Effects of fire return rates on traversability of lodgepole pine forests for mountain pine beetle (Coleoptera: Scolytidae) and the use of patch metrics to estimate traversability

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Abstract—A Monte-Carlo simulation was used to examine the effects of fire return rates on the equilibrium age structure of a one-million-hectare lodgepole pine forest (*Pinus contorta* var. *latifolia* Engelm. *ex* S. Wats.; Pinaceae) and yielded a mosaic of ages over the one million hectares for each fire regime modelled. These mosaics were used to generate mosaics of susceptibility to mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins, 1902) attack. This susceptibility was related to the age distribution to calculate the mean susceptibility of the forest. Susceptibility maps were produced for two timber supply areas in British Columbia, as well as for the whole of B.C. In addition, we defined a quality, called traversability, that describes the ability of a beetle population to disperse across a landscape according to defined rules of susceptibility and maximum distance for dispersal through unsuitable habitat. Using each of 40 combinations of susceptibility classifications and dispersal limits, the landscape was categorized as traversable or non-traversable. This represents the suitability of a landscape to the unimpeded spread of an incipient beetle population. It was found that (*i*) long fire cycles yield an age structure highly susceptible to beetle attack; (*ii*) fire suppression reduces the frequency of fires and yields an age structure highly susceptible to beetle attack; and (*iii*) harvesting one age class reduces the mean susceptibility to MPB attack, and this reduction decreases with increasing harvest age and increasing fire cycle length. When fires were limited in size to less than 100 ha, the area was always traversable. For larger fires, traversability declined, and for the largest fires (up to one million hectares), the area was often not traversable. Harvesting reduced the mean susceptibility and traversability, often substantially. Traversability was calculated for the whole of B.C. in blocks of about one million hectares using B.C. Ministry of Forests and Range inventory data for the year 2000. The area most traversable was the area around Tweedsmuir Park and the Lakes Timber Supply Area, where most of the present outbreak of MPB is centred. FRAGSTATS patch metrics were calculated for each of the simulations and were related to traversability using discriminant analysis. This analysis was then applied to the B.C. inventory; the concordance was high, with 93.3% of conditions being correctly classified.

Résumé—Une simulation de Monte Carlo nous a servi à examiner les effets de la fréquence des feux sur la structure d'âges à l'équilibre d'une forêt d'un million d'hectares de pins vrillés (*Pinus contorta* var. *latifolia ex* S. Wats.; Pinaceae) et a fourni une mosaïque des âges sur le million d'hectares pour chacun des régimes de feux modélisés. Ces mosaïques permettent de générer des mosaïques de vulnérabilité aux attaques du dendroctone du pin ponderosa (MPB) (*Dendroctonus ponderosae* Hopkins, 1902). Cette vulnérabilité associée à la distribution des âges sert à calculer la vulnérabilité moyenne de la forêt. Nous avons produit des cartes de vulnérabilité pour deux régions de production de bois en Colombie-Britannique, ainsi que pour l'ensemble de la province.

Received 23 February 2005. Accepted 12 August 2005.

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De plus, nous définissons une caractéristique, la pénétrabilité, qui décrit la possibilité qu'a une population de coléoptères de se disperser dans un paysage d'après des règles définies de vulnérabilité et de la distance maximale de la dispersion à travers un habitat défavorable. À l'aide de 40 combinaisons de catégories de vulnérabilité et de limites à la dispersion, le paysage peut être caractérisé comme pénétrable ou non pénétrable. Cela représente la possibilité de dispersion sans encombre d'une nouvelle population de coléoptères dans un paysage donné. Nous avons observé que (*i*) les longs cycles de feux entraînent des structures d'âges qui sont très vulnérables à l'attaque des coléoptères, (*ii*) la suppression des feux réduit la fréquence des feux et permet une structure d'âges très vulnérable aux coléoptères et (*iii*) la récolte d'une classe d'âge réduit la vulnérabilité moyenne aux attaques de MPB et cette réduction diminue en fonction de l'accroissement de l'âge de la classe récoltée et de la longueur des cycles de feux. Quand les feux sont limités à des surfaces de moins de 100 ha, la région est toujours pénétrable. La pénétrabilité décline lors les feux plus importants et elle devient souvent nulle lors des feux les plus étendus (jusqu'à 1 million d'hectares). La récolte réduit la vulnérabilité moyenne et la pénétrabilité, souvent de façon substantielle. Nous avons calculé la pénétrabilité pour l'ensemble de la C.-B. en parcelles d'environ 1 million d'hectares à l'aide des données d'inventaire de l'an 2000 du Ministère des forêts et des prairies (Ministry of Forests and Range). La région la plus facilement pénétrable est celle des environs du parc Tweedsmuir et de la région de production de bois des Lacs, où l'épidémie actuelle de MPB est concentrée. Nous avons calculé les métriques des parcelles par FRAGSTATS pour chacune des simulations et les avons reliées à la pénétrabilité par analyse discriminante. Nous avons appliqué le modèle à l'inventaire de la C.-B. et obtenu une concordance élevée puisque 93,3 % des situations sont classées correctement.

[Traduit par la Rédaction]

Introduction

Forest fires, attack by mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins, 1902) (Coleoptera: Scolytidae), and harvesting are the three major sources of mortality for mature lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. *ex* S. Wats.) (Pinaceae) in the interior of British Columbia, Canada. Although fires can occur in stands of any age, fire and MPB attack occur mainly when trees are of harvestable age, and it is often a challenge for forest managers to plan harvesting to occur before a stand has been devastated by either fire or the beetle. Fire is usually more severe, and an MPB outbreak more likely, in years with hot, dry summers (Safranyik 2004), and both are suppressed in years with cool, moist summers, although if a beetle epidemic is in progress, a cool, moist summer may not stop it or even slow it down significantly. It is thus reasonable to expect that there may be an interaction between wild fires and MPB in terms of the probability of occurrence. Also, once a stand has been burned, it may be less susceptible to attack by MPB, as there are fewer live trees (or maybe none) for the beetle to attack; on the other hand, stands that have been recently attacked by the beetle may be more susceptible to fire because the foliage dries out on the trees that are killed, although evidence for such an increase in susceptibility is lacking. It seems likely, in fact, that there might be an interaction between several factors such as climate, weather variations, condition of the trees, and species mix. Another such factor is the age structure of the forest, which will depend partly on forest fire return rates and fire sizes (Van Wagner 1978; Armstrong 1999; Li and Barclay 2001). This age structure, in turn, will influence the susceptibility of the forest to attack by MPB (Shore and Safranyik 1992; Shore *et al.* 2000).

Dispersal of MPB consists of two broad kinds: short-distance dispersal, in which movement is predominantly by direct flight, and long-distance dispersal, in which movement is mostly on air currents. MPB can fly for up to 4 h, but only at speeds of 3–6 km/h, and thus cannot overcome the effects of winds at higher velocities (Safranyik 1978). During short-distance dispersal, the beetles usually fly within the canopy for the purpose of attacking trees, mating, *etc.*, often in response to pheromone (Cerezke 1989). This occurs within suitable habitats and between patches of suitable habitat. When suitable habitat is depleted or when beetles fly into unsuitable habitat, they may rise above the canopy and become wind-borne. They may be carried for hundreds of kilometres in this way (Furniss and Furniss 1972), and when they encounter cold air they fall to earth (Safranyik 2004); they may or may not land in suitable habitat, and many perish (Furniss and Furniss 1972). In addition, such long-distance dispersal tends to dilute the beetles, as they do not all fall in the same place. Once an epidemic is well under way, however, the beetles are so numerous that even long-distance dispersal results in sufficient numbers of beetles falling into suitable habitat, so the epidemic can effectively move to new areas and be self-sustaining (Safranyik 2004). Thus, the concept of traversability of a landscape is most applicable to beetle populations in the endemic and incipient stages, which will move mostly by short-distance dispersal.

It seems likely that the rate of spread of MPB will depend not only on the susceptibility of the surrounding trees, but also on the fragmentation and connectivity of the forest with respect to susceptibility. Random recurring fires would tend to produce a mosaic of forest ages and thus also a mosaic of susceptibilities, yielding patches of higher and lower susceptibility. Short-distance dispersal of MPB is partly mediated by pheromones, which are attractive over moderate distances (Safranyik *et al.* 1989; Barclay *et al.* 1998); beyond these distances, dispersal is probably fairly random or oriented towards vertical silhouettes or upwind. Since MPBs are slow fliers, their maximum dispersal distance is probably only a few kilometres, and thus habitat fragmentation will be important. Dispersal models for pine beetles have been constructed by several workers, notably Polymenopoulos and Long (1990), Turchin and Thoeny (1993), Logan *et al.* (1998), and Hughes (2002), and these reinforce the idea that spatial pattern is important.

One purpose of this paper is to quantify the effects of fire size and fire cycle in a lodgepole pine forest on the susceptibility of that forest to attack and spread by MPB. The susceptibility rating system of Shore and Safranyik (1992) is used to derive susceptibility for each cell (hectare) in a one-million-hectare simulated mosaic of stand ages, where the cell ages have been determined by the frequency and size of random fires. As proof of concept we calculate susceptibility to attack by MPB for two timber supply areas in British Columbia and also produce susceptibility maps for these areas and the whole of B.C.

The fires also determine the spatial structure of the cell ages and thus also the spatial structure of susceptibility to attack by MPB. By making certain assumptions about the dispersal ability of MPB through non-susceptible habitat, we can relate the spatial structure of susceptibility of a forest to the ability of MPB to traverse the landscape. This addresses the question of the ability of an MPB population to move across large areas and possibly proceed towards epidemic status. For fires of unit size (in this case, 1 ha), percolation theory states that there is a proportion (0.59) of susceptible forest ages that will provide a continuous cluster of adjacent susceptible cells — a spanning cluster — that will stretch from top to bottom and from side to side of the square lattice (mosaic) under consideration (Stauffer and Aharony 1992). If the proportion of susceptible cells is 0.59, then the probability of such a spanning cluster being present is 0.5, and this probability rapidly increases as the proportion of susceptible cells increases beyond 0.59. If cells are not required to be adjacent, but could provide a connection by touching only at the corners, then this condition is relaxed, and the critical density is 0.41. Since a range of ages allow a path for the beetles, the annual density of fires required to create such a path is much less than it would be if only one age were suitable. In addition, if beetles are capable of crossing patches of unsuitable habitat in search of suitable habitat, then patches of suitable habitat need not be contiguous to provide a landscape enabling beetle movement across it.

Finally, we relate this traversability to readily available spatial statistics to allow easy calculation of traversability once the spatial variation in age structure and species mix is known. We then apply this relationship to the whole of British Columbia using the letter blocks of the British Columbia Geographic System of Mapping (BCGS) to assess the traversability of these blocks. The letter blocks are, on average, slightly over one million hectares, and thus similar in size to the simulated mosaics.

Methodology

Effects of fire size and frequency on age structure

A Monte-Carlo simulation study was done to determine the effects of burn probabilities (*i.e.*, the probability of a fire igniting) and fire sizes, which combine to yield fire return intervals (or, equivalently, fire cycles), on the equilibrium age structure of a lodgepole pine forest consisting of a mosaic of one million 1-ha cells. Both

Table 1. Definitions of the age and density factors used to determine susceptibility of lodgepole pine (*Pinus contorta* var. *latifolia*) to attack by mountain pine beetle (*Dendroctonus ponderosae*).

Factor	
Age	
$0 \le A < 40$	$AF = 0.1$
$40 \le A < 80$	$AF = 0.1 + 0.1[(A - 40)/10]^{1.585}$
$80 \le A < 120$	$AF = 1.0$
$120 \le A < 520$	$AF = 1.0 - 0.05[(A - 120)/20]$
$520 \le A$	$AF = 0.002$
Density	
$0 < D < 650$	$DF = 0.0824(D/250)^2$
$650 \le D < 750$	$DF = 1.0 - 0.7(3 - D/250)^{0.5}$
$750 \le D < 1500$	$DF = 1.0$
$1500 \le D$	$DF = 1.0/\{0.9 + 0.1 \exp[0.4796(D/250 - 6)]\}$

Note: A is age in years, AF is the age factor, D is density in stems per hectare, and DF is the density factor. The susceptibility index is then $S = AF \times DF \times 100$.

the initial ignition of a cell and the subsequent size of the resulting fire were treated as random events, being determined by comparing random numbers with predetermined probabilities. Burn probability was independent of age, and three burn probabilities were used: 0.05, 0.01, and 0.004. These represent fire cycles of 20, 100, and 250 years, respectively, encompassing most of the fire cycles likely to be found in British Columbia. For each cell, the probability of burning was compared with a random number from a negative exponential distribution to determine whether or not the cell burned (uniform and normal distributions were also used (to provide other distribution shapes), but the results were very similar for all three, so only the results using the exponential distribution are presented here). Fire sizes were determined by assigning a maximum size (1 ha to 1×10^6 ha, in powers of 10) and then drawing a random number from the negative exponential distribution (again, uniform and normal distributions were also tried, with similar results) and multiplying the maximum fire size by the random number. These fire sizes span the range observed by Hawkes (1979), who estimated fires in Kananaskis Provincial Park to be between 49 and 9132 ha during the period 1712 to 1973, and by Armstrong (1999), who presented data for fires in northern Alberta ranging from 4.5 to 708 172 ha between 1961 and 1995. Once a cell burned, its age was reset to zero. Each simulation was run for 2000 iterations and the age distribution from the 2000th iteration was used to construct a mosaic of ages over the one million cells. By the 2000th iteration, the age structure had equilibrated in all except the very large fires.

Susceptibility model

We used the susceptibility model of Shore and Safranyik (1992), updated (T. Shore, unpublished data) for continuity. This model includes four factors: age, density, species mix, and location. We assume here that the stand under consideration is 100% lodgepole pine, and so the species mix factor is 100.0. Also, we assume that we are considering the same stand in an ideal location in making the various comparisons due to age structure, so the location factor can be taken as 1.0. The age and density factors are defined in Table 1, and when these are determined, they are simply multiplied together to arrive at the susceptibility index, S_a (see Eq. 4).

Stand age and density will be related for natural stands, and these have been abstracted from stand tables for lodgepole pine in the interior of British Columbia (Goudie *et al.* 1990). The stand tables contain height data; age, diameter at breast height (dbh), and stand density are determinable from height. We used the following regression of top height (H; mean height (m) of the 100 tallest trees per hectare) *versus* age (A):

$$H = 30.0 - 29.2 \exp(-0.0174A) \qquad [1]$$

The regression of dbh (D; cm) *versus* top height (H) was

$$D = 0.357H^{1.28} \qquad [2]$$

The regression of stem density (ρ; stems/ha) *versus* top height (H) was

$$\begin{aligned} \rho &= 3060\exp(-0.107H)+6930 && \text{if } H < 10\text{ m} \\ \rho &= 17\,017-900H && \text{if } 10 \le H \le 14\text{ m} \\ \rho &= 30\,600\exp(-0.148H)+505 && \text{if } H > 14\text{ m} \end{aligned} \quad [3]$$

Thus, we can derive density from age. Knowing both age and density, we can calculate susceptibility for that age (S_a) using the appropriate age factor (AF) and density factor (DF) (see Table 1) and the following equation:

$$S_a = \text{AF} \times \text{DF} \times 100 \quad [4]$$

Van Wagner (1978) found that when fires were small, the resulting age distributions closely approximated a negative exponential distribution (NED) of the form

$$f(x) = \lambda\exp(-\lambda x) \quad [5]$$

where λ is the parameter and x is the variable. For this distribution, the mean and standard deviation are both equal to $1/\lambda$. For a forest that is a mosaic of stands of different ages but has an overall negative exponential age distribution, we can calculate the susceptibility of a given age class weighted by the relative frequency of that class (S_e) as follows:

$$S_e = \lambda\exp(-\lambda a)S_a \quad [6]$$

where a is the cell's age and $\lambda\exp(-\lambda a)$ is the relative frequency of age class a in the NED. Using Equation 6, we can calculate the mean susceptibility of the forest (the one-million-hectare mosaic) (S_λ) by means of the following equation:

$$S_\lambda = \int\lambda\exp(-\lambda a)S_a\,\mathrm{d}a \quad [7]$$

The integral is taken over all ages of the forest. S_λ can then be graphed for a range of values of λ, and this can be used to quickly assign mean susceptibility to stands if the value of λ is known. Figure 1 shows S_λ (determined using Equation 7) *versus* λ for values of λ from 0.0002 to 0.08, representing forests with mean ages from 12.5 to 5000 years. For forests whose age distributions closely follow the NED, λ can be estimated as the reciprocal of the mean age of the forest, although this estimation is slightly biased as a result of the denominator being estimated imprecisely because of sampling error.

If the forest age structure deviates significantly from the NED, then Equation 7 becomes

$$S = \int f(a)S_a\,\mathrm{d}a \quad [8]$$

where $f(a)$ is the observed age distribution of the forest in question. This integral will need to be determined numerically for each forest considered.

Effects of fire return rates on susceptibility

For each of the 21 fire conditions (seven fire sizes and three burn probabilities), the mean susceptibility over the one million hectares was computed using Equation 8. These computations were made based on the results of the 2000th iteration (year), at which time equilibrium had been established, except for those cases involving large fires in which the system was inherently unstable.

Effects of harvesting and fire control

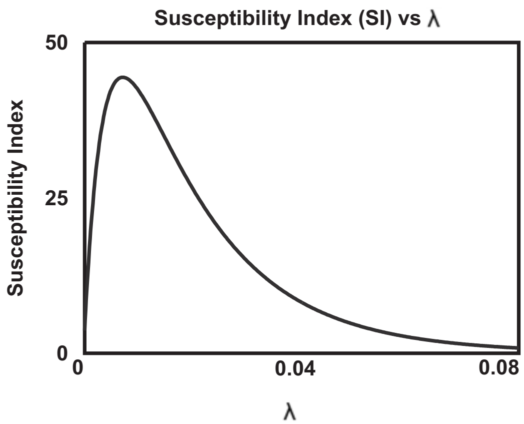
A simple harvesting model was included to determine whether harvesting would change the conclusions of the model with only fires killing trees. Here an entire age class of trees was harvested. In the first year, all trees over the harvest age (80, 100, or 120 years) were harvested, and in subsequent years only trees from the target age class were harvested; this was done to facilitate the establishment of an equilibrium. Trees killed by fire were not harvested, but such stands were regenerated immediately. The harvesting model was not designed to yield quantitatively accurate estimates, but rather to determine the dynamic effects of harvesting on the forest age structure when in combination with fire.

Fire control was modelled by disallowing a certain percentage of fires that would have otherwise occurred. Four percentages were used: 0, 50, 80, and 95, and these were used in combination with harvesting.

Susceptibility of selected stands

The values of the susceptibility index calculated in the preceding sections used only tree age and stand density as components; stands were assumed to be pure lodgepole pine and to be ideally located. The Shore and Safranyik

Fig. 1. Mean susceptibility (susceptibility index, S_λ) of a lodgepole pine (*Pinus contorta* var. *latifolia*) forest with a negative exponential age distribution for a given value of λ, where $S_\lambda = \int \lambda \exp(-\lambda a) S_a da$, where a is stand age, S_a is the susceptibility of a stand of age a, and λ is the parameter of the negative exponential distribution. The integral is taken over all ages of the forest.



(1992) susceptibility index also requires a percent pine factor and a location factor, and when these are included in real forest situations, the susceptibility values will be altered considerably. The percent pine factor is the percentage of the total basal area (of trees >7.5 cm dbh) represented by susceptible lodgepole pine (>15 cm dbh). To calculate the location factor, the value of Y is first calculated as follows:

$$Y = 24.4 \times \text{longitude} - 121.9 \times \text{latitude} - \text{elevation} + 4545.1 \quad [9]$$

where longitude and latitude are in degrees and elevation is in metres. Then, the location factor (Shore and Safranyik 1992) is

$$\begin{cases} 1.0 & \text{if } Y > 0.0 \\ 0.7 & \text{if } -500 < Y < 0 \\ 0.3 & \text{if } Y < -500 \end{cases} \quad [10]$$

Two timber supply areas (TSAs) in British Columbia were chosen to illustrate the effects of including the percent pine and location factors. These two areas are the Lakes TSA, with a centroid approximately at lat 54°N, long 125.5°W, just northeast of Tweedsmuir Provincial Park, and Merritt TSA, with a centroid near lat 49.8°N, long 120.5°W. The first location is in the Boreal Interior Cordilleran ecoclimatic region, whose major overstory components are lodgepole pine, trembling aspen (*Populus tremuloides* Michx.; Salicaceae), paper birch (*Betula papyrifera* Marsh.; Betulaceae), and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco; Pinaceae) (Ecoregions Working Group 1989). The second location is in the Vertically Stratified Interior Cordilleran ecoclimatic region, where the major overstory components vary with altitude. The Lakes TSA was not attacked by the beetles in the 1980s but is being attacked now. Although the Merritt TSA was attacked by the beetles in the 1980s (Taylor and Carroll 2004), it has not been as severely affected by the current outbreak as the Lakes TSA.

Inventory data for the year 2000 were obtained from the B.C. Ministry of Forests and Range for the whole province of British Columbia, including these two TSAs, at a resolution of 400 m × 400 m squares. For each square, mean age and percent pine were available, although density was not. We also obtained a digital elevation map and, on the assumption that the density was the same as that predicted by Goudie's yield tables (Goudie *et al.* 1990), we calculated the susceptibility index for each 400 m × 400 m cell in each of the TSAs. These were then averaged, and the individual susceptibilities of the cells were mapped. Using the same approach, we also computed susceptibility for the whole of British Columbia and created a susceptibility map for B.C.

Spread propensity: traversability

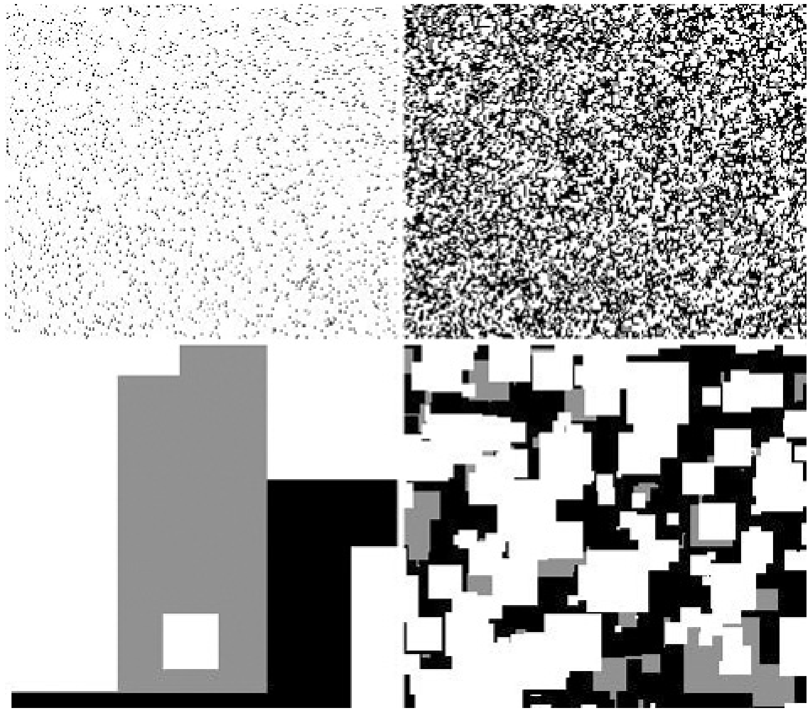
We present a methodology to allow assessment of the propensity of a mountain pine beetle population to traverse (spread across) a million-hectare forest based on the characteristics of the forest. These characteristics include age structure, and hence susceptibility to attack by MPB, as well as patchiness and connectivity of the susceptible areas of forest. Susceptibility is based on stand age, while patchiness and connectivity are based on spatial structure and the rules outlined below. In total, 21 such forest mosaics were examined, being the combinations of seven maximum fire sizes (1 to 1 000 000 ha) and three nominal burn probabilities (0.05, 0.01, and 0.004). All fires were of variable size, with the sizes drawn from a negative exponential distribution.

We define here a quality, called traversability (closely related to percolation, but not the same as traversability of FRAGSTATS (McGarigal and Marks 1995)), describing the ability of a beetle population to spread across the surrounding landscape. Since beetles can disperse through limited areas of non-susceptible forest (or across grassland, *etc.*) to arrive at tracts of susceptible forest, a landscape can be characterized as traversable or non-traversable depending on whether or not a beetle population could cross it while obeying certain rules that are appropriate to its ability to disperse. We deal here only with short-distance dispersal, not long-distance dispersal above the canopy in a wind stream. Traversability will depend on the maximum distance that beetles can travel through non-suitable habitat in search of susceptible forest to attack, and also on the value of the susceptibility index, which represents the boundary between suitability and non-suitability for attack by an incipient beetle population. The spatial structure of the forest, as well as the overall susceptibility, is important in determining traversability. Thus, a methodology was devised to detect possible routes across the million-hectare forest at various thresholds of distance that the beetle could travel through non-susceptible habitat as well as various thresholds of what is considered susceptible. Lower limits of susceptibility (*S*) of 20, 30, …, and 90 were used for a cell to be considered susceptible to attack by MPB. For each million-hectare forest mosaic obtained from the 2000th iteration (year) of the simulation, susceptibilities were assigned to each cell using the Shore and Safranyik (1992) rating system, and then the image-analysis software eCognition (Definiens Inc. 2004) was used to segment and dichotomously classify the million cells into susceptible and non-susceptible classes based on the limits of *S* being less than, or greater than or equal to, 20, 30, …, or 90. For each combination of susceptible and non-susceptible classes, the million-hectare forest was examined under a given set of fire conditions for the ability of a beetle to get from one side to the other without having to travel more than 1, 2, 3, 4, or 5 km through unfavourable habitat in search of susceptible habitat. This was done by using the Nearest Feature extension (courtesy of Jeff Jenness and Lois Engleman) of ArcView® (Environmental Systems Research Institute, Inc. 2000) to identify susceptible patches and then drawing lines between patches that were within the distance limits specified. Following this, the possibility of traversing the area was assessed visually by following the connections between susceptible patches and searching for a path across the mosaic. If such a path existed, then that image was given a coding of one and the mosaic was called traversable; otherwise, it had a coding of zero and was not traversable. These ones and zeros were tabulated for each combination of the eight bounding susceptibility values and the five limiting dispersal distances for each million-cell mosaic. An index (called τ) was calculated as the mean of the 40 ones and zeros. The bounding susceptibility index in reality puts bounds on the tree ages that the beetles could successfully attack.

Spatial indices

There exists a variety of spatial indices, most of which can be classified as areal, linear, or topological (Baskent and Jordan 1995). Many of them are sensitive to grain and spatial scale (Haines-Young and Chopping 1996). The Monte-Carlo simulation yielded output of age structure of the forest and also age and density for each hectare (cell) in the million-hectare forest in the simulation. This information was obtained for each combination of mean fire size and burn probability. Susceptibility to MPB was calculated for each cell. From these output files, FRAGSTATS and the Patch Analyst (Elkie *et al.* 1999) extension of ArcView® were used to define patches of these susceptibility classes and to compute several spatial statistics that might be useful in describing the ease of dispersal of MPB over the susceptible cells in the million-hectare forest. These spatial statistics included the following: PLC, proportion of susceptible land cover; NP, number of susceptible patches; MPS, mean patch size; ED, edge density (calculated as the total edge of a given class divided by the total area of that class; m/ha); MSI, mean shape index; LPI, largest patch index; FD, fractal dimension; NND, mean nearest-neighbour distance; CN, connectance; and AI, aggregation index. MSI is the mean of an index that calculates the patch perimeter (in terms of cell faces) divided by the minimum possible perimeter of a maximally compact patch of the same area. FD is twice the logarithm of the adjusted patch perimeter divided by the logarithm of the patch area, and it reflects the shape complexity across a range of scales. CN is an index that tallies the number of patches of a given type that are within a specified distance of each other as a proportion of all possible patch pairs of that type. For

Fig. 2. Four susceptibility maps resulting from fire sizes (hectares) of 1.0 (upper left), 100 (upper right), 10 000 (lower right), and 1 000 000 (lower left). All were generated using a nominal burn probability of 0.01.



connectance, a threshold distance must be specified above which flights from one favourable patch to another cannot be made. We used 3 km, as this is what was suggested by Shore and Safranyik (1992) as being a reasonable upper limit for easy dispersal. Typical susceptibility mosaics of 1 000 000 ha from the simulations are shown in Figure 2 for fire sizes of 1, 100, 10 000, and 1 000 000 ha.

A stepwise discriminant analysis was performed on the spatial statistics in an attempt to discriminate traversable from non-traversable landscapes. Discriminant analysis calculates a regression line that divides a set of dichotomous data into two sets in such a way as to maximize the separation of the two kinds of data. One analysis was run for each of the limiting dispersal distances of 1 to 5 km. Each analysis used the value of the maximum fire size as well as the 10 spatial statistics listed above as variables. The classification variable was traversability, being one if the area was traversable and zero if the area was not traversable. The discriminant analysis yielded a set of spatial variables capable of discriminating traversable landscapes and also two equations of the discriminating hyperplane for each limiting dispersal distance. In this way the landscape could be characterized with respect to the ease with which MPB could traverse the mosaic from one side to the other, *i.e.*, spread across the landscape. This would allow an assessment of the likelihood of uncontrolled spreading occurring from an incipient infestation or an epidemic in progress. The spatial variables are easily computed using FRAGSTATS or Patch Analyst and could be used as a surrogate for the time-consuming process of computing traversability the way it was done here.

The three best patch measures (PLC, ED, and LPI) were computed for each of three areas in British Columbia: the Lakes and Merritt TSAs and the Tweedsmuir Park forest. The data used were from the B.C. Ministry of Forests and Range inventory for the year 2000. These data consisted of mean age and percent pine for grids of these areas at a resolution of 400 m × 400 m. The discriminant equations were then applied to these areas to estimate traversability. The patch measures PLC, ED, and LPI were computed for each of the letter blocks of the BCGS map for B.C., and each letter block was assessed for traversability using the methods outlined above. The discriminant equations

Table 2. Mean values of the susceptibility index (*S*) for one million simulated hectares for three nominal burn probabilities and six fire sizes (1 – 100 000 ha).

	Mean *S*					
Burn probability	1 ha	10 ha	100 ha	1000 ha	10 000 ha	100 000 ha
0.05	4.58	6.19	8.79	5.67	3.99	4.20
0.01	44.53	46.63	48.21	46.29	45.66	43.00
0.004	46.29	44.89	41.80	45.54	43.30	41.90

were then applied to the same data to estimate traversability for each letter block for the whole of B.C. using the patch metrics.

Results

Effects of fires on forest age distribution

It was found that when fires were small (less than 100 ha), the resulting age distributions closely approximated the negative exponential distribution (NED). When mean fire sizes were an appreciable proportion of the million hectares (greater than approximately 50 000 – 100 000 ha), no equilibrium was reached and the resulting distribution was not close to the NED, often having several peaks and varying over time. The agreement of the age distributions with the NED was also better for shorter fire cycles than for longer ones. Fire size distribution had no significant effect on equilibrium age distribution. The fire cycle was approximately the reciprocal of the burn probability.

Mean susceptibility of a forest with a negative exponential age distribution

The mean susceptibility (*S*) was calculated from Equation 8 and the results are shown in Table 2 for three burn probabilities and six fire sizes (the maximum fire size of 10^6 ha was excluded because the results were so erratic). An analysis of variance of the *S* values showed that nominal burn probability significantly affected mean susceptibility to beetle attack ($P < 0.0001$), with *S* values being much lower for higher burn probabilities (shorter fire cycles).

Lower limits on susceptibility

The use of the susceptibility index implicitly requires that one recognizes whether a given value of *S* implies susceptibility or lack of susceptibility to attack by MPB. The general wisdom is that lodgepole pine trees are susceptible to attack if the trees are greater than 15 cm in diameter at breast height or less than about 200 years old (Hopping and Beale 1948; Cole and Amman 1969). Using Equations 1 to 4, it can be shown that a value of *S* of 10% corresponds to a mean tree dbh between 14.2 and 27.7 cm; trees in this range are usually considered prone to attack if beetle pressure is moderate to high. Thus, even fairly low values of *S* appear to be consistent with the risk of trees being attacked.

Shore *et al.* (2000) tested the susceptibility model and found a linear relationship between the susceptibility index and the basal area (BA) killed during a beetle epidemic. Their regression was as follows:

$$\text{percent BA killed} = 0.68 \times \text{susceptibility index} \quad [11]$$

Thus, all positive values of *S* are consistent with some positive probability of attack.

Effects of harvesting and fire control on susceptibility

Several trends emerge clearly when harvesting is considered (Table 3). The mean susceptibility of the forest to beetle attack increases with age at harvest; thus, mean *S* is lower when harvests are done at 80 years than at 120 years. Furthermore, volume harvested decreases with age at harvest, presumably as a result of the balance between the current and mean annual increments, so harvesting earlier minimizes susceptibility to beetle attack and also maximizes harvest. Also, mean *S* increases with the extent of fire control, as does the volume harvested. There is a positive interaction between age of harvest and fire suppression, so that the greatest difference in *S* between harvests at 80 and 120 years is seen for 95% fire control. It appears that both late harvesting and extensive fire control allow a greater proportion of the forest to be in age classes that are susceptible to beetle attack. However, comparing data in

Table 3. Mean susceptibility (*S*) values for three burn probabilities (0.05, 0.01, and 0.004), three harvesting ages (H.A.) (80, 100, and 120 years), and four levels of fire suppression (0%, 50%, 80%, and 95% of fires prevented from burning following the determination of the burn status for each cell).

		Percentage of fires suppressed							
		0		50		80		95	
Burn probability	H.A.	Mean *S*	Vol	Mean *S*	Vol	Mean *S*	Vol	Mean *S*	Vol
0.05	80	2.683	0.7	3.262	1.0	5.162	2.1	12.892	4.7
	100	4.052	0.3	5.156	0.4	11.412	1.2	16.646	3.6
	120	4.397	0.1	5.678	0.2	13.825	0.6	26.542	2.4
0.01	80	12.771	4.9	13.398	5.2	14.650	6.4	16.285	7.9
	100	21.78	3.4	23.919	4.0	26.570	5.1	32.103	6.7
	120	26.362	2.3	27.293	3.1	32.581	4.1	41.958	6.0
0.004	80	15.163	6.6	15.209	7.4	15.942	7.7	16.560	8.6
	100	27.249	5.8	29.000	5.9	31.806	6.5	32.590	7.4
	120	35.647	4.8	38.100	5.3	41.402	5.9	45.062	6.6

Note: All fires had a maximum size of 10 000 ha. "Vol" is volume harvested (m^3/ha).

Tables 2 and 3, we see that harvesting at all three ages reduced the value of *S* compared with no harvesting, and this reduction increased with fire cycle length but decreased with harvest age. The optimal combination appears to be early harvesting with intensive fire control: although the susceptibility increases with fire control, it is drastically decreased by early harvesting.

Susceptibility of selected areas

The mean values of the susceptibility index calculated using only tree age and stand density as components were 68.2% for the Lakes TSA and 70.3% for the Merritt TSA. If location and percent pine were also included, then the *S* values were 40.2% for the Lakes TSA and 31.9% for the Merritt TSA. The first pair of values correspond approximately to a lower limit on dbh of 18.2 cm and are thus both normally considered to be susceptible. Age-class distributions for the two areas are shown in Figure 3, and they are quite similar. Maps of susceptibility over the two TSAs using all four factors are shown in Figure 4. Black indicates values of *S* >80% and white indicates values of *S* <20%; it is clear that large proportions of both TSAs were highly susceptible in the year 2000.

Traversability and dispersal potential

Values of the index τ, mean traversability, for the 21 million-hectare simulated mosaics are shown in Table 4 for the three burn probabilities and seven fire sizes. A value of 1.0 in Table 4 indicates that the mosaic was traversable for all eight bounding susceptibility percentages and all five limiting distances, and thus would easily be capable of allowing an

Fig. 3. Age distributions of predominantly lodgepole pine stands in two areas of British Columbia: the Lakes Timber Supply Area (L) and the Merritt Timber Supply Area (M).

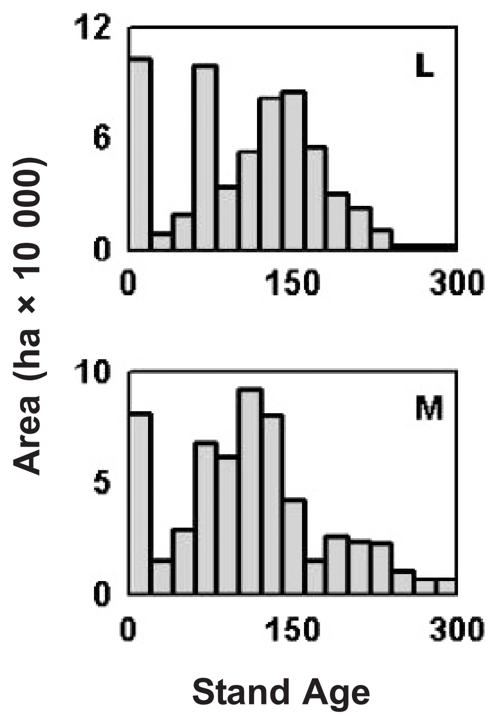


Fig. 4. Maps of the susceptibility index in the year 2000 for the Lakes Timber Supply Area (L) and the Merritt Timber Supply Area (M) determined using the four factors age, density, location, and percent lodgepole pine. Five susceptibility classes were used, ranging from 0–20 (white) to 80–100 (black).

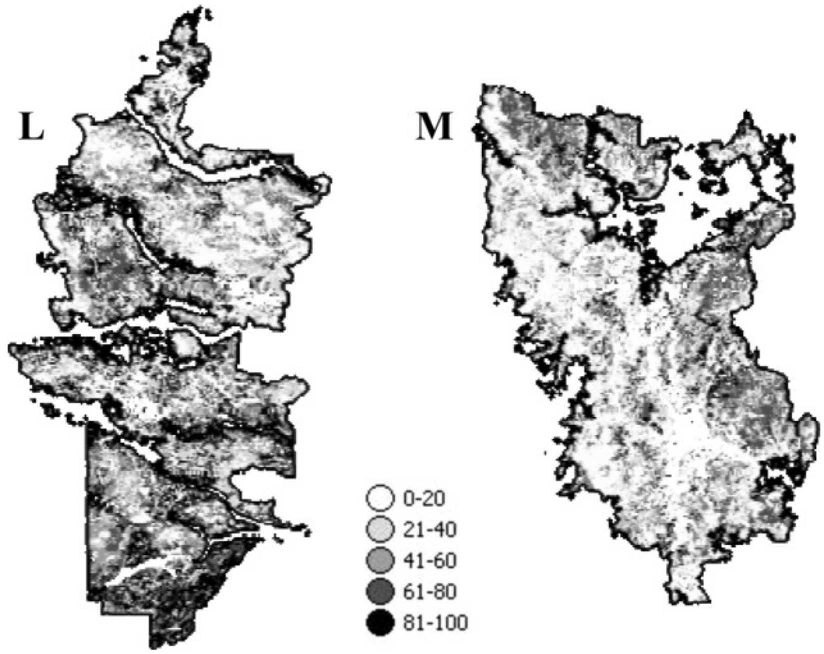


Table 4. Index of mean traversibility (τ) for three burn probabilities and seven fire sizes for the one-million-hectare simulated lodgepole pine forest.

	Fire size (ha)						
Burn probability	1	10	10^2	10^3	10^4	10^5	10^6
0.05	1.0	1.0	1.0	0.65	0.00	0.00	0.00
0.01	1.0	1.0	1.0	1.0	0.95	0.70	0.85
0.004	1.0	1.0	1.0	0.97	0.80	0.45	0.25

infestation to travel from one side to the other. A value of 0.00 indicates that such traversal might be impossible unless long-distance dispersal occurred. For most fire sizes, values for the 40 combinations of *S* and dispersal distance were either all ones or all zeros. Values of τ between zero and one mean that traversal across the landscape might well happen, but the values of *S* and dispersal distance that would allow transmission need to be empirically determined to put a boundary on the types of fire regimes that would permit such traversal. For fire sizes of 1000, 10 000, and 100 000 ha, in many cases ones changed to zeros as the bounding value of *S* increased and (or) the dispersal distance decreased. Fires of a maximum size of 1, 10, or 100 ha produced patterns of susceptible forest that were traversable for all burn probabilities, and thus $\tau = 1$ throughout. For larger fires, the index τ generally decreased as fire size increased, so that large, infrequent fires tended to yield a landscape that MPB cannot easily traverse. The values for fires of a maximum size of 1 000 000 ha formed a continually changing distribution of forest ages, so that equilibrium was never achieved for fires of that size.

Fire control and harvesting: effects on traversability

Fire control increased traversability when burn probability was high and fire cycles were short, and decreased traversability when burn probability was low and fire cycles were long (Table 5). Harvesting at 80 and 100 years

Table 5. Index of mean traversibility (τ) for harvesting at three ages (H.A.) (or no harvest), fire suppression at four levels, three nominal burn probabilities, and a maximum fire size of 10 000 ha for the one-million-hectare simulated lodgepole pine forest.

		Percentage of fires suppressed			
Burn probability	H.A.	0	50	80	95
0.05	none	0.00	0.40	0.55	0.93
	80	0.00	0.00	0.00	0.10
	100	0.03	0.03	0.15	0.20
	120	0.00	0.05	0.20	0.58
0.01	none	0.95	0.90	0.93	0.60
	80	0.28	0.18	0.13	0.20
	100	0.60	0.63	0.45	0.65
	120	0.73	0.63	0.70	0.85
0.004	none	0.80	0.80	0.75	0.38
	80	0.30	0.25	0.13	0.20
	100	0.75	0.68	0.53	0.68
	120	0.93	0.93	0.90	0.98

consistently reduced traversability, but values of τ were often larger when harvesting occurred at 120 years than when no harvesting occurred, especially when burn probability was very low. Harvesting and fire control interacted to yield a minimum value of traversability when fire control was about 80%. For the burn probability of 0.01 (100-year fire cycle), the best combination to reduce traversability was early harvest with moderate fire suppression.

Spatial indices

Ten spatial statistics were computed for each of the 21 combinations of factors. These statistics were computed for patches of high susceptibility, defined as $S \geq 20, 30, \ldots,$ and 90, successively. Fire size highly significantly affected six spatial statistics (NP, PLC, NND, FD, CN, and AI), and burn probability highly significantly affected all except CN and NND. Pairwise correlations among these 10 statistics were all significant except for the pair CN and NND.

Variation of spatial indices with susceptibility

In the treatment above, the spatial statistics were examined for patches of susceptibility above 20, 30, …, and 90, successively. A stepwise discriminant analysis showed that the two most important variables for discriminating traversability were PLC and ED. These two variables were most important for each of the five limiting dispersal distances, although the sum of the R^2 values for these two variables decreased monotonically from 0.80 for 1 km to 0.56 for 5 km, limiting dispersal distance. The next most important variables for predicting traversability were LPI and NP. The susceptibility boundary was also tried as a discriminating variable, but it was not significant. Discriminant analyses were performed on the best two (PLC and ED), the best three (PLC, ED, and LPI), and then on all four variables to predict traversability. The best discrimination was with the three variables PLC, ED, and LPI. The coefficients of the discriminant equations for these three variables are shown in Table 6 for the five maximum dispersal distances (1 to 5 km). Graphic results using PLC and ED (Fig. 5) showed strong trends, with groupings attributable to fire size. Discrimination was very good, and over 90% of traversability conditions (Trav; “yes” or “no”) were correctly classified. Each discrimination has two equations, one for Trav = 0 (“no”) and one for Trav = 1 (“yes”). For a given set of values of PLC, ED, and LPI, both equations are computed and the one with the larger result determines the value of Trav. Although both vertical and horizontal traversability were derived, it appears that horizontal traversability is likely a more useful indicator of potential movement, as prevailing winds are generally from west to east at those latitudes.

Table 6. Coefficients of discriminant equations to predict traversability (Trav: 1 = yes; 0 = no) using the three variables PLC (proportion of susceptible land cover), ED (edge density), and LPI (largest patch index).

			Variable		
Maximum dispersal distance (km)	Trav	Constant	PLC	ED	LPI
1	0	–0.735	13.623	0.009	–0.057
	1	–9.077	39.603	0.042	–0.087
2	0	–0.507	11.311	0.007	–0.053
	1	–7.450	36.318	0.035	–0.107
3	0	–0.385	9.705	0.005	–0.048
	1	–6.407	32.931	0.030	–0.108
4	0	–0.252	7.914	0.004	–0.040
	1	–5.891	32.331	0.027	–0.117
5	0	–0.179	6.787	0.004	–0.034
	1	–6.027	34.300	0.027	–0.132

Note: Ten sets of coefficients are shown, representing the two equations for each of the five dispersal distances (1–5 km).

Considering mean traversability for each letter block in B.C. in 20% classes, the greatest area judged to be traversable was for $S \geq 20$ and the smallest area was for $S \geq 80$, centred around Tweedsmuir Park and the Lakes TSA. Figure 6 shows mean susceptibility and traversability for the whole of B.C. as well as the extent of the current outbreak in 2004. Both susceptibility and traversability are highest in the area around Tweedsmuir Park and the Lakes TSA, exactly where the current outbreak (Fig. 6) originated and still continues (Wilson 2004).

The discriminant equations applied to the three best patch metrics for each of the 89 provincial letter blocks, at each of four susceptibility boundaries, correctly classified 93.3% of cases. The best prediction was for non-traversable blocks in which the mean traversability, τ, was zero, and then there was a decline in predictability for larger values of τ, especially for $\tau \approx 0.5$. There was little difference in predictability among the four boundary susceptibility percentages or the five maximal dispersal distances.

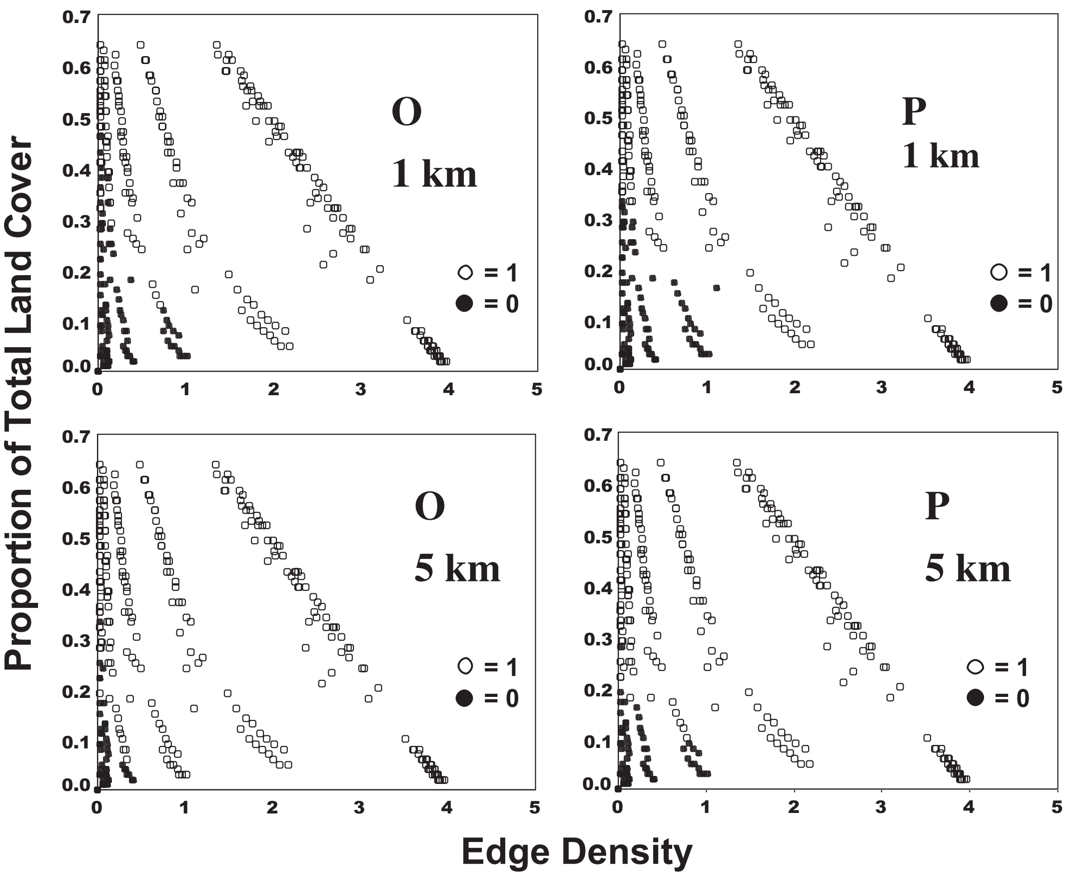
Over the past century, the number of fires has decreased (Fig. 7) and the area attacked by MPB has increased. Data from the B.C. Ministry of Forests Annual Reviews have been compiled by one of us (S.T.) and have been grouped into decades, starting in 1912 and ending in 2000. Figure 7 shows mean areas burned by fire and mean areas attacked by MPB for each decade of the 20th century except the first. It is worth noting that the area attacked by MPB since 2000 is much higher than the area attacked in the 1980s, and the present epidemic is the largest on record.

Discussion

Our results build linkages between fire size and frequency and the resulting susceptibility of the stands and larger forested landscape to attack by mountain pine beetles. Once these linkages are established, an assessment of risk from an incipient beetle population can be established under the appropriate weather conditions.

The major conclusions from the simulations are that (*i*) long fire cycles yield an age structure that is highly susceptible to beetle attack by preserving trees in older age classes; (*ii*) fire suppression, which reduces the frequency of fires, also yields an age structure highly susceptible to beetle attack; (*iii*) harvesting, especially harvesting of younger age classes (*i.e.*, 80 years), considerably reduces the mean susceptibility of the forest to beetle attack and also reduces traversability, although Fall *et al.* (2004) pointed out that early harvest may result in harvest shortfalls; and (*iv*) the occurrence of many small fires yields a landscape structure susceptible to sustaining beetle dispersal throughout the landscape, as the distances that must be travelled over hostile habitat are all within the beetles' short-distance dispersal capabilities.

Fig. 5. Observed (O) and predicted (P) distributions of traversability (1, yes; 0, no) plotted against two spatial statistics from FRAGSTATS: proportion of susceptible land cover (PLC) and edge density (ED). These are shown for two maximum dispersal distances: 1 km (upper panels) and 5 km (lower panels). Predicted values were obtained from a discriminant analysis of traversability *versus* PLC and ED. Both the observed and predicted values fall into seven groupings corresponding to the seven maximum fire sizes, from 1 ha (on the right) to 10^6 ha (on the left).



For random fires of 1 ha, percolation theory predicts that there will be a mean threshold proportion (0.59) of susceptible age classes above which susceptible cells will form a continuous network across the mosaic, with the contact between cells being a common edge. Thus, if highly susceptible cells ever exceed a proportion of 0.59 of the total mosaic, then it would presumably be easy for a beetle population to traverse the mosaic and proceed from there. It is apparent from Figure 1 that highly susceptible cells approach a proportion of 0.59 of the total mosaic only when $\lambda \approx 0.005$, which would imply a mean age of 200 years, which is unlikely to occur often with lodgepole pine.

Traversability has been established using two sets of rules: one set of rules involves the distinction between susceptible and non-susceptible forest, while the other involves the distance that beetles can disperse over non-suitable habitat in search of susceptible forest. Both the boundary between high and low susceptibility and the maximum distance that beetles can disperse across non-suitable habitat must be empirically determined. Once these two factors are known and the fire cycle and size distribution are known, then a judgement can be made regarding the traversability of the forest and the consequent danger of a beetle population moving across the landscape. Maximum dispersal distances of 1 to 5 km were used, although it seems likely that even 5 km is a conservative estimate of the distance that MPB can disperse (L. Safranyik, personal communication).

The use of square fires in the simulations may have some influence on the results but

Fig. 6. Mean susceptibility (*a*) and traversability (*b*) for the province of British Columbia calculated over four susceptibility boundaries and five maximum dispersal distances. Each polygon in the grid is one letter block in the British Columbia Geographic System of Mapping. Also shown (*c*) is the state of the current infestation in British Columbia at the year 2004.

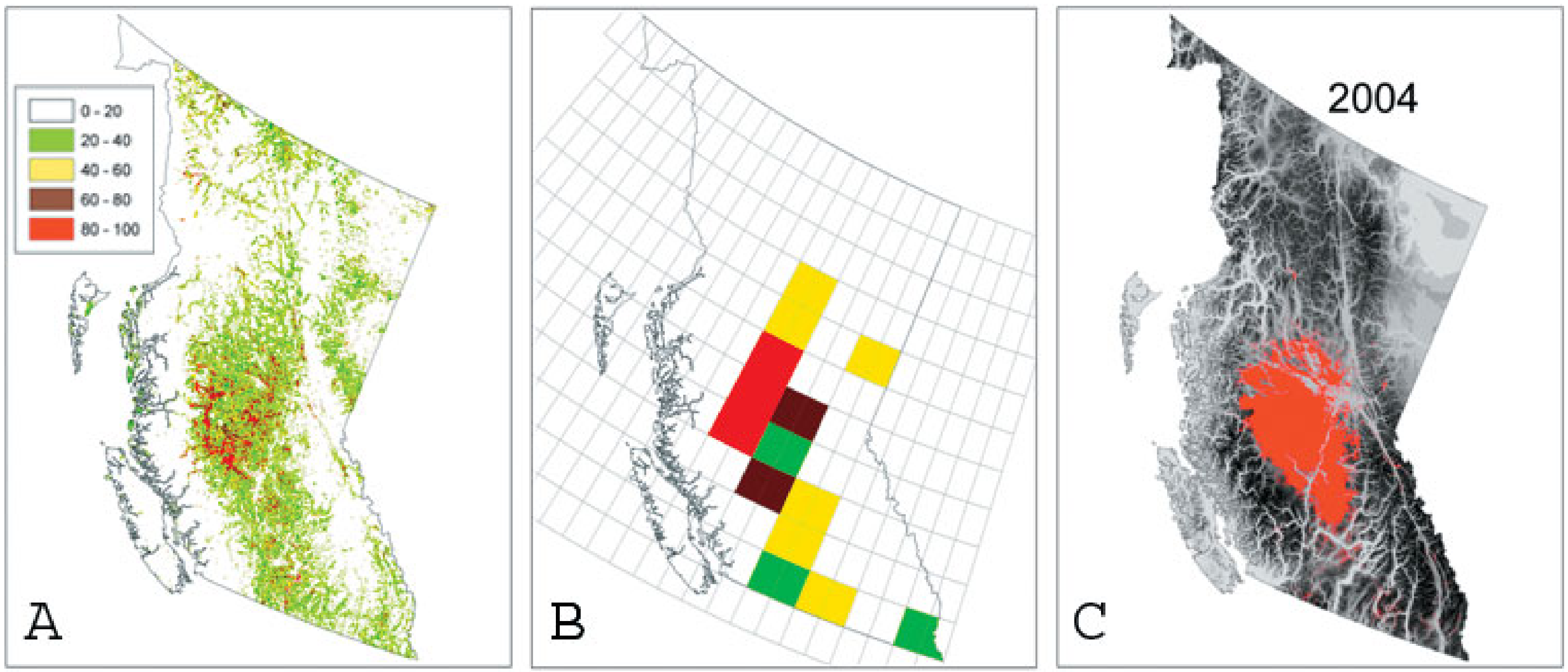
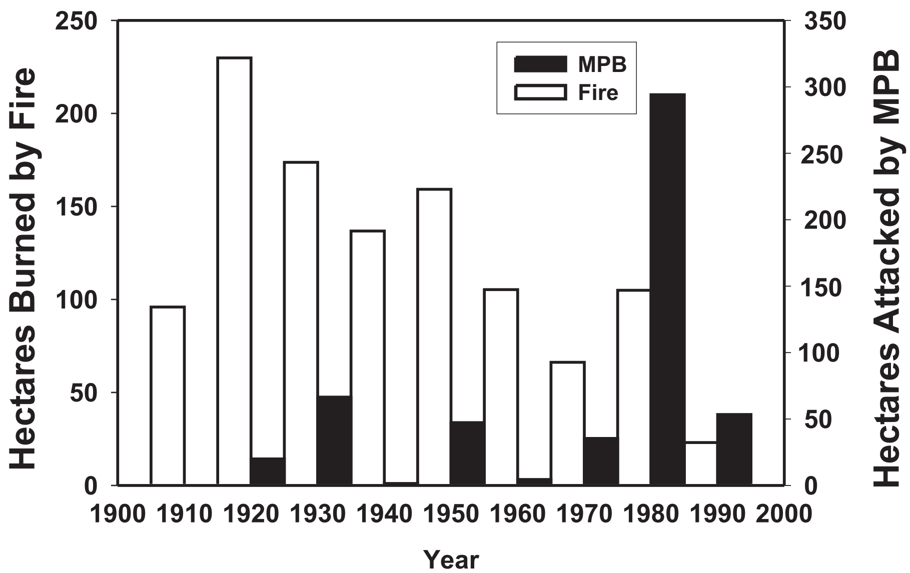


Fig. 7. Mean annual area burned by wildfires (hectares, times 1000) and areas attacked by mountain pine beetle (hectares, times 10 000) for each of nine decades starting in 1912 and ending in 2000.



would be noticeable mostly in computing indices such as the fractal dimension, which depends on the shape of the resulting sections of susceptible forest. However, the agglomeration of several areas of forest that are of similar susceptibility but due to fires in different years would likely eliminate most artifacts due to the square nature of the burns, except for those resulting from the largest fires, which produce very angular susceptible blocks (Fig. 2).

Although it is possible to compute traversability for a real forest using our methodology, once the forest is modelled in a geographic information system (GIS) format, as we have done for B.C., the discriminant functions will allow the use of spatial statistics as a surrogate for traversability. Once the forest inventory is in GIS format, one can calculate the spatial statistics using software such as ArcView® and then apply the discriminant functions to assess traversability. Our results indicate that the predictive power of the discriminant functions is quite good. The discriminant functions were derived from simulated landscapes determined by random fires, without lakes and mountains, and assuming 100% pine. Landscapes in nature are not random (as large-scale geological and geographic features are not random) and are of mixed species. In spite of these differences, the discriminant functions did quite well for B.C. as a whole, with 93.3% of predictions being correct, and thus the discrepancies between the conditions used to derive the discriminant functions and those of a real forest did not seem to matter.

Traversability in the year 2000 was highest in the Lakes and Merritt TSAs. The Lakes TSA is the area in which the present MPB epidemic is concentrated. Thus, traversability appears to be an effective indicator of the likelihood of an outbreak if weather conditions are favourable. Since the determination of traversability is rather labour-intensive, the use of FRAGSTATS metrics together with discriminant equations is a shortcut that is readily available once electronic inventory maps are available. The maps we used were for the year 2000, and the measured traversability correlates well with the observed beetle epidemic. The information in the 2000 map is already out of date, but subsequent inventories following the collapse of the current epidemic will lay the foundation for prediction of the likelihood of future epidemics starting throughout British Columbia.

There remains a discrepancy between our *S* values from the models and those that would be computed in the field, as we used only two factors whereas those in the field would be computed with all four factors. This must be taken into account in relating susceptibility to spatial pattern. The values we computed for the two TSAs using all four factors were about half of those computed by excluding the percent pine factor. In other areas, values computed in the field are often quite low as a result of species mixes and unsuitable locations (Dymond *et al.* 2005).

The simulation results presented here are all from forests at equilibrium. Equilibrium results are not only easy to obtain, but also reduce complexity, as there is usually only one equilibrium for a given set of parameter values, whereas there is an infinite number of possible trajectories for transient behaviour of the models. Since equilibrium age distributions are close to negative exponential for all except the large fire sizes, the use of Equation 7 or Figure 1 to estimate susceptibility provides a shortcut to assessment of the overall susceptibility of a tract of forest to attack by MPB. In a forest whose age structure is negative exponential, the parameter λ is the reciprocal of the mean age of the forest, and this provides an estimate of the mean fire cycle. These relationships facilitate quick estimation of the susceptibility of the forest. Since most forested areas in British Columbia are presently far from equilibrium, as a result of harvesting, fire control, and beetle activities, these shortcuts are not presently available to forest managers. The results presented in this paper should be useful to forest managers developing strategies for long-term, sustainable forest management.

Historical records of the number of fires and the area attacked by MPB show inverse trends (Fig. 7). Fire control was begun about a century ago and was intensified and made more efficient with the advent of airborne reconnaissance about 50 years ago. However, pine was not much harvested until about the early 1970s. These factors have allowed an ageing of the forest and a consequent increase in mean susceptibility to MPB attack, as pointed out by Taylor and Carroll (2004). The same trends are predicted by our models (Table 3). It appears that the pine trees not burned by fire will become prime habitat for the beetle. However, the situation may be even more extreme, inasmuch as the beetle occurs in epidemics that may attack a greater area of trees than the fire would have taken if allowed to burn. In the long term, strategies to save more timber for harvesting might involve either planting other species instead of pine, where possible, or harvesting at an earlier age. Neither of these would be totally satisfactory. An alternative strategy would be to plant other species as well as lodgepole pine in mosaics such that the spatial arrangement would minimize the probability of both fire and attack by MPB.

Acknowledgements

We thank M. Eng for supplying the inventory data for the B.C. forests, G. Thandi for providing the digital elevation model and for advice on the Nearest Feature facility of ArcView®, B. Riel for the updated susceptibility equations, H. Chen for advice on using eCognition, A. Carroll for the map of the epidemic status of MPB in 2004, and L. Safranyik, B. Hawkes, and C. Stockdale for fruitful discussions and information. This research was supported by a grant from the Mountain Pine Beetle Initiative.

References

Armstrong, G.W. 1999. A stochastic characterization of the natural disturbance regime of the boreal mixedwood forest with implications for sustainable forest management. Canadian Journal of Forest Research, **29**: 424–433.

Barclay, H.J., Safranyik, L., and Linton, D. 1998. Trapping mountain pine beetles *Dendroctonus ponderosae* (Coleoptera: Scolytidae) using pheromone-baited traps: effects of trapping distance. Journal of the Entomological Society of British Columbia, **95**: 25–31.

Baskent, E.Z., and Jordan, G.A. 1995. Characterizing spatial structure of forest landscapes. Canadian Journal of Forest Research, **25**: 1830–1849.

Cerezke, H.F. 1989. Mountain pine beetle aggregation semiochemical use in Alberta and Saskatchewan, 1983–1987. *In* Proceedings of a Symposium on the Management of Lodgepole Pine to Minimize Losses to the Mountain Pine Beetle, Kalispell, Montana, 12–14 July 1988. *Compiled by* G.D. Amman. General Technical Report INT-262, USDA Forest Service, Intermountain Research Station, Ogden, Utah. p. 113.

Cole, W.E., and Amman, G.D. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. Research Note INT-95, Intermountain Range and Experiment Station, USDA Forest Service, Ogden, Utah.

Definiens Inc. 2004. eCognition: a user's guide. Definiens Inc., Boulder, Colorado.

Dymond, C., Wulder, M., Shore, T., Nelson, T., Boots, B., and Riel, B. 2005. Evaluation of risk assessment of mountain pine beetle infestations using GPS survey points. Western Journal of Applied Forestry. In press.

Ecoregions Working Group. 1989. Ecoclimatic regions of Canada. Ecological land classification series. No. 23. Canadian Wildlife Service, Environment Canada, Ottawa, Ontario.

Elkie, P., Rempel, R., and Carr, A. 1999. Patch Analyst user's manual. TM-002. Ontario Ministry of Natural Resources, Northwest Science and Technology, Thunder Bay, Ontario.

Environmental Systems Research Institute, Inc. 2000. ArcView®. Version 3.2*a* [computer program]. Environmental Systems Research Institute, Inc., Redlands, California.

Fall, A., Fortin, M.-J., Kneeshaw, D.D., Yamasaki, S.H., Messier, C., Bouthillier, L., and Smyth, C. 2004. Consequences of various landscape-scale ecosystem management strategies and fire cycles on age-class structure and harvest in boreal forests. Canadian Journal of Forest Research, **34**: 310–322.

Furniss, M.M., and Furniss, R.L. 1972. Scolytids (Coleoptera) on snowfields above timberline in Oregon and Washington. The Canadian Entomologist, **104**: 1471–1478.

Goudie, J.W., Mitchell, K.J., and Polsson, K.R. 1990. Managed stand and product yield tables for interior lodgepole pine: initial density and precommercial thinning. Available from B.C. Ministry of Forests, Research Branch, Victoria, BC V8W 3E7.

Haines-Young, R., and Chopping, M. 1996. Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. Progress in Physical Geography, **20**: 418–445.

Hawkes, B.C. 1979. Fire history and fuel appraisal study of Kananaskis Provincial Park, Alberta. M.Sc. thesis, University of Alberta, Edmonton, Alberta.

Hopping, G.R., and Beale, G. 1948. The relation of diameter of lodgepole pine to incidence of attack by the bark beetle *Dendroctonus monticolae* Hopkins. Forestry Chronicle, **24**: 141–145.

Hughes, J. 1998. Modeling the effect of landscape pattern on mountain pine beetles. M.Sc. thesis, School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia.

Li, C., and Barclay, H.J. 2001. Fire disturbance patterns and forest age structure. Natural Resource Modeling, **14**: 495–521.

Logan, J.A., White, P., Bentz, B.J., and Powell, J.A. 1998. Model analysis of spatial patterns in mountain pine beetle outbreaks. Theoretical Population Biology, **53**: 236–255.

McGarigal, K., and Marks, B. 1995. FRAGSTATS: a spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351, US Department of Agriculture, USDA Forest Service, Northwest Research Station, Portland, Oregon.

Polymenopoulos, A.D., and Long, G. 1990. Estimation and evaluation methods for population growth models with spatial diffusion: dynamics of mountain pine beetle. Ecological Modelling, **51**: 97–121.

Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. *In* Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. Proceedings of a Symposium, Pullman, Washington, 25–27 April 1978. *Edited by* A.A. Berryman, G.D. Amman, and R.W. Stark. University of Idaho, Moscow, Idaho. pp. 77–84.

Safranyik, L. 2004. Mountain pine beetle epidemiology in lodgepole pine. *In* Proceedings of the Mountain Pine Beetle Symposium: Challenges and Solutions, Kelown, British Columbia, 30–31 October 2003. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Information Report BC-X-399, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia. pp. 33–40.

Safranyik, L., Silversides, R., McMullen, L.H., and Linton, D.A. 1989. An empirical approach to modelling the dispersal of the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (Col., Scolytidae) in relation to sources of attraction, wind direction and speed. Journal of Applied Entomology, **108**: 498–511.

Shore, T.L., and Safranyik, L. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Information Report BC-X-336, Forestry Canada, Victoria, British Columbia.

Shore, T.L., Safranyik, L., and Lemieux, J.P. 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. Canadian Journal of Forest Research, **30**: 44–49.

Stauffer, D., and Aharony, A. 1992. Introduction to percolation theory. Taylor and Francis, London.

Taylor, S.W., and Carroll, A.L. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: a historical perspective. *In* Proceedings of the Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, British Columbia, 30–31 October 2003. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Information Report BC-X-399, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia.

Turchin, P., and Thoeny, W.T. 1993. Quantifying dispersal of southern pine beetles with mark–recapture experiments and a diffusion model. Ecological Applications, **3**: 187–198.

Van Wagner, C.E. 1978. Age-class distribution and the forest fire cycle. Canadian Journal of Forest Research, **8**: 220–227.

Wilson, B. 2004. An overview of the mountain pine beetle initiative. *In* Proceedings of the Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, British Columbia, 30–31 October 2003. *Edited by* T.L. Shore, J.E. Brooks, and J. Stone. Information Report BC-X 399, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia. pp. 3–9.