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Mountain Pine Beetle Initiative
Working Paper 2006-01

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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* Englm. Ex S. Wats; Pinaceae). A mosaic of ages over the one million hectares was produced for each fire regime modelled. These were used to generate mosaics of susceptibilities to mountain pine beetle attack. This susceptibility is 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, which 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 allow an incipient beetle population to spread unimpeded across the landscape under consideration. It was found that (i) long fire cycles yield an age structure that is highly susceptible to beetle attack; (ii) fire suppression reduces the frequency of fires and yields an age structure highly susceptible to beetle attack; (iii) harvesting one age class reduced the mean susceptibility to mountain pine beetle attack, and this reduction decreased with increased harvest age and increased 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 ha) the area was often not traversable. Harvesting reduced the mean susceptibility and traversability, often substantially. Traversability was calculated for the whole of British Columbia in blocks of about one million ha using B.C. Ministry of Forests and Range inventory data for the year 2000. The area most traversable was the area in Tweedsmuir Park and the Lakes Timber Supply Area, where most of the present outbreak is centred. FRAGSTATS patch metrics were calculated for each of the simulations and these were related to traversability using discriminant analysis. This was then applied to the B.C. inventory; the concordance was high with 93.3% of conditions being correctly classified.

Résumé

Nous avons eu recours à une simulation de Monte Carlo pour examiner les effets de la fréquence des feux sur la structure par âge à l'équilibre d'une forêt de pin tordu latifolié (*Pinus contorta* var. *latifolia* Engelm. *ex* S. Wats; Pinacées) d'une superficie d'un million d'hectares et produire une mosaïque des âges à l'échelle de cette forêt pour chacun des régimes de feux modélisés. Nous avons ensuite utilisé ces résultats pour générer des mosaïques de vulnérabilité au dendroctone du pin ponderosa (DPP). En associant cette vulnérabilité à la répartition selon l'âge, nous avons calculé la vulnérabilité moyenne de la forêt et produit des cartes de vulnérabilité pour deux zones d'approvisionnement forestier de la Colombie-Britannique et pour l'ensemble de la province. Nous avons également défini une caractéristique, la pénétrabilité, qui décrit la capacité d'une population de DPP de se disperser à l'échelle d'un paysage selon des règles définies de vulnérabilité et la distance de dispersion maximale à travers un habitat défavorable. En utilisant les 40 combinaisons de catégories de vulnérabilité et de limites de dispersion, nous avons caractérisé le paysage comme pénétrable ou non pénétrable. Cette information nous renseigne sur la capacité qu'a une nouvelle population de DPP de se disperser librement dans un paysage donné. Nous avons constaté que : i) les longs cycles de feu produisent des structures par âge très vulnérables au DPP; ii) la suppression des feux réduit la fréquence des feux et génère des structures par âge très vulnérables au DPP; iii) la récolte des arbres d'une classe d'âge réduit la vulnérabilité moyenne de la forêt au DPP, et cette réduction diminue en fonction de l'âge de la classe récoltée et de la longueur des cycles de feux. Quand les incendies couvrent des superficies inférieures à 100 ha, la région est toujours pénétrable. La pénétrabilité est inversement proportionnelle à la superficie brûlée et souvent nulle lorsque cette superficie est très grande (jusqu'à un 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 Colombie-Britannique, par blocs d'environ un million d'hectares, à l'aide des données d'inventaire de l'an 2000 du B.C. Ministry of Forests and Range. La région la plus facilement pénétrable se trouvait dans le parc provincial Tweedsmuir et la zone d'approvisionnement forestier des Lacs (Lakes Timber Supply Area), où l'infestation actuelle est concentrée. Pour chacune des simulations, nous avons calculé à l'aide de FRAGSTATS les valeurs pour les parcelles et les avons mises en relation avec la pénétrabilité par analyse discriminante. Nous avons ensuite appliqué le modèle aux données d'inventaire de la Colombie-Britannique. Une forte concordance a été observée, 93,3 % des situations étant classées correctement.

Introduction

Forest fires, attack by mountain beetle (MPB) (*Dendroctonus ponderosae* Hopk.) and harvesting are the three major sources of mortality for mature lodgepole pine (*Pinus contorta* var. *latifolia* Englm. Ex S. Wats; Pinaceae) in the interior of British Columbia, Canada. Although fires can occur in stands of any age, all three events occur mainly when the trees are of harvestable age and often it is challenging for forest managers to schedule harvesting before a stand has been devastated by either fire or the beetle. Fire is usually more severe in years with hot dry summers and the probability of an MPB outbreak is similarly higher in hot dry summers (Safranyik 2004). Both fires and outbreaks 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 wildfires 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 (or no) live trees left for the beetle to attack. On the other hand, stands that have been recently attacked by the beetle may be more susceptible to fire as 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 several factors contributing to an interaction, such as climate, weather variations, condition of the trees, species mix, etc. One such factor is the age structure of the forest, which depends partly on the forest fire return rates and fire sizes (van Wagner 1978; Armstrong 1999; Li and Barclay 2001). This in turn will influence the susceptibility of the forest to attack by MPB (Shore & Safranyik 1992; Shore et al. 2000).

Dispersal in mountain pine beetles 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 four hours, but only at speeds of 3-6 km/hr, and thus cannot overcome the effects of winds at higher velocities (Safranyik 1978). In 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 land in suitable habitat or perish in unsuitable habitat (Furniss and Furniss 1972). In addition, such long-distance dispersal tends to dilute the numbers of MPB, as they don't all fall in the same place. Once an epidemic is well underway, however, the numbers are so large that even long-distance dispersal results in sufficient numbers of beetles falling into suitable habitat that the epidemic can effectively move to new areas and become self-sustaining (Safranyik 2004). Thus, the concept of traversability is most applicable to beetle populations in the endemic and incipient stages, which will move mostly by short-distance dispersal.

It seems likely that spread rates of MPB will depend not only on the susceptibility of surrounding trees, but also on fragmentation and connectivity of the forest with respect to susceptibility. Recurring random 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 in MPB is in part mediated by pheromones that are attractive over moderate distances (Safranyik et al. 1989; Barclay et al. 1998), but beyond that dispersal is probably fairly random or oriented towards vertical silhouettes or up-wind. Since MPB 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 most notably by Polymenopoulos and Long (1990), Turchin and Thoeny (1993), Logan et al. (1998) and Hughes (2002), which 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 MPB attack and spread. The susceptibility rating system of Shore and Safranyik (1992) is used to derive susceptibility for each cell (hectare) in a one million ha 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 the MPB for two timber supply areas in British Columbia and produce susceptibility maps for these areas as well as the whole of the province.

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 one hectare) percolation theory states that, as an expected value, 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 past 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 suitable ages allows a path for the beetles, the annual density of fires required to create such a path is much less than if only one age was 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 suitable for 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 ha, 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 one-hectare cells. Both the initial ignition of a cell and the subsequent size of the resulting fire were treated as random events, 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, encompassing most of those likely to be found in British Columbia. For each cell, the probability of burning was compared with a random number from the negative exponential distribution (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), to determine whether or not the cell burned. Fire sizes were determined by assigning a maximum size (1 ha to 1 X 10^6 ha in powers of ten) and then drawing a random number from the negative exponential distribution (again, uniform and normal were tried, and the results were similar) 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 from 1712 to 1973, and by Armstrong (1999) who presented data for fires in northern Alberta ranging from 4.5 to 708172 ha from 1961 to 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 (Shore in preparation) for continuity which 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 when 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.

Table 1. Definitions of the effects of age and density on stand susceptibility of lodgepole pine to attack by mountain pine beetle. 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) x (DF) x 100.

Age	Age factor
$0 \leq A < 40$	$AF = 0.1$
$40 \leq A < 80$	$AF = 0.1 + 0.1\,[(A - 40) / 10]^{1.585}$
$80 \leq A < 120$	$AF = 1.0$
$120 \leq A < 520$	$AF = 1.0 - 0.05\,[(A - 120) / 20]$
$520 \leq A$	$AF = 0.002$

Density	Density Factor
$0 < D < 650$	$DF = 0.0824\,(D / 250)^2$
$650 \leq D < 750$	$DF = 1.0 - 0.7\,(3 - D/250)^{0.5}$
$750 \leq D < 1500$	$DF = 1.0$
$1500 \leq D$	$DF = 1.0 / [0.9 + 0.1 \exp\{0.4796\,(D/250 - 6)\}]$

Age and stand 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 are given in terms of height, with age, diameter at breast height (dbh) and stand density being determinable from height. We have used a regression for height vs age: the regression of top height (H; being mean height (m) of the 100 tallest trees per ha.) versus age (A):

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

The regression of dbh (D, diameter at breast height; cm) versus height (H) was

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

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

$$\rho = 3060 \exp(-0.107\,H) + 6930 \quad \text{if } H < 10\text{m}$$
$$\rho = 17017 - 900\,H \quad \text{if } 10 \leq H \leq 14\text{m} \quad [3]$$
$$\rho = 30600 \exp(-0.148\,H) + 505 \quad \text{if } H > 14\text{m}$$

Thus, we can derive density from age. Knowing both age (AF) and density (DF), we can calculate susceptibility for that age, S_a, as

$$S_a = AF * DF * 100 \quad [4]$$

using the values in Table 1.

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

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

in which λ is the parameter and x is the variable. For this distribution, the mean and standard deviation are both equal to 1/λ. For a forest that is a mosaic of stands of different ages but with an overall negative exponential age-distribution, we can calculate the susceptibility of a given age class weighted by the relative frequency of that class as

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

in which *a* is the cell age and λ exp (-λa) 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 ha mosaic) by means of the equation:

$$S_\lambda = \int \lambda \exp(-\lambda a)\, S_a \, da \qquad [7]$$

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 as a quick method of assigning mean susceptibility to stands if the value of λ is known. Equation 7 is shown in Figure 1 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 due to sampling error.

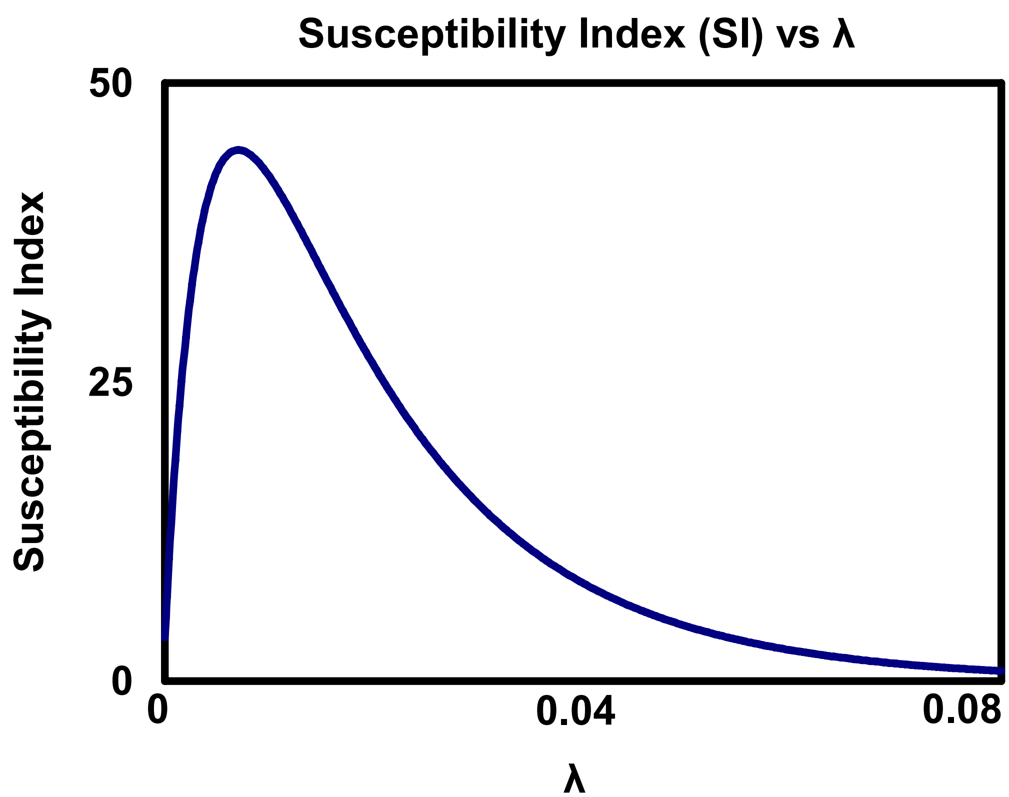

Figure 1. The mean susceptibility of a forest for a given value of λ, where the age distribution is negative exponential, is $S_\lambda = \int \lambda \exp(-\lambda A)\, S(A)\, dA$, in which A is the stand age, S(A) is the susceptibility a stand of age A, and λ is the parameter of the negative exponential distribution. The integral is taken over all ages of the forest.

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

$$S = \int f(a) S_a \, da \qquad [8]$$

in which 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 on the results of the 2000th iteration (year), at which time equilibrium had been established, except for those cases involving large fires when the system was inherently unstable.

Effects of harvesting and fire control

A simple harvesting model was included to determine if 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 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 done 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-Safranyik (1992) susceptibility index also requires the percent of susceptible pine and a location factor, and when these are included in real forest situations, the susceptibility values will be altered considerably. The percent of susceptible pine factor is the percentage of the total basal area (of trees > 7.5 cm dbh) represented by susceptible lodgepole pine (> 15 cm dbh). The location factor is calculated using

$$Y = [24.4 \text{ Longitude}] - [121.9 \text{ Latitude}] - [\text{Elevation (m)}] + [4545.1] \qquad [9]$$

where longitude and latitude are in degrees, and then the location factor (Shore & Safranyik 1992) is

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

Two timber supply areas in British Columbia were chosen to illustrate the effects of including the percent pine and location factors. These two areas are the Lakes Timber

Supply Area (TSA), with a centroid approximately at lat 54^{o} N, long 125.5^{o} W, being just northeast of Tweedsmuir Provincial Park, and Merritt TSA, with a centroid near lat 49.8^{o} N, and long 120.5^{o} W. The first location is in the Boreal Interior Cordilleran ecoclimatic region, whose major overstory components are lodgepole pine, trembling aspen, paper birch and Douglas-fir (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 was attacked during the early 2000s outbreak. The Merritt TSA was attacked by the beetles during both outbreaks (Taylor & Carroll 2004), but not as severely as the Lakes TSA (as at 2003).

Inventory data for the year 2000 were obtained from the B.C. Ministry of Forests for the whole province of British Columbia, including these two TSAs, at a resolution of 400 m by 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 predicted by Goudie's yield tables (Goudie et al. 1990), we calculated the susceptibility index for each 400 m by 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 the province.

Spread propensity: traversability

We present a methodology to allow assessment of the propensity of a beetle population to traverse (spread across) a million ha of forest based on the characteristics of the forest. These include age structure, and hence susceptibility to attack by MPB, and 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 rules as outlined below. In total, 21 such forest mosaics were examined, being the combinations of seven maximum fire sizes (1 to 1000000 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 a quality called traversability, [closely related to percolation, but not the same as traversability of FRAGSTATS (McGarigal & Marks 1995)], 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 for its ability to disperse. We deal here only with short-distance dispersal, not with 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 that 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 with various thresholds of distance that the beetle could travel through non-susceptible habitat and for various thresholds of what is considered susceptible. Lower susceptibility (S) limits of

20, 30, …, 90 were used for a cell to be susceptible to attack by MPB. For each million ha forest mosaic obtained from the 2000th iteration (year) of the simulation, susceptibilities were assigned to each cell using the Shore-Safranyik (1992) rating system, and then the image-analysis software eCognition (Definiens Imaging 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 these limits, the million ha forest under a given set of fire conditions was examined 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 using the Nearest Feature extension (courtesy of Jeff Jenness and Lois Engleman) of ArcView® (Environmental Systems Institute, Inc. 2000) for identifying the patches within these limits and then draw lines between patches that were within the distance limits specified. Then, 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 percentage of the 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 and most of them can be classified as areal, linear or topological indices (Baskent & Jordan 1995). Many of them are sensitive to grain and spatial scale (Haines-Young & Chopping 1996). The Monte-Carlo simulation yielded output of both age-structure of the forest and also age and density for each hectare (cell) in the million-hectare forest. This information was obtained for each combination of various mean fire sizes and burn probabilities. Susceptibility to MPB was calculated for each cell. From these output files, FRAGSTATS and the Patch Analyst (Elkie, Rempel and Carr 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. The spatial statistics we calculated include: PLC = proportion 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; 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 connectance, a threshold distance must be specified above which flights from one favourable patch to another cannot be made. We used three kilometres, as suggested by Shore and Safranyik (1992) as being a reasonable upper limit for easy dispersal. Typical susceptibility mosaics of one million ha from the simulations are shown in Fig. 2 for fire sizes of 1 ha, 100 ha, 10000 ha and 1000000 ha.

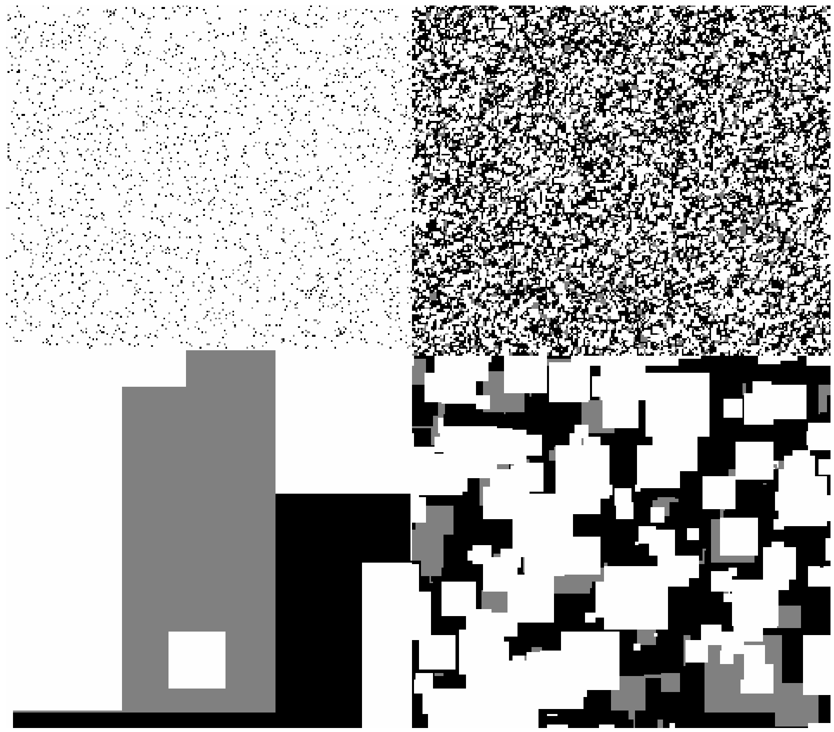

Figure 2. Four susceptibility maps resulting from fire sizes (ha) of 1.0 (upper left), 100 (upper right), 10000 (lower right) and 1000000 (lower left). All used a nominal burn probability of 0.01.

A step-wise 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 one to five kilometres. Each analysis used the value of the maximum fire size as well as the ten spatial statistics listed above as variables. The classification variable was traversability, being one if the area was traversable, and zero if not traversable. The discriminant analysis yielded a set of spatial variables capable of discriminating traversable landscapes and also two equations of the discriminating hyper-plane 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 Timber Supply Areas and also to the Tweedsmuir Park forest. The data used were from the British Columbia Ministry of Forests inventory were for the year 2000. These data consisted of mean age and percent pine for grids of these areas at a resolution of 400 m by 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 by the methods outlined above. Then the discriminant equations were 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 (below 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 (above about 50000-100000 hectares), 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 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, excluding the maximum fire size of 10^6 where the results were so erratic. An analysis of variance on 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 high burn probabilities (short fire cycles).

Table 2. Mean values of the susceptibility index (S) for one million simulated hectares for three nominal burn probabilities and six fire sizes (1 – 100000 ha).

Burn Probability	1 Mean S	10 Mean S	100 Mean S	1000 Mean S	10,000 Mean S	100,000 Mean S
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

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 at dbh or less than about 200 years old (Hopping and Beale 1948; Cole and Amman 1969). From the regressions shown in equations 1 and 2 we can infer that a value of S of 10% corresponds to a mean tree dbh between 14.2 and 27.7 cm, sizes 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 the trees being attacked.

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

$$\text{Percent BA killed} = 0.68 * \text{Susceptibility Index} \quad [11]$$

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 considering harvesting (Table 3). The mean susceptibility (S) 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. On the other hand, 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 maximizes harvest as well. Also, mean S increases with the extent of fire control, as also does 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 Tables 2 and 3, we see that harvesting at all three ages reduced the value of S compared to 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.

Table 3. Mean susceptibility (S) values for three burn probabilities (0.05, 0.01, 0.004), three ages of harvesting (80, 100, 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). All fires were of maximum size 10000 ha. Volumes harvested (Vol) are also shown (cubic metres per hectare).

		Percent of Fires Suppressed							
Burn Prob	**H.A.**	**0**		**50**		**80**		**95**	
		Mean S	**Vol**	**Mean S**	**Vol**	**Mean S**	**Vol**	**Mean S**	**Vol**
	80	2.683	0.7	3.262	1.0	5.162	2.1	12.892	4.7
0.05	**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
	80	12.771	4.9	13.398	5.2	14.650	6.4	16.285	7.9
0.01	**100**	21.780	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
	80	15.163	6.6	15.209	7.4	15.942	7.7	16.560	8.6
0.004	**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

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, the values were 40.2% for the Lakes TSA and 31.9% for the Merritt TSA. The first pair correspond approximately to lower limits on dbh of 18.2 cm and are thus both normally considered to be susceptible. Age class distributions for the two areas are quite similar, as shown in Fig. 3. Maps of the 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 a large proportion of both TSAs were highly susceptible in the year 2000.

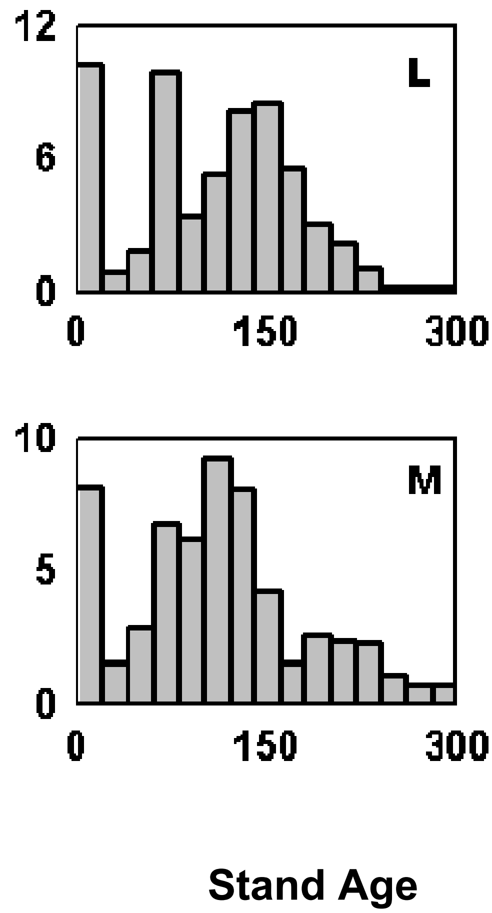

Figure 3. Age distributions of predominantly lodgepole pine stands in two areas of British Columbia: the Lakes TSA (L), and the Merritt TSA (M).

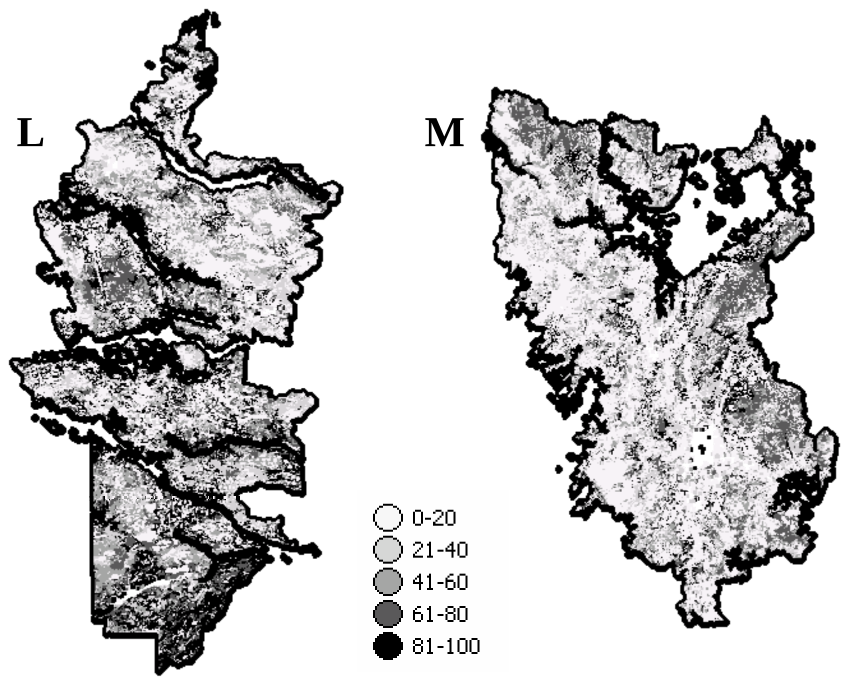

Figure 4. Maps of the susceptibility index in year 2000 for the Lakes TSA (L) and the Merritt TSA (M) using the four factors: age, density, location and percent pine. Five susceptibility classes are used, ranging from 0 – 20 (white) through grey to 80 – 100 (black).

Traversability and dispersal potential

Values of the index τ, mean traversability, for the 21 million-ha simulated mosaics are shown in Table 4 for three values of the burn probability and the seven fire sizes. A value of one 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 infestation to travel from one side of the mosaic to the other. A value of zero indicates that such traversal might be impossible unless long-distance dispersal occurred. For most fire sizes, these 40 values were either all ones or all zeros. Values between zero and one mean that such traversal might well happen, but the values of S and dispersal distance that would allow transmission need to be empirically determined in order to put a boundary on the types of fire regimes that would permit such traversal. For fire sizes of 1000, 10000 and 100000, in many cases, ones changed to zeros as the bounding value of S was increased and/or the dispersal distance decreased. Fires of maximum size of 1, 10 and 100 produced patterns of susceptible forest that were traversable for all burn probabilities, and thus τ = 1 throughout. For larger fire sizes, the index τ generally decreased as fire size increased, so that large infrequent fires tended to yield a landscape that MPB cannot easily traverse, and the values for fires of maximum size 1000000 formed a continually changing distribution of forest ages, so that equilibrium was never achieved for fires of that size.

Table 4. Index of mean traversibility (τ) for burn probability (IP) and fire size (Size) for the one million hectare simulated lodgepole pine forest.

IP	Size						
	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

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 consistently reduced traversability, but values of τ when harvesting occurred in the 120^{th} age class were often larger than when harvesting did not occur, especially when burn probability was very low. Harvesting and fire control in combination yielded 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.

Table 5. Index of mean traversibility (τ) for harvesting at three ages (H.A.) and fire suppression at four levels, three nominal burn probabilities (IP) and maximum fire size of 10000 ha for the one million hectare simulated lodgepole pine forest.

IP	H.A.	Percent of Fires Suppressed			
		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

Spatial indices

Ten spatial statistics were computed for each of the 21 combinations of factors. These statistics were computed for patches of high susceptibility, being defined as $S \geq 20$, 30, … 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 connectance and nearest neighbour distance. Pairwise correlations among these 10 statistics were all significant, except for the pair connectance and nearest neighbour distance.

Variation of spatial indices with susceptibility

In the treatment above, the spatial statistics were examined for patches of susceptibility above 20, 30, … 90 successively. A step-wise discriminant analysis showed that the two most important variables for discriminating traversability were 'proportional cover of susceptible forest' (PLC) and 'edge density' (ED), and 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 one kilometre to 0.56 for five kilometres, limiting dispersal distance. The next most important variables for predicting traversability were 'largest patch index' (LPI) and 'number of patches' (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, and then on all four variables to predict traversability. The best discrimination was with the three variables, PLC, ED and LPI, and the coefficients of the discriminant equations for the best three variables are shown in Table 6 for the five maximum dispersal distances (one to five km). Graphic results using PLC and ED are shown in Fig. 5 showing strong trends, with groupings attributable to fire size. Discrimination was very good, and over 90% of traversability conditions ('yes' or 'no') were correctly classified. Each discrimination has two equations, one for Trav=0 and one for Trav=1. 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 in those latitudes.

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 is for $S \geq 80$, centred around Tweedsmuir Park and the Lakes TSA. Fig. 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).

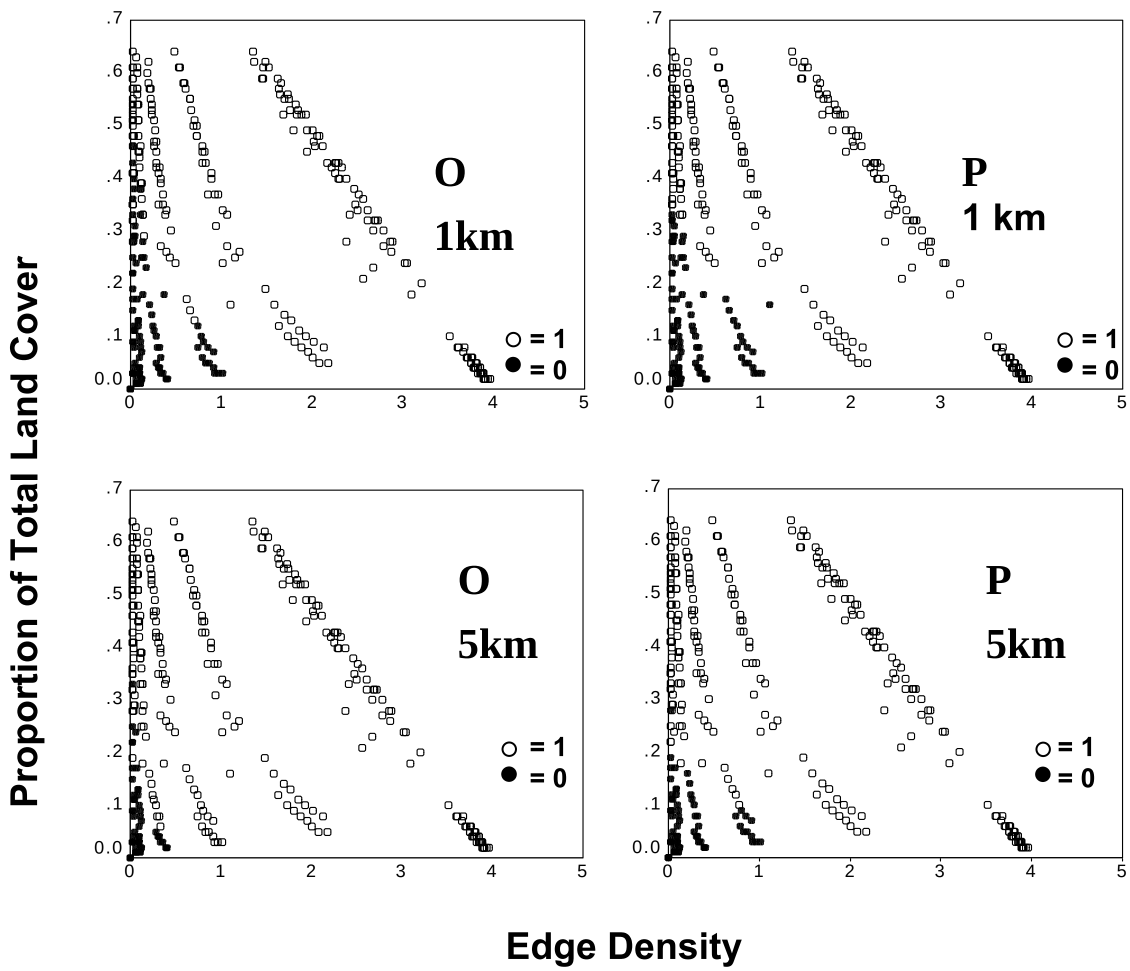

Figure 5. Observed (O) and Predicted (P) distributions of traversability (Tr: 1=yes; 0=no) graphed against the two spatial statistics from FRAGSTATS, percent susceptible land cover (PLC) and edge density (ED). These are shown for the two maximum dispersal distances, one km (on the left) and five km (on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

Table 6. Coefficients of discriminant equations to predict traversability (Trav: 1=yes; 0=no) using the three variables of proportion susceptible land cover (PLC), edge density (ED) and largest patch index (LPI). Ten sets of coefficients are shown, representing the two equations for each of the five dispersal distances (1-5 km).

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

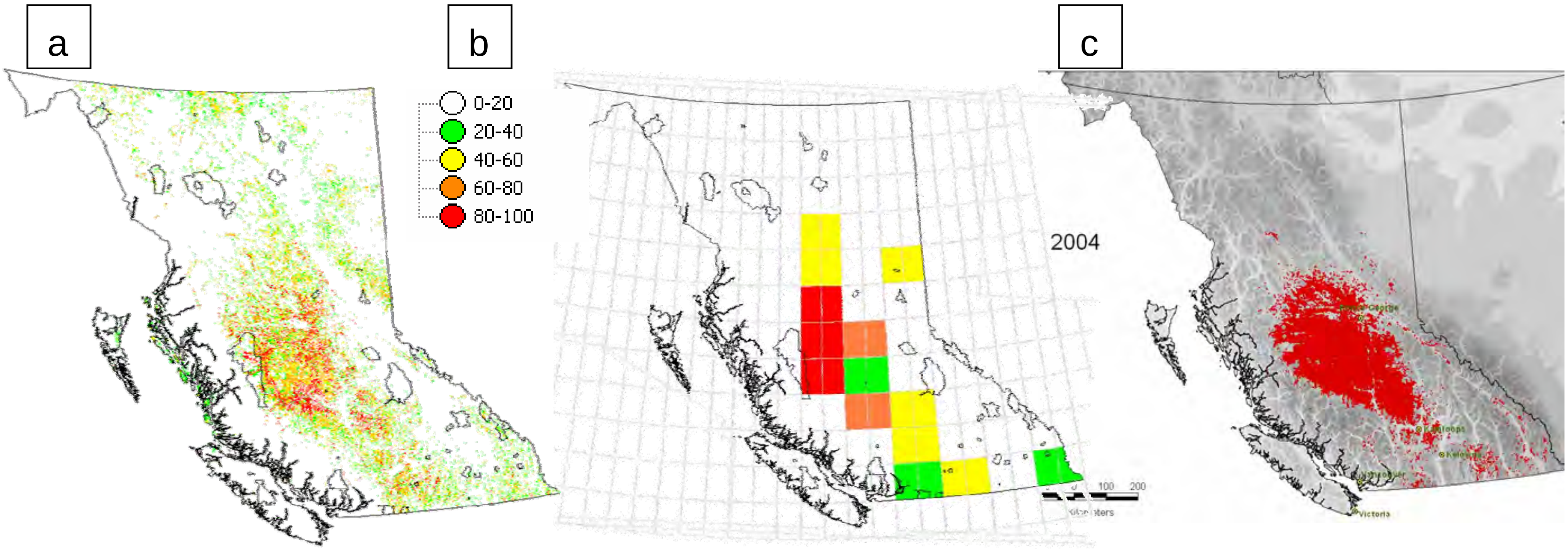

Figure 6. Mean susceptibility (a) and traversability, τ, (b) for the province of British Columbia calculated over four susceptibility boundaries and the five Maximum dispersal distances. Each polygon in the grid is one letter block in the British Columbia Geographic System of Mapping (BCGS). Also shown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

The discriminant equations applied to the three best patch metrics for each of the 89 provincial letter blocks, each at four levels of 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 τ ≈ 0.5. There was little difference in predictability for the four boundary percentages of susceptibility of the five maximal dispersal distances.

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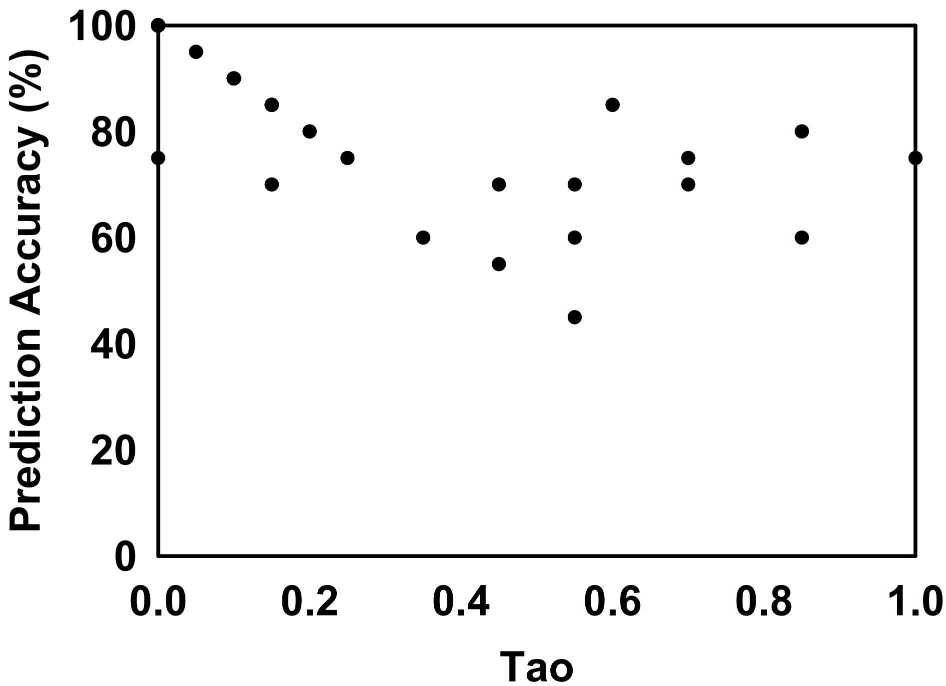

Figure 7. Accuracy of the discriminate equations in predicting traversability plotted against mean measured traversability (τ) for the 89 letter blocks covering British Columbia.

Over the past century, the number of fires has decreased (Figure 8) 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 (ST) and grouped into decades starting in 1912 and ending in 2000. Figure 8 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 has been much larger than in the 1980s, and the present epidemic is the largest on record.

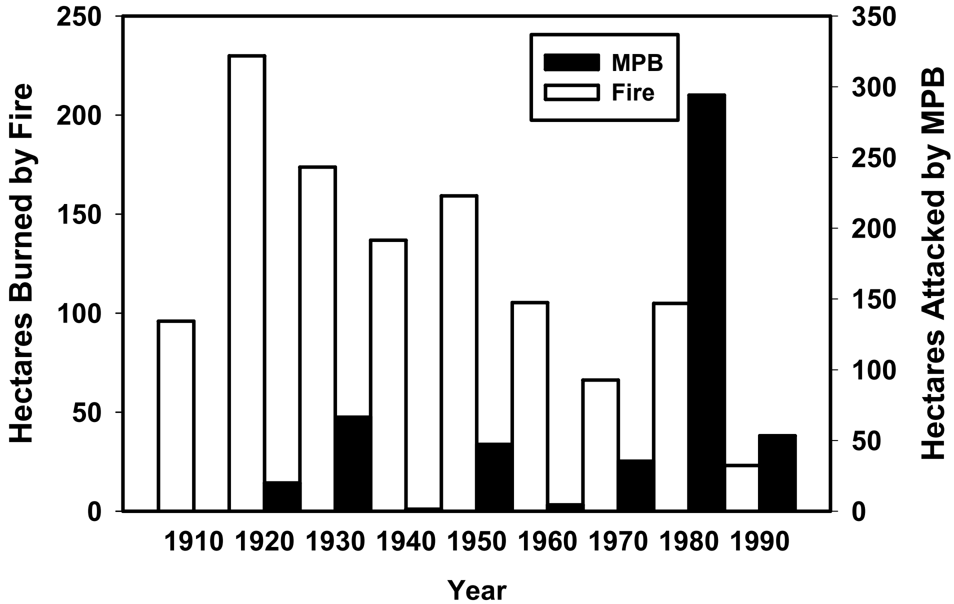

Figure 8. Mean annual area burned by wildfires (hectares, times 1000) and areas attacked by mountain pine beetles (hectares, times 10000) for each of nine decades starting in 1912 and ending in 2000.

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 beetle. Once this is established, an assessment of risk from an incipient beetle population could 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 considerably reduces the mean susceptibility of the forest to beetle attack, and also reduces traversability, especially harvesting of younger age classes (i.e., 80 years), although Fall et al. (2004) point out that early harvest may result in harvest shortfalls; (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.

For random fires of one hectare, percolation theory predicts that there will be a mean threshold proportion (0.59) of susceptibility classes above which the class in question will form a continuous network across that 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 Fig. 1 that highly susceptible cells only approach a proportion of 0.59 of the total mosaic when $\lambda \approx 0.005$, which would imply a mean age of 200 years, which is unlikely to often occur 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 is 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 distance of one to five km were used, although it seems likely that even five km is a conservative estimate of the distance that MPB can disperse (L. Safranyik, pers. comm.).

The use of square fires in the simulations may have some influence on the results, but would be mostly noticeable in computing indices such as the fractal dimension, that 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 the largest fire sizes, in which the susceptible blocks are very angular (Fig. 2).

Although it is possible to compute traversability for a real forest using our methodology once the forest was modelled in a 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 in B.C. as a whole, with 93.3% correct predictions, although only complete lack of traversabilty was predicted with 100% certainty. The least accurate predictions were for intermediate levels of traversability. 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 TSA areas. The Lakes TSA is where the present MPB epidemic is concentrated. Thus, traversability appears to be an effective indicator of the likelihood of an outbreak if weather conditions favour such an outbreak. Since the determination of traversability is rather labour-intensive, the use of the FRAGSTATS metrics together with discriminant equations represents 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 present 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).

All the results presented here are from simulated forests at equilibrium. Equilibrium results are not only easy to obtain, but also reduce the complexity, as usually there is 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. Thus, the results are most useful for long-term management and especially in developing strategies for long-term sustainable forest management.

Since equilibrium age distributions are close to negative exponential for all except the large fire sizes, the use of equation 7 or Fig. 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 NED, 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 in planning for long-term sustainable forest management.

Historical records of the number of fires and the area attacked by MPB show inverse trends (Figure 8). 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.

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