A population dynamics model for the mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera : Scolytidae)

L. Safranyik, H. Barclay, A. Thomson, and W.G. Riel

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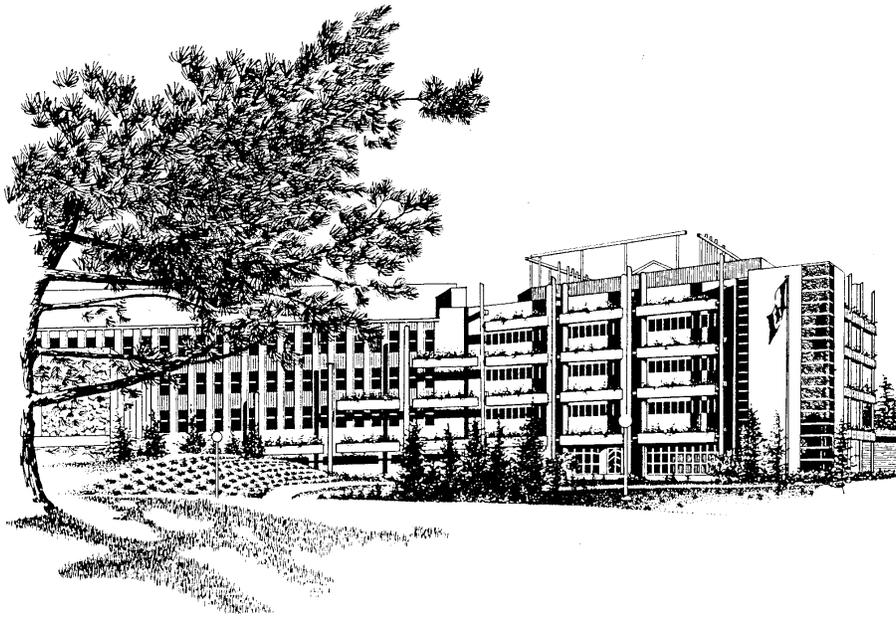
The Pacific Forestry Centre, Victoria, British Columbia

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Integrated Pest Management Network

The protection of Canada's forest resource against damaging insects, disease-causing organisms, and competing vegetation is essential to sustainable development from both environmental and economic perspectives.

The methods used to reduce depletion of our forest resources must be effective without having a negative impact on public health or ecological diversity. There is a continuing social and economic demand for safe, effective methods to control forest pests. Research expertise within the Canadian Forest Service (CFS) plays a central role in developing and assessing forest pest management alternatives, which provide additional incentives to commercial pest control industries.

The Integrated Pest Management Network advances the development of cost-effective and ecologically acceptable methods for managing forest pests and contributes to the establishment of integrated pest management and sustainable forest development in partnership with other CFS networks and external clients and collaborators.

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Canadian Forest Service
Pacific Forestry Centre

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Abstract

An interactive simulation model of mountain pine beetle population dynamics was developed in the Windows-95 environment. A 1-ha area of pure lodgepole pine is simulated. The model is composed of four main parts: a forest stand sub-model, a mountain pine beetle biology sub-model, beetle management sub-models, and an input-output interface. The forest stand sub-model predicts lodgepole pine growth and yield and is based on previously published yield tables. The mountain pine beetle biology sub-models are process-based and simulate attack dynamics within and among trees, brood establishment, development and survival in relation to tree, site and stand factors, temperature and natural enemies. These sub-models are based on published information and, where data were lacking, on the experience of the authors with mountain pine beetle biology and management and simulation modeling. The beetle management sub-models simulate individual tree treatments, pheromone baiting, removal of infested or uninfested trees, and tree spacing. Theoretical control scenarios can also be explored by introducing control factors at specified stages of brood development. The interface allows for interactive manipulation of tree, site and insect variables in order to assess effects on the course of an infestation evaluated by graphical or tabular outputs of results. The model has not been tested against data because the type of complex data that would be required are lacking. In simulated runs, the model generally gave qualitatively accurate descriptions of the course of infestations in terms of the relative effects of tree and site factors and management interventions.

Résumé

Un modèle interactif de simulation de la dynamique des populations de dendroctones du pin argenté a été mis au point sous Windows-95. Le modèle simule l'évolution des insectes sur une surface de 1 ha couverte en exclusivité de pins de Murray. Il comprend quatre composantes principales : un module pour la simulation du peuplement forestier, des modules « biologiques » servant à simuler l'évolution de la population de dendroctones, des modules pour la simulation du contrôle des insectes et un module d'interface permettant d'entrer les données et de recueillir les résultats. Le module de simulation du peuplement forestier prédit le taux de croissance des pins de Murray et la productivité du peuplement en se basant sur des tables de rendements connues. Les modules de simulation de la population de dendroctones fonctionnent en faisant appel aux processus eux-mêmes et permettent de simuler la dynamique de l'infestation à l'intérieur des arbres et d'un arbre à l'autre, l'établissement du couvain, le développement et la survie de l'insecte en fonction des facteurs liés aux arbres, au site et au peuplement, de la température et des ennemis naturels. Ces modules sont basés soit sur des données connues soit sur des données issues de l'expérience des auteurs dans le domaine de la biologie et du contrôle des dendroctones ainsi que de la simulation numérique. Le module de simulation du contrôle des insectes simule l'action de certains traitements appliqués aux arbres, l'efficacité des pièges sexuels, l'effet du retrait des arbres infestés ou sains, et l'effet de l'espacement des arbres. Des scénarios théoriques de contrôle peuvent également être explorés en introduisant des facteurs de contrôle à des étapes spécifiques du développement du couvain. L'interface permet la manipulation des variables décrivant les arbres, le site et les insectes de manière à pouvoir évaluer l'effet de ces variables sur l'évolution de l'infestation grâce à la représentation graphique ou tabulaire des résultats. On n'a pas encore pu tester le modèle en comparant les simulations obtenues à des données réelles car ces dernières, très complexes, ne sont pas disponibles. Les simulations ont néanmoins généré des descriptions précises – du point de vue qualitatif – de l'évolution des infestations en fonction des effets engendrés par les facteurs liés aux arbres et au site ainsi qu'aux interventions de contrôle

Acknowledgements

Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopk.) is the most destructive insect of mature pine forests in western North America (Wood 1963). In western Canada, lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) is the main host species. Periodic outbreaks result in catastrophic losses in terms of killed trees (Safranyik et al. 1974; Unger 1993). Historically, the greatest damage has occurred in the southern interior regions of British Columbia (Unger 1993). In addition to tree mortality, outbreaks impact on other resource values, increase fire hazard, and may force changes in resource management plans.

Due mainly to the severity of these impacts on forest resource values, the biology and management of the mountain pine beetle has been researched extensively over the past 50 years, and a large body of published information exists. The earlier publications are referenced in Safranyik et al. (1975); examples of more recent work are found in the publications Amman and Cole (1983), Cole et al. (1985), Berryman (1976), Burnell (1977), Bentz et al. (1991), Borden et al. (1983a, b), Raffa and Berryman (1983 and 1986), Logan et al. (1998), and Powell et al. (1998). This knowledge base, augmented by similar information on other *Dendroctonus* species and the authors' experience, was used to develop an interactive model of mountain pine beetle population dynamics. The main objective of this model was to provide specific information for a computer-based decision support system being developed at the Pacific Forestry Centre.

The model runs interactively and allows evaluation of a number of biological factors, including tree and stand factors, climatic variables and management practices on mountain pine beetle populations and damage levels. The objectives of this report are to describe the development and structure of the model and evaluate its performance.

Overview of mountain pine beetle biology

The range of the mountain pine beetle extends from northern Mexico (latitude 31 °N) to northwestern British Columbia (latitude 56 °N) and from the Pacific Coast east to the Black Hills of South Dakota. In Canada, the beetle is found as far east as the Cypress Hills in Alberta. The elevational range is from sea level to about 750 m near the northern limit, and up to 3650 m in the most southerly regions (Safranyik 1978). The principal hosts are lodgepole pine (*Pinus contorta* var *latifolia*), ponderosa pine (*P. ponderosa* Laws.), western white pine (*P. monticola* D. Don.), and sugar pine (*P. lambertiana* Douglas) (Amman 1978). All native pines and several exotic species within the beetle's range can be infested and killed.

The length of the life cycle varies depending on temperature conditions. There is normally one generation per year in Canada. During warmer than average summers, parent adults may re-emerge to establish a second brood (Reid 1962a). In cooler summers, which often occur at high elevations, some or all of the brood may require two years to mature.

The onset of the emergence and flight period is generally preceded by warm, dry weather. Daily emergence and flight activity begins when air temperatures exceed 16 °C. The maximum rate occurs at air temperatures above 20 °C, but is reduced at temperatures exceeding 32 °C (Gray et al. 1972; Reid 1962a). Emergence and flight normally occurs over a 7-day to 10-day period in late July to mid August. Following an exceptionally warm spring and early summer, the median emergence time can be advanced by up to one month over abnormally cool weather. There is some evidence that adult females emerging early in the emergence period search at random for suitable host trees (Hynum and Berryman 1981), and visually select the larger trees (Shepherd 1966). Upon finding a suitable host, the female beetle initiates attack by boring through the bark and beginning excavation of a vertical egg gallery in the phloem parallel to the grain of the wood. The male joins the female and mating takes place in the lower end of the egg gallery.

During egg gallery initiation, the female produces an aggregating pheromone, which attracts mainly males and mediates mass attack on the tree. The male produces an aggregating pheromone that attracts mainly females. Some host volatiles synergize the effect of the aggregating pheromones. During host colonization, an anti-aggregating pheromone is produced by auto-oxidation of alpha-pinene and microbial conversion of the female-produced aggregating pheromone. The function of the anti-aggregating pheromone is regulation of attack density and close-range redirection of attacks to nearby trees (Borden et al. 1986).

Mating takes place near the lower end of the egg gallery and the male aids in gallery construction, pushing debris out the entry hole, and eventually plugging the entrance and the lower end of the gallery with packed boring dust. The males usually die in the gallery shortly after mating, and are sealed in by the female as she continues packing the lower gallery with debris. The female lays 40 to 60 eggs singly into niches in the sides of the egg gallery, and covers them with packed frass. Egg galleries average 30 cm in length, and may be as long as 2 m. The lower temperature limit for egg gallery elongation and egg laying is 1.7 °C (Reid 1962a) and activity increases curvilinearly with temperature (Amman 1972). In lodgepole pine, oviposition ceases and females tend to abandon the egg gallery when the moisture content of the inner bark falls below about 105% of oven dry weight ((wet weight - dry weight)/dry weight; Reid 1962b) and the outer sapwood below 60%.

Eggs hatch between 4.4 and 35.0 °C. The optimum temperature range is 21.0 - 25.0 °C (Reid and Gates 1970). Eggs normally hatch within a week or so following deposition and the larvae construct tunnels in the phloem at right angles to the egg gallery as they feed. There are four larval stages (instars) which range in head capsule width from 0.5 mm (first instar) to 1.25 mm (fourth instar). Larvae may reach third and early fourth instar before the onset of winter in October and November when they become dormant. The larvae resume feeding in April and complete their development by June. The low temperature threshold for larval development is near 2.2 °C (McCambridge 1974), and the rate of development near this threshold is inversely related to larval instar (Amman and Cole 1983). Pupae held at a constant temperature of 30 °C die before completing pupal development (Amman and Cole 1983) and all larvae die within a few days of hatching at constant temperatures of 32 °C and 35 °C (Safranyik and Whitney 1985). Temperatures above 43 °C kill all brood (Patterson 1930). At 24 °C, 674 degree-days above 5.6 °C (a degree-day is 1 °C above the threshold temperature for 24 hours) were required for development from egg to the tanned (dark) adult stage.

Eggs freeze at -18 °C (Reid and Gates 1970); consequently, most eggs are killed during the winter in Canada. When beetles infest trees in late August, there may be insufficient heat accumulation before the onset of cold weather for all eggs to hatch. The lethal low temperature for larvae is between -34 °C and -38 °C (Wygant 1940; Somme 1964). Cold hardiness of larvae generally increases upon exposure to freezing temperatures; hence cold-hardiness is greatest from mid to late winter.

Mountain pine beetles pupate in cells that the larvae excavate in the bark and sapwood. Pupae transform into adults during late June to mid-July. Brood adults typically mature in July. Prior to emergence, the young beetles resume feeding on the inner bark and ingest spores of blue stain fungi and yeasts that line the inner walls of the pupal chambers. During this feeding, the flight muscles increase in size (Reid 1958), and the mycangia (organs on the mandibles evolved to carry fungal spores) become charged with spores, which ensures transport of the fungi to new trees (Safranyik et al. 1975).

Those trees that are able to prevent the establishment of beetles and blue stain fungi are termed resistant. Trees resist invasion with an initial flow of liquid resin from severed resin ducts (Reid et al. 1967). Living cells next to wounds produce additional liquid resin and other substances normally present in heartwood. This process is accelerated by the presence of blue-stain fungi. The phloem and sapwood surrounding wounds become impregnated by resinous substances that are detrimental to the establishment of beetles and blue-stain fungi. Resistance is affected by a number of environmental factors including tree age, stand density, and temperature (Safranyik et al. 1974; Thomson et al. 1985).

When mountain pine beetle populations are low, a number of factors interact to restrain the potential of such populations to increase. These include climatic effects, natural enemies, competition within and among species, and host resistance. Relaxation of one or a combination of these factors may result in the development of an outbreak. During outbreaks, it appears that beetle survival is not regulated by natural within-tree factors such as competition, predators, parasites, resinosis and phloem drying (Amman and Cole 1983). Beetle survival is more closely related to tree diameter and phloem thickness than any other factor. Tree resistance is usually greatest in the largest diameter, fastest growing trees (Shrimpton 1973, 1978). At low beetle population levels, the success of resistance and a tree's subsequent suitability as mountain pine beetle habitat depend on beetle numbers (Raffa and Berryman 1983). Consequently, as the number of beetles increases, trees of higher resistance become available for colonization. Outbreaks are triggered when a threshold number of beetles that can successfully colonize large diameter trees with thick phloem is attained (Berryman 1978). This threshold may be exceeded in stands temporarily weakened by disease, drought, defoliation, senility, or where large numbers of beetles have arrived from other nearby infestations. If weather conditions are unfavourable, incipient infestations will decline, and several years may elapse before conditions again become suitable.

Model development

The model is composed of four main sections: two biological sections – the forest stand model and the mountain pine beetle biology model; and two non-biological sections – a management submodel and a section that controls input, output and interactive simulation. The original model was written in FORTRAN to run on a Vax 8650 under VMS. It has since been converted to a Windows 95-based PC environment with a user interface developed in Visual Basic

The forest stand submodel is based on variable density yield tables for lodgepole pine developed by Johnstone (1976) and simulates the growth (DBH, height, natural mortality) and yield of a pure, unmanaged lodgepole pine stand as a function of site quality, initial density and age.

The mountain pine beetle biology and management submodels simulate the processes of host colonization, brood development and survival, tree mortality, and control interventions (direct control, host density manipulation and biological control). The model simulates the course of a beetle infestation in a 1-ha stand using a daily time step. Although the number of adult beetles dispersing out of the area is calculated for each beetle generation, the fate of these beetles is not considered in the model. Stand parameters, temperature regime, host resistance, the initial size of the beetle population, and control interventions by type, magnitude and duration, can all be specified at the beginning of each run.

The development of this model involved two approaches: 1) empirical models from published sources, and 2) conceptual models. The empirical models were based on regressions such as surface area equations or growth and yield functions, or they consisted of tabular data from which intermediate values were interpolated, such as the data for brood development as a function of temperature. The general structures of conceptual models and their parameters were based on published sources whenever data were available. The functions relating egg and larval survival to attack density were derived in this manner. Where data were not available, the parameters were derived from the known or assumed limits of the dependent variable and its rate of change with respect to the explanatory variable. The sub-model for the effect of host resistance on brood survival (e.g. Fig. 2) was derived this way. In situations where only general information was available, the structure and parameters of sub-models were developed on hypothetical grounds. For example, to examine the effects of bait on attack density and tree mortality, we assumed that the inter-bait distance commonly used in experiments is the practical limit for attraction or repellency, and that relative bait effects increase exponentially with bait density.

The output is in the form of tables showing changes through time in a number of stand and insect variables, which can be plotted against each other, or as functions of time. A large number of variables are included in the

simulation; only a subset of these variables of interest mainly to forest managers and students of insect population dynamics, are output.

Forest stand sub-model

The forest sub-model predicts lodgepole pine growth based on yield tables published by Johnstone (1976), converted to metric form and extended to age 120 years as described in Thomson (1987a). The equations predict stand attributes based on three parameters – age, site productivity index (*PI*), and development index (*DI*) — and have been used as the basis of stand table construction (Thomson 1987b, 1993).

The program generates a stand table of stem diameters based on *PI*, *DI*, and the initial number of stems per hectare. The stand table describes conditions between a starting and a final age, and outputs the number of stems per hectare in 2.5-cm size classes for each year of the simulation (Table 1).

Table 1. Example of stand table. The stand started with 9964 stems per hectare (SPH) and an average DBH of 3.25 cm at age 21. Stems per hectare in 2.5-cm DBH classes between age 36 and 40 are illustrated.

Age	Mean DBH	SPH	DBH class (mid points)					
			2.5	5.0	7.5	10.0	12.5	15.0
36	6.85	6477	1211	1856	1942	1105	363	0
37	7.03	6306	1104	1751	1915	1145	391	0
38	7.20	6141	1007	1629	1882	1168	418	37
39	7.37	5983	915	1527	1852	1192	419	48
40	7.54	5831	828	1442	1811	1220	466	64

Mountain pine beetle biology and management sub-models

General structure

The size of the attacking beetle population (*N*) in generation *t*+1 is given by equation 1a.

$$N_{t+1} = (N_t - L_t)P_t \sum_i (AP_i \times S_i \times E_i) \tag{1a}$$

Where the summation is over DBH classes, and *i* designates the *i*-th infested DBH class, *APi* is the normalized proportion of beetles allocated to a DBH class, *N* is number of adult beetles, *L* is number of beetles lost due to inability to fly or dispersal out of the area, *S* is across-generation survival, *E* is average number of eggs laid per female beetle, and *P* and is proportion of adults that are female.

The size of the attacking female population (*F*) in generation *t*+1 is given by equation 1b.

$$F_{t+1} = (N_t - L_t)P_t \sum_i (AP_i \times S_i \times E_i \times P_i) \tag{1b}$$

Beetle survival across generations (*S*) in DBH class *i* was expressed as the product of a number of stage-specific survival factors (equation 2)

$$S_i = S_e \times S_1 \times S_p \times S_y \times S_n \tag{2}$$

Where the letters e, l, p, y, and m designate survival of the eggs, larvae, pupae, young adults and mature adults. Because the rate of progress through the various brood stages was simulated as a function of temperature, based on data in Safranyik and Whitney (1985), the length of the life cycle varies depending on temperature conditions.

The number of trees attacked (*TA*) in generation $t+1$ is expressed as follows:

$$TA_{t+1} = F_{t+1} \sum_i \left(\frac{AP_i}{(Am_i \times Bm_i)} \right) \tag{3}$$

Where *TA*, *Am* and *Bm* designate, the total number of attacked trees, mean attack density and mean infested bark surface area per tree and the other symbols are as described earlier. A flow diagram of the general structure of the mountain pine beetle model is given in Appendix A.

Attack sub-models

The attack sub-models determine by DBH class, the numbers of successfully and unsuccessfully attacked trees, and the number of emigrated beetles, for each beetle generation. They also calculate average attack density and the average infested bark area per tree. Attack during the initial year is handled differently than in subsequent years. During the initial year, the simulation begins with the attack event, and all attacks are deemed to occur on a single day at the end of July (Julian day 208). This corresponds with the usual timing of peak attack in southern British Columbia. The hatching of 50% of the eggs is also deemed to occur on this date. In subsequent beetle generations, the duration of each development stage and the emergence period are determined internally as described under the section entitled Beetle development period. The following is a description of the important fragmental equations.

Infested bole surface area (S_i) was modeled as in Safranyik (1988, equations 6 to 8). The general form of this is given by equation 4. Where f_1 estimates total bole surface area as a function of DBH and tree height and f_2 estimates the proportion of the total bole surface area contained below a given (infested) height. The product $f_1 \times f_2$ therefore gives an estimate of infested bole surface area (S_i). The form of equation 4 is illustrated in Fig. 1.

$$S_i = \left[f_1(DBH, \text{ Tree height}) \right] \times \left[f_2 \left(\frac{\text{Infested height}}{\text{Tree height}} \right) \right] \tag{4}$$

(Note: In this and following equations, the symbol f is used as a function. The same symbol is used in several equations but the particular function is specific to each equation. The simulation is conducted by DBH class.)

Infested height was modeled as a function of DBH and site index (*SI*) based on the results of Amman and Cole (1980).

$$\text{Infested height} = a(\text{DBH} - b)^{cSIh} \tag{5}$$

SIh is the site index and *a*, *b*, and *c* are constants.
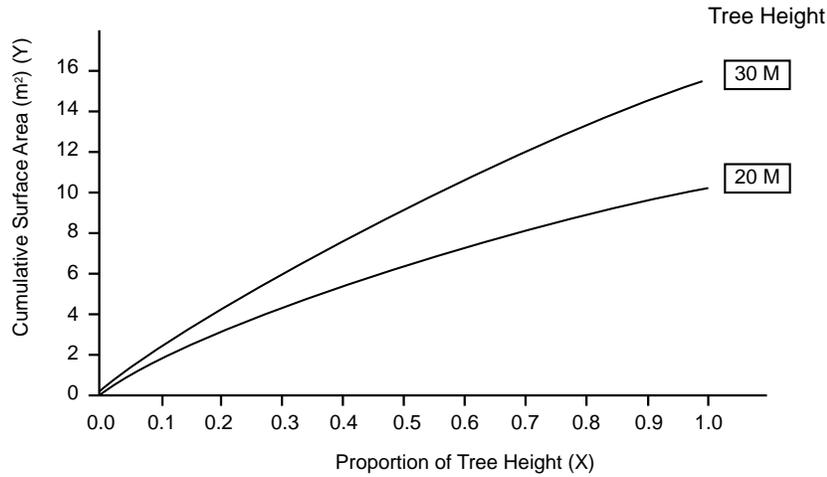
Figure 1. Cumulative bole surface areas (Y) in two 25-cm-DBH lodgepole pines of different tree heights. $Y = [0.3455 + 1.9708\ DH]\ [0.0059 + 1.6761X - 0.6657\ X^2]$ (Safranyik 1988) where D and H are DBH and tree height, respectively, in metres and X = (height on the bole to a given point)/(tree height).

Allocation of attacking beetles to DBH classes (APi) is based on the observation that frequency of attack is directly related to tree size (DBH) and the relative frequency of trees in a size class. In addition, the average number of attacks per tree is related to DBH (Safranyik et al. 1973). For other than the initial attack (start of simulation), attacking beetles were allocated to the DBH classes based on the normalized proportions given in equation 6.

$$AP_i = \frac{\left(M_i \times \mathrm{DBH}_i\right)}{\sum_i \left(M_i \times \mathrm{DBH}_i\right)} \tag{6}$$

Where the sum is taken over all attacked DBH classes, subscript i designates the i-th DBH class, M is the number of live trees and the other symbols are as described earlier.

For the initial attack, AP_i was weighted by the expected number of attacks per tree in each DBH class (Safranyik et al. 1975) and average maximum attack density was set at $110/m^2$. The total number of trees attacked in a DBH class (Tai) was modeled as a ratio of the number of female beetles and the average number of attacks per tree in that DBH class as shown in equation 3.

In subsequent generations, the initial number of attacked trees in each DBH class was determined in the same manner as described above, but was based on the number of beetles emerging during day one of the emergence period. Following the first day of attack, attack density was simulated by allocating beetles to randomly selected attacked trees in proportion to (i) the relative attractiveness of a tree based on pheromone production as modeled in Geiszler et al. (1980) and (ii) current attack density relative to the average maximum density given above. Attack stopped once a tree ceased to be attractive and/or it attained maximum attack density. If attacks ceased on all of the initially attacked trees before the end of the emergence period, additional trees were selected and mass attack was simulated as described earlier. This process of "pioneering" attack and subsequent mass attack occurred recursively until the end of the attack period. Any beetles that were not allocated by this process (Le) were deemed to have dispersed out of the simulation area.

A proportion of beetles are lost during emergence and dispersal due to inability to fly (*Lu*) and sub-optimal stand conditions (*Ld*). There is little published information on either of these variables. Disease (Whitney et al. 1978), mites (Moser 1975), and nematodes (Massey 1966) can have significant effect on the flight ability of bark beetles, but functional relationships have not been developed. During dispersal studies involving a large number of beetles, Linton et al. (1987) found that 6.3% of the beetles were unable to fly. Although some of the beetles in those experiments may have been injured during handling, in the absence of other data, we used the constant, 6.3% for *Lu*. Amman and Cole (1983) stated that losses of 40% or more can occur during beetle dispersal. We modeled dispersal loss due to sub-optimal stand conditions (*Ld*) simply as a function of the geometric mean of stand age, mean DBH of lodgepole pine, and mean nearest-neighbour distance among living lodgepole pine with DBH greater than 10 cm (equation 7) expressed as proportion.

$$Ld = \left\{ \left[f_1(\text{Distance}) \right] \times \left[f_2(\text{Stand age}) \right] \times \left[f_3(\text{Mean DBH}) \right] \right\}^{1/3} \tag{7}$$

The components of this model were based on the premise that the suitability of a stand for attack is directly related to age over 40 yr and average DBH, and inversely related to the mean distance among living trees. The parameters were fitted so that dispersal loss due to stand unsuitability would be about 50% in a 40-year-old stand with an average DBH of 8 cm and average density of 1500 stems per ha. On the other hand, an 80-year-old stand with an average density of 1500 stems per ha and an average DBH of 20 cm or greater would sustain no such loss. Total loss of emerged beetles (*L*) was modeled as: *Le* + (Number of Emerged Beetles) × (*Lu* + *Ld*).

Minimum DBH limit for attacks was set at 10 cm at the beginning of the simulation. This corresponds with the approximate DBH limit normally observed during epidemics in mature stands (Hopping and Beall 1948). Beetles fly toward dark silhouettes in the final stages of host location (Shepherd 1966). Attacks switch from one (focus) tree to another (recipient) tree during the process of mass attack. Geizler and Gara (1978) found that as the distance between the focus and recipient trees increased, the diameter of the recipient trees increased. The largest trees closest to a focus tree are attacked first. As the progressively smaller diameter classes are killed, the reduction of silhouette size combined with the ever-increasing distance between living trees makes it much more difficult for the beetles to successfully instigate mass attack, and the infestation will eventually abate. We used an exponential model to simulate the effect of tree spacing on minimum DBH attacked (equation 8). The parameters were established so that in a 70-year-old stand at the lowest average density in this model, the minimum size of trees attacked will be approximately 10 cm DBH. At 400 stems per ha the minimum size of tree that will be attacked will have a DBH of about 18 cm.

$$\text{DBH}_{Min} = \frac{175}{\left[5 + 27 \times \text{Exp}(-0.35 \times \text{Distance}) \right]} \tag{8}$$

Where Distance is defined as the average nearest-neighbour distance (in metres) among living pine with DBH 10 cm or more.

The number of successfully attacked trees is modeled as a product of the number of attacked trees in a DBH class (*Ta_i*) and the probability of successful attack (*AS_i*). In turn, AS_i was described by a sigmoid function of average attack density (*A_i*) and relative host resistance (*R_i*) (equation 9):

$$AS_i = \frac{1}{\left[1 + \exp\left(-b(XO - R_i) \right) \right]} \tag{9}$$

Where *b* is a constant R_i is relative host resistance (0 = not resistant, 1 = fully resistant) and *XO* is a linear function of average attack density. Equation 9 is illustrated in Fig. 2. Successfully attacked trees were those that died because
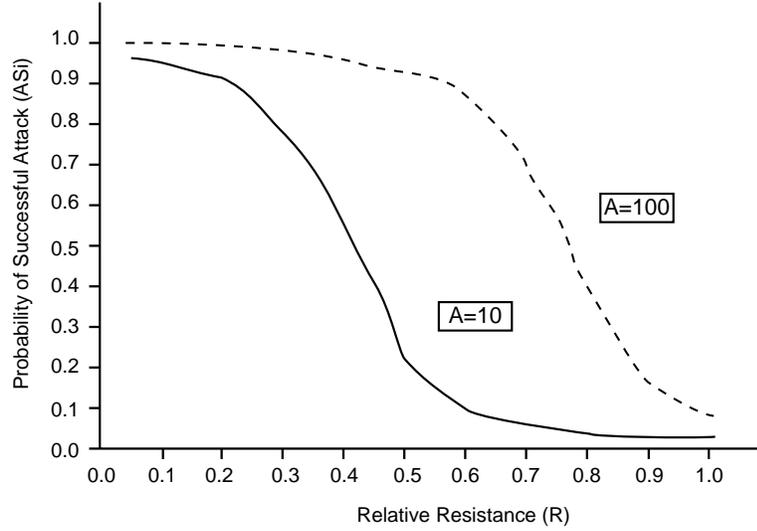
Figure 2. Sub-model for the probability of successful attack by mountain pine beetle in lodgepole pine (*ASi*).
ASi = 1 / [1 + exp(-12 (*Xo* - *R*))], where *Xo* = 0.4 + 0.04((*A*-10)/10)
A = mountain pine beetle attack density/m², *R* = relative host resistance(range: 0-1).

of the attacks, regardless of whether or not any broods matured. The general form of equation 9 is based on the results of Berryman (1976), Raffa and Berryman (1983), and Thomson et al. (1985). These authors and others have shown that attack success in individual trees increases asymptotically with attack density and decreases with increased resin production. The importance of concentration of attacks through the synchrony of emergence on attack success has been demonstrated in a model analysis of local spatial spread of mountain pine beetle infestations (Logan et al. 1998). We assumed that the proportion of attacked trees has the same general relation to attack density and host resistance as the proportion of successful attacks within trees. The constants *b* and *X0* were determined by the following conditions: at attack density (A_i) = 100/m² and R_i = 0, $AS_i \cong 1$; A_i = 100 and R_i =1, $AS_i \cong 0.05$; A_i = 10 and R_i = 0, $AS_i \cong 1$; A_i = 10 and R_i = 1, $AS_i \cong 0$. In the model, R_i can also be specified by the user at the start of the simulation.

Beetle survival sub-models

The number of eggs laid per female (*E*) was modeled as a product of average egg gallery length per attack (G) and number of eggs laid per unit length of egg gallery (*Eu*) (equation 10).

$$E = a \times G \times Eu \tag{10}$$

Where a is a constant, *Eu* is determined from an array relating beetle size to egg production per unit egg gallery length based on McGhehey (1971). G was modeled in terms of female size (*Sf*) (width of the pronotum) relative to the average size which was assumed to be 2.1 mm (Safranyik and Jahren 1970; McGhehey 1971), attack density (*A*), and relative host resistance (*R*) (equation 11).

$$G = a\left[\frac{Sf}{2.1}\right] \times \left[(bA)^{-0.33}\right] \times [1 - f(R)] \tag{11}$$

Where *a* and *b* are constants and the other symbols are as defined earlier.

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Figure 3. Sub-model for average egg gallery length (G) for mountain pine beetle in lodgepole pine.
$G = 0.8338 \,[Sf\,/\,\text{Avg. width}]\,[1 - f(R)]\,A^{-0.33}$
$f(R) = M\,/\,(1 + \exp(-0.2667\,R^{0.5}))$

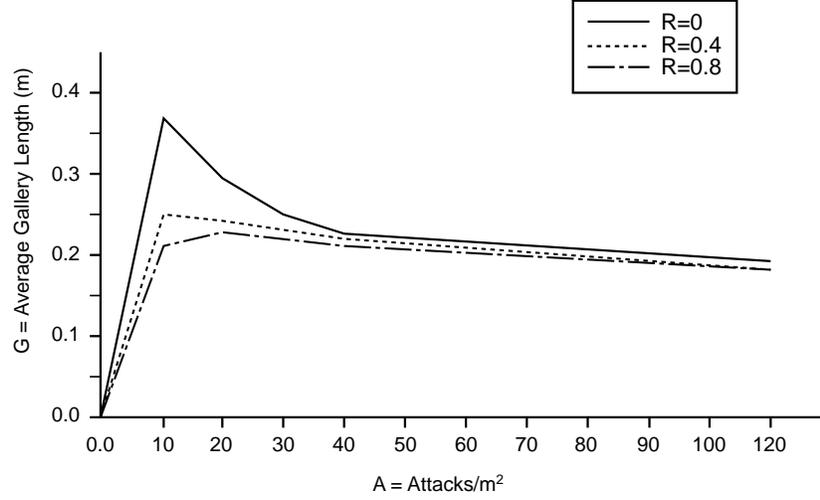$$M = \begin{cases} 0.9\,R^{0.5}\,; A < 10 \\ [0.9 - (A - 10)\,/\,A]\,R^{0.5}\,;\, 10 < A < 100 \\ (0\,;\,A > 100 \end{cases}$$

Sf = female adult head capsule width (mm); A = attacks / m^2
R = relative host resistance (range: 0 - 1); Avg. width = average head capsule width (2.1 mm)
G was solved for an Sf value of 2.0 mm

In turn, female size in equation 11 was modeled as a function of average daily temperature, DBH, and egg gallery length density (Gd) (equation 12).

$$Sf = \left[1 - a(\text{Avg. daily Temp.} - 15)\right] \times \left[b + cDBH - \left(e(Gd)^3\right)\right] \tag{12}$$

Here, a, b, c, and e are constants. The term inside the first set of square brackets represents a decrease in adult size with increasing temperature above 15 °C. The term inside the second set of square brackets was modeled after Amman and Pace (1976). Safranyik and Whitney (1985), and Amman and Cole (1983) found that mountain pine beetle larvae did not mature at temperatures lower than 15 °C. Average egg gallery length increases with female size and decreases with attack density and host resistance (equation 11 and Fig. 3).

Egg survival (Se) was modeled in terms of attack density, average daily temperature (Temp.), and relative host resistance (R) (eqn 13). The expression inside the first set of square brackets indicates that egg survival is a declining sigmoid function of attack density (modeled after Raffa and Berryman (1983)). This basic relationship is modified by two factors: temperature effects (f_1 (Temp.)) and relative host resistance, the first of which was obtained by interpolation from an array of survival values modified from Safranyik and Whitney (1985) and McGhehey (1971). Effects of natural enemies were not included, as this aspect of beetle biology is poorly understood. The constants a and b were determined by assuming that in logs (no host resistance) free from competition and under temperature conditions of 24-27 °C, average egg survival was 83% (McGhehey 1971) and at A= 100/m^2, Se = 0.53 (Cole et al. 1985). The function f_2 (A,R) was modeled as in Figure 4. This model was developed based on the conditions that at A =10 and R=0.5, f_2 (A,R) $\cong$ 0.5; A = 100 and R =0.5, f_2 (A,R) $\cong$ 1; A = 100 and R = 1, f_2 (A,R) $\cong$ 0.05.
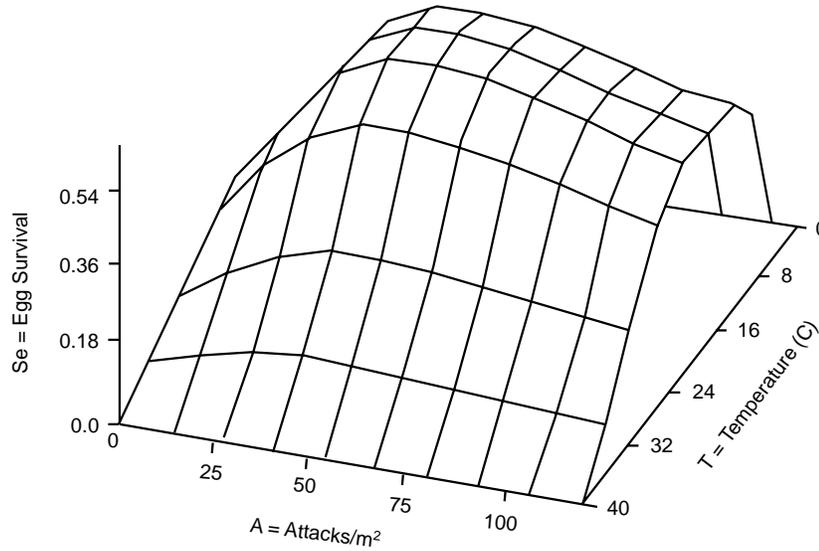
Figure 4. Sub-model for mountain pine beetle egg survival (*Se*).
$Se = 1.1857 \exp(-0.0045 / (A-1)) (f_2(A,R)) (f_1 (\text{Temp.}))$
$f_2(A,R) = 1 / (1 + \exp(-2.4 - 0.0672\, A + 12\, R^2))$
$f_1(\text{Temp.})$ = temperature effect obtained by interpolation from Safranyik and Whitney (1985).
R = relative host resistance (range: 0 - 1)
$f_2(A,R)$ was solved for $R = 0.5$.
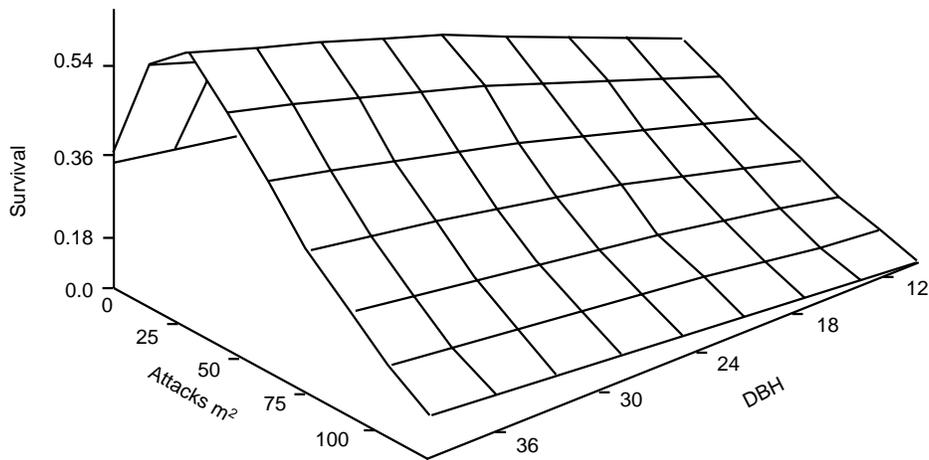
Figure 5. Larval survival as affected by attack density (*A*), relative host resistance (*R*), phloem thickness (PH) and tree age (A). Where DBH = diameter at 1.3 m (in inches), *PH* = phloem thickness at 1.3 m (in inches), ln = natural logarithm. The sub-model was solved for Age = 80 years, and *R*=0.5.

$\ln(PH) = -3.3843 + 0.6314 \times (\ln (\text{DBH})) - 0.0043 \times \text{Age}$ (Cole 1973).
$RPH = 0.1465 + 8.308 \times \exp(\ln(PH))$
$Sa = 0.7482 \times \exp(-0.004877A(1+R)^{0.5})$
$Sr = 1/(1+\exp(-12(0.2+0.0056A - R^2)))$
$\text{Survival} = [Sa \times Sr \times RPH]$

$$S_e = a\left[\exp\left(-b(\text{Avg. Attack Density} - 1)\right)\right] \times \left[f_1(\text{Temp.})\right] \times \left[f_2(A, R)\right] \qquad (13)$$

Where a and b are constants. The egg survival sub-model, at relative host resistance held constant, is shown in Figure 4.

Larval survival (S_l) was modeled similarly to egg survival, but includes the effects of phloem thickness (f_1 (PHt)), phloem drying (f_2 (PHd)), competition among larvae, expressed as a function of average attack density and relative host resistance ($f_3(A,R)$), and natural enemies (f_4 (Mn)) (equation 14). The model is multiplicative: specific effects on overall survival are represented by the various sub-models.

To set values for the constants in the sub-model describing the effects of attack density (equation 14) we assumed that in the absence of resistance, enemies and competition, average larval survival at optimum temperature was 65% (Safranyik and Whitney 1985). With R = 0.5 average survival was 44% and under average conditions survival was 39% (Cole et al. 1985).

Phloem thickness was modeled as a function of DBH and age (Cole 1973), and its relative effect on larval survival was modeled from data shown in Amman (1969, Table 1). The phloem is the principal source of food for the larvae. Phloem thickness was used as an indicator of the relative amount of food per unit bark area.

Phloem drying is considered an important factor in larval mortality (Amman and Cole 1983). Bark moisture in an infested tree is directly related to DBH (Amman 1977). Bark drying was therefore assumed to be a linear function of tree diameter, and its relative effect on larval survival was modeled as a parabolic function of DBH such that survival is zero for trees with a DBH 6 cm or less, and increases with larger DBH. In addition to DBH, temperature was assumed to have an important effect on larval survival, indirectly through phloem drying. The effect of temperature was modeled by expressing the deviation of heat accumulation from its norm as a proportion of the norm. These proportions were grouped into 20% classes, and assigned an "effect index" for each class. The index values ranged from 1.0 for heat accumulation in the coolest years to 0.35 in the warmest year.

Mortality from insect enemies and disease are user-defined inputs to the model which default to the assumed average values for these variables (Amman and Cole 1983). The survival from the effects of natural enemies was modeled simply as: (1- mortality from natural enemies). Larval survival as a function of attack density, relative host resistance and phloem thickness (expressed in terms of DBH and age) is shown in Fig. 5.

$$S_l = \left[f_1\right](A, R) \times \left[f_2(PHt)\right] \times \left[f_3(PHd)\right] \times \left[f_4(\text{Temp.})\right] \times \left[f_5(Mn)\right] \qquad (14)$$

Survival of pupae and adults was modeled as a constant proportion of the survival of the preceding stage (80% and 90%, respectively) which approximated average natural within-stage survival rates.

Winter survival (Sw) of the various brood stages was modeled in terms of (i) cold temperature effects on short exposure (Wt), based on Safranyik et al. (1974, Fig. 25), (ii) duration of lethal low temperatures (Dt) in days, (iii) tree diameter (DBH), (iv) a larval stage susceptibility function (Rs), based on Amman and Cole (1983, Fig. 34) and (v) mortality from woodpeckers (Kw) (equation 15). The DBH effect was expressed relative to a DBH of 30 cm, and the power b (=1/4) in equation 15 was estimated so that the relationship between relative effect and DBH would be similar to that of Amman and Cole (1983, Fig. 31).

The rate of cooling of a tree is inversely related to both its moisture content and diameter. Wt was expressed as [1-$((ta\text{-}tm)/ta)^{0.23}$] where tm is the weekly minimum temperature and ta is the absolute lethal temperature. A different ta is specified for each of the stages; egg, larva, pupa and adult. The power, 0.23, was set so that at 5% deviation of

tm from *ta*, *Wt* would be about 0.5. This is a relatively moderate mortality but we felt that, because underbark temperature follows ambient temperature with a time lag, short exposure of the cold-hardened larvae (the common over-wintering stage) to ambient temperatures even near *ta*, would cause only moderate mortality. Because duration of exposure to a particular temperature affects cumulative mortality, and much of the mortality tends to occur within the first day of exposure, relative mortality from this source was modeled as a logarithmic function with a slope (a= 0.315) equal to the rate of mortality at -32 °C in a laboratory experiment conducted on infested bolts containing mountain pine beetle larvae (L. Safranyik, unpublished). *Wt* and *Dt* are assessed weekly and applied to the survivors of each life stage present.

$$Sw = \left\{ \left[1 - (Wt) \right] \left[Dt^a \right] \left[Rs \right] \right\} \times \left[(DBH \div 30)^b \right] \times \left[1 - Kw \right] \tag{15}$$

Where *Rs* is 1 for all stages but the larvae. Because larval survival was modeled using a common ta for all instars, relative susceptibility of larvae to low temperature was determined based on Amman and Cole (1983; Fig. 34) (equation 16).

$$Rs = 1 - 0.125(5 - \text{Stage}); \text{ stage } = 2\text{-}5 \text{ for instars 1-4, respectively} \tag{16}$$

Mortality from woodpecker predation (*Kw*) is a user defined variable. *Kw* is an index with a range from 0 to 1.

Beetle development sub-models

Beetle development period is determined stage by stage from temperature-based studies by Safranyik and Whitney (1985). The per day portion of the total development period for a specific stage at a given temperature is determined through interpolation between data points. The per day portions are summed until the total is equal to one. The corresponding number of days is the development period. The standard deviation is based on the sum of the variances corresponding to the development rates.

Following the first generation, the mid-point of the attack period was defined as the date by which 50% of the adults had emerged. The length of the attack period was therefore dependent on the temporal distribution of adult maturation. The mid-point of the egg laying period occurred when 50% of the eggs had been laid, and the limits were defined by the temporal distribution of attack and egg gallery establishment. The midpoints of the development stages were defined as the dates by which 50% of the brood had developed to the respective stages. The beginning and end of the dormant period (called the winter period in the model) were defined as the dates corresponding to no development for six consecutive days and development for 15 consecutive days, respectively.

Temperature data used in the model are of two types: synthetic data, and weather records. Both types of data consist of minimum and maximum daily temperatures. The synthetic data are generated by sine functions with amplitudes corresponding to specified maxima and minima in periods equal to a calendar year. There are four synthetic temperature regimes covering a range from very hot to cool climates, which correspond to daily average temperature maxima of 27 and 22 °C, respectively. These regimes were generated to explore the effects of temperature on insect dynamics. The weather records are maximum and minimum daily temperatures for a 30-year period from Kamloops, B.C. During simulation, the first year is picked at random from this record and progresses through consecutive years. If the simulation runs past the last year of the data file, it loops back to the first year. Similar data from other locations could be substituted.

Management sub-models

User-defined mortality events are used to explore the effects of introducing a level of mortality at specified stages of development (theoretical control) and implementing bark beetle management which consists of six control methods (operational control). Three control methods involve large-scale tree removal: spacing, harvesting infested trees, and harvesting uninfested trees. The other control methods are single tree treatments – pesticides (such as MSMA), fell-and-burn, or single tree removal, baiting with attractive pheromone, and baiting with repellent pheromone. The pheromone treatments are not considered control methods on their own. However, using them in the model without any control treatment enables us to simulate the possible effects of baiting stands. Any combination of these control measures can be used, but spacing or harvesting of the uninfested trees can only be implemented once at the start of the simulation.

The theoretical control option is implemented by specifying the desired level of beetle mortality at any stage of development. This mortality is implemented in the sub-model for the survival of that stage.

Spacing reduces stand density but will not alter the DBH frequency distribution or the relative probabilities of attack for the various DBH classes in the first year of the simulation. The main effect of spacing is to reduce the success of host finding and colonization because of the increased average distance among live trees. In this option, regular spacing (as opposed to thinning) is assumed even though in practice the same density, and mean inter-tree distance, could be achieved through both operations. Removal of some of the uninfested trees through thinning may change the pre-attack DBH distribution (and the resulting beetle productivity) and thus differs from the spacing treatment. If trees are removed in blocks, live tree density in the remaining stand is not affected. Removal of various proportions of live trees from a number of DBH classes can be specified.

The logging of infested trees can be mimicked by taking the same or different proportions of trees from affected DBH classes. It is assumed that all of the beetles are removed with each cut tree. For the single tree treatments (MSMA and fell-and-burn), the efficacy of treatment, in addition to the proportion of trees treated, must also be specified.

The effects of attractive and repellent baits on the concentration of attacks, in terms of attack density and the number of attacked trees, were simulated based in part on the results of baiting trials published by Amman et al. (1989), Borden et al. (1983a, b), Gibson et al. (1991), Gray and Borden (1989), and Lindgren et al. (1989).

For the attractive bait sub-model, we assumed that a maximum of 25 baits per hectare could be used and the baits are attached singly to large, evenly spaced trees. Average maximum attack density is $110/m^2$. At all lower average attack densities in any given DBH class that would occur without baiting (A_i), baiting can induce more attacks. The rate of increase in attack density due to baiting is reduced with increased bait density (B) and attack density (equation 17). The bait treatment will reduce the number of beetles dispersing out of the area, and may thus result in an increase in the number of successfully attacked trees.

$$A_a = A_i \left\{ 1 + \left[1 - \left(A_i \div 110 \right) \right] 0.2 B^{0.5} \right\} \tag{17}$$

Where A_a = attacks/m^2 resulting from attractive baiting, and the other symbols are as given earlier.

Repellent baits are assumed to be distributed evenly over the 1-ha area, in the same manner as attractive baits, with a maximum of 100 baits allowed. We assume that the baiting will reduce attack density. As above, the relative effectiveness of increased baiting will decrease as bait density (C) increases, and that a maximum reduction of 30% in average attack density will occur at 100 baits per hectare (equation 18).

$$Ar = A_i \left[1 - 0.03 C^{0.5} \right] \tag{18}$$

Where Ar = attacks/m^2 due to repellent baiting and the other symbols are as defined earlier.

The simulation

In the following simulations we explored the effects of various site and stand factors, and methods of beetle management on the course of an infestation in terms of the cumulative number of trees killed and the cumulative number of adults produced during the infestation (Table 2). In addition, we have simulated the DBH distribution of the residual stand at the beginning and end of the infestation as a function of site quality. In all simulations, mortality from insect natural enemies, woodpeckers, and disease were held constant at their default values of 0.05, 0.04, and 0.01, respectively. The main results from these simulations are summarized below.

- For an initial stand density of 950 trees per hectare at all three sites, site quality in a mature stand affected both the duration and the intensity of the infestation, in terms of the average number of trees killed per generation (Fig. 6). The infestation continued for 11 years and 15 beetle generations on the best site (site 1) and 5 years and six beetle generations on the poor site (site 3); the duration of the infestation on the medium site was 10 years and 13 beetle generations. Total tree mortality was similar on the medium and good sites but considerably higher than on the poor site. The average rate of tree mortality per beetle generation, however, was highest for the poor site, lowest for the good site and intermediate for the medium site. This trend in total numbers of trees killed was generally reflected by beetle production (Fig. 7), as the total numbers of emerged beetles during the infestation increased with site quality. Peak tree mortality, however, was not consistently associated with peak brood production (Fig. 6 vs. Fig. 7).

- Stand age affected both the duration and intensity of the infestation on a medium quality site (Fig. 8). Although the average and peak mortality rates were directly related to age, duration of the infestation and total mortality were lowest and highest in the 50-year-old stand and 75-year-old stand, respectively. Total mortality for the two oldest stands was nearly identical.

- The infestation peaked at a higher level, and collapsed sooner, in the stand with the hot climate in comparison with stands with cool and moderate climate (Fig. 9). Total mortality, however, was similar for all three climate regimes. Beetles in the stand with the moderate climate produced one generation each year; in the stand with hot climate two generations were produced in three different years and one generation was produced in the other years; in the stand with cool climate one generation (the sixth) had a two-year cycle and the balance had one-

Table 2. Site and stand factors, direct control methods, and initial beetle population sizes used in simulation runs to illustrate relative effects on numbers of killed trees and beetle population size per generation. When a variable was being tested, all values in the table were used. All other variables were assigned the values in bold.

Variable	Attributes/Values
Site Quality	Good, **Medium**, Poor
Age (years)	50, 75, **100**
Stand climate	Cool, Warm, **Hot**
MSMA treatment (%)	**0%**, 40%, 80% mortality per year
Tree spacing (done at start of simulation)	**Not spaced**, 4m, 5m.
Removal of infested trees (%)	**0%**, 40%, 80%
Remove uninfested trees (%)	**0%**, 40%, 80%
Apply repellent baits (no./ha)	**0**, 4, 16, 25
Apply attractive baits (no./ha)	**0**, 4, 16, 25
Initial female adult density (in one ha)	2000, **10 000**
Relative host resistance	0.5 (default), or **resistance function applied**
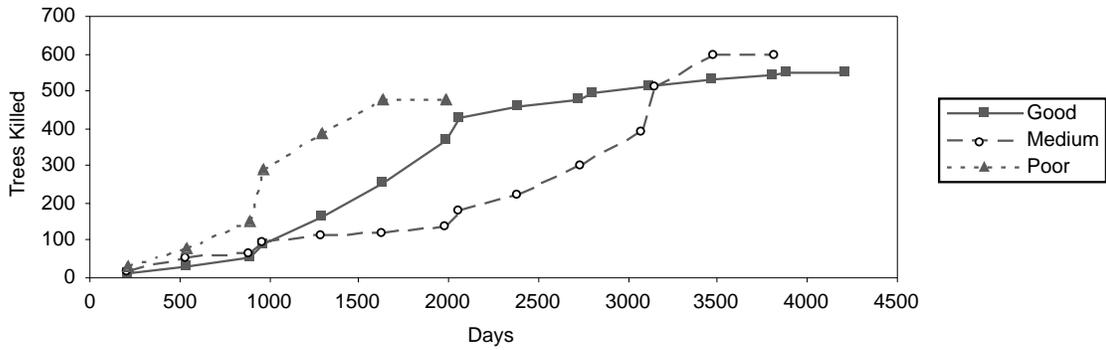
Figure 6. Effect of site quality on cumulative number of trees killed by mountain pine beetle during an infestation. Initial stand density was 950 trees per hectare and initial stand age was 100 years. The simulations used the synthetic hot temperature data. Mountain pine beetle infestations were simulated for one hectare of pure lodgepole pine. The infestation was assumed to have collapsed when less then 200 adult beetles were produced in a generation or no trees were successfully attacked. Tree mortality and adult populations occurred in the model at discrete time intervals corresponding to beetle generations. Data for consecutive generations were connected by lines to better highlight trends.
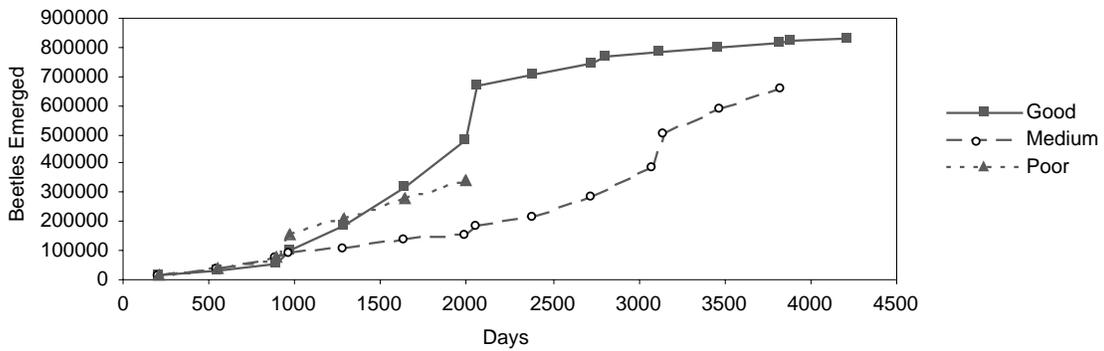
Figure 7. Effect of site quality on cumulative number of adult mountain pine beetles produced during the infestation. The same conditions were used as in Figure 6.
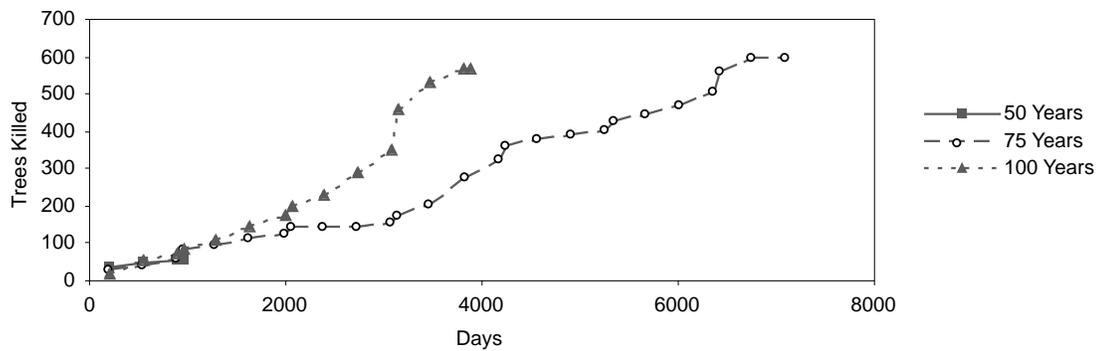
Figure 8. Effect of initial stand age on the cumulative number of trees killed by mountain pine beetle during an infestation. Site quality was medium, and the synthetic hot temperature data were used.
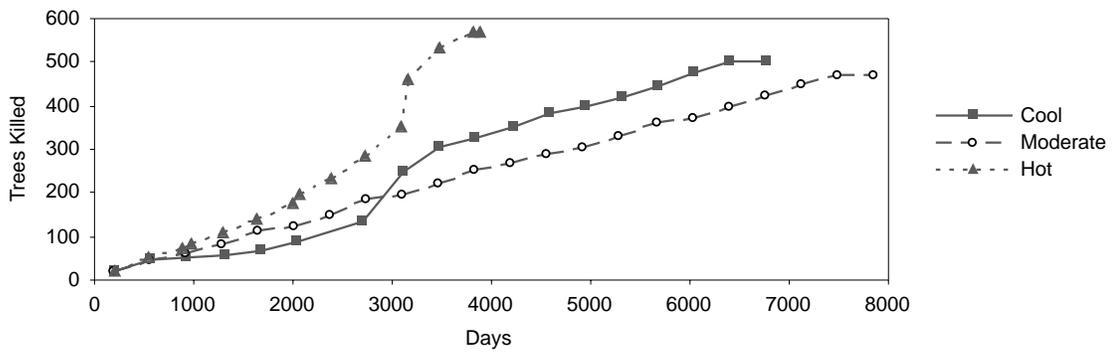
Figure 9. Effect of stand temperature on the cumulative number of trees killed. Site quality was medium and initial stand age was 100 years.
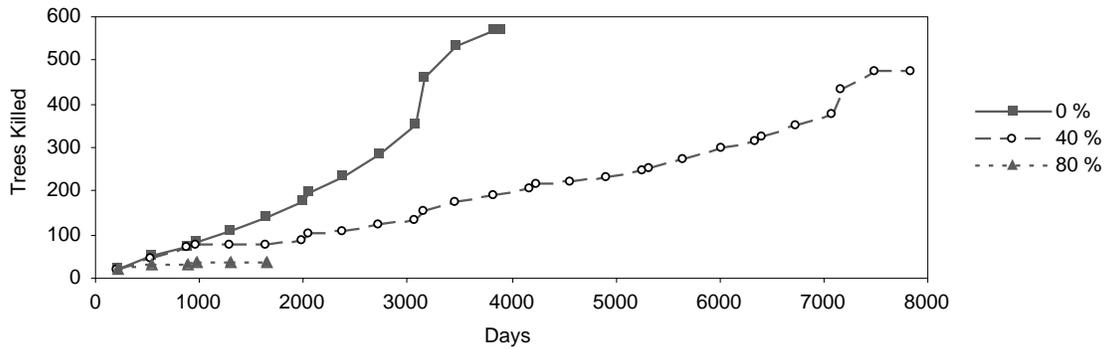
Figure 10. Effect of single tree treatments of 40% and 80% efficacy and no control each beetle generation on cumulative number of trees killed. Site quality was medium, initial stand age was 100 years and the synthetic hot temperature data were used.
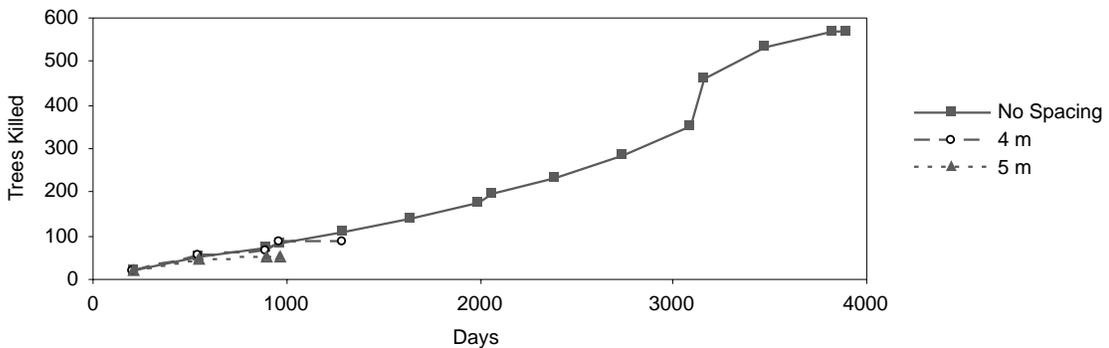
Figure 11. Effect of no spacing and two spacing regimes on the cumulative number of trees killed. Stands were spaced once at the beginning of the simulation. Site quality was medium, initial stand age was 100 years and the synthetic hot temperature data were used.

year cycles (Fig. 9). Initially, the rate of tree mortality was lower in the stand with the cold climate compared with the stand with the moderate climate but the mortality rates became approximately equal two years or so following the time when beetle broods in the cool climate stand developed on a two-year cycle. These results correspond with field observations. At colder sites, such as at high elevations or near the northern parts of the beetle's range, in some years completion of the life cycle may take longer than one year. Conversely, in areas with hot climate or during unusually hot years in areas with moderate climate more than one generation of beetles can be produced per year. In the southern parts of the beetle's range, outbreaks tend to be more intense and of shorter duration than those near the northern edge of the range. There is, however, no major difference in the final amount of stand depletion between these regions.

• Individual tree treatments that destroyed only a moderate proportion of the brood (40%) each beetle generation prolonged the infestation to beyond the no-control alternative (Fig. 10), although somewhat fewer trees were killed over the duration of the infestation. Reductions in attack density and consequent mortality from crowding are the main reasons for such an outcome. This treatment is called MSMA in the simulation model, but the same procedure is used to simulate the effects of any single tree treatment such as fall-and-burn or bark peeling.

• Spacing living trees at the beginning of the simulation resulted in reduced peak and total mortality and reduced infestation duration as distance among residual trees increased (Fig. 11). There is experimental evidence to indicate that greater distances between neighbouring trees reduces "switching" of attacks, hence affecting attack success (Geiszler et al. 1980). Bentz et al. (1996) found that the largest distance between consecutively attacked trees was 3.2 m. Raffa and Berryman (1983) stated that no trees greater than 6 m apart were attacked. Geiszler et al. (1980) suggested that no switching of attacks occurred at distances greater than 7.3 m between adjacent trees. Preisler and Mitchell (1993) on the other hand, working in thinned stands, found that tree spacing between 4.3 m and 6.9 m appeared to have had no effect on the switching of attacks to neighbouring trees. However, switching is also affected by tree size, vigour, and some other factors.

• Harvesting the same percentage of infested trees following each attack during an infestation (Fig. 12) as the percent beetle mortality used in simulations of MSMA treatment effects (Fig. 10) resulted in the same pattern and total mortality from mountain pine beetle. This is mainly because in the simulation of the harvesting operation the distribution of the DBH classes for the infested trees and harvested trees were identical. Also, the sub-model for harvesting infested trees assumes that all of the beetles contained in the cut trees are removed during the harvesting operation.

• The harvesting of uninfested trees assumes that they are removed in one or more blocks. The density of the residual trees therefore remains unchanged, but the size of the stand is reduced. If tree removal through thinning is assumed, the course of the infestation will be the same as for spacing (Fig.11) because, not being spatially explicit, the simulation uses the mean distance among residual trees.

• The use of attractive baiting for each beetle generation during the infestation tends to reduce the peak intensity of the infestation and total tree mortality but, depending on baiting intensity, may increase the duration of the infestation (Fig. 13). In some years, however, tree mortality may be greater in baited stands than in unbaited stands. This happens mainly because attractive baiting tends to increase attack density and reduce brood survival and dispersal. Hence, depending on the changes in the values of these factors relative to those in the unbaited stand, beetle populations in attractively baited stands may build up faster and persist longer but cause less tree mortality.

• In general, repellent baiting produced effects similar to attractive baiting (Fig. 14). except that total mortality was reduced and the duration of the infestation increased for a given density of baits. These results are likely to be caused by the reduced attack density on individual trees which may decrease attack success and brood survival on successfully attacked trees.
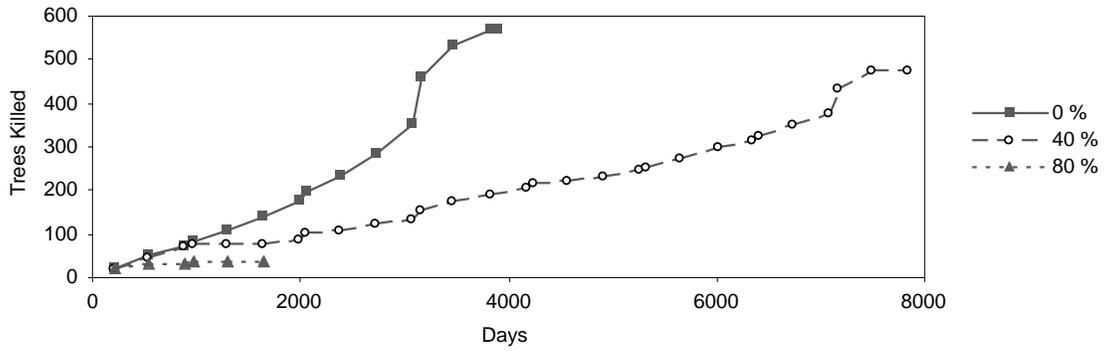
Figure 12. Effect of harvesting infested trees each year during the infestation on cumulative number of trees killed. Site quality was medium, initial stand age was 100 years and the synthetic hot temperature data were used.
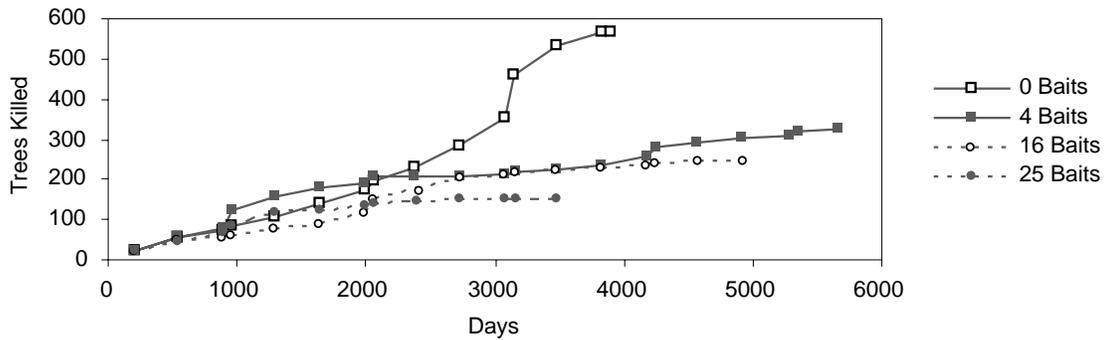

Figure 13. Effect of applying 0-25 attractive baits per hectare each year during the infestation on cumulative number of trees killed. Site quality was medium, initial stand age was 100 years, and the synthetic hot temperature data were used.
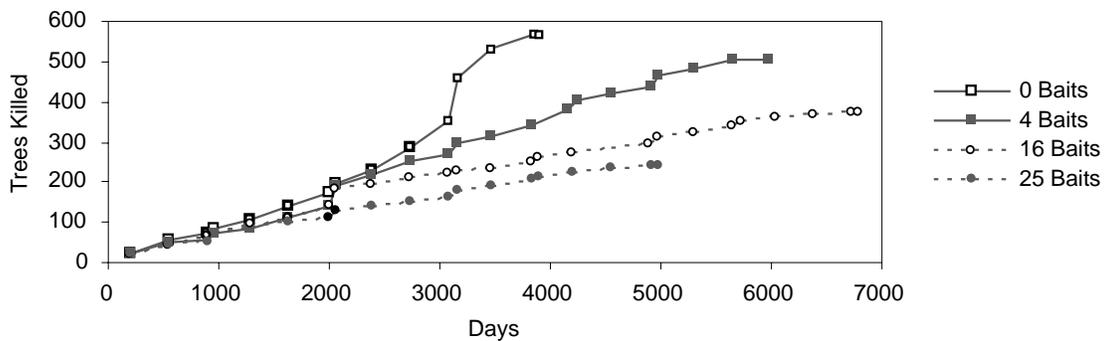
Figure 14. Effect of applying 0-25 repellent baits per hectare each year during the infestation on cumulative number of trees killed. Site quality was medium, initial stand age was 100 years, and the synthetic hot temperature data were used.
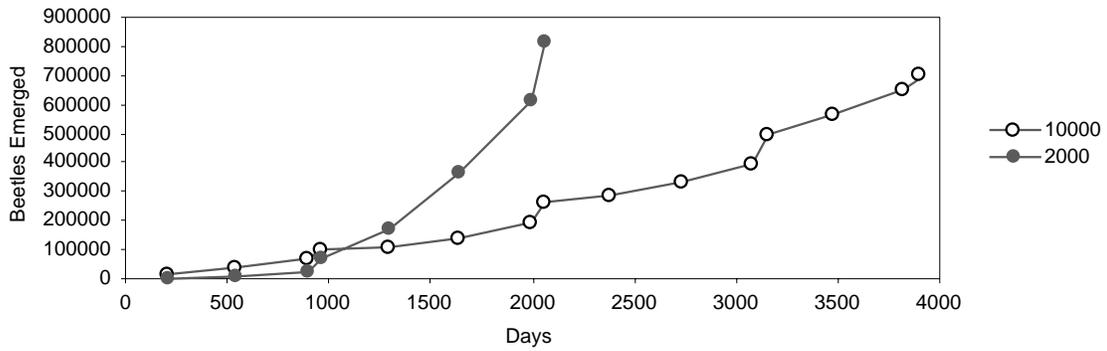
Figure 15. Effect of initial beetle population size of 2000 and 10 000 on cumulative numbers of adult mountain pine beetles. Site quality was medium, initial stand age was 100 years, and the synthetic hot temperature data were used.
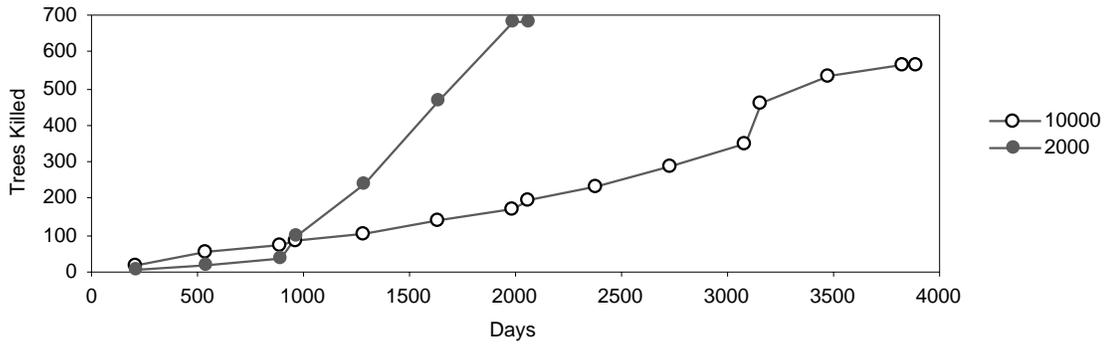
Figure 16. Effect of initial beetle population size of 2000 and 10 000 on cumulative number of trees killed. Site quality was medium, initial stand age was 100 years, and the synthetic hot temperature data were used.
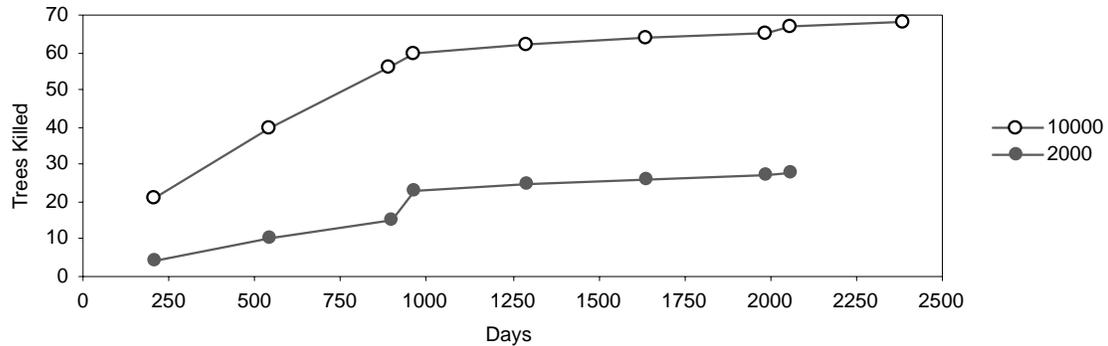
Figure 17. Effect of holding relative host resistance constant at 0.5 on cumulative number of trees killed by mountain pine beetle during the infestation. Site quality was medium, initial stand age was 100 years, and the synthetic hot temperature data were used. (Compare this with Figure 16, where each year relative host resistance was determined by the host resistance sub-model.)

• The size of the initial beetle population (Fig. 15 vs. Fig. 16) and host resistance (Fig. 15 vs. Fig. 17) can affect the duration, intensity and total tree mortality of an infestation. The size of the initial beetle population had the greatest impact on the duration of the infestation, whereas host resistance substantially affected all three factors.

Tree mortality by DBH class and total stand depletion are affected by site quality (Fig. 18 vs. Fig. 19). This effect is mainly due to the differences in the DBH distributions of trees in sites of different qualities, and DBH-related attack and beetle productivity.

Sensitivity analysis

A sensitivity analysis was performed on the effects of five control parameters: (i) spacing, (ii) cutting of uninfested trees, (iii) direct control of beetles by killing them , (iv) the use of attractive baits, and (v) the use of repellent baits. In each case the variable graphed was the total number of trees killed during the outbreak. The results are shown for three stand ages, three temperatures, three levels of site quality, and four values of the control variable (Appendix B, Figs. I-V). Spacing had a strong effect in stands initially of 75 and 100 years of age, but had less effect on stands of 50 years (Appendix B, Fig. I). Harvesting uninfested trees during an outbreak greatly reduced the number of trees killed and this effect was greater for 75 and 100 years and for poor and medium quality sites (Appendix B, Fig II). Direct control of beetles through individual tree treatments reduced the number of trees killed, but the effectiveness is much greater in poor and medium quality sites than in good quality sites; control has to be very high (80%) before this reduction is substantial (Appendix B, Fig. III). There was little effect of direct control in 50-year-old stands. Attractive baits resulted in modest reduction in the number of trees killed, and again mainly in low and medium sites (Appendix B, Fig. IV). The use of repellent baits is ineffective in good sites and most effective in older stands. Temperature had little effect on any of the control methods (Appendix B, Fig. V).

Discussion

Simulation outputs of the numbers of trees killed, beetles produced, and the duration of infestations (Figs. 6-19) generally corresponded to qualitative expectations, for the various site and stand factors and management options tried. This was true for simulations involving manipulation of site quality, age, stand climate, host resistance, individual tree treatments (MSMA), and the relationship between tree mortality and DBH.

The results of some simulations, however, were unexpected:

• The simulated rates of brood production (Fig. 15) and tree mortality (Fig. 16) during the infestation were much higher after the first three beetle generations when initial female adult population size was 2000 compared to an initial female adult population size of 10 000. Although total tree mortality and total adult beetle production for the infestation were comparable in both simulations, the infestation with an initial 2000 female adults had much shorter duration. The generally grater rates of dispersal out of the area combined with reduced brood survival owing to greater attack densities in simulations with an initial 10 000 female adults appear to be mainly responsible for these results. When brood production was reduced substantially owing to host resistance, the pattern of tree mortality relative to the size of the initial female beetle population conformed to expectation (Fig. 17).

• Simulations of attractive baiting effects also produced some unexpected results. Although, as expected, both average annual tree mortality and total tree mortality tended to decline with increased bait density (Fig. 14), tree mortality in some years was greater for the two lowest bait density treatments compared with mortality in the untreated stand. The two lowest bait density treatments also increased the duration of the infestation. These
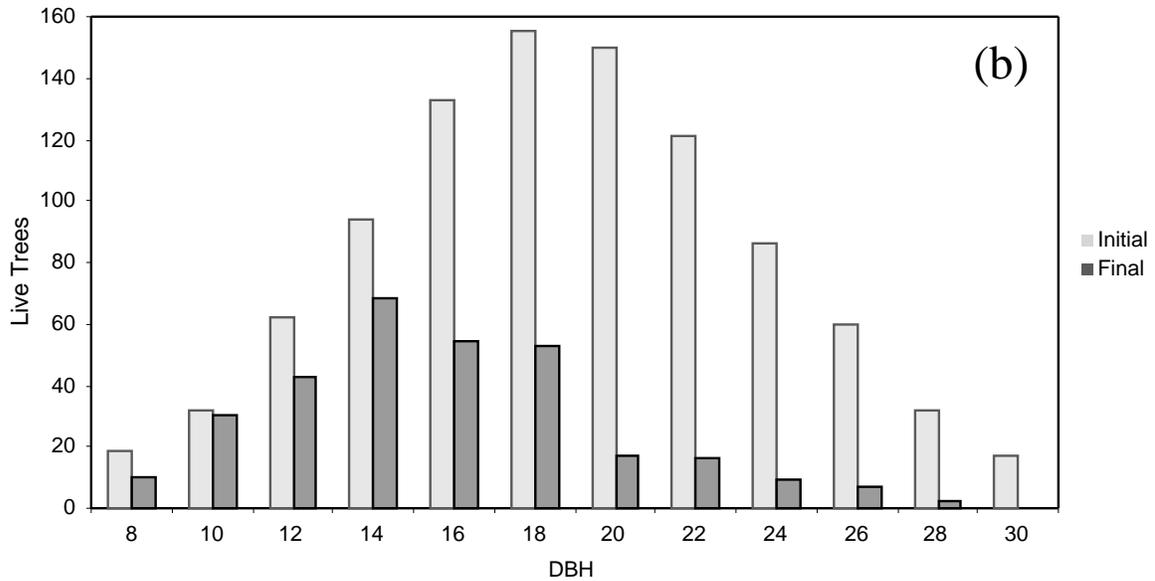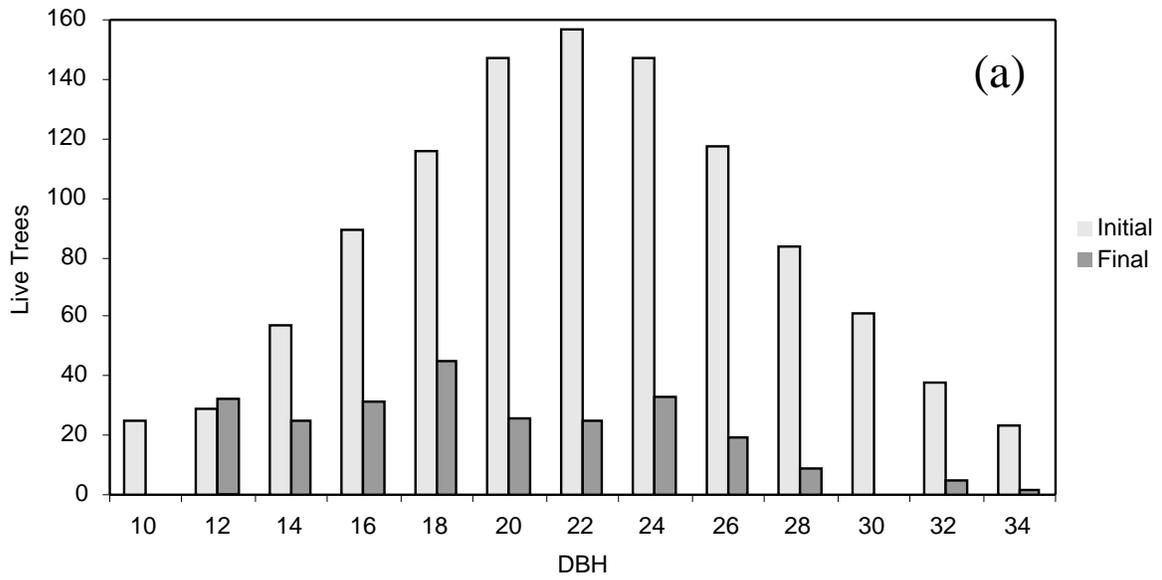
Figure 18. Effect of good (a) and medium (b) site quality on initial and final distribution of living lodgepole pine in different diameter classes at the end of an infestation by mountain pine beetle. Initial stand age was 100 years and the synthetic hot temperature data were used. Note that in (a) the number of living trees in the 12-cm-DBH class was greater at the end of the infestation than at the beginning. This is because few trees were killed in this DBH class and trees from the 10-cm-DBH class grew into it during the infestation period.

results suggest that, under some conditions at least, continuous baiting may result in increased tree mortality during some years and increased infestation duration but reduced total tree mortality.

• Repellent baiting had an effect similar to that of attractive baiting, except that for a given bait density there was less decline in total tree mortality and a more pronounced increase in the duration of the infestation compared to the untreated stand (Fig. 15). Hence, surprisingly, these simulations indicated that for the same bait densities continuous attractive baiting may result in reduced total tree mortality compared with continuous repellent baiting.

• Substantial reduction in both total tree mortality and the duration of the infestation resulted when trees were spaced to 3 m (1111.1 stems per ha). Experience indicates, however, that during actual outbreaks high tree mortality can occur at similar tree densities. Theoretical modeling of the attack process (Powell et al. 1998) suggested that thinning reduces attack success mainly through interference with chemical ecology due to changes in microclimate. Similar conclusions were reached based on field experiments (Amman et al. 1988).

All of these apparently anomalous simulation results could be tested by experiment.

In addition to the insect, tree, and stand variables currently output from the model, numerous other variables are available for output. A number of variables concerning beetle biology are useful for exploring various aspects of their population dynamics. Others are useful for investigating the consequences of various management practices in terms of tree mortality, which could include some theoretical methods such as the introduction of a mortality factor at a specific life stage.

A number of sub-models have not been validated experimentally because the available field data consist mainly of the number of infested or killed trees and, in some cases, densities of attacks and emerged adults per unit of bark area are included. While these are the important variables from the point of view of bark beetle management, additional data would be required on beetle survival and tree characteristics to properly test the model. Such data should include stage-specific survival, as well as tree and stand variables such as phloem thickness, tree density, DBH distribution and age. Nevertheless, comparisons of observed and predicted tree mortality during the course of an infestation could be made provided that initial beetle population size was known (or could be estimated), and yearly tree mortality and daily weather data (in terms of maximum and minimum temperatures) were available. However, a good fit to the available field data would not necessarily validate the model (likewise, a poor fit would not necessarily invalidate it) for reasons discussed above. Since the host tree sub-model is based on growth and yield functions, for the validation exercise the initial tree density and DBH distributions would need to be adjusted to correspond with observed values.

The current version of the model operates on a 1-ha area of pure lodgepole pine. Future development may involve expanding the host base to the stand level and allowing for mixed stands with the main objective of exploring the effect of beetle dispersal on outbreak dynamics.

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Appendix A

Flow diagram for the mountain pine beetle population dynamics model

```
┌──────────────┐
│  Initialize  │
│ Input/Output │
└──────────────┘
        │
        ▼
  ┌───────────┐                                    ┌──────────────┐
  │ Start main │◄──────────────────────────────────│  Increment   │
  │program loop:│◄──────────────────────────┐      │    output    │
  └───────────┘                             │      │  variables   │
        │                                   │      └──────────────┘
        ▼                                   │             │
┌──────────────┐                            │             ▼
│Initialize beetle│◄─────────────────────────┼──────┌──────────────┐
│ & tree variables│                          │      │    Beetle    │
└──────────────┘                            │      │   dynamics   │
        │                                   │      │  sub-models  │
        ▼                                   │      └──────────────┘
┌──────────────┐                            │             │
│ Allocate adult │                          │             ▼
│ beetles to trees│                         │      ┌──────────────┐
│  by dbh class  │                          │      │Lodegepole pine│
└──────────────┘                            │      │model: implement│
        │                                   │      │ growth & yield │
        ▼                                   │      └──────────────┘
┌──────────────┐                            │             │
│   Determine   │                           │             ▼
│attack dynamics│                           │      ┌──────────────┐
└──────────────┘                            │      │  Increment   │
   │      │      │                          │      │   day, year  │
   ▼      ▼      ▼                          │      └──────────────┘
┌────┐ ┌────┐ ┌────┐                        │             │
│No. │ │Attack│ │Volume│                    │             ▼
│trees│ │durations│ │killed│                │      ┌──────────────┐
│attacked│ │& density│ └────┘               └──────│   Output     │
└────┘ └────┘                                      │   results    │
          │                                        └──────────────┘
          ▼
┌──────────────┐
│   Determine   │
│oviposition rates│
│ & egg survival │
└──────────────┘
        │
        ▼
┌──────────────┐
│   Determine   │
│  median date  │
│  of egg hatch │
└──────────────┘
        │
        ▼
┌──────────────┐
│Determine median│
│duration of larval│
│  development  │
└──────────────┘
        │
        ▼
┌──────────────┐
│Determine larval│
│   survival    │
└──────────────┘
        │
        ▼
┌──────────────┐
│Determine median│
│duration of pupal│
│  development  │
└──────────────┘
        │
        ▼
┌──────────────┐
│Determine pupal│
│   survival    │
└──────────────┘
        │
        ▼
┌──────────────┐
│Determine median│
│duration of adult│
│  development  │
└──────────────┘
        │
        ▼
┌──────────────┐
│Determine adult│
│survival & rates│
│ of emergence  │
└──────────────┘
```

29

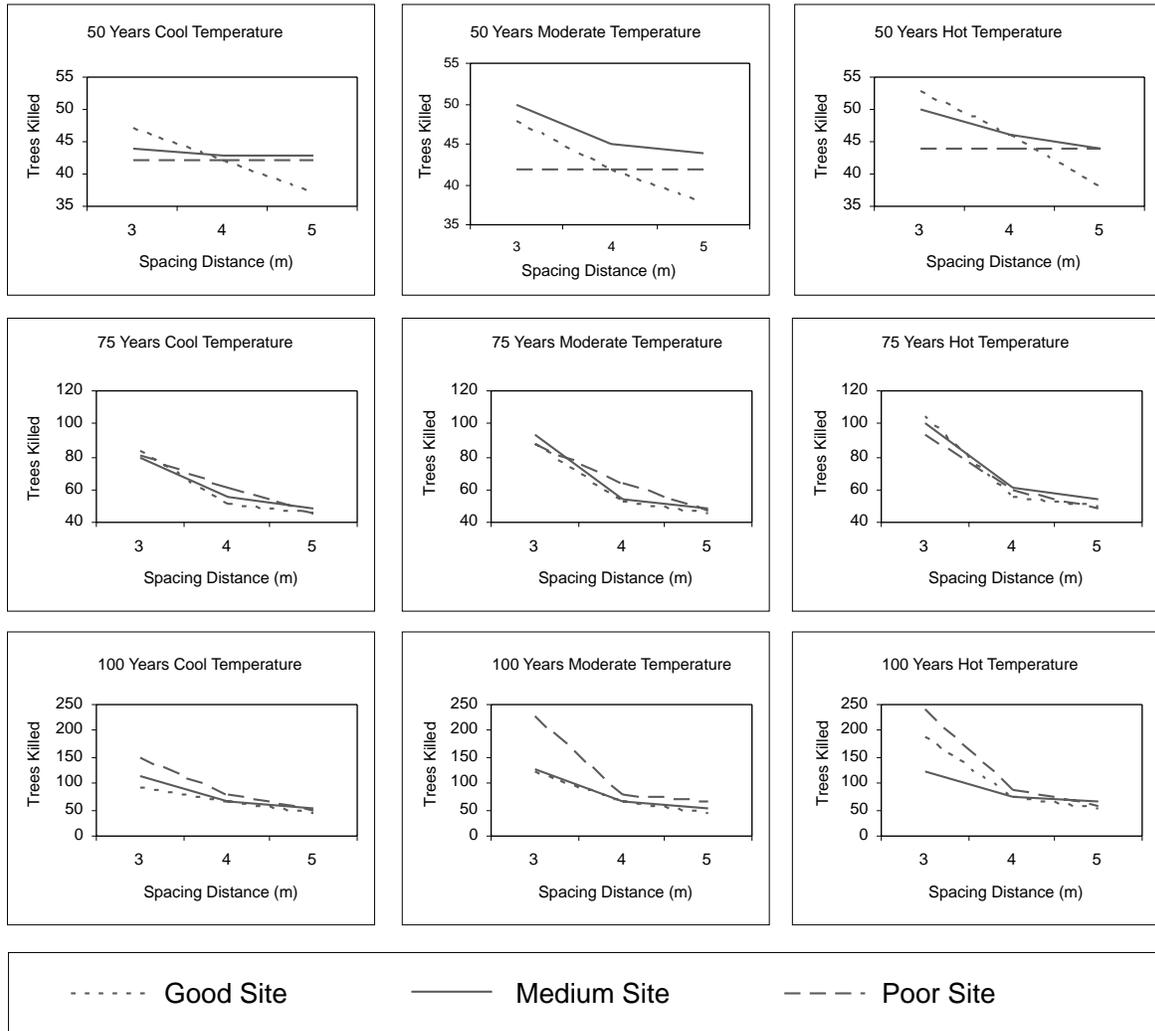# Appendix B

Sensitivity analysis diagrams

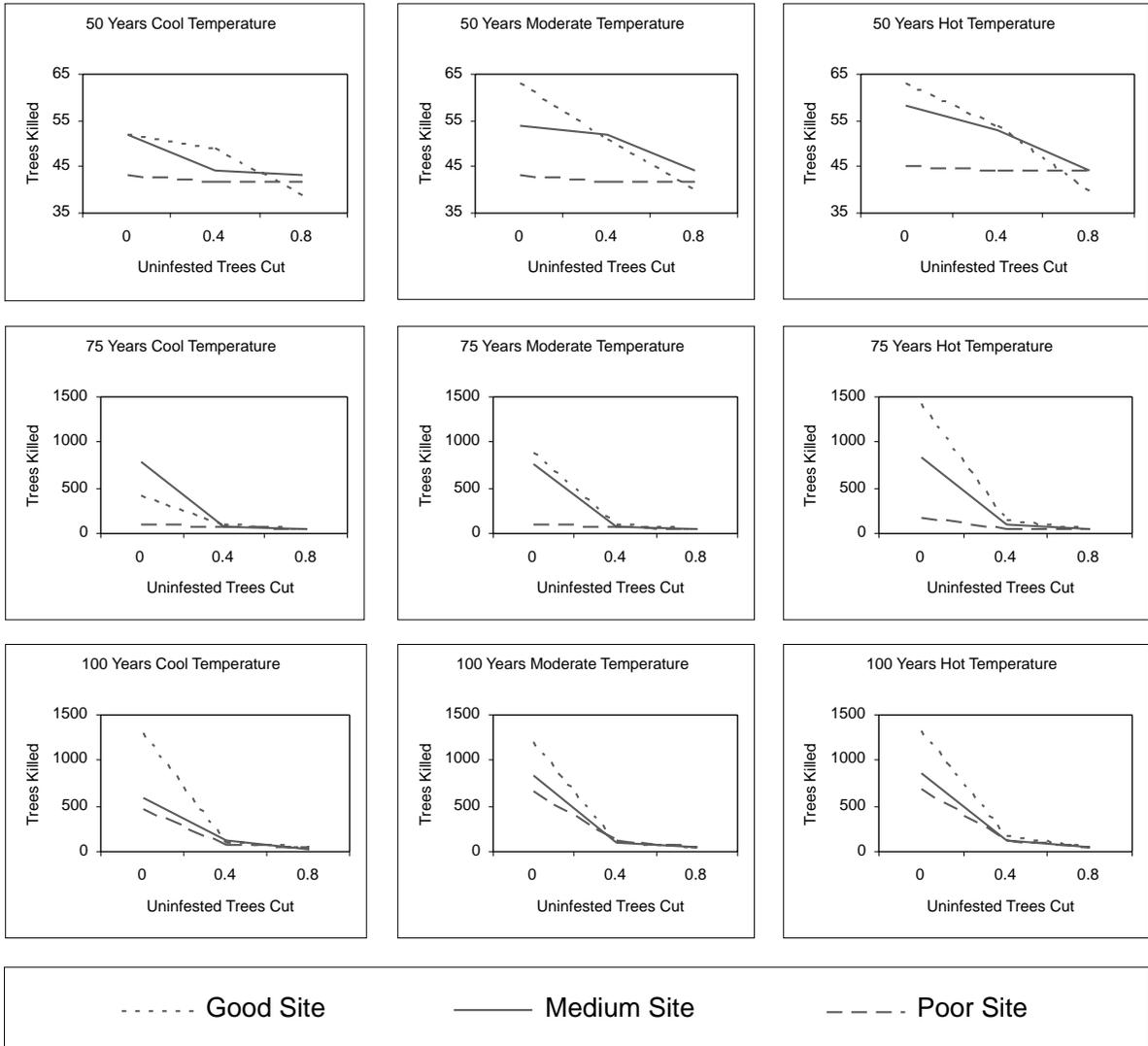**Fig. I**. Effects of tree spacing on the total number of trees killed.

Fig. II. Effects of the cutting 0, 40% and 80% of non-infested trees on the total number of trees killed.
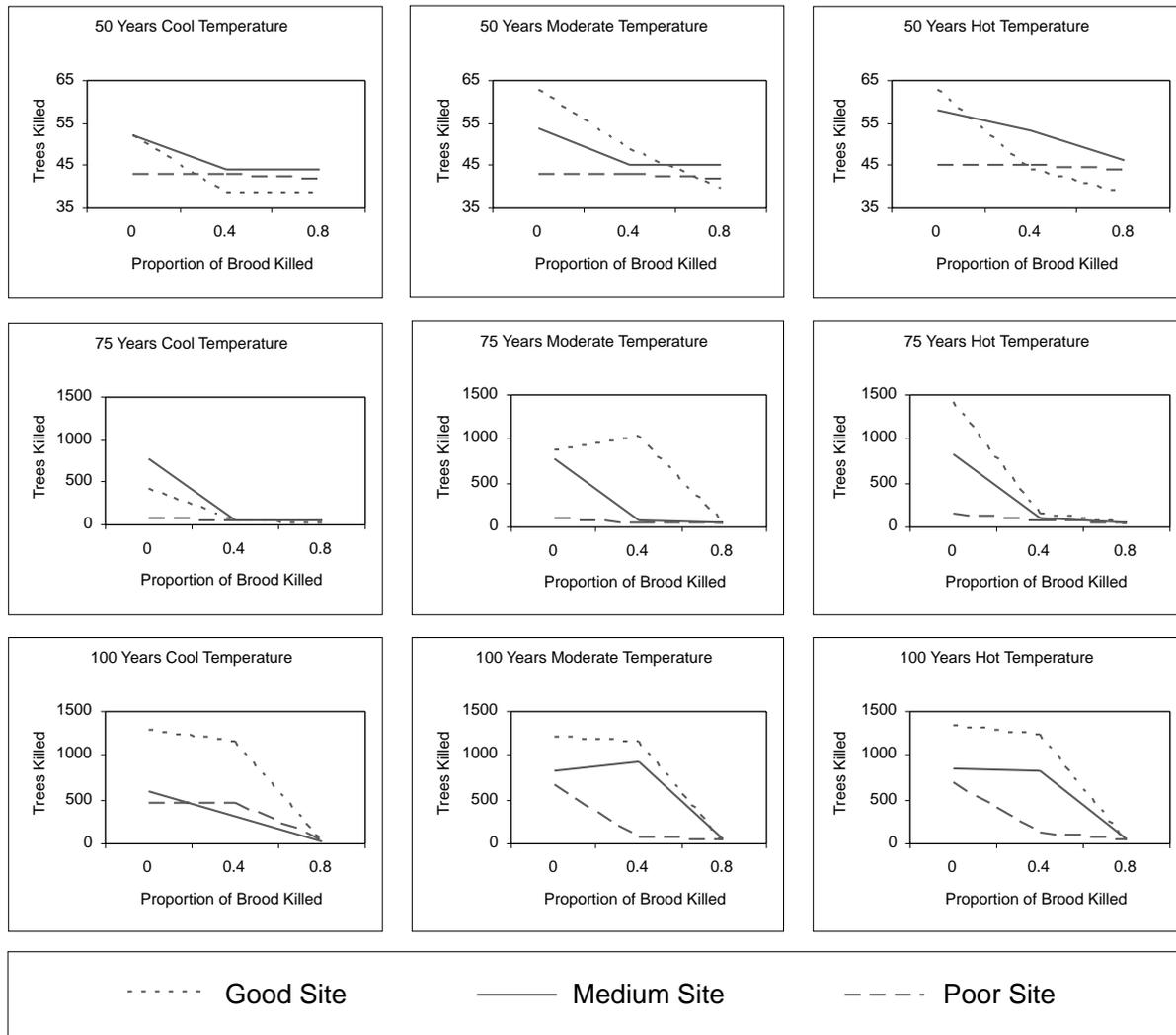
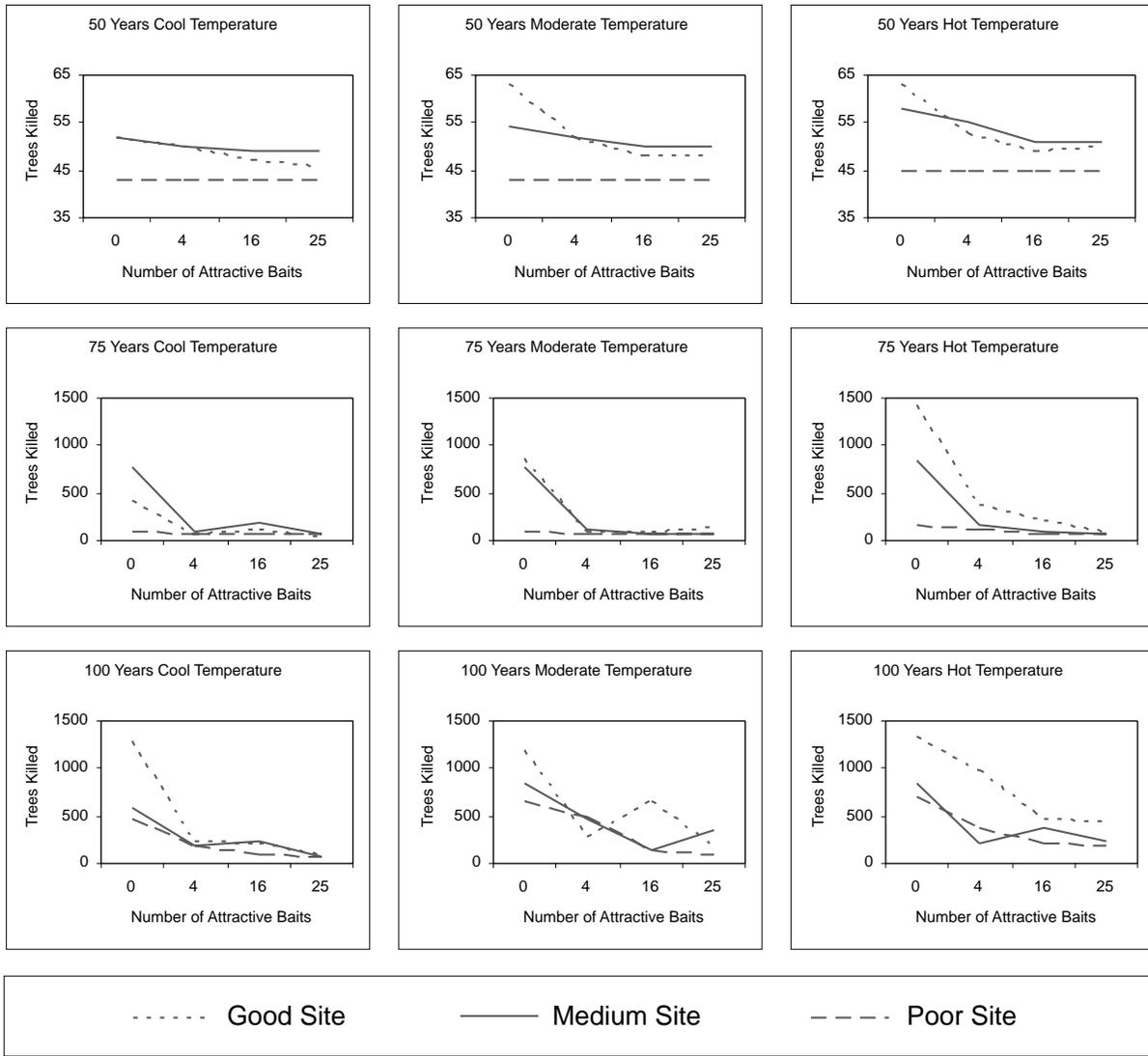**Fig. III**. Effects of killing 0, 40% and 80% of beetles by direct control on the total number of trees killed.

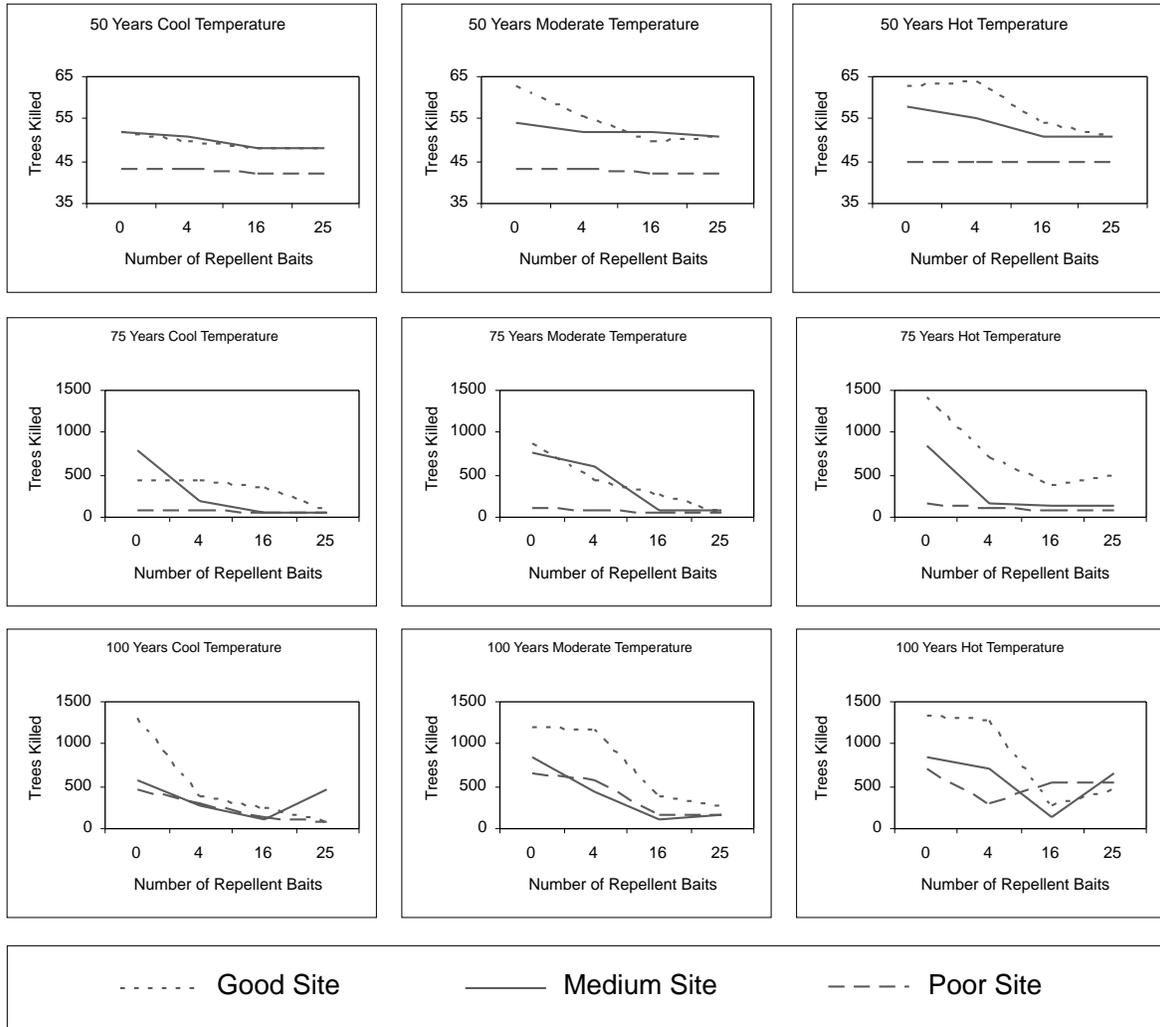**Fig. IV**. Effects of attractive baits on the total number of trees killed.

Fig. V. Effects of repellent baits on the total number of trees killed.