Maritime pine reduced its susceptibility to the pitch moth *Dioryctria sylvestrella* Ratz., indicating that this monoterpene may be an important defensive compound in some conifers.

Lodgepole pine reacts to invasion by insects and disease by primary resinosis, involving preformed oleoresin, and secondary resinosis, involving an induced response to the invasion (REID et al., 1967; RAFFA and BERRYMAN, 1982). Our sampling methods were designed to study primary resin only, and did not measure any quantitative or qualitative aspects of secondary resinosis. Resin present in pitch masses of the Douglas-fir pitch moth, although composed of both primary and secondary resin, probably contains far more of the latter, because resin is continuously exuded throughout larval development. Nevertheless, our results show that the chemical composition of primary resin affects the susceptibility or suitability of lodgepole pine to pitch moth attacks.

ROCCHINI (1997) showed that previous attack was important in determining attack distribution in the seed orchards at the PGTIS. Thus, it appears that females may orient to exuding pitch for oviposition. If so, susceptibility is due at least in part to female choice of oviposition site. In Washington State, Douglas-fir pitch moths were attracted to relatively fresh pruning wounds that exuded oleoresin (JOHNSON, 1993). He found that 73% of Douglas-fir pitch moth oviposited only on trees that were pruned just prior to the onset of insect flight, an additional 22% oviposited on trees that were pruned during the first 4 weeks of flight, whereas no ovipositions occurred on wounds pruned during the bulk of the flight (JOHNSON, 1993). His findings indicate that secondary resin is more attractive to ovipositing females than primary resin. We do not know if δ -3-carene is primarily affecting oviposition choice or if it prevents larval establishment due to its toxicity, i.e. making the tree unsuitable. Further research is required to determine this, and to elucidate the role of limonene on host selection.

Acknowledgements

This research was funded by a Forest Renewal BC research grant to Dr R. G. BENNETT, B.C. Ministry of Forests. We thank Dr C. WAYNE BERISFORD for helpful comments on the manuscript; Dr M. GILLINGHAM for statistical advise and, along with Dr K. J. LEWIS, for helpful suggestions during the completion of L.A.R.'s graduate research; ANN MARIE MACISAAC, KRISTEN WELGAN, SHELLEY ROSENTHAL, and RICHARD CROMBIE for assistance in the laboratory and field; KIMBERLEY WALLIN and Dr GÖRAN BIRGERSSON for advice on GC-MS analysis; REGINE GRIES for confirming identities of monoterpenes; and CAROLE FLEETHAM and staff at the Prince George Tree Improvement Station for providing access and support for this research.

References

BARBOSA, P.; WAGNER, M. R., 1989: Introduction to Forest and Shade Tree Insects. San Diego: Academic Press.

- CHRISTIANSEN, E., 1989: *Ips typographus* and *Ophiostoma polonicum* versus Norway spruce: joint attack and host defense. In: Forest Insect Guilds: Patterns of Interaction with Host Trees. Ed. by BARANCHIKOV, Y. N.; MATTSON, W. J.; HAIN, F. P.; PAYNE, T. L. Gen. Technical Report NE-153. Radnor, PA: US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, 321–334.
- COOK, S. P.; HAIN, F. P., 1988: Toxicity of host monoterpenes to *Dendroctonus frontalis* and *Ips calligraphus* (Coleoptera: Scolytidae). J. Entomol. Sci. **23**, 287–292.
- HODGES, J. D.; LORIO, P. L. JR., 1971: Comparison of field techniques for measuring moisture stress in large loblolly pines. For Sci. **17**, 220–223.
- JACTEL, J.; KLEINHENTZ, M., 1997: Intensive silvicultural practices increase the risk of infestation by *Dioryctria sylvestrella* Ratz (Lepidoptera: Pyralidae), the Maritime pine stem borer. In: Integrating Cultural Tactics Into the Management of Bark Beetle and Reforestation Pests. Proceedings. Ed. by GRÉGOIRE, J.-C.; LIEBHOLD, A. M.; STEPHEN, F. M.; DAY, K. R.; SALOM, S. M. Gen. Technical Report NE-236, Radnor, PA: US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, 177–190.
- JACTEL, J.; KLEINHENTZ, M.; MARPEAU-BEZARD, A.; MARION-POLL, F.; MANASSIEU, P.; BUBAN, C., 1996: Terpene variations in maritime pine constitutive oleoresin related to host tree selection by *Dioryctria sylvestrella* Ratz. J. Chem. Ecol. **22**, 1037–1050.
- JOHNSON, J. M., 1993: Flight, emergence, and oviposition patterns of the Douglas-fir pitch moth *Synanthedon novaroensis* (Hy. Edwards) (Lepidoptera: Sesiidae), in Western Washington. MSc Thesis. Seattle, WA: University of Washington.
- LINDGREN, B. S.; NORDLANDER, G.; BIRGERSSON, G., 1996: Feeding deterrence of verbenone to the pine weevil, *Hylobius abietis* (L.) (Col., Curculionidae). J. Appl. Ent. **120**, 397–403.
- NORDLANDER, G. 1990: Limonene inhibits attraction to α -pinene in the pine weevils *Hylobius abietis* and *H. pinastri*. J. Chem. Ecol. **16**, 1307–1320.
- RAFFA, K. F.; BERRYMAN, A. A., 1982: Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. Environ. Entomol. **11**, 486–492.
- REID, R. W.; WATSON, J. A., 1966: Sizes, distributions, and numbers of vertical resin ducts in lodgepole pine. Can. J. Bot. **44**, 519–525.
- REID, R. W.; WHITNEY, H. S.; WATSON, J. A., 1967: Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue stain fungi. Can. J. Bot. **45**, 1115–1126.
- ROCCHINI, L. A., 1997: Variation in lodgepole pine susceptibility to pitch moth (Lepidoptera: Sesiidae and Pyralidae) attack at the Prince George Tree Improvement Station. MSc Thesis., Prince George, BC: University of Northern British Columbia.
- SPSS INC., 1996: Systat 7.0 for Windows: Statistics. Chicago, IL: SPSS Inc.
- VITÉ, J. P., 1961: The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosae*. Contrib. Boyce Thomson Inst. **21**, 67–78.
- WERNER, R. A., 1995: Toxicity and repellency of 4-allyl-anisole and monoterpenes from white spruce and tamarack to the spruce beetle and eastern larch beetle (Coleoptera: Scolytidae). Environ. Entomol. **24**, 372–379.
- WHITE, E. E.; NILSSON, J. E., 1984: Genetic variation in resin

- canal frequency and relationship to terpene production in foliage of *Pinus contorta*. *Silva Genetica* **33**, 79–84.
- WILKINSON, R. C., 1979: Oleoresin Crystallization in Eastern White Pine: Relationships with Chemical Components of Cortical Oleoresin and Resistance to the White Pine Weevil. NE For. Exp. Stn., Res. Paper no. NE-438. Radnor, PA: US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station.
- WILKINSON, L.; BLANK, G.; GRUBER, C., 1996: Desktop Data Analysis with SYSTAT. Upper Saddle River. NJ: Prentice Hall Inc.
- ZAR, J. H., 1984: *Biostatistical Analysis*. 2nd edn. Englewood Cliffs, NJ: Prentice Hall, Inc.
- Author's addresses:** LYNN A. ROCCHINI, B. STAFFAN LINDGREN (corresponding author), College of Science and Management, University of Northern British Columbia, Prince George, BC V2N 5A4, Canada. E-mail: lindgren@unbc.ca; ROBERT G. BENNETT, BC Ministry of Forests, 7380 Puckle Road, Saanichton, BC V8M 1W4, Canada

Copyright of Journal of Applied Entomology is the property of Blackwell Publishing Limited and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.