Characteristics of subalpine fir susceptible to attack by western balsam bark beetle (Coleoptera: Scolytidae)

Katherine P. Bleiker, B. Staffan Lindgren, and Lorraine E. Maclauchlan

Abstract: A diameter distribution survey at three sites in the interior of British Columbia revealed that the western balsam bark beetle (*Dryocoetes confusus* Swaine) predominately attacked trees from the three to four largest diameter classes at each site. However, the mean diameter of attacked trees was significantly different among sites, indicating that factors other than diameter contribute to the susceptibility of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) to the western balsam bark beetle. A number of tree characteristics, including measures of growth, age, crown size, and phloem thickness, were compared among a total of 22 successfully attacked, 26 unsuccessfully attacked, and 28 unattacked trees at three sites. Of the 12 tree characteristics measured, five showed significant differences between successfully attacked and unattacked trees. Successfully attacked trees had a lower percentage of the bole covered with constant crown, lower crown volume, lower radial growth in the last 5 years, and were older than unattacked trees. Successfully attacked trees also produced less induced resinosis than unsuccessfully attacked trees. The results of this study suggest that western balsam bark beetle mortality may be limited by the presence and distribution of susceptible hosts. The study also identifies a number of variables that could be used in a susceptibility and risk rating model for western balsam bark beetle.

Résumé : Un inventaire de la distribution du diamètre des arbres dans trois sites à l'intérieur de la Colombie-Britannique montre que le scolyte du sapin de l'Ouest (*Dryocoetes confusus* Swaine) attaque surtout les arbres dans les trois ou quatre plus fortes classes de diamètre dans chaque site. Cependant, le diamètre moyen des arbres attaqués est significativement différent selon le site, indiquant que d'autres facteurs que le diamètre contribuent à la susceptibilité de sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.) au scolyte du sapin de l'Ouest. Plusieurs caractéristiques des arbres, incluant des mesures de croissance, d'âge, de dimension de la cime et d'épaisseur du phloème, ont été comparées pour 22 arbres sur lesquels l'attaque avait réussi, 26 arbres sur lesquels l'attaque n'avait pas réussi et 28 arbres qui n'avaient pas été attaqués répartis dans les trois sites. Parmi les 12 caractéristiques individuelles mesurées, cinq étaient significativement différentes selon que les arbres avaient été attaqués avec succès ou qu'ils n'avaient pas été attaqués. Les arbres sur lesquels l'attaque avait réussi avaient un plus faible pourcentage du tronc couvert par une cime persistante, un volume de cime plus faible, une croissance radiale plus faible au cours des cinq dernières années et étaient plus vieux que les arbres non attaqués. Les arbres sur lesquels l'attaque avait réussi produisaient également moins de résine que les arbres qui n'avaient pas été attaqués. Les résultats de cette étude indiquent que la mortalité due au scolyte du sapin de l'Ouest est possiblement limitée par la présence et la distribution d'hôtes susceptibles. L'étude identifie également plusieurs variables qui pourraient être utilisées dans un modèle d'évaluation de la susceptibilité et du risque pour le scolyte du sapin de l'Ouest.

[Traduit par la Rédaction]

Introduction

Most species of bark beetles inhabit down or dying trees (Rudinsky 1962). At high population levels, some species that prefer dead or moribund trees have the ability to mass attack and kill healthy hosts (Furniss and Carolin 1977). The specific events that trigger insect outbreaks and allow less aggressive beetles to kill healthy hosts are the subject of numerous studies, but are not well understood for most species. Epidemics of many tree-killing bark beetles have been linked to substantial increases in susceptible host material (Berryman 1972). Past studies exploring the nature of tree and stand susceptibility for major tree-killing bark beetles, such as mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Amman 1972; Waring and Pitman 1983, 1985; Shore and Safranyik 1992), spruce beetle (*Dendroctonus rufipennis* Kirby) (Hard et al. 1983; Safranyik et al. 1983), and Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) (Furniss et al. 1981; Shore et al. 1999), have contributed significantly to the development of relevant management strategies and options.

The western balsam bark beetle (*Dryocoetes confusus* Swaine (Coleoptera: Scolytidae)) is the most destructive in-

---

Received 3 April 2002. Accepted 25 February 2003. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 14 July 2003.

K.P. Bleiker[1] and B.S. Lindgren.[2] University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada.
L.E. Maclauchlan. British Columbia Ministry of Forests, 515 Columbia Street, Kamloops, BC V2C 2T7, Canada.

[1] Present address: School of Forestry, University of Montana, Missoula, MT 59812, U.S.A.
[2] Corresponding author (e-mail: lindgren@unbc.ca).

Can. J. For. Res. **33**: 1538–1543 (2003)

doi: 10.1139/X03-071

sect pest of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in British Columbia (Garbutt 1992). Western balsam bark beetle selectively kills small groups of subalpine fir at a relatively low, but constant, level each year in infested stands (Stock 1991; Unger and Stewart 1992). Although cumulative mortality may reach significant levels in chronically infested stands (Garbutt and Stewart 1991), western balsam bark beetle is less aggressive than other tree-killing bark beetles at epidemic levels. This selective and patchy distribution of mortality suggests that western balsam bark beetle may be limited by the abundance and distribution of susceptible hosts. Identifying the characteristics of susceptible hosts may contribute to a broader understanding of the ecology of the beetle and aid in developing effective management practices.

Trees in the genus *Abies* lack extensive vertical resin canals (Bannan 1936) and rely on induced resinosis as their defense against attack by bark beetles and fungi. Host vigor has been identified as the main factor affecting the ability of a tree to defend itself (Berryman 1982). Tree vigor, usually indicated by measures of radial growth, may be influenced by senescence, defoliation, pathogens, as well as other factors that cause stress (Coulson 1979; Kaufman and Ryan 1986; Waring 1987; Yoder et al. 1994; Nebeker et al. 1995).

The objective of this study was to identify characteristics of subalpine fir trees susceptible to western balsam bark beetle.

Materials and methods

Study sites

Field sampling was conducted at three sites in the Engelmann Spruce – Subalpine Fir (ESSF) biogeoclimatic zone (Meidinger and Pojar 1991) in the interior of British Columbia during the summers of 1998 and 1999. The Cherry Ridge site (Zone 10 Universal Transverse Mercator (UTM) 393300E 5573300N) was in the wet cold subzone of the ESSF, the Lumby site (UTM 362300E 5551700N) was in the very dry cold subzone of the ESSF, and the Milk River site (UTM 5914800E 655000N) was in the transition zone between the moist mild subzone of the ESSF and the moist cold subzone of the Interior Cedar–Hemlock zone. Subalpine fir was the leading and dominant species at all sites followed by Engelmann spruce (*Picea engelmanni* Parry ex Engelm.) at the Cherry Ridge and Lumby sites, or its hybrid with white spruce (*Picea glauca* (Moench) Voss) at the Milk River site. Patches of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were common in the understory at Milk River. There was no evidence of past logging activity in any of the stands.

Tree characteristics

In August and September 1998, 6 to 10 transects 10 m wide and 50 m apart were established at each site to map and relocate specific trees. Subalpine fir trees attacked in 1998 that occurred in the transects were initially classified using external signs as either unsuccessfully or successfully attacked. Trees classified as unsuccessfully attacked had fresh resin streaming on the bole, with very little or no frass present; successfully attacked trees had frass accumulated at the base, and moderate, light, or no resin on the bole.

A subset of the attacked trees was selected for felling and intensive sampling at each site. To ensure that the sampled trees were independent and not a result of spillover attack from an adjacent sampled tree, all attacked trees selected for felling were located at least 15 m apart, with a minimum of two mature unattacked subalpine fir trees between them. After felling, trees were reclassified as unsuccessfully or successfully attacked based on an additional set of criteria: unsuccessfully attacked trees had no live larvae present, and no live adults present or a limited number of live adults struggling in short galleries inundated with resin; successfully attacked trees had live adults and larvae present. All unsuccessfully attacked trees were correctly classified; however, of trees originally classified as successfully attacked, 2 of 8, 2 of 12, and 3 of 9 trees at Cherry Ridge, Lumby, and Milk River, respectively, were reclassified as unsuccessfully attacked. The corrected classifications were used for all analyses. Unattacked trees were selected as controls for approximately half of the felled trees by identifying the nearest live, unattacked subalpine fir of similar (±10%) diameter at breast height (DBH). Sample sizes were as follows: 7 unsuccessfully attacked, 6 successfully attacked, and 8 unattacked trees were sampled at Cherry Ridge; 11 unsuccessfully attacked, 10 successfully attacked, and 12 unattacked trees were sampled at Lumby; and 8 unsuccessfully attacked, 6 successfully attacked, and 8 unattacked trees were sampled at Milk River.

The following variables were measured for each tree: DBH (cm), height (m), mean crown width (m) (from two measurements taken at 90° angles to each other), mean phloem thickness (mm) (derived from measurements taken on the east and west aspects at 1, 4, 8, 12, and 16 m), percentage of bole with live crown, and percentage of bole with constant crown (used length of the bole with complete and continuous whorls of branches). Crown volume (m^3) was estimated using mean crown width and the length of constant crown to calculate the volume of a cone. Attacked trees with new resin present on the bole were given one of the following three resin ratings: light, resin beads or a few streams present with a large part of the bole lacking resin; moderate, resin streaming pronounced but covers only a short length of the bole or partial circumference; or heavy, bark obscured by resin in the area of the bole with streaming.

Stem disks were taken at 0.5 m above the ground from each felled tree, except at the Milk River site where disks were recut in 1999 at 1.3 m because the flared bases of some trees obscured the growth pattern. Two radii per disk were selected for measurement using the method outlined by Chapman and Meyer (1949). A number of cumulative and periodic growth indices were calculated using the data averaged from the two radii. Because of autocorrelation between the indices, only 5-year cumulative diameter growth was used in the analyses. Age and canopy age, at 0.5 or 1.3 m, were recorded from one of the radii. Canopy age was taken from the time when the tree showed evidence of sustained release. In cases where there was no significant sustained increase in ring width over the radii, canopy age was the same as age. Disks were measured using Windendro software (Regent Instruments Inc., Québec, Que.) and a Hewlett-Packard ScanJet 4c/T scanner (Hewlett-Packard Ltd., Palo Alto, Calif.).

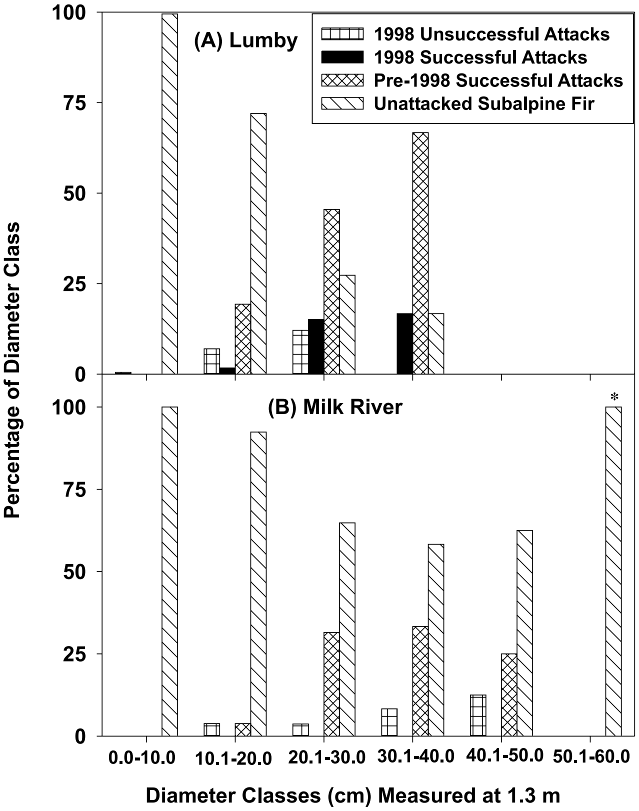
Diameter survey

Six to 12 strip plots, 20 × 5 m, were systematically located along the established transects at each site. Species and DBH of every tree greater than 1.3 m in height occurring in the plot were recorded. Subalpine fir trees were classified according to one of the following conditions: 1, live unattacked; 2, 1998 unsuccessful attack; 3, 1998 successful attack; or 4, pre-1998 successful attack (fading, red, or grey attack).

Data analysis

Data from the diameter distribution survey were graphed to determine the diameter distribution of attacked trees at each site. Site differences in the DBH of attacked trees were tested using a one-factor analysis of variance (ANOVA). Pearson correlation matrices were used to examine the associations among growth indices and tree characteristics. Tree characteristics were analyzed for differences among attack classes (unattacked, unsuccessfully, and successfully attacked) and sites using a three-factor nested ANOVA. Attack class and site were entered in the model as fixed factors, and individual trees were nested under attack class and site and entered as a random factor. A logarithmic transformation was applied to crown volume prior to analysis to correct for non-normality. Significant ANOVAs ($P < 0.05$) were followed by Bonferroni's multiple comparisons test. Pearson chi-square was used to test for independence between attack class and resin production. To avoid bias from small frequencies, data for resin production rating were pooled across sites resulting in a mean expected frequency of at least six (Zar 1999). Data were analyzed using SYSTAT 9.0 (SPSS Inc., Chicago, Ill.).

Fig. 1. Percentage of standing subalpine fir in each diameter class by attack status at Lumby (A) and Milk River (B) sites. There were only two trees in the DBH class denoted by an asterisk.



Results

Diameter survey

The diameter survey measured 64 trees at Cherry Ridge, 354 trees at Lumby, and 468 trees at Milk River.

Mean diameter (±SE) of attacked trees was significantly different among sites, with the largest trees at Cherry Ridge (44.4 ± 3.3 cm), followed by Milk River (31.2 ± 1.0 cm) and Lumby (22.3 ± 1.0 cm) ($F_{[2,103]} = 39.086$, $P < 0.001$; Bonferroni's multiple comparisons test $P < 0.001$). The majority of attacks occurred in the top three diameter classes at Lumby (Fig. 1). Larger trees were also attacked at Milk River; however, the two trees that composed the largest diameter class were not attacked (Fig. 1). Because of the small number of trees sampled in the diameter survey at Cherry Ridge, it was excluded from Fig. 1; however, the 11 attacked trees that were surveyed at Cherry Ridge were in the top three diameter classes (30–60 cm DBH). Western balsam bark beetle contributed to the mortality of over three-quarters of the subalpine fir in the top two diameter classes (20–40 cm DBH) at Lumby, and to that of half the subalpine fir in three of the four largest diameter classes (20–50 cm DBH) at Milk River (Fig. 1).

Tree characteristics

Of the tree characteristics analyzed, age, 5-year cumulative growth, percentage of bole with constant crown, and crown volume showed significant differences among attack classes (Table 1). Successfully attacked trees were significantly older than unattacked trees, had significantly lower growth over the last 5 years, had a lower percentage of their bole covered in constant crown, and had a smaller crown volume (Table 1). Although unsuccessfully attacked trees did not differ significantly from successfully attacked trees or unattacked trees in terms of age, 5-year cumulative growth, and percentage of the bole covered in constant crown, the means were in between those of successfully attacked and unattacked trees (Table 1). Of the tree characteristics that differed significantly among attack classes, percentage of bole with constant crown and crown volume were significantly correlated at all three sites ($P < 0.05$). Five-year cumulative growth and percentage of bole with constant crown were moderately correlated, but only at the Cherry Ridge site ($P < 0.05$).

Resin production was not independent of attack class ($\chi^2 = 12.509$, $P < 0.001$). Eighteen of 26 unsuccessfully attacked trees were classified as having moderate to heavy resin present, whereas only 4 of 22 successfully attacked trees had moderate resin (Table 2).

Discussion

Susceptibility of subalpine fir to attack by western balsam bark beetle was associated with tree diameter, age, recent radial growth, induced resinosis, the percentage of the bole with constant crown, and crown volume.

Table 1. A comparison of tree characteristics among unattacked, unsuccessfully attacked, and successfully attacked trees at Lumby, Cherry Ridge, and Milk River sites.

	Unattacked trees		Unsuccessfully attacked trees		Successfully attacked trees	
	n	Mean (SE)	*n*	Mean (SE)	*n*	Mean (SE)
Diameter (cm)	28	33.7 (1.9)a	26	34.7 (1.7)a	22	32.7 (1.8)a
Height (m)	28	24.4 (0.8)a	26	24.4 (0.6)a	22	24.2 (0.9)a
Age (years)	25	179.6 (8.9)a	19	196.6 (12.3)ab	18	213.4 (12.1)b
Canopy age (years)	26	117.9 (3.7)a	23	116.7 (3.3)a	20	121.5 (2.4)a
5-year growth (mm)	27	4.5 (0.3)a	26	3.7 (0.3)ab	22	2.8 (0.4)b
% bole with live crown	28	69.0 (2.6)a	26	68.4 (2.4)a	22	62.4 (2.4)a
% bole with constant crown	28	56.0 (2.0)a	26	54.6 (1.8)ab	22	48.7 (1.9)b
Mean crown width (m)	28	3.0 (0.1)a	26	3.1 (0.2)a	22	2.8 (0.2)a
Crown volume (m^3)	28	36.3 (4.1)a	26	36.6 (4.5)a	22	27.0 (3.7)b
Mean phloem (mm)	27	5.4 (0.3)a	26	5.4 (0.3)a	22	5.7 (0.3)a

Note: Means within rows followed by the same letter are not significantly different (ANOVA, $P > 0.05$).

Table 2. Number of trees in each resin category by attack class (Lumby, Cherry Ridge, and Milk River sites combined).

	No resin	Light resin	Moderate resin	Heavy resin
Unsuccessful	0	8	18	3
Successful	2	18	4	0

Large diameter is a common characteristic of hosts susceptible to attack by tree-killing bark beetles (Cole and Amman 1969; Baker and Kemperman 1974; Furniss et al. 1981; Shore et al. 1999). Larger diameter trees may provide a more suitable habitat or food source for attacking adults and developing offspring because of increased phloem thickness (Amman 1972; Cole 1973; Amman and Pace 1976; Cole and Cahill 1976; Haack et al. 1987). Phloem thickness, as it affects host suitability, may explain the preference of beetles for larger diameter trees as seen in Fig. 1; however, attacking beetles did not differentiate among trees of comparable diameter based on phloem thickness in our study.

Western balsam bark beetle predominantly attacked trees from the three to four largest diameter classes at each site, with the exception of the largest diameter class at Milk River, which only contained two trees. Thus, a large-diameter, highly susceptible tree at one site may be only a medium-sized, less-susceptible tree at another site. This indicates that factors other than diameter also contribute to the susceptibility of subalpine fir to western balsam bark beetle. Smaller-diameter attacked trees were usually located next to larger mass-attacked trees (K.P. Bleiker, personal observations). Beetles attracted to the larger-diameter mass-attacked trees may have landed on smaller adjacent trees as a result of increasing levels of anti-aggregation pheromones produced by mated females (Stock and Borden 1983).

Tree diameter and age are usually correlated, with the oldest trees in a stand being the largest. Therefore, the increase in the susceptibility of subalpine fir to attack by western balsam bark beetle with tree age may be due, in part, to the effects of diameter. However, given that there was no significant difference in the mean diameters of unsuccessfully and successfully attacked trees (unattacked trees were selected to be of similar diameter to attacked trees), the increase in susceptibility with age may be related to the effects of senescence. Senescence has been associated with a decline in host vigor, although the nature of the relationship has not been resolved (Coulson 1979; Kaufman and Ryan 1986; Yoder et al. 1994). Studies by Furniss et al. (1981) and Shore et al. (1999) have shown that Douglas-fir beetle, which prefers down or weakened hosts, preferentially attacks older trees.

The decline in host vigor, as indicated by declining recent radial growth from unattacked to unsuccessfully attacked to successfully attacked trees, suggests that western balsam bark beetle may not be able to overcome the defenses of more vigorous hosts. Other studies have also associated susceptibility to bark beetle attack with reduced growth and vigor (Ferrell 1973*a*, 1973*b*; Ferrell and Hall 1975; Hard 1985; Larsson et al. 1983; Waring and Pitman 1985; Lessard and Schmid 1990; Shore et al. 1999). Beetles may be able to recognize low-vigor hosts and preferentially select them for attack.

Faster-growing trees were less susceptible to attack by western balsam bark beetle than slower-growing trees, which may be due to the higher quantities of induced resinosis that were observed on fast-growing trees. Induced resinosis is responsible for repelling attacks by adult beetles, inhibiting the establishment of blue-stain fungi associated with bark beetles, deterring oviposition, and increasing brood mortality (Reid et al. 1967; Berryman 1969; Berryman and Ashraf 1970; Christiansen 1985). Host vigor may also affect qualitative aspects of the induced response, e.g., relative amounts of toxic compounds or viscosity (Wong and Berryman 1977; Bordasch and Berryman 1977; Raffa and Berryman 1983; Raffa et al. 1985; Lewinsohn et al. 1993; Rohde and Lunderstadt 1996; Nagy et al. 2000).

Reduced photosynthetic ability may affect the induced response, which depends on the efficient translocation of current photosynthate to the invasion site (Christiansen and Ericsson 1986; Miller and Berryman 1986). Defoliation and pruning may increase susceptibility to bark beetles or their symbiotes (Wright et al. 1979; Miller and Berryman 1986; Christiansen and Fjone 1993). The tendency of successfully attacked trees to have a smaller crown suggests that crown size may be related to resistance. Increased susceptibility of trees with a lower proportion of the bole with constant crown could also be due to higher rates of successful landings on such trees. Branches may inhibit incoming beetles from locating and landing on the bole. Although beetles may land lower on the bole and walk up the tree before attacking, the relatively high flight path of western balsam bark beetle, as shown by Stock (1991), suggests that this beetle may also land on the upper bole.

The preference of western balsam bark beetle for low-vigor hosts is shared by most other species of bark beetles (Rudinsky 1962). Stressed and downed trees may emit volatiles that enable insects to locate weakened hosts. Furthermore, weakened hosts may have lowered defense systems (White 1969), which would increase the likelihood of successful brood production. The results of this study suggest that western balsam bark beetle may be limited by the presence and distribution of susceptible hosts. Therefore, stand management practices that increase host vigor could be used to reduce mortality caused by western balsam bark beetle. The factors that affect susceptibility identified in this study should also be considered in the development of a susceptibility and risk rating model for western balsam bark beetle.

Acknowledgements

We thank Riverside Forest Products for welcoming research in their operating area; C. Ferguson, K. Buxton, S. Nesbitt, S. Moraes, T. Rimmer, S. Collingridge, J. Clarke, A.M. MacIsaac, C. Gauthier, K. Lagrandeur, P. Hulka, and T. Gainer for field and laboratory assistance; K.J. Lewis, P. McMillan, M. Gillingham, and D. Ayres for valuable comments and discussion during the course of the research; L. Safranyik for review of the manuscript prior to submission; and two anonymous reviewers for comments. Funding for the project was provided by a GREAT Scholarship to K.P.B. from the Science Council of British Columbia, a Forest Renewal B.C. grant to L.E.M., Natural Sciences and Engineering Research Council of Canada operating grant to B.S.L., Zeidler Forest Industries, and Bugbusters Pest Management.

References

Amman, G.D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. J. Econ. Entomol. **65**: 138–140.

Amman, G.D., and Pace, V.E. 1976. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. USDA For. Serv. Res. Pap. INT-209.

Baker, B.H., and Kemperman, J.A. 1974. Spruce beetle effects on a white spruce stand in Alaska J. For. **72**: 423–425.

Bannan, M.W. 1936. Vertical resin ducts in the secondary wood of the Abietinae. New Phytol. **35**: 11–46.

Berryman, A.A. 1969. Responses of *Abies grandis* to attack by *Scolytus ventralis* (Coleoptera: Scolytidae). Can. Entomol. **101**: 1033–1041.

Berryman, A.A. 1972. Resistance of conifers to invasion by bark beetle–fungus associations. Bioscience, **22**: 598–602.

Berryman, A.A. 1982. Population dynamics of bark beetles. *In* Bark beetles in North American conifers. *Edited by* J.B. Mitton and K.B. Sturgeon. University of Texas Press, Austin, Tex. pp. 264–314.

Berryman, A.A., and Ashraf, M. 1970. Effects of *Abies grandis* resin on the attack behavior and brood survival of *Scolytus ventralis* (Coleoptera: Scolytidae). Can. Entomol. **102**: 1229–1236.

Bordasch, R., and Berryman, A.A. 1977. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae) 2. Repellency of *Abies grandis* resins and some monoterpenes. Can. Entomol. **109**: 95–100.

Chapman, H.H., and Meyer, W.H. 1949. Forest mensuration. McGraw-Hill, New York.

Christiansen, E. 1985. *Ceratocystis polonica* inoculated in Norway spruce: blue-staining in relation to inoculum density, resinosis and tree growth. Eur. J. For. Pathol. **15**: 160–167.

Christiansen, E., and Ericsson, A. 1986. Starch reserves in *Picea abies* in relation to defence reaction against a bark beetle transmitted blue-stain fungus, *Ceratocystis polonica*. Can. J. For. Res. **16**: 78–83.

Christiansen, E., and Fjone, G. 1993. Pruning enhances the susceptibility of *Picea abies* to infection by the bark beetle-transmitted blue-stain fungi, *Ophiostoma polonicum*. Scand. J. For. Res. **8**: 235–245.

Cole, W.E. 1973. Interaction between mountain pine beetle and dynamics of lodgepole pine stands. USDA For. Serv. Res. Pap. INT-197.

Cole, W.E., and Amman, G.D. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA For. Serv. Res. Pap. INT-97.

Cole, W.E., and Cahill, D.B. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. J. For. **74**: 294–297.

Coulson, R.N. 1979. Population dynamics of bark beetles. Annu. Rev. Entomol. **24**: 417–447.

Ferrell, G.T. 1973*a*. Stand and tree characteristics influencing density of fir engraver attack scars in white fir. USDA For. Serv. Res. Pap. PSW-97.

Ferrell, G.T. 1973*b*. Weather, logging, and tree growth associated with fir engraver attack scars in white fir. USDA For. Serv. Res. Pap. PSW-92.

Ferrell, G.T., and Hall, R.C. 1975. Weather and tree growth associated with white fir mortality caused by fir engraver and roundheaded fir borer. USDA For. Serv. Res. Pap. PSW-109.

Furniss, M.M., Livingston, R.L., and McGregor, M.D. 1981. Development of a stand susceptibility classification for Douglas-fir beetle. *In* Proceedings: Symposium on Hazard Rating Systems in Forest Pest Management, 31 July – 1 August 1980. *Edited by* R.L. Hedden, S.J. Barras, and J.E. Coster. USDA For. Serv. Gen. Tech. Rep. WO-27. pp. 115–128.

Furniss, R.L., and Carolin, V.M. 1977. Western forest insects. USDA For. Serv. Misc. Publ. 1339.

Garbutt, R. 1992. Western balsam bark beetle. Can. For. Serv. Pac. For. Res. Cent. For. Pest Leafl. 64.

Garbutt, R., and Stewart, A. 1991. Forest insect and disease conditions. Prince Rupert Forest Region, 1990. Can. For. Serv. Pac. For. Res. Cent. For. Insect Dis. Surv. Rep. 91-5.

Haack, R.A., Wilkinson, R.C., Foltz, J.L., and Corneil, J.A. 1987. Spatial attack pattern, reproduction, and brood development of *Ips calligraphus* (Coleoptera: Scolytidae) in relation to slash pine phloem thickness: a field study. Environ. Entomol. **16**: 428–436.

Hard, J.S. 1985. Spruce beetles attack slowly growing spruce. For. Sci. **31**: 839–850.

Hard, J.S., Werner, R.A., and Holsten, E.H. 1983. Susceptibility of white spruce to attack by spruce beetles during the early years of an outbreak in Alaska. Can. J. For. Res. **13**: 678–684.

Kaufmann, M.R., and Ryan, M.G. 1986. Physiographic, stand, and environmental effects on individual tree growth and growth efficiency in subalpine forests. Tree Physiol. **2**: 47–59.

Larsson, S., Oren, R., Waring, R.H., and Barrett, J.W. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. For. Sci. **29**: 395–402.

Lessard, E.D., and Schmid, J.M. 1990. Emergence, attack densities, and host relationships for the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in northern Colorado. Great Basin Nat. **50**: 333–338.

Lewinsohn, E., Gijzen, M., Muzika, R.M., Barton, K., and Croteau, R. 1993. Oleoresinosis in Grand fir (*Abies grandis*) saplings and mature trees. Plant Physiol. **101**: 1021–1028.

Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. British Columbia Ministry of Forests, Research Branch, Crown Publications, Victoria, B.C.

Miller, R.H., and Berryman, A.A. 1986. Carbohydrate allocation and mountain pine beetle attack in girdled lodgepole pines. Can. J. For. Res. **16**: 1036–1040.

Nagy, N.E., Franceschi, V.R., Solheim, H., Krekling, T., and Christiansen, E. 2000. Wound-induced traumamtic resin duct development in stems of Norway spruce (Pinaceae): anatomy and cytochemical traits. Am. J. Bot. **87**: 302–313.

Nebeker, T.E., Schmitz, R.F., Tisdale, R.A., and Hobson, K.R. 1995. Chemical and nutritional status of dwarf mistletoe, Armillaria root rot, and Comandra blister rust infected trees which may influence tree susceptibility to bark beetle attack. Can. J. Bot. **73**: 360–369.

Raffa, K.F., and Berryman, A.A. 1983. Physiological aspects of lodgepole pine wound response to a fungal symbiont of the mountain pine beetle. Can. Entomol. **115**: 723–734.

Raffa, K.F., Berryman, A.A., Simasko, J., Teal, W., and Wong, B.L. 1985. Effects of grand fir monoterpenes on the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae), and its symbiotic fungus. Environ. Entomol. **14**: 552–556.

Reid, R.W., Whitney, H.S., and Watson, J.A. 1967. Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue stain fungi. Can. J. Bot. **45**: 1115–1126.

Rohde, M., and Lunderstadt, W.R. 1996. Induced defence reaction in the phloem of spruce (*Picea abies*) and larch (*Larix decidua*) after attack by *Ips typographus* and *Ips cembrae*. For. Ecol. Manage. **86**: 51–59.

Rudinsky, J.A. 1962. Ecology of Scolytidae. Annu. Rev. Entomol. **7**: 327–348.

Safranyik, L., Shrimpton, D.M., and Whitney, H.S. 1983. The role of host–pest interaction in populatioin dynamics of *Dendroctonus rufipennis* (Kirby) (Coleoptera: Scolytidae). *In* The role of insect–plant relationships in the population dynamics of forest pests. *Edited by* A.S. Isaev. Reprinted by the Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C. pp. 2–12.

Shore, T.L., and Safranyik, L. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Can. For. Serv. Pac. For. Res. Cent. Inf. Rep. BC-X-336.

Shore, T.L., Safranyik, L., Riel, W.G., Ferguson, M., and Castonguay, J. 1999. Evaluation of factors affecting tree and stand susceptibility to the Douglas-fir beetle (Coleoptera: Scolytidae). Can. Entomol. **131**: 831–839.

Stock, A.J. 1991. The western balsam bark beetle, *Dryocoetes confusus* Swaine. Impact and semiochemical based management. Ph.D. thesis, Simon Fraser University, Burnaby, B.C.

Stock, A.J., and Borden, J.H. 1983. Secondary attraction in the western balsam bark beetle, *Dryocoetes confusus* (Coleoptera: Scolytidae). Can. Entomol. **115**: 539–550.

Unger, L., and Stewart, A.J. 1992. Forest insect and disease conditions: Nelson Forest Region 1991. Can. For. Serv. Pac. For. Res. Cent. For. Insect Dis. Surv. Rep. 92-3.

Waring, R.H. 1987. Characteristics of trees predisposed to die: stress causes distinctive changes in photosynthate allocation. Bioscience, **37**: 569–574.

Waring, R.H., and Pitman, G.B. 1983. Physiological stress in lodgepole pine as a precursor for mountain pine beetle attack. Z. Angew. Entomol. **96**: 265–270.

Waring, R.H., and Pitman, G.B. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. Ecology, **66**: 889–897.

White, T.C.R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of Psyllids in Australia. Ecology, **50**: 905–909.

Wong, B.L., and Berryman, A.A. 1977. Host resistance to the fir engraver beetle. 3. Lesion development and containment of infection by resistant *Abies grandis* inoculated with *Trichosporium symbioticum*. Can. J. Bot. **55**: 2358–2365.

Wright, L.C., Berryman, A.A., and Gurusiddaiah, S. 1979. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera:Scolytidae). 4. Effect of defoliation on wound monoterpene and inner bark carbohydrate concentrations. Can. Entomol. **111**: 1255–1262.

Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., and Kaufman, M.R. 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. **40**: 513–527.

Zar, J.H. 1999. Biostatistical analysis. Prentice Hall, N.J.