Forest Ecology and Management 257 (2009) 233–237

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Can predicted mountain pine beetle net production be used to improve stand prioritization for management?

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ARTICLE INFO

*Article history:*
Received 9 April 2008
Received in revised form 25 August 2008
Accepted 29 August 2008

*Keywords:*
Stand susceptibility index
Susceptibility rating
Mountain pine beetle
Brood productivity
Stand-level mortality
Net brood production
*Dendroctonus ponderosae*
*Pinus contorta* var. *latifolia*

ABSTRACT

Stand-level planning of lodgepole pine management can benefit from the use of mountain pine beetle susceptibility-risk model analyses to assign treatment priority. Priority is currently assigned based solely on relative levels of expected volume loss in the event of a mountain pine beetle outbreak. We evaluated the possibility to predict the relative contribution of brood beetles, by infested stands, to the next beetle generation. Existing data were used to develop generalized parameters for inclusion in predictive models of stand-level mortality and brood production. Model output for independent stands achieved a highly significant relationship with measured outcomes of brood productivity, indicating that relative levels of brood production can be predicted and incorporated into decision-models.

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## 1. Introduction

Outbreaks of the mountain pine beetle, *Dendroctonus ponderosae* Hopk., can have devastating effects on lodgepole pine, *Pinus contorta* Dougl., forests in western North America (Amman and Cole, 1983). To minimize negative economic impacts of such outbreaks, it is often necessary to prioritize forest stands for treatment, e.g., clear-cutting and thinning. Prioritization is usually assigned to stands based on a stand susceptibility rating model, which provides a measure of potential losses in the event of a mountain pine beetle invasion. In Canada, the most frequently used model was developed by Shore and Safranyik (1992) and Shore et al. (2000). This model assigns a stand susceptibility value, which reflects the potential percent of basal area lost to bark beetles. Basal area is the total cross-sectional area of trees, measured at breast height (1.4 m), per area unit, and it is used to calculate volume, and hence the economic value of a stand. A measure of the percentage of basal area killed is, therefore, a primary concern for forest managers. However, infested stands also provide the host material for the next generation of beetles and thereby constitute a risk for neighboring stands. There is large variation among stands in terms of the number of brood beetles that are produced, which may be due to differences in tree diameter distribution, attack densities, etc. (Safranyik et al., 1975; Safranyik, 1988). It would, therefore, be valuable if stand-level assessments of the relative contribution by infested stands to the next beetle generation could be used together with the stand susceptibility rating system to aid in stand prioritization.

On average, large trees produce more brood beetles than small trees (Safranyik et al., 1975; Safranyik, 1988), but there is also vast variation in brood production between similarly sized trees growing in different stands (Safranyik and Carroll, 2006). Such differences may be due to variation among stands with regard to temperature, moisture, intraspecific competition, host quality, host defenses, natural enemies, etc. Thus, the only way to obtain a precise estimate of the net brood production of any given stand is to do field sampling. Appropriate sampling techniques have been developed for sampling mountain pine beetles in lodgepole pine (Safranyik, 1968). To use net brood production within a stand as a tool for stand prioritization, however, it must be possible to generate a brood production estimate before any beetle attack occurs. In this study, we evaluated the possibility of using general

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doi:10.1016/j.foreco.2008.08.034

mountain pine beetle–lodgepole pine parameters to estimate stand-level net brood production.

## 2. Materials and methods

We calculated "general" mountain pine beetle–lodgepole pine parameters based on data from an independent large-scale study by Shore et al. (2000). In addition, we intensively sampled 26 stands at the end of mountain pine beetle infestations, i.e., when most or all susceptible trees had been attacked and killed, for stand specific attack and emergence densities. To evaluate the accuracy of estimates of stand-level net brood production based on "general" parameters generated from Shore et al. (2000) study stands, the relationship between these estimates and data from the sampled stands were calculated.

The following four-step procedure was carried out to determine the influence of stand-level differences in mountain pine beetle attack and emergence densities on estimates of stand-level net production of beetles, based on general mountain pine beetle–lodgepole pine parameters obtained from the independent study.

(1) Data from Shore et al. (2000) were used to obtain measures of the relationships between diameter-at-breast-height (DBH) vs. percent tree mortality, and DBH vs. net brood production (i.e., number of beetles that emerge from an individual tree minus number of beetles that attacked that tree), respectively. The relationship between DBH and percent tree mortality was obtained by calculating the proportion of lodgepole pine killed for each diameter class (i.e., 0–5, 5–10 cm, etc.). To determine the relationship between DBH and tree-level net brood production, the following relationships were calculated: (i) DBH vs. attack height, (ii) DBH vs. number of attacks per $m^2$ at 1.4 m above ground (attacks were multiplied by 1.6 to compensate for the skewed sex ratio (Reid, 1963)), (iii) DBH vs. number of emerged beetles per $m^2$ (the number of emerged beetles was corrected as per Safranyik and Linton (1985) (see Eq. (2) below) to compensate for the fact that more than one beetle will emerge per hole at high attack densities). The total number of attacks and total number of emerged beetles per tree were then estimated according to Safranyik (1988), taking the taper of the trees and the lower attack densities higher up along the bole into account. Based on these calculations, a formula was developed to estimate the net brood production for a tree with a given DBH, taking the DBH-related probability of attack into account.

(2) Field data to calculate beetle productivity for individual stands were obtained by intense sampling of 26 lodgepole pine stands, where a mountain pine beetle infestation had run its course or was close to the end. The stands were widely distributed within British Columbia, Canada (Table 1). Within each stand, 8–11 variable radius plots were established according to the following procedure. A transect line was laid out at a random bearing, and plots were placed along the transect with random distances of between 80 and 120 m separating them. If the boundary of the stand was reached, a new transect was established at a random distance of between 80 and 120 m, parallel to the original transect. Within each plot, a prism (BAF 5) was used to select trees for sampling. On each tree, at 1.4 m above ground, the number of attacks and the number of exit holes were counted within 15 cm × 30 cm rectangles, one on the north- and one on the south-facing side of the tree. Ventilation holes and exit holes made by other insects can look very similar to mountain pine beetle exit holes (Safranyik and Linton, 1985), so to make sure that we only included mountain pine beetle exit holes, we also removed the bark and examined the associated gallery systems.

(3) Since trees were selected with prisms, we calculated a density factor for each tree as follows (Husch et al., 2003):

$$\mathrm{TDF} = \mathrm{BAF} \times \left(\frac{T_N}{\mathrm{BAF} \times P_N}\right) \qquad (1)$$

**Table 1**

Parameters related to the net production of *Dendroctonus ponderosae* and stand characteristics of the studied lodgepole pine forests in British Columbia, Canada

| Forest district | Latitude (N) | Longitude (W) | Elevation | # Plots | # Pines[a] | % Pine | Age | DBH of pine | Attack density[b] | Intercept[c] |
|---|---|---|---|---|---|---|---|---|---|---|
| Prince George | 53.6 | 123.0 | 855 | 10 | 84 | 79 | 120 | 24 | 126 | 493 |
| Prince George | 53.4 | 123.0 | 872 | 10 | 68 | 82 | 103 | 23 | 105 | 642 |
| Prince George | 53.4 | 123.7 | 783 | 11 | 86 | 88 | 147 | 18 | 110 | 457 |
| Prince George | 54.4 | 122.6 | 764 | 10 | 71 | 86 | 115 | 20 | 135 | 383 |
| Prince George | 54.2 | 122.8 | 751 | 10 | 83 | 76 | 82 | 23 | 104 | 164 |
| Prince George | 53.7 | 123.4 | 950 | 11 | 110 | 75 | 124 | 17 | 84 | 457 |
| Prince George | 53.7 | 123.4 | 850 | 11 | 60 | 79 | 151 | 20 | 86 | –38 |
| Prince George | 53.8 | 123.5 | 883 | 10 | 111 | 97 | 89 | 16 | 91 | 871 |
| Prince George | 53.5 | 123.3 | 765 | 10 | 67 | 68 | 116 | 20 | 161 | 165 |
| Prince George | 53.4 | 123.7 | 898 | 10 | 78 | 82 | 137 | 16 | 82 | 708 |
| Vanderhoof | 53.6 | 124.9 | 850 | 10 | 75 | 95 | 58 | 15 | 145 | 476 |
| Vanderhoof | 53.9 | 124.4 | 1013 | 10 | 80 | 90 | 89 | 17 | 105 | 539 |
| Vanderhoof | 53.9 | 124.4 | 805 | 10 | 90 | 99 | 65 | 16 | 108 | 131 |
| Vanderhoof | 53.9 | 124.4 | 832 | 10 | 92 | 86 | 61 | 16 | 722 | 666 |
| Vanderhoof | 53.8 | 124.3 | 735 | 10 | 102 | 84 | 93 | 19 | 147 | 351 |
| 100 Mile House | 51.6 | 121.4 | 1147 | 10 | 41 | 64 | 62 | 14 | 132 | 959 |
| 100 Mile House | 52.0 | 121.3 | 956 | 10 | 95 | 99 | 120 | 27 | 73 | 733 |
| 100 Mile House | 52.0 | 121.2 | 1003 | 10 | 123 | 94 | 122 | 23 | 789 | 545 |
| Columbia | 51.1 | 116.5 | 1302 | 10 | 43 | 39 | 124 | 30 | 136 | 127 |
| Columbia | 51.2 | 116.6 | 1120 | 10 | 57 | 67 | 119 | 26 | 160 | –78 |
| Columbia | 51.2 | 116.6 | 1140 | 10 | 75 | 93 | 84 | 20 | 188 | 388 |
| Rocky Mountain | 49.6 | 116.2 | 1500 | 8 | 61 | 91 | 111 | 19 | 148 | 482 |
| Rocky Mountain | 49.6 | 116.2 | 1756 | 10 | 101 | 92 | 107 | 12 | 88 | 499 |
| Rocky Mountain | 49.6 | 116.2 | 1473 | 10 | 99 | 99 | 110 | 15 | 163 | 233 |
| Rocky Mountain | 49.6 | 116.2 | 1707 | 10 | 49 | 74 | 105 | 19 | 131 | 746 |
| Rocky Mountain | 49.6 | 116.2 | 1296 | 10 | 50 | 57 | 94 | 14 | 152 | 226 |

[a] Number of pines that were sampled.

[b] Mean number of attacks per $m^2$ (adjusted for skewed sex ratio) at 1.4 m above ground.

[c] Intercept value for the stand-specific version of Eq. (6) which was used to calculate the DBH-related number of emerged beetles per $m^2$ (see Section 2).

where TDF = tree density factor (trees/ha), BAF = basal area factor, $T_N$ = number of trees sampled, and $P_N$ = number of plots sampled.

The generalized net brood production of each stand, defined as the net brood production based on the beetle–lodgepole pine parameters from the independent study (Shore et al., 2000), was then calculated for each of the 26 stands as the sum of the net brood production for each sampled tree, multiplied by the tree density factor for that tree.

(4) The stand-specific net brood production per ha, defined as the net production based on stand-specific beetle attack and emergence data from sampling, was calculated as in "step 3" except that: (i) a stand-specific number of attacks per unit area, multiplied by 1.6 to compensate for the skewed sex ratio normally found in mountain pine beetle populations (Reid, 1963), was inserted in the formula described in "step 2" instead of the value from the independent study, and (ii) a stand-specific regression line, representing the relationship between DBH and number of exit holes per unit area sampled in that stand, was used in the formula described in "step 2", instead of the generalized regression line based on the independent dataset. We calculated a stand-specific intercept of the line based on the mean DBH and the mean number of exit holes per unit area for all trees within a stand. We assumed that the slope of this line is always the same. Emergence was adjusted to compensate for the fact that, according to Safranyik and Linton (1985), more than one beetle emerges from each exit hole at high attack densities (Eq. (2)):

$$y = 1.2635x - 0.3300 \tag{2}$$

where $y$ = log (number of emerged mountain pine beetles/ 0.125 $m^2$) and $x$ = log (number of holes in the bark/0.125 $m^2$).

A stand susceptibility index (SSI) was calculated for each of the 26 stands sampled. We used a modification of the Shore and Safranyik (1992) system where some discrete functions had been replaced with continuous functions according to Shore et al. (2006).

To determine if the estimated net brood production can provide an additional aid for stand prioritization, we calculated the correlation between stand susceptibility index and stand net brood production. We should expect a correlation since a stand's net brood production is related to the four variables that are used to calculate the index, i.e., percentage of susceptible pine basal area, age, tree density and location (latitude, longitude and elevation). If this correlation explains most of the variation, then we would conclude that the estimated net brood production would not add to the index, and hence would not be a useful tool for stand treatment prioritization.

The relationship between a stand's net brood production and its stand susceptibility index is, to a large extent, determined by the relationships between DBH vs. tree-level net brood production and DBH vs. basal area. Basal area, i.e., the area of the cross-section of a tree trunk at breast height, is the metric used in the stand susceptibility rating system to quantify tree mortality, and increases exponentially with increasing DBH. The net production of beetles per tree also increases exponentially with increasing DBH. We generated curves of the rate of increase for these two relationships to determine the tree diameters that contribute most, per tree, to any discrepancy between net brood production and stand susceptibility rating. The estimated generalized net brood production was calculated according to "step 1" described above.

Risk Rating Software (v.3) was used to calculate stand susceptibility index. The rest of the data analyses were performed using SigmaPlot® 9.0 (Systat Software Inc., Point Richmond, CA, USA).

## 3. Results

Eqs. (3)–(9) presented below were calculated from the independent study and represent the "general" mountain pine beetle–lodgepole pine parameters:

DBH (cm) vs. proportion of lodgepole pine killed by mountain pine beetle (Fig. 1):

$$y = \frac{a}{1 + \exp(-(x - x_0)/b)}, \quad a = 0.8049, \; b = 5.3411, \; x_0 = 20.1662; \; R^2 = 0.98; \; P = <0.0001 \tag{3}$$

DBH (cm) vs. attack density per $m^2$ (adjusted for skewed sex ratio):

$$y = 0.9395x + 130.4526, \quad r^2 = 0.0063; \; P = 0.2545 \tag{4}$$

Since there was no significant relationship between DBH and attack density (Eq. (4)) the mean attack density was used instead (Eq. (5)).

Mean attack density per $m^2$ (adjusted for skewed sex ratio):

$$y = 153.7305 \tag{5}$$

DBH (cm) vs. number of emerged beetles per $m^2$:

$$y = 36.8046x - 399.0261, \quad r^2 = 0.0478; \; P = 0.002 \tag{6}$$

DBH (cm) vs. attack height (m):

$$y = 0.3320x - 1.0589, \quad r^2 = 0.3040; \; P = <0.0001 \tag{7}$$

The mean number of beetles attacking a tree with a certain DBH, including the probability that the tree will be attacked, was calculated as follows (based on Eqs. (3), (5), and (7) from the present study and Eq. (13) in Safranyik (1988), which states that $T_a = 129.2189\ (X_a^{0.2964})(D^{1.7665})(H_i^{0.9430})$; $T_a$ = attack totals in individual trees; $X_a$ = attack density per square metre at 1.22 m on the bole; $D$ = tree diameter (m) at 1.37 m; $H_i$ = infested bole height (m)):

$$y = (3)(5)(7)\ (13\ \text{in Safranyik, 1988}) \tag{8}$$

The mean number of beetles emerging from a tree of a given DBH, including the probability of attack on that tree, was calculated as follows (based on Eqs. (3) and (5)–(7) above and Eq. (14) in Safranyik (1988), which states that $T_b = 48.0586\ (X_b^{0.6386})(D^{1.3264})(H_i^{0.7465})$; brood totals in individual trees; $X_b$ = brood density per square metre at 1.22 m on the bole; $D$ = tree

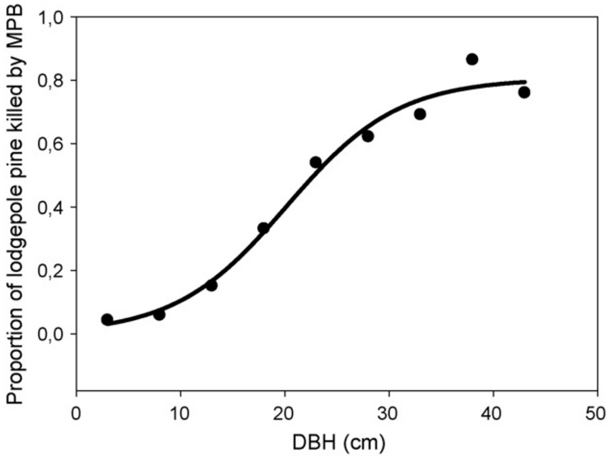

**Fig. 1.** Relationship between the DBH of a lodgepole pine tree and its probability of being killed by mountain pine beetles (MPB), *Dendroctonus ponderosae*. The relationship could be characterized by a three-parameter sigmoid equation.

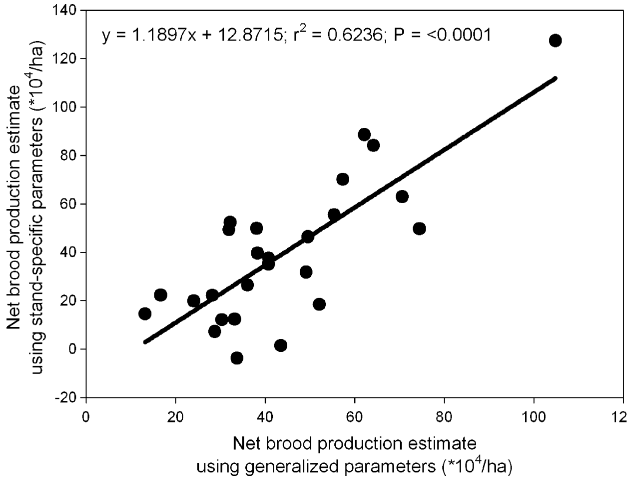

**Fig. 2.** Relationship between estimates of net brood production based on generalized *D. ponderosae–Pinus contorta* parameters vs. stand-specific parameters, i.e., attack and emergence data from Shore et al. (2000) vs. from that specific stand. Each dot represents one stand.

diameter (m) at 1.37 m; $H_i$ = infested bole height (m)):

$$y = (3)(5)(6)(7)(14\ \text{in Safranyik, 1988}) \tag{9}$$

The mean net brood production for a tree of a given DBH, including the probability of attack for that tree, was calculated as follows (based on Eqs. (8) and (9)):

$$y = (9) - (8) \tag{10}$$

The stand-specific parameters from the 26 stands that were intensively sampled in the present study are given in Table 1. There was great variation in mountain pine beetle productivity among stands, which was mainly due to large variation in the number of beetles that emerge per unit area (Table 1, intercept values for the stand-specific version of the equation that were used to calculate the DBH-related number of emerged beetles per m$^2$).

The relationship between estimates of net brood production per ha, based on generalized vs. stand-specific mountain pine beetle–lodgepole pine parameters, is shown in Fig. 2. This relationship can be described with the following equation:

$$y = 1.1897x + 12.8715, \quad R^2 = 0.6236; P = \ < 0.0001 \tag{11}$$

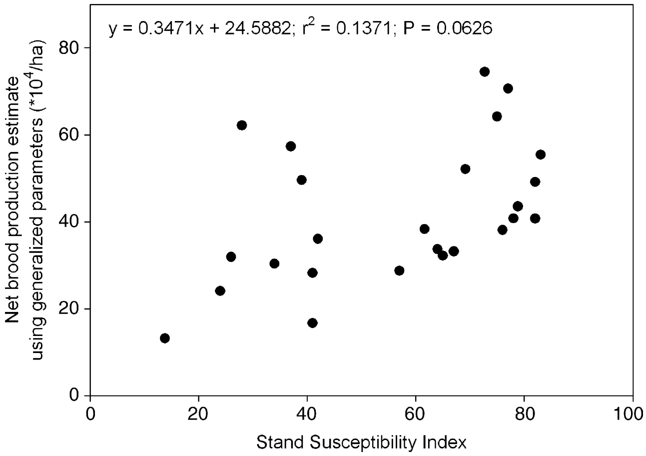

**Fig. 3.** Relationship between stand susceptibility index and estimates of net brood production based on stand-specific *D. ponderosae–Pinus contorta* parameters. N.B.: the aim of the stand susceptibility index is not to predict net brood production.

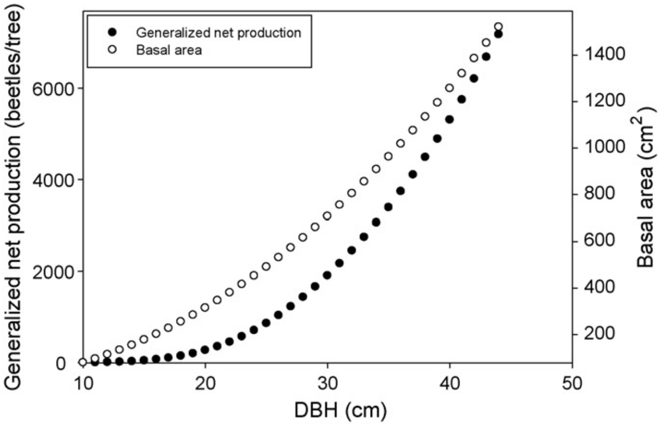

**Fig. 4.** Relationship between a tree's DBH and its estimated net brood production based on generalized *D. ponderosae–Pinus contorta* parameters (including the probability of beetle caused mortality (see text)). To make a comparison to measures that are based on basal area possible the DBH vs. basal area relationship were also plotted.

There was no significant relationship between Stand Susceptibility Index ratings and stand-specific net brood production estimates (Fig. 3, Eq. (12)):

$$y = 0.3471x + 24.5882, \quad R^2 = 0.1371; P = 0.0626 \tag{12}$$

The relationship between DBH and basal area is described in Eq. (13) and plotted in Fig. 4. For comparative purposes, the relationship between the DBH of a lodgepole pine and its net brood production (described in Eq. (10)) is also plotted in Fig. 4.

$$y = \pi\left(\frac{x}{2}\right)^2 \tag{13}$$

## 4. Discussion

The objective of this study was to develop a simple index of mountain pine beetle net brood production based on stand parameters and known tree–insect interactions. We assumed that in addition to potential stand volume losses, treatment priority should also take into account the potential contribution by a stand to the next generation of beetles. In other words, we assumed that there is a direct relationship between the number of brood beetles contributed by a stand to the next generation, and the impact on outbreak progression by treatment activities such as harvesting. Thus, when assigning harvesting priority among stands with similar susceptibility scores, those with the highest estimated net production of beetles should be given preference.

As expected, there was great variation in beetle productivity among similar sized trees in different stands. This variation may be due to variation among stands with regard to climatic suitability, host defenses, etc. (Safranyik and Carroll, 2006). However, this variation had only a minor influence compared to that of the tree diameter distribution on a stand's net production of brood beetles. Thus, before any beetle attack occurs, calculations can be made, based solely on tree diameter distributions and generalized parameters, which explain a large part of the variation in expected stand-level net brood production (Fig. 2).

There were two reasons why larger trees generally produced more beetles than the small trees: (i) the relationship between tree diameter and percent beetle-caused tree mortality tended to follow a sigmoid distribution with larger trees being attacked more frequently (Fig. 1); and (ii) among attacked trees the larger ones generally had a higher net production of beetles. The higher net production was due to larger trees having a higher maximum height of attack, i.e., they were attacked over a much larger surface area than smaller diameter trees, they produced more beetles per $m^2$ of bark at DBH, and other general factors that are summarized in Safranyik (1988).

There was no significant correlation between the diameter of the attacked trees and beetle attack density and there was only a weak correlation between the diameter of attacked trees and the number of emerged beetles per $m^2$. Tree diameter may be a significant variable when individual stands are analyzed separately (Reid, 1963; Cole and Amman, 1969) but when data from several separate locations are incorporated into a single regression the strength of such correlations tend to be noticeably weaker (Berryman, 1976). The average attack density was relatively high, but not extreme (see Berryman et al. (1985) for a literature review). This suggests that the vigor of the sampled trees was relatively high (Raffa and Berryman, 1983).

Estimates of net brood production can provide an additional aid for stand prioritization since the stand susceptibility index explains little of the variation in net brood production (Fig. 3). The largest trees contributed most, per tree, to the discrepancy between net brood production and stand susceptibility rating (Fig. 4). For example, a 35 cm DBH tree have a basal area that is approximately twice as large as a 25 cm DBH tree whereas the net production of beetles is more than three times as high in a 35 cm DBH tree compared to a 25 cm DBH tree. Thus, the higher the proportion of a stand that is made up of large trees the larger the discrepancy between net brood production and stand susceptibility.

The estimates of the net brood production should be treated with some caution since they are based on a limited number of parameters and, most likely, simplified relationships. It is, for example, likely that the calculated net production in small trees is slightly overestimated since we used a linear regression to represent the relationship between DBH and number of emerged beetles per $m^2$. In reality the net production probably drops sharply when the phloem is too thin for the beetle to survive. This has, however, only a minor influence on the stand-level net production estimate.

The precision of the net brood production estimates based on generalized parameters can probably be improved if the larger dataset, which we used to evaluate the model in the present study, was used to calculate the mountain pine beetle–lodgepole pine parameters, i.e., DBH vs. brood production per $m^2$, etc. We also used the Shore and Safranyik (1992) location factor in the calculation of the stand susceptibility index. Björklund and Lindgren (in preparation) showed by meta analysis that the location factor explained 53% of the variation of stand-level mortality of lodgepole pine during mountain pine beetle outbreaks. Changing climatic conditions have led to the development of a more sensitive climatic suitability index (Carroll et al., 2004), so it is possible that further improvement might be accomplished if this index is incorporated in the model (Cudmore, in preparation).

To our knowledge, this is the first time that stand parameters have been used to predict insect population parameters for the explicit purpose of forest management. The approach used in this study, i.e., to evaluate the precision of net beetle production estimates made before the host is attacked, may be useful also in other systems with aggressive bark beetle species where managers need to rank areas in order of priority with regard to treatments.

## Acknowledgements

This project was funded by the Government of Canada through the Mountain Pine Beetle Initiative and administered by Natural Resources Canada, Canadian Forest Service. Publication does not necessarily signify that the contents of this report reflect the views or policies of Natural Resources Canada—Canadian Forest Service. Mention in this publication of any commercial product or service does not constitute endorsement of such by the Canadian Forest Service or the Government of Canada. Les Safranyik and one anonymous referee are acknowledged for comments on an earlier version of the manuscript. We thank Simon Goring, Marnie Graf, Erin Carlson, Mirco Muntener, Crystal Braun, Khya Saban, and Jeff Selesnic for assistance in the field, and employees of the BC Ministry of Forests and Range for help with locating field sites.

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