Relationship between spruce beetle and tomentosus root disease: two natural disturbance agents of spruce

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Abstract: This project investigated the interaction between tomentosus root disease of spruce, caused by *Inonotus tomentosus* (Fr.:Fr.) S. Teng, and spruce beetle (*Dendroctonus rufipennis* (Kirby)). Both organisms are important agents of mortality and volume loss in boreal and sub-boreal spruce forests of British Columbia. They also occur in similar stand types with respect to species composition and tree age. One study involved an intensive survey of 23 spruce stands, where trees were sampled for both beetle and root disease. Tree condition (dead standing, live, windthrown) was also recorded. Few stands showed a significant relationship between incidence of spruce beetle and incidence of root disease, regardless of tree condition. Observations indicated that beetles actually tended to avoid severely infected trees. A second study involved pheromone baiting of paired healthy and infected trees, and measurements of phloem thickness. Two sites were used, one with very high (epidemic) populations of beetles, and the second with low (endemic) levels. Spruce beetle attacks were more successful on infected trees compared with healthy trees only at the site with endemic levels of beetle. Collectively, the results indicate that tomentosus root disease helps to maintain endemic levels of spruce beetle, and disease incidence may be useful as a tool to identify areas that may have endemic populations of spruce beetle.

Résumé : Cet article traite de l'interaction entre la carie rouge alvéolaire du pied de l'épinette causée par *Inonotus tomentosus* (Fr.:Fr.) S. Teng et le dendroctone de l'épinette (*Dendroctonus rufipensis* (Kirby)). Les deux organismes sont des causes importantes de mortalité et de perte de volume dans les forêts boréales et sub-boréales d'épinette en Colombie-Britannique. Ces organismes sont également présents dans des types de peuplement similaires par leur composition en espèces et par l'âge des arbres. Une étude comportait un inventaire intensif de 23 peuplements d'épinette dans lesquelles les arbres ont été échantillonnés pour la présence du dendroctone et de la carie du pied. La situation de chaque arbre (mort debout, vivant ou renversé par le vent) a également été notée. Peu de peuplements montraient une relation significative entre l'incidence du dendroctone de l'épinette et celle de la carie du pied peu importe la condition de l'arbre. Les observations révèlent que les dendroctones avaient en fait tendance à éviter les arbres sévèrement infectés. Une deuxième étude comportait des paires d'arbres sains et infectés traités avec une phéromone et la mesure de l'épaisseur du phloème. Deux sites ont été utilisés : l'un avec des populations très élevées (épidémiques) et l'autre avec des populations faibles (endémiques) de dendroctones. Les attaques du dendroctone de l'épinette étaient plus fortes sur les arbres infectés que sur les arbres sains seulement sur le site où les populations de l'insecte étaient endémiques. Dans l'ensemble, les résultats montrent que la carie rouge alvéolaire du pied favorise le maintien de populations endémiques du dendroctone de l'épinette et que l'incidence de la maladie peut être utile comme outil pour identifier les zones où sont présentes des populations endémiques du dendroctone de l'épinette.

[Traduit par la Rédaction]

Introduction

The root disease fungus *Inonotus tomentosus* (Fr.:Fr.) S. Teng and the spruce beetle (*Dendroctonus rufipennis* (Kirby)) are both important agents of spruce mortality in the boreal and sub-boreal forests of British Columbia. Both can cause significant timber volume losses (Humphreys and Safranyik 1993; Lewis 1997), and they also have important roles as natural disturbance agents, especially in the wetter spruce ecosystems where fires are infrequent (Lindgren and Lewis 1997; Veblen et al. 1991).

The spruce beetle preferentially attacks recently windthrown or severely stressed trees (Furniss and Carolin 1977; Safranyik 1995). Spruce stands that are in the climax stage of succession usually have endemic populations of spruce beetles, and rapid population build-up results when availability of breeding resources increases. In particular, scattered windthrow can lead to rapid increases in populations, while sheet blowdown tends to produce relatively less brood per available surface area of bark (Safranyik 1985). This is due to the fact that spruce beetles prefer shaded locations, and will only use the bottoms of logs that are completely exposed.

Infection by *I. tomentosus* causes root dysfunction, resulting in tree stress as evidenced by crown symptoms and re-

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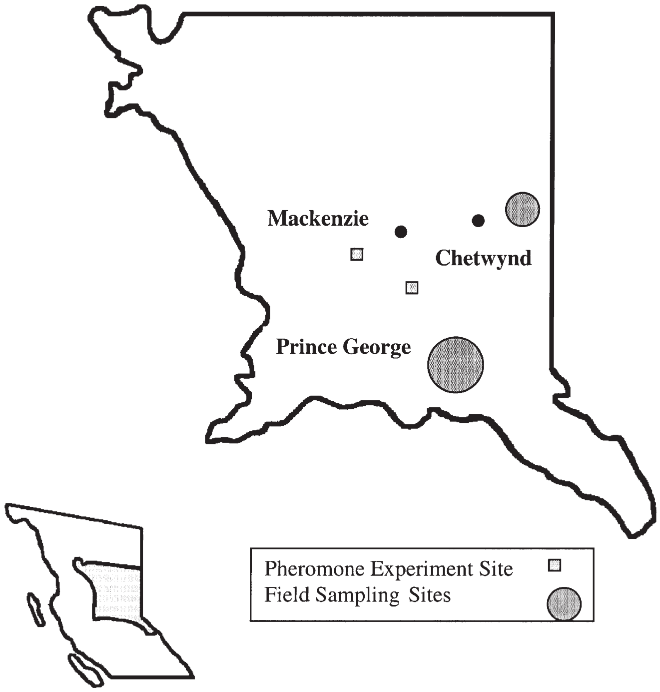
Fig. 1. Map of study areas.



duced growth (Lewis 1997), and loss of structural integrity resulting in windthrow. Tomentosus root disease is distributed patchily throughout infected spruce stands (Lewis and Hansen 1991). These patches could provide suitable habitat for the maintenance of endemic levels of spruce beetles and, combined with wind events that blow down healthy and infected trees, contribute to build-up of spruce beetle populations to epidemic levels.

Bark beetles are often associated with trees of low vigour. It is thought that beetles are either attracted to stressed trees by the chemicals that such trees release, or stressed trees are less able to respond to attack by pitching out the beetles (Tkacz and Schmitz 1986). Root pathogens are known to be important in predisposing trees to attacks by some bark beetle species (Cobb et al. 1974; Hadfield 1985; Lessard et al. 1985; Hadfield et al. 1986; Tkacz and Schmitz 1986; Goheen and Hansen 1993). Cobb (1989) further describes a pattern of beetle population increase in areas of high root disease incidence when combined with a short-term triggering event such as drought. *Dendroctonus pseudotsugae* Hopkins is most likely to be found attacking Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees infected by *Phellinus weirii* (Murrill) R.L. Gilbertson. Low-level beetle populations are maintained in root disease stressed hosts (Hadfield 1985; Hadfield et al. 1986). Tkacz and Schmitz (1986) observed a relationship between endemic levels of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and armillaria root disease (caused by *Armillaria* sp.). Gara et al. (1984) further suggested that *D. ponderosae* is preferentially attracted to lodgepole pine trees with root disease. Lessard et al. (1985) also found a significant association between mountain pine beetle and *Armillaria* in the northern Black Hills of South Dakota. Ponderosa pine trees infected with the root pathogen *Heterobasidion annosum* (Fr.:Fr.) Bref. were frequently attacked by mountain pine beetles and western pine beetles (*Dendroctonus brevicomis* LeConte) (Hadfield et al. 1986). Several authors have documented associations between root pathogens and *Scolytis ventralis* LeConte on *Abies* spp. in western North America (Cobb et al. 1974; Miller and Partridge 1974; Hertert et al. 1975; Lane and Goheen 1979; James and Goheen 1981).

Given these associations, the following study was initiated to determine if tomentosus root disease does provide substrate that contributes to the maintenance, or possible increase, of spruce beetle populations. The objectives of this study were to (*i*) determine if there is a consistent association between bark beetles and tomentosus root disease; (*ii*) determine the nature of that association between infected trees in different categories (windthrown, standing, dead) and bark beetle infestation frequency and population size; (*iii*) determine whether or not spruce beetles are attracted specifically to tomentosus root diseased trees; and (*iv*) examine the relationship between loss of vigour and success or frequency of attack.

Materials and methods

Two approaches were used in this study. The first was a survey of stands with root disease to determine if spruce beetle was associated with root diseased trees. The second was an experiment that involved baiting pairs of infected and healthy trees with pheromones to determine if there was a difference in attack success.

Field surveys

Stands were surveyed in spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm.) dominated forests, 80 years old or more, with *I. tomentosus* present. Candidate stands were identified from forest cover maps and were assessed by walk-through surveys to determine if tomentosus root disease existed on each site. Sites with tomentosus root disease were selected for survey. A total of 23 stands were surveyed; 20 of these were in the Prince George area (Fig. 1) and 3 were in the Chetwynd area (Sub-Boreal Spruce and Boreal White and Black Spruce biogeoclimatic zones, respectively (Meidinger and Pojar 1991)).

At least 1000 m of 10 m wide transect line was surveyed at each site giving a minimum sample coverage of 1 ha. Every spruce tree (15 cm diameter at breast height (DBH) or greater) within the transect was recorded and mapped using the following categories: standing live, standing dead, windthrown, or broken. Every spruce tree in the transect was also assessed for the presence of root disease and spruce beetle. Infected trees were identified by their location relative to infected windthrown and dead standing trees, crown symptoms, and root chopping to look for the reddish brown stain, and (or) pitted decay indicative of *I. tomentosus*. Beetle attack was determined by examining trees for pitch and frass, and by removing patches of bark to observe beetle activity. Trees were recorded as healthy, infected with root disease, attacked by beetle or with both agents present. Data from the field surveys were analyzed at the tree level by constructing contingency tables for each study site. *G* tests for independence of the two factors (root rot and bark beetles) were applied to the data from each site, according to procedures in Sokal and Rohlf (1995).

At the stand level, percent trees attacked by beetle at each site was plotted against the percentage of trees infected with root disease to determine if bark beetle attack increased with root disease incidence. Also, maps of the transect lines were made to show the location, tree condition, and infection or attack status of each tree. The number of trees attacked by beetles and (or) infected with root disease in each 20-m section of transect was recorded and plotted for a subsample of the ten stands that had the highest incidence of disease and beetle. Correlation analyses (SYSTAT version 9) were run on each of these stands to determine if spruce beetle was spatially clumped around root disease infection centres.

Pheromone baiting experiment

The effect of pheromone baiting is to attract beetles to baited trees. Baited trees must be harvested before the beetle flight the following year to avoid increasing beetle populations. Therefore, the sites had to be selected from those scheduled for the next winter's harvest. All candidate sites were surveyed to determine if root disease was present in adequate levels for the experiment. Two stands were selected for pheromone baiting. One (McLeod Lake site) was southwest of Mackenzie (Fig. 1), in a wet, cool part of the Sub-Boreal Spruce (SBS) zone. This site had outbreak levels of spruce beetles. A beetle survey performed the year before the trees were baited determined that 21% of the spruce were attacked and 85% of these were recent attacks (Bugbusters Pest Management, unpublished data[2]). The second site (Mackenzie site) was south of Mackenzie in a moist, cool part of the SBS zone, and had light, endemic levels. A beetle survey in the area found 10% of trees attacked, but only 10% of these attacks were current (D. Devlin, unpublished data[3]). Trees for pheromone baiting were selected systematically by walking transects through the stand and looking for *I. tomentosus* infected trees. Once an infected tree was located, its DBH was determined and the closest healthy tree with a similar DBH (within ±5 cm) was selected to make a pair. Both trees were baited with spruce beetle pheromone (frontalin and α-pinene; Phero Tech Inc., Delta, B.C.) by attaching the bait approximately 2 m off the ground, usually on the north side of the tree. Trees were tagged with a number and flagged for later identification. Infected trees were further classified by light, moderate, or severe crown symptoms. At the McLeod Lake site, 40 pairs of trees (80 trees in total) were baited, and at the Mackenzie site, 26 pairs of trees were baited. Pheromone baiting was done in May 1998 before the spruce beetle flight.

In August and September 1998, the baited trees were sampled for spruce beetle attack and quantification of root disease severity. To quantify beetle attack, 20 × 20 cm bark patches, at a height of 1.5 m, were removed from four quadrants on the tree corresponding to cardinal bearings. The number of successful galleries originating in the patches was counted, as well as the number of pitch-outs, or unsuccessful attacks. In the most heavily attacked quadrant, the brood were counted and recorded by developmental stage (larvae, pupae, and adult). To quantify disease severity, four roots were selected that were closest to the cardinal bearings. Each root was sampled between 0.5 and 1.0 m from the root collar, using a battery-powered drill or a pulaski. Each root was rated for disease severity as follows: (0) no root disease; (1) infected, incipient decay or stain stage; and (2) advanced decay stage. The disease severity rating (DSR) for each tree was calculated by adding the disease ratings for all four roots, to arrive at a number between 0 (healthy trees) and 8.

Additional notes were made regarding the location of the fungus in the roots (heartwood, sapwood, inner bark). Also, the location of the bait was recorded if different from north (closest cardinal bearing), and subjective estimates of pitch and boring dust levels were made. Each tree was rated for attack as follows: (0) no attack; (1) successful full attack; (2) unsuccessful full attack; (3) successful strip attack; and (4) unsuccessful strip attack.

Phloem thickness was measured on all trees by removing a sample of bark with a bark punch, from two approximately equidistant locations on each tree, avoiding areas where the cambium had died and dried out because of spruce beetle activity. The phloem thickness of each sample was measured, and the mean thickness was determined for each tree.

Comparisons of successful attacks (full and strip), unsuccessful attacks (full and strip), and number of brood beetles were made between infected and healthy pairs of trees using a paired t test. The number of successful galleries, the number of pitch-outs, the number of brood insects, and the phloem thickness of infected trees were regressed on DSR.

Differences in phloem thickness between crown symptom categories were also analyzed by analysis of variance (ANOVA) and means separated using a Tukey's test.

Results

Sampling of stands

At the individual tree level, there is no consistent statistically significant evidence that spruce beetles preferentially infest *I. tomentosus* infected trees. Figure 2 shows results of the contingency table G tests. Data from two stands were eliminated from further analysis, because no evidence of beetle infestation was detected during the survey. Six of 21 sites showed a significant P value ($P < 0.05$), however, the remaining 15 stands showed no relationship. Figure 2 shows a plot of G test P values plotted against the percent root disease and the percent bark beetle attack for each stand to determine if the stands showing a significant relationship were those with higher amounts of either root disease or beetle. The figure indicates that the significant P values are from stands that have varying levels of both root disease and bark beetle. A G test on the contingency table of the windthrown trees alone indicated only one stand that showed a significant association between beetle attack and root disease (P = 0.02, site number 12).

When bark beetle incidence (percent trees attacked) for each stand was regressed against root disease incidence (Fig. 3), there was a weak, but significant, relationship between attack by beetles and root disease incidence (r^2 = 0.392, P = 0.038).

[2] Bugbusters Pest Management Inc., 3810 18th Avenue, Prince George, BC V2N 4V5, Canada.
[3] Darrell Devlin, B.C. Hydro, 3333 22nd Avenue, Prince George, BC V2N 2K4, Canada.

Fig. 2. *P* values from contingency table *G* tests, plotted against (A) percent root disease in each stand and (B) percent bark beetles in each stand. Each solid circle is one site. Points below 0.05 on the *Y* axis are sites that had significant *P* values (<0.05).

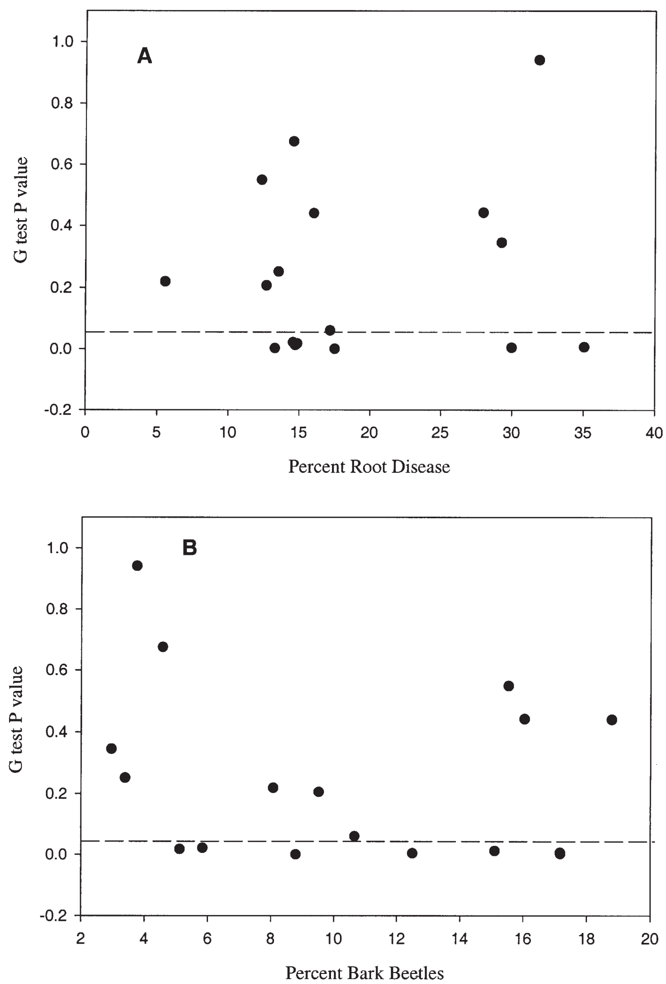


Fig. 4. Difference in number of successful and unsuccessful attacks between infected and healthy trees: (A) Mackenzie site; (B) McLeod Lake site.

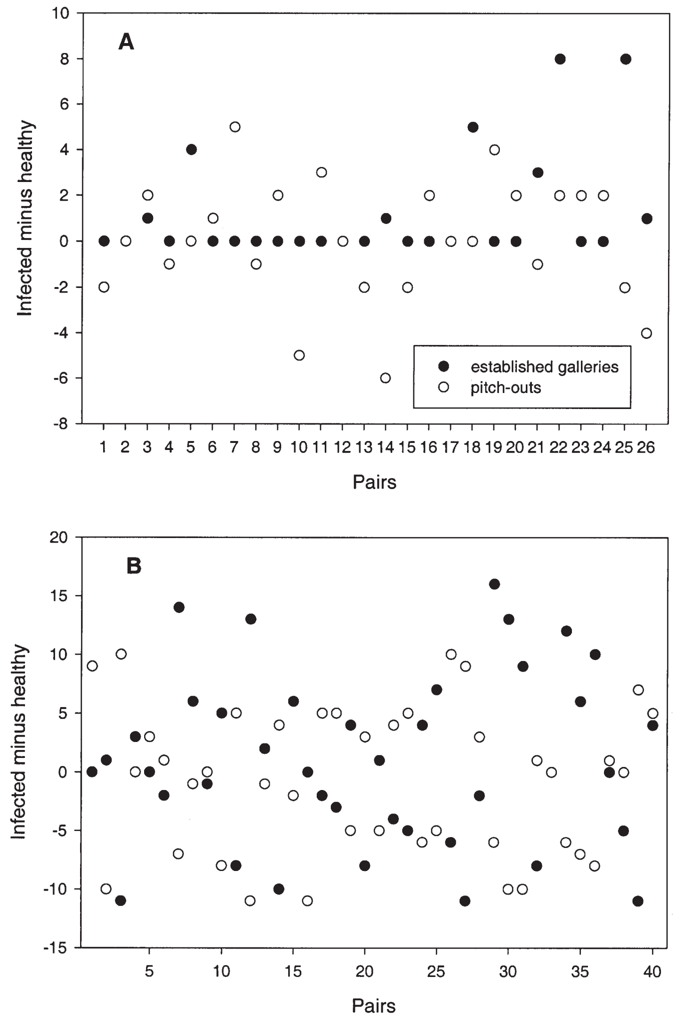
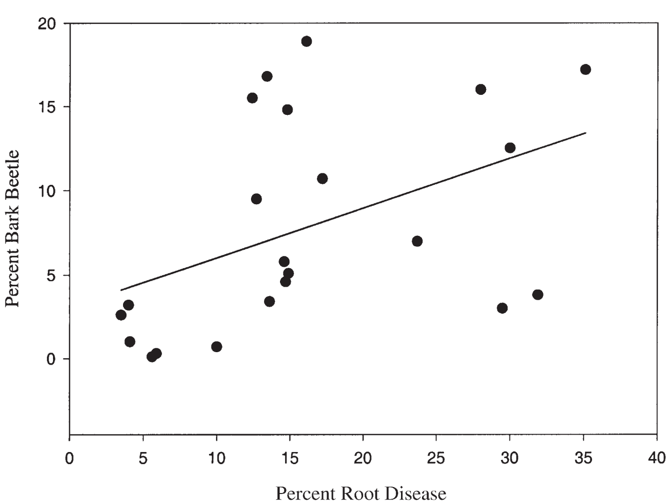


Fig. 3. Percentage of trees attacked by bark beetle plotted against percent trees infected with root disease for each stand surveyed.



Inonotus tomentosus usually occurs in small patches of trees (two to five trees per patch) (Lewis and Hansen 1991). In severely diseased areas, these can coalesce into larger areas of infected trees interspersed with healthy trees. To examine the effect of patches of root disease on bark beetle incidence, frequency plots of root disease and beetle incidence in 20-m intervals were made for the 10 stands with the highest incidence of beetles. These plots showed limited overlap between high beetle incidence and high root disease incidence. Only 4 of the 10 sites analyzed showed a significant positive spatial correlation ($P < 0.05$). Three of these were also shown to have significant relationships at the tree level according to the *G* tests.

Experiment with pheromone baiting

Paired *t* tests on the data from the Mackenzie site showed significant differences between healthy and infected trees for the number of successful galleries established (means 0.35 and 1.54, respectively, 95% CI = [0.22, 2.16], $P = 0.018$), and the number of brood produced (means 0.81 and 4.08, respectively, 95% CI = [0.68, 5.86], $P = 0.015$). The number of unsuccessful attacks (pitch-outs) and phloem thickness were not significantly different between infected and healthy trees. Figure 4A shows the differences in the numbers of successful galleries and unsuccessful pitch-outs in infected trees relative to healthy trees for each of the pairs. None of the infected trees at the Mackenzie site had fewer successful galleries than their healthy mate. Although only 8 of the 26 infected trees baited had successful attacks, in all of these cases, the number of attacks was greater than that in the healthy counterpart. This was not the case at the heavily infested McLeod Lake site (Fig. 4B) where none of the *t* tests showed significant results. Infected trees were no different from healthy trees in terms of successful or unsuccessful beetle attack in this stand with epidemic levels of spruce beetles.

Regression analysis of the relationship between disease severity and the number of successful attacks, unsuccessful attacks, brood density, and phloem thickness showed no consistently significant relationships at either site. However, the Mackenzie data indicated some weak relationships between successful galleries, and number of brood, on disease severity ($P = 0.062$ and 0.067, respectively). Analysis of variance of DSR on crown symptoms showed a significant relationship at both sites ($P < 0.001$ for both). Therefore, the above variables were analyzed by ANOVA on crown symptoms. At the Mackenzie site, the number of successful attacks on trees with severe symptoms was significantly greater than trees classified as healthy ($P = 0.002$) or lightly symptomatic ($P = 0.003$) according to Tukey's post-hoc comparisons. Brood density had a similar relationship with the severely symptomatic trees having significantly greater numbers of brood than healthy and lightly symptomatic trees ($P < 0.001$ and $P = 0.002$, respectively). The number of pitch-outs was not related to crown symptoms ($P = 0.991$). No significant relationships between crown symptoms and brood numbers or attack success were found at the McLeod Lake site.

Paired *t*-test comparisons of phloem thickness between trees with disease severity of 0 and those with disease severity greater than 0 indicated no significant differences between these two classes. However, at the Mackenzie site, trees with a severity rating of 4 or more had significantly thinner phloem than their healthy counterparts ($P = 0.018$). Furthermore, when phloem thickness was compared between trees exhibiting different symptom classes (none, low, moderate, high), phloem of trees infected with tomentosus root disease was significantly thinner ($P = 0.019$) than phloem of healthy trees (Table 1). A Tukey's mean separation test indicated that the phloem of trees recorded as having moderate crown symptoms was significantly thinner than phloem of healthy and lightly symptomatic trees ($P = 0.041$ and 0.038, respectively). Trees with severe crown symptoms were not different, probably because of the low sample size. No significant relationships were observed at the McLeod Lake site.

Table 1. Mean phloem thickness by crown symptom category at the Mackenzie site.

Crown symptom category	Sample size	Mean phloem thickness (mm)	SE
Healthy	26	3.59	0.14
Light	14	3.68	0.28
Moderate	6	3.06*	0.3
Severe	3	2.63	0.14

*Significantly different from healthy and lightly symptomatic trees ($P < 0.05$).

Discussion

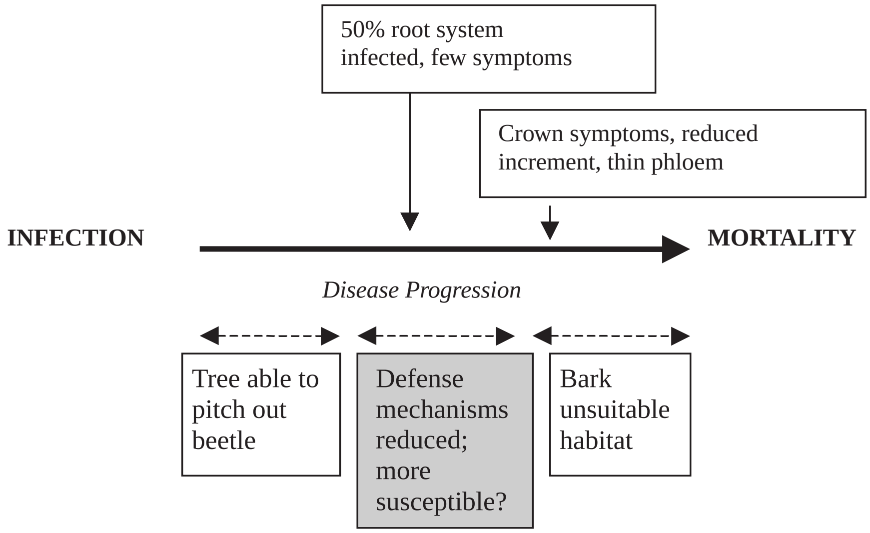
Results from the sampling phase of this project indicate that tomentosus root disease probably does not make a significant contribution to the development of epidemic spruce beetle populations. There may, however, be a weak relationship between the two organisms as indicated by the significant *G* test values in one quarter of the stands surveyed, the overlapping frequency peaks in some of the correlation plots, and the results from the pheromone experiment.

At endemic levels, spruce beetle is found primarily in recently windthrown trees, stumps, or weakened trees (Furniss and Carolin 1977). In this study, trees windthrown as a result of tomentosus root disease usually showed no sign of attack by spruce beetle, even though many of these trees were in shady locations and were suitable sizes for beetle habitat. One possible explanation for this is that spruce beetle may not use such diseased dead trees after the phloem has deteriorated because of drying or invasion by saprophytes. Although some live *I. tomentosus* infected trees are windthrown (K.J. Lewis, personal observations), the number of standing dead trees infected with *I. tomentosus* is much greater than the number of infected windthrown trees (K.J. Lewis, unpublished data). Therefore, it is suspected that most infected windthrown trees examined in this study died before they were blown over. Furthermore, to have significant weakening of structural roots, there must be fairly severe root disease. Results from the site least impacted by beetles indicate that the phloem of severely infected trees is quite thin and may not be suitable habitat for bark beetles. This may explain the lack of spruce beetle attack in downed infected trees.

At endemic levels, spruce beetles are rarely found in living trees unless these trees are severely weakened (Safranyik 1988). Results from the surveys and the measurements of phloem thickness indicate that this may result in a weak association between the two organisms for several reasons. First, when spruce beetles attack living trees, they usually attack trees of larger diameter because of their preference for thick phloem (Humphreys and Safranyik 1993). In stands with low to moderate levels of root disease (less than approximately 15% incidence), large trees are more likely to become infected than small trees because of their larger root systems and the root-to-root spread of *I. tomentosus* (Lewis 1997). Therefore, both the beetle and the fungus commonly attack the same type of tree.

Secondly, trees infected with *I. tomentosus* decline very slowly; large trees can be infected for several decades before they die. In the early stages of colonization, the fungus is limited to heartwood of larger roots, although the cambium of smaller roots (<4 cm diameter) can be killed (Lewis et al. 1992). At this stage it is presumed that the fungus has little

Fig. 5. Conceptual model of the relationship between endemic levels of spruce beetle and tomentosus root disease.



impact on tree physiology and that such trees can successfully pitch out beetles under normal circumstances. As colonization progresses and more roots are killed, the tree begins to decline as evidenced by the development of crown symptoms (thin foliage, chlorosis, reduced leader growth, distress cone crop) and eventually a measurable reduction in tree volume (Lewis 1997). Trees with moderate to severe crown symptoms had significantly thinner phloem than healthy trees or trees with slight symptom development. It is expected that there are other changes (e.g., moisture content, chemical composition) associated with thinner phloem. These changes may explain why spruce beetles were not found in many of the infected trees. However, trees in the middle stages of *I. tomentosus* colonization may have phloem that is less affected by the root disease that would provide suitable beetle habitat. Even though crown symptoms have not developed, or are minimal, and there is no significant loss of volume increment, such trees may be physiologically altered to such a degree that resin flow is impaired and (or) stress chemicals released. This would enable greater success by bark beetles and could explain the inconsistent and weak association between the two organisms observed in the sampling phase of the study. The pheromone experiment supports this explanation by suggesting that there was indeed a relationship between the number of successful galleries and the presence of root disease at the site with low levels of spruce beetle. Of the 26 infected trees baited, 16 had no successful attack, and neither did their healthy mate. Eight infected trees did have successful attack, and in all cases, the number of successful galleries was greater than the number shown by their healthy mate. Collectively, these results suggest that *I. tomentosus* infected trees are not more attractive to spruce beetle but that at a certain stage in disease development they provide a more suitable environment for brood establishment than healthy trees because of reduced defence capabilities. As disease progresses, the tree's defences become more limited and success rate improves as seen in the results from the regression analysis of the Mackenzie data. The experiment demonstrated that beetles can establish a successful brood at a higher rate in infected trees than in healthy trees. At the point in disease development when the fungus has advanced into the sapwood and inner bark, shortly before tree death, the environment for the beetle must become less suitable. This was supported by observations from the sampling phase of the study where severely infected standing trees and infected windthrown trees were infrequently attacked. This may be partly explained by the observation that phloem thickness of infected trees is not different from that of healthy trees until the disease has progressed to the point that the tree is showing moderate to severe symptoms.

Other root disease – beetle associations reported in the literature (e.g., Cobb et al. 1974; Hertert et al. 1975; Tkacz and Schmitz 1986) have indicated stronger associations. However, most other root disease fungi, such as *Armillaria ostoyae* (Romagnesi) Herink and *Phellinus weirii*, kill trees much faster than *I. tomentosus* does. Tomentosus root disease causes a slower decline or chronic stress that may affect beetle behaviour and success differently than the more acute stresses induced by more aggressive root pathogens. Furthermore, spruce trees are very shallow rooted, and in sub-boreal forests they are often found in wet areas with thin soils. As a result, windthrown spruce are common in most spruce stands and the availability of this resource to spruce beetles may outweigh the effects of root disease on host trees. The results from the pheromone experiment support this hypothesis. The positive relationship between spruce beetle attack success and disease severity observed at the site with endemic beetle levels was not observed at the site with epidemic beetle levels. Furthermore, stands with high incidence of spruce beetle attacks sampled in the first phase of the study showed very little association between beetle and root disease. It is suggested that at high beetle populations, the pressure of attack on the host is greater than the effect of the root disease on defence response and therefore overwhelms the root disease effect.

At endemic beetle levels, the association between root disease and beetle is conceptually modelled in Fig. 5. The figure indicates a window of opportunity in root-diseased trees where host suitability for bark beetle is greater than in healthy trees. At epidemic, or outbreak populations, there are other factors that have more influence on beetle success than the presence of root disease.

The results indicate that spruce beetles are probably not specifically attracted to infected trees. However, their success rate in these trees is significantly greater in the period between infection and development of severe crown symptoms. However, it is important to note that these interpretations are based partly on an experiment that was performed only once and on only two sites.

Although tomentosus root disease does not appear to contribute to the development of outbreak populations of spruce beetle under the conditions of this study, infected trees appear to have the potential to harbour greater numbers of beetles at low populations than do healthy trees. Therefore, the incidence of root disease on a site can be used as a tool to indicate areas where other events (e.g., windthrow) may lead to problematic population levels. We have also increased our understanding of the influences on beetle population dynamics, particularly the observation that at outbreak levels, beetle pressure itself has an overwhelming influence on successful attack rates that apparently negates any effects of root disease and reduced phloem thickness.

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