

Resistance of fast- and slow-growing subalpine fir to pheromone-induced attack by western balsam bark beetle (Coleoptera: Scolytinae)

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- Abstract**
- 1 We investigated the resistance of fast- and slow-growing subalpine fir to pheromone-induced attack by western balsam bark beetle at two sites in the interior of British Columbia, Canada.
 - 2 Attack success by the beetle and subsequent tree mortality were higher in slow-growing trees than in fast-growing trees.
 - 3 Fast-growing trees were more likely to produce secondary resin, and in greater quantities, than slow-growing trees after attack.
 - 4 Host vigour (indicated by recent radial growth) was positively related to the induced defense response and resistance of subalpine fir to bark beetle attack. These results are discussed in the context of plant defense and plant–herbivore interaction hypotheses.
 - 5 Given the preference of western balsam bark beetle for weakened trees, as well as the reduced defenses and increased mortality rates in less vigorous trees, effective management tactics for this beetle may include strategies that increase the growth and vigour of its subalpine fir host.

Keywords *Abies lasiocarpa*, bark beetles *Dryocoetes confusus*, growth, growth–differentiation balance hypothesis, host vigour, induced defense, plant defense, plant–insect interactions, plant stress.

Introduction

Tree-killing bark beetles must overcome the defenses of live hosts to successfully colonize trees and produce brood. Plants possess two general types of defense systems to combat attacking organisms: (i) a constitutive defense system, also known as passive, primary or preformed resistance, and (ii) an induced defense system, also known as active, secondary or induced resistance, or dynamic wound response (Klement & Goodman, 1967; Berryman, 1972; Paine *et al.*, 1997). The constitutive defense system of a conifer consists of an extensive system of resin-filled canals that exist in the tree before attack. Attacking beetles may sever the preformed canals and be deterred, drowned, or physically expelled by a short-lived flow of resin. Extensive resin canals are present in many of the Pinaceae, including

trees in the genera *Larix*, *Pseudotsuga*, *Picea* and *Pinus*; however, trees in the genera *Abies*, *Tsuga* and *Cedrus* lack extensive preformed resin canals, and rely mainly on the induced response for defense (Bannan, 1936; Berryman, 1972).

The induced defense response is a rapid reaction by a plant to mechanical wounding or invasion by organisms (e.g. insects, pathogens, viruses, or bacteria) (Klement & Goodman, 1967). The induced reaction involves immediate changes in the function, division, and differentiation of cells adjacent to the attack site (Rohde & Lunderstadt, 1996; Franceschi *et al.*, 2000). These changes lead to cell necrosis (hypersensitivity), decreased sugar concentrations, increased quantities of toxic and/or inhibitory substances, formation of traumatic resin ducts, induced resinosis and wound periderm formation (Reid *et al.*, 1967; Berryman, 1969; Shrimpton, 1973; Wong & Berryman, 1977; Raffa & Berryman, 1983a; Raffa *et al.*, 1985; Lewinsohn *et al.*, 1993; Rohde *et al.*, 1996; Wallin & Raffa, 1999; Nagy *et al.*, 2000). Conifers, such as subalpine fir *Abies lasiocarpa* (Hook.) Nutt., that lack extensive vertical resin canals rely

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on the induced defense response to fend off attack by insects and microorganisms. Even in trees with a constitutive defense system, the induced response may still be an important factor in determining host resistance because some organisms may bypass or survive preformed defenses (for a review, see Fernandes, 1990 and references therein; see also Långström *et al.*, 1992).

The ability of a tree to defend itself against bark beetle attack has long been associated with host vigour, which is often correlated with growth (e.g. Berryman, 1972; but see Baier, 1996; Baier *et al.*, 2002). It is generally accepted that weaker trees are more susceptible to bark beetle attack due to lowered defenses (Mattson & Haack, 1987; Waring, 1987). However, brood production and fitness may be higher in more vigorous trees that are successfully attacked (i.e. defenses overwhelmed) due to a relatively higher quantity or quality of food (phloem). Stated another way, more vigorous trees are predicted to be more resistant to attack, but they may also be more suitable for bark beetles than low vigour trees if the defenses can be overcome.

Many bark beetles release aggregation pheromones to attract conspecifics and attack trees *en masse*. There is a positive correlation between tree vigour and the number of bark beetles required to overwhelm tree defenses (called 'threshold of successful attack') (Berryman, 1972; Waring & Pitman, 1980; Mulock & Christiansen, 1986). This threshold of successful attack predicts that, as beetle numbers increase and more beetles are available to attack *en masse*, the defenses of more vigorous trees can be overcome. This may result in positive density-dependent feedback (until host depletion and/or intraspecific competition becomes a factor leading to delayed negative density-dependent feedback) because the number of susceptible hosts essentially increases as beetle populations increase (Berryman, 1986).

A number of plant defense and plant–herbivore interaction hypotheses may be applied to predict how host vigour affects tree defenses and resistance to bark beetle attack. Most widely applied to bark beetles is the plant stress hypothesis (Waring & Pitman, 1983; Mattson & Haack, 1987; Waring, 1987) and the environmental constraint hypothesis (for reviews, see Herms & Mattson, 1992; Stamp, 2003), which predict that increased stress will result in lower resistance to insect attack due to changes in plant defense during stress. Lorio (1986) applied the growth–differentiation balance hypothesis to explain seasonal variation in bark beetle attack success. The growth–differentiation balance hypothesis also predicts that stressed plants have lower defenses; however, the relationship is curvilinear across the resource gradient (for reviews, see Herms & Mattson, 1992; Stamp, 2003).

Western balsam bark beetle *Dryocoetes confusus* Swaine (Coleoptera: Scolytinae) is the most destructive insect pest of subalpine fir in British Columbia, Canada (Garbutt, 1992). The beetle selectively kills small groups of subalpine fir at a relatively low level each year in infested stands, although cumulative mortality may reach significant levels in chronically infested stands (Stock, 1991; Unger & Stewart, 1992). However, western balsam bark beetle is

less aggressive than other tree-killing bark beetles at epidemic levels, such as the mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytinae), which may kill all mature pine hosts in a geographical region (Wood, 1982). Because western balsam bark beetle preferentially attacks the larger, older, and slower growing subalpine fir trees in a stand, it has been hypothesized that this beetle may be limited by the abundance and distribution of susceptible (weakened) hosts (Bleiker *et al.*, 2003). Indeed, fast-growing trees appear to be capable of eliciting a more rapid defense response than slow-growing trees when inoculated with a bluestain fungus associated with western balsam bark beetle (Bleiker & Uzunovic, 2004). The induced defense reaction was larger in fast- vs. slow-growing trees shortly after inoculation, but there was no significant difference in the size of the induced reaction 41 days after inoculation (Bleiker & Uzunovic, 2004).

We investigated the defense response of fast- and slow-growing subalpine fir to pheromone-induced attack by western balsam bark beetle. The objectives of this study were: (i) to determine the attack success of western balsam beetle in fast- and slow-growing trees and (ii) to determine the rate and extent of the induced defense response of fast- and slow-growing trees to attack by western balsam bark beetle.

Materials and methods

Site description and tree selection

Fifty-two trees were selected for pheromone baiting at two sites in the Engelmann spruce-subalpine fir (ESSF) biogeoclimatic zone (Meidinger & Pojar, 1991) in the interior of British Columbia, Canada. The ESSF is the highest forested ecosystem in mountainous and rugged terrain. The climate is cold, with much of the precipitation in the form of snow. Elevations range from 1000 to 2000 m, and mean annual temperatures are near 0 °C, with up to 2 months of frost-free days (Farnden, 1994). Forests are predominantly dominated by hybrid white spruce, *Picea glauca* (Moench) Voss × *P. engelmanni* (Parry) Engelmann, and subalpine fir. Ten fast- and 11 slow-growing trees were selected at a site (53°19'39"N, 120°41'9"W) in the Milk River drainage in the Robson Valley Forest District. The Milk River site was located at 1350 m elevation on a south-facing 35% slope in the moist mild subzone of the ESSF. Sixteen fast- and 15 slow-growing trees were selected at a site (50°5'59"N, 118°55'31"W) south of Lumby, in the Vernon Forest District. The Lumby site was located at 1700 m elevation on a slope of less than 10% in the very dry cold subzone of the ESSF.

To identify fast- and slow-growing trees, transects 20 m wide, and spaced at intervals of 50 and 100 m were established at Lumby and Milk River, respectively. Two increment cores were collected from each subalpine fir with a diameter exceeding 20 cm along the transects and used to calculate mean cumulative growth for the last 5 years

(CUM5). Cores were taken perpendicular to the slope at the Milk River site, and from east and west aspects at the Lumby site, where slope was negligible. The mean CUM5 of nonattacked trees, unsuccessful attacks and successful attacks identified by Bleiker *et al.* (2003) were used to classify trees into fast- and slow-growing categories. Trees were classified as slow-growing if the mean CUM5 was 2.8 mm or less and fast-growing if the mean CUM5 was equal to or greater than 4.0 mm. Trees with a mean CUM5 between 2.8 and 4.0 mm were excluded from the study. A minimum distance of 15 m was left between fast- and slow-growing trees selected for baiting to avoid saturating the stand with pheromones.

At Milk River, selected trees ranged in age from 85–189 years at breast height and in diameter from 26.5–56.9 cm at breast height. At Lumby, selected trees ranged in age from 93–266 years at breast height, and in diameter from 20.8–37.2 cm at breast height. These trees corresponded to mid- to large diameter classes in the two stands.

Tree baiting and data collection

The 52 selected trees were baited with the commercially available (+/-)-*exo*-brevicomin bait for western balsam bark beetle (Phero Tech Inc., Canada) in late May and mid June of 1999 at Milk River and Lumby, respectively, before the main beetle flight. Trees at the Milk River site were assessed for resin production approximately 3, 5 and 6 weeks after the main flight. At each observation time, resin production was rated as: none, no resin present on the bole; 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 of partial circumference; or heavy, resin streaming on main part of bole and covers majority of circumference (Bleiker *et al.*, 2003). Trees at the Lumby site were assessed once for resin production at approximately 7 weeks after the main flight.

Trees were felled approximately 6–7 weeks after the main flight at each site, and the following information was recorded for each tree: d.b.h., tree height, height of lowest and highest unsuccessful and/or successful attack if present, and attack class. Attack classes were assigned as: unsuccessful, no live adults or larvae present in phloem and discolored lesions from unsuccessful attacks present; light, live adults or larvae present with phloem discolored around galleries, but lines of periderm present with live phloem left between attacked areas (some lesions from unsuccessful attacks may also be present); or successful, live adults or larvae present with highly discolored phloem throughout the attack zone. Five 400-cm² (20 × 20 cm) bark samples were taken at random heights and aspects in the attack zone (between the lowest and highest attack regardless of success). For each bark sample, the following information was recorded if applicable: number of unsuccessful attacks, length and width of each lesion associated with an unsuccessful attack, number of successful attacks (gallery systems), number of female galleries in each gallery system, and the mean female gallery length per gallery system. Data

from the bark samples were collated and, for each tree, the following variables summarizing attack were constructed: density of unsuccessful attacks in the attack zone; density of successful attacks in the attack zone; density of total attacks (unsuccessful and successful) in the attack zone; proportion of tree's total height successfully attacked; mean length of lesion; mean width of lesion; mean number of female galleries per gallery system; and mean female gallery length per gallery system.

Data analysis

Analysis of variance (ANOVA) procedures were used to test for differences in basic tree characteristics between sites and tree growth categories. The proportions of fast- and slow-growing trees that produced resin were compared using Fisher's exact test for small sample sizes. The frequency of occurrences in tree growth categories, resin ratings and attack classes were not statistically compared due to small sample sizes. Variables summarizing attack were analysed for relationships with site and tree growth using ANOVA. Attack variables that could not be normalized with standard transformations were pooled between the two sites and analysed using a nonparametric one-factor ANOVA (Mann–Whitney test). The nonparametric one-factor ANOVAs were repeated on the attack variables using site as the grouping variable and pooling the data from fast- and slow-growing trees at each site. Results from the nonparametric tests were compared with results from parametric two-factor ANOVAs conducted on each attack variable using site and tree growth as factors. Statistical significance did not differ between the parametric and nonparametric tests (*P*-values were within 0.002 of each other). Because the results of the two methods were similar, the planned two-factor design of the experiment, and the robustness of parametric ANOVA to violations of normality (Zar, 1999), the results presented are for the parametric tests performed on nontransformed data. Data were analysed using SYSTAT 9.0 (SPSS Inc., Chicago, Illinois).

Results

Site characteristics

Mean ± SE d.b.h. of baited trees was significantly greater at the Milk River site than at the Lumby site (38.5 ± 1.6 cm and 26.0 ± 0.8 cm, respectively) ($F_{1,48} = 55.181$, $P < 0.001$). Mean d.b.h. of fast- and slow-growing trees did not differ significantly within sites ($F_{1,48} = 0.308$, $P = 0.582$). Height of baited trees did not differ significantly between fast- and slow-growing trees ($F_{1,48} = 0.340$, $P = 0.563$) or between sites ($F_{1,48} = 1.295$, $P = 0.261$).

Host defense and tree growth

All 52 baited trees were attacked by western balsam bark beetles. Six to 7 weeks after the main beetle flight, 29 of the

52 baited trees had produced resin. Fast-growing trees were more likely to have resin present and in greater quantities than slow-growing trees 7 weeks after attack at both sites (Tables 1 and 2); however, the difference was only statistically significant at the Milk River site (Fisher's exact test, $P = 0.008$), and not at the Lumby site (Fisher's exact test, $P = 0.479$).

During the first observation of baited trees at the Milk River site on 21 July 1999, approximately 2–3 weeks after the main beetle flight, two of the 21 baited trees had resin present (one fast- and one slow-growing tree). At this time, all 21 baited trees had beetle frass present, either on the bole or accumulated at the base of the tree, indicating that all trees had received some degree of attack. On 4 August 1999, nine of the 21 baited trees had resin present (six fast- and three slow-growing trees). By 11 August 1999, nine of the 10 fast-growing trees had resin present, and there was no change in the number of slow-growing trees with resin present.

Fast-growing trees were rated slightly higher for resin production than slow-growing trees at the Lumby site (Table 1). This relationship was not discernable at the Milk River site due to the low number of slow-growing trees that produced resin.

The majority of slow-growing trees at both sites were successfully attacked by western balsam bark beetle regardless of the presence of resin or the amount of resin produced (Table 1). Fast-growing trees that produced resin tended to have unsuccessful or light attacks, whereas fast-growing trees that did not produce resin tended to have successful attacks. Fast-growing trees that produced resin had an increased chance of resisting attack (having unsuccessful or light attacks) as resin rating increased.

Attack success and tree growth

The distribution of fast-growing trees into attack categories varied between sites (Table 1). At the Lumby site, fast-growing trees were equally divided between the three attack classes: unsuccessful, light and successful. At the Milk River site, 70% of the fast-growing trees had light attacks, whereas 30% had unsuccessful attacks and no fast-growing trees were successfully attacked. The distribution of slow-growing trees into attack categories followed the same trend at both the Lumby and Milk River sites with the majority being successfully attacked (86% and 73%,

respectively) with the remainder either lightly or unsuccessfully attacked.

The eight fast- and two slow-growing unsuccessfully attacked trees did not differ significantly in mean lesion length ($F_{1,6} = 0.003$, $P = 0.959$), mean lesion width ($F_{1,6} = 0.049$, $P = 0.465$), density of unsuccessful attacks in the attack zone ($F_{1,6} = 0.289$, $P = 0.610$) and proportion of the bole attacked ($F_{1,6} = 105.679$, $P = 0.398$). Site had no significant effect on these variables ($F_{1,6} = 1.873$, $P = 0.220$; $F_{1,6} = 0.791$, $P = 0.408$; $F_{1,6} = 0.921$, $P = 0.374$; $F_{1,6} = 3.822$, $P = 0.098$, respectively).

The six fast- and 21 slow-growing successfully attacked trees did not differ significantly in density of successful attacks in the attack zone ($F_{1,24} = 0.521$, $P = 0.477$), density of total attacks in the attack zone ($F_{1,24} = 1.669$, $P = 0.209$), proportion of the bole successfully attacked ($F_{1,24} = 0.426$, $P = 0.520$), mean number of females per male ($F_{1,24} < 0.001$, $P = 0.996$) and mean gallery length per female ($F_{1,24} = 1.428$, $P = 0.244$). (Because there were no successfully attacked fast-growing trees at the Milk River site an interaction between site and tree growth was not tested for.) Successfully attacked trees at Lumby had a significantly higher density of successful attacks ($F_{1,24} = 4.833$, $P = 0.038$) and total number of attacks ($F_{1,24} = 13.005$, $P = 0.001$) in the attack zone than successfully attacked trees at Milk River. The mean \pm SE number of females per male for successfully attacked trees was significantly higher at Milk River (4.111 ± 0.463) than Lumby (3.243 ± 0.130), although the difference was less than one ($F_{1,24} = 5.008$, $P = 0.035$). The significantly higher mean gallery length per female in successfully attacked trees at Milk River compared with Lumby ($F_{1,24} = 5.886$, $P = 0.023$) was probably due to flight and sampling time differences.

The 12 fast- and three slow-growing lightly attacked trees did not differ significantly in density of successful attacks ($F_{1,11} = 0.002$, $P = 0.966$) or total attacks in the attack zone ($F_{1,11} = 0.035$, $P = 0.854$), proportion of the bole successfully attacked ($F_{1,11} = 0.003$, $P = 0.957$), mean number of females per male ($F_{1,11} = 0.173$, $P = 0.685$) and mean gallery length per female ($F_{1,11} = 1.721$, $P = 0.222$). Site had no significant effect on these variables either ($F_{1,11} = 0.714$, $P = 0.416$; $F_{1,11} = 0.009$, $P = 0.926$; $F_{1,11} = 0.674$, $P = 0.429$; $F_{1,11} = 0.222$, $P = 0.647$; $F_{1,11} = 0.207$, $P = 0.660$, respectively). However, lightly attacked fast-growing trees at Lumby had a higher density of successful attacks in the attack zone than lightly attacked

Table 1 Number and attack status of fast- and slow-growing baited trees by resin production for Lumby site

	Fast-growing ($n = 16$)				Slow-growing ($n = 15$)			
	No Resin	Light Resin	Mod. Resin	Heavy Resin	No Resin	Light Resin	Mod. Resin	Heavy Resin
Unsuccessful	0	1	3	1	0	1	0	0
Light	1	2	2	0	0	1	0	0
Successful	5	1	0	0	8	5	0	0
Total	6	4	5	1	8	7	0	0

n-values are total number of fast- or slow-growing trees that were pheromone-baited.

Table 2 Number and attack status of fast- and slow-growing baited trees by resin production for Milk River research site

	Fast-growing ($n = 16$)				Slow-growing ($n = 11$)			
	No Resin	Light Resin	Mod. Resin	Heavy Resin	No Resin	Light Resin	Mod. Resin	Heavy Resin
Unsuccessful	0	2	1	0	1	0	0	0
Light	1	0	6	0	1	0	1	0
Successful	0	0	0	0	6	0	2	0
Total	1	2	7	0	8	0	3	0

n -values are total number of fast- or slow-growing trees that were pheromone-baited.

slow-growing trees, whereas this pattern was reversed at Milk River, but the interaction was not significant ($F_{1,11} = 3.842$, $P = 0.076$).

Discussion

The higher mortality rate for slow- vs. fast-growing trees indicates that resistance of subalpine fir to attack by western balsam bark beetle is associated with host vigour. This is consistent with other studies, which have found that the induced defense response of trees to bark beetle attack is compromised under stress conditions (for review, see Christiansen *et al.*, 1987 and references therein; see also Wallin & Raffa, 1999; Wallin *et al.*, 2003). Fast-growing trees were probably more resistant to attack than slow-growing trees because they were more likely to produce resin, and in greater quantities. Although resin flow was not sampled before attack, host resistance has been linked to secondary resin production in other systems as well (e.g. lodgepole pine and mountain pine beetle, Reid *et al.*, 1967; Raffa & Berryman, 1982a) and grand fir and fir engraver beetle (Berryman, 1969). Furthermore, the quantity of induced resin produced has also been positively correlated with tree resistance to blue-staining fungal associates of bark beetles (Shrimpton, 1973; Christiansen, 1985; Horntvedt, 1988; Lieutier *et al.*, 1993; Croisé *et al.*, 2001). Attacking adults may be inhibited by resin production as they are physically expelled from the host, drowned in their galleries, or deterred from continuing attack by volatiles in the resin. In addition, induced resin may deter oviposition, increase brood mortality and inhibit the establishment of blue-stain fungi associated with bark beetles (Reid *et al.*, 1967; Berryman, 1969; Berryman & Ashraf, 1970; Shrimpton, 1973; Raffa & Berryman, 1982a, 1982b; Christiansen, 1985; Horntvedt, 1988).

In addition to the quantity of resin produced, tree vigour may also affect the chemical composition or quality of induced resin, as well as other aspects of the induced defense response (e.g. cellular necrosis or wound periderm formation), which are also important factors in host defense (Wong & Berryman, 1977; Raffa & Berryman, 1982b; Raffa *et al.*, 1985; Lewinsohn *et al.*, 1993; Klepzig *et al.*, 1995; Wallin & Raffa, 1999; Nagy *et al.*, 2000; Wallin & Raffa, 2001; but see Kytö *et al.*, 1996; Viiri *et al.*, 2001; Baier *et al.*, 2002). Although these variables were not

measured in this study, attack success tended to be higher in slow- vs. fast-growing trees within the same resin category, suggesting that tree vigour may also affect the quality of the induced response.

Increased resistance in the fastest growing trees is inconsistent with the growth-differentiation balance hypothesis, which predicts that during favourable environmental conditions resources are allocated to growth at the cost of defense (Herms & Mattson, 1992). According to the growth-differentiation balance hypothesis, very stressed and very vigorous plants have the lowest defenses. Lorio (1986) applied the growth-differentiation balance hypothesis to explain the seasonal timing of southern pine beetle attacks *Dendroctonus frontalis* Zimmerman, and why attacks in the spring (when tree growth was high) were more likely to be successful than attacks in the summer (when tree growth was somewhat reduced due to moderate water shortages). The hypothesis explains why even vigorously growing trees may vary in their resistance to bark beetle attack over 1 year; however, the hypothesis was not used to explain variation in beetle attack success and tree defense responses among trees with varying vigour at the same point in time. In our study, the fast- and slow-growing trees were sampled at the same time and were mixed together throughout the stand. Although the cause of the reduced growth is unknown, slow-growing trees were probably significantly older with lower crown volumes than fast-growing trees (Bleiker *et al.*, 2003). Thus, photosynthesis and growth were probably reduced in slow-growing trees resulting in lower defense as predicted by both plant stress and growth-differentiation balance hypotheses. The location of fast-growing trees along the growth-differentiation balance curve is unknown. Although these were some of the fastest growing trees in the stand, competition in a mature stand may still limit resources to some extent. In addition, Wallin & Raffa (1999, 2001) found temporal variation (time after stress) in tree stress and defense relationships based on three sample periods over 1 year starting 1 year after the original stress. An initial parabolic relationship between tree stress and defense supporting the growth-differentiation balance hypothesis was replaced by a negative inverse relationship supporting the plant stress hypothesis. The trees in this study had sustained fast- or slow-growth for an extended period of time, which may have favoured a negative inverse relationship.

Our results support a trade-off between growth and defense, as predicted by the environmental constraint hypothesis (for reviews, see Herms & Mattson, 1992; Stamp, 2003) and the plant stress hypothesis (Waring & Pitman, 1983; Mattson & Haack, 1987; Waring, 1987). The positive relationship between host vigour and resistance to bark beetle attack has been well established for a number of species (Lorio & Hodges, 1977; Ferrell, 1978; Waring & Pitman, 1980; Raffa & Berryman, 1982a; Hard *et al.*, 1983; Hard, 1985; Mulock & Christiansen, 1986; Shore *et al.*, 1999), including western balsam bark beetle (Bleiker *et al.*, 2003). A positive relationship between growth and inducible defenses also supports the results of Lombardero *et al.* (2000) that induced resin flow in *Pinus taeda* L. was greatest for the fastest growing trees during the season of most rapid growth. However, *P. taeda* also has an extensive preformed resin system, and constitutive resin flow was higher in less vigorous trees, supporting the growth-differentiation balance hypothesis (Lombardero *et al.*, 2000). Thus, the authors argue that carbohydrates may be preferentially invested in growth at the cost of constitutive defenses, but allocation of resources to induced defenses becomes a priority when wounding has occurred. Because bark beetles attack *en masse*, wounding would mean a high probability of continued attacks, selecting for a rapid induced response (Lombardero *et al.*, 2000). Because subalpine fir lacks extensive preformed resin canals and relies mainly on induced defenses to fend off bark beetle attack, this may explain why our results support the plant stress hypothesis. Thus, to create an integrative model of plant defense, we may also need to consider the defense system being invoked.

The relatively high number of fast-growing trees that failed to produce resin and were successfully mass attacked at Lumby compared with Milk River may be a function of the higher beetle pressure in Lumby [based on the number of red trees (dead trees likely to contain brood), the beetle numbers were higher at Lumby]. Very rapid attack by a large number of beetles may have interrupted the induced defense response before traumatic resin could be produced. Because there was no significant difference in the variables describing attack between fast- and slow-growing trees in the same attack class (successful, light or unsuccessful attack), this suggests that once the defenses of the host had been overwhelmed, colonization was similar in both fast- and slow-growing trees. This is in contrast with the threshold of successful attack model and studies on the mountain pine beetle and European spruce beetle, which found higher attack densities on more vigorous hosts (Waring & Pitman, 1980; Mulock & Christiansen, 1986). In the mountain pine beetle, the female-produced aggregation pheromone is an oxidation product of one of the principal monoterpenes of lodgepole pine, which leads to a correlation between attack density and vigour (Raffa & Berryman, 1983b). By contrast, the aggregation pheromone of the western balsam bark beetle is not tied to the tree's defenses, and attack density regulation is more likely a function of anti-aggregation (spacing) pheromones (Stock, 1991). This may explain why attack densities were not

higher on the few fast-growing trees that were successfully attacked compared with the slow-growing trees. Western balsam bark beetle preferentially attacks downed trees, and may act as an opportunist attacking trees with weakened defense systems. Even at high population levels, this beetle may be restricted by the defenses of its host tree. However, the sample sizes within attack classes were small and unequal. The significantly higher density of attacks on successfully attacked trees at Lumby compared with Milk River was probably due to the relatively high beetle pressure recorded at Lumby.

Although western balsam bark beetle preferentially attacks slow-growing trees (Bleiker *et al.*, 2003), the results of this study demonstrate that this beetle is capable of successfully attacking pheromone-baited vigorous trees at relatively high beetle population densities. However, western balsam bark beetle failed to induce mass attacks on many of the fast-growing trees, despite high beetle populations and the attraction of pheromone baits. Due to the more effective induced defense response of fast-growing trees, pioneering beetles may be unable to establish attack quickly and release aggregation pheromones to induce the mass attack needed to overwhelm the tree's defenses. Although the synthetic pheromone bait used in this study provided a constant source of attraction, western balsam bark beetle responds to increasing levels of pheromones (Stock, 1991). Therefore, dispersing beetles may have been drawn to the stronger pheromone plume associated with baited slow-growing trees where attack was established quickly due to less resistance from the host tree. If the pheromone baits had been removed from trees as soon as attack was initiated, it is likely that attacks on the more vigorous hosts would not have been sustained, and even fewer attacks would have been successful on these trees.

Given the apparent preference of western balsam bark beetle for weakened trees, as well as the reduced defenses and increased mortality rates in less vigorous trees, effective management of this beetle may include strategies that increase the growth and vigour of subalpine fir. Silvicultural practices, such as thinning or selective cutting, may be used to increase stand vigour and resistance of subalpine fir to western balsam bark beetle. The results of the present study may also be applied to increase the efficacy of using pheromone-baited trees to trap, contain, and (or) concentrate western balsam bark beetle populations (Stock *et al.*, 1994; Maclauchlan *et al.*, 2003). It may be advantageous to preferentially select less vigorous trees for pheromone baiting if the objective is to trap or concentrate beetles in a given tree or patch of trees. If male beetles, which attack first and are polygamous, are unable to successfully establish in high vigour baited trees, then the trees will probably fail to capture or concentrate many female beetles from the population. Smaller crown volume may potentially be used to identify less vigorous trees, which have lower resistance to attack (Bleiker *et al.*, 2003). Thus, the efficacy of pheromone baiting to trap, contain, and (or) concentrate western balsam bark beetle before single tree selection, clear cutting, selective cutting, or patch cutting may be improved by preferentially placing baits on less

vigorous trees where attack is likely to be successful and draw more beetles.

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