Effects of Climate Change on Range Expansion by the Mountain Pine Beetle in British Columbia

Allan L. Carroll, Steve W. Taylor, Jacques Régnière* and Les Safranyik

Canadian Forest Service, Pacific Forestry Centre, 506 W. Burnside Rd., Victoria, BC V8Z 1M5
*Canadian Forest Service, Laurentian Forestry Centre, PO Box 3800, Sainte Foy, QC G1V 4C7

Abstract

The current latitudinal and elevational range of mountain pine beetle is not limited by available hosts. Instead, its potential to expand north and east has been restricted by climatic conditions unfavorable for brood development. We combined a model of the impact of climatic conditions on the establishment and persistence of mountain pine beetle populations with a spatially explicit, climate-driven simulation tool. Historic weather records were used to produce maps of the distribution of past climatically suitable habitats for mountain pine beetles in British Columbia. Overlays of annual mountain pine beetle occurrence on these maps were used to determine if the beetle has expanded its range in recent years due to changing climate. An examination of the distribution of climatically suitable habitats in 10-year increments derived from climate normals (1921-1950 to 1971-2000) clearly shows an increase in the range of benign habitats. Furthermore, an increase (at an increasing rate) in the number of infestations since 1970 in formerly climatically unsuitable habitats indicates that mountain pine beetle populations have expanded into these new areas. Given the rapid colonization by mountain pine beetles of former climatically unsuitable areas during the last several decades, continued warming in western North America associated with climate change will allow the beetle to further expand its range northward, eastward and toward higher elevations.

Introduction

Every aspect of an insect's life cycle is dependent upon temperature because they are cold blooded. Therefore, these organisms should respond quickly to changing climate by shifting their geographical distribution and population behaviour to take advantage of new climatically benign environments. Rapid ecological and genetic adaptation by insects in response to global warming has already been documented in Europe (Thomas et al. 2001). However, for North America, despite the development of several models predicting climate change impacts (e.g., Logan and Powell 2001), there is little empirical evidence that global warming has affected insect populations.

In long-lived ecosystems such as forests, insects are often primary disturbance agents (e.g., Dale et al. 2001; Logan et al. 2003). The mountain pine beetle, *Dendroctonus ponderosae* (Hopkins), is one of the most

---

Mountain Pine Beetle Symposium: Challenges and Solutions. October 30-31, 2003, Kelowna, British Columbia. T.L. Shore, J.E. Brooks, and J.E. Stone (editors). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC. 298 p.

significant sources of mortality in mature pine forests in western North America (Safranyik et al. 1974). Mountain pine beetles will successfully attack most western pines, but lodgepole pine is its primary host throughout most of its range. Although it is widespread – occurring from northern Mexico, through 12 U.S. states and 3 Canadian provinces – mountain pine beetle outbreaks in Canada are mainly restricted to the southern half of British Columbia (BC) and the extreme south-western portion of Alberta (note: one outbreak has been recorded in the Cypress Hills at the southern junction of the Alberta – Saskatchewan border). Despite its significant distribution, the current latitudinal and elevational range of mountain pine beetle in western Canada is not restricted by the availability of suitable host trees. Indeed, lodgepole pine extends north into the Yukon and Northwest Territories, and east across much of Alberta. Instead, the potential for mountain pine beetles to expand north and east is currently limited by climate (e.g., Safranyik 1978). It is anticipated that under global warming, former climatically hostile environments will become climatically benign, allowing mountain pine beetle to significantly expand its range (Logan and Powell 2001).

Currently, mountain pine beetle populations are at epidemic levels in BC. Observations suggest that infestations may be occurring in areas previously considered climatically unfavorable (Safranyik et al. 1975). This study was initiated to determine if (i) there has been a shift in climatically benign habitats for mountain pine beetles during the recent past, and (ii) mountain pine beetle populations have expanded into these new habitats.

Methods

Climatic suitability for mountain pine beetle

To quantify the climatic suitability of habitats for mountain pine beetles, we adapted a model of the impact of climatic conditions on the establishment and persistence of mountain pine beetle populations originally developed by Safranyik et al. (1975). The model combines the effects of several critical aspects of climate on the beetle and its host trees (Table 1). It was developed from the analysis of climatic variables measured at 42 locations for the period 1950 to 1971 (Safranyik et al. 1975). The locations were chosen to represent the historic range of mountain pine beetle in BC.

An index of climatic suitability for mountain pine beetle (F) was derived as follows:

$$F = P_i \sqrt{X_1 \times X_2} \tag{1}$$

where P_i is the number of years with the joint occurrence of P_1 through P_4 in runs of ≥2 consecutive years divided by the total number of years (see Table 1). The values of F range from 0 to 1. Climatic suitability classes (CSCs; Table 2) were created by comparing index values with the frequency of mountain pine beetle infestations across its historic range (Powell 1966).

Table 1. Description of climatic variables utilized to construct a model of climatic suitability of habitats to mountain pine beetle populations (adapted from Safranyik et al. 1975).

Variable	Description	Rationale
P_1	> 305 degree-days above 5.5°C from Aug. 1 to end of growing season (Boughner 1964), *and* >833 degree-days from Aug. 1 to Jul. 31	A univoltine life cycle synchronized with critical seasonal events is essential for mountain pine beetle survival (Logan and Powell 2001). The minimum heat requirement is 305 degree-days from peak flight to 50% egg hatch, and 833 degree-days is the minimum required for a population to be univoltine (adapted from Reid 1962).
P_2	Minimum winter temperatures >-40°C	Under-bark temperatures at or below -40°C causes 100% mortality within a population (Safranyik and Linton 1998).
P_3	Average maximum Aug. temperatures ≥18.3°C	The lower threshold for mountain pine beetle flight is ≈18.3°C (McCambridge 1971). It is assumed that when the frequency of maximum daily temperatures ≥18.3°C is ≤5% during August, the peak of mountain pine beetle emergence and flight will be protracted and mass attack success reduced.
P_4	Total precipitation Apr. to Jun. < long-term average	Significant increases in mountain pine beetle populations have been correlated with periods of two or more consecutive years of below-average precipitation over large areas of western Canada (Thomson and Shrimpton 1984).
X_1	Variability of growing season precipitation	Since P_4 is defined in terms of a deviation from average, the coefficient of variation of precipitation was included. Its numerical values were converted to a relative scale from 0 to 1 (see Safranyik et al. 1975).
X_2	Index of aridity[1]	Water deficit affects the resistance of lodgepole pine to mountain pine beetle, as well as subsequent development and survival of larvae and associated blue stain fungi. An index of aridity (Ung et al. 2001) was used to approximate water deficit.

[1] The index of aridity replaces the water deficit approximation (National Atlas of Canada 1970) in the original model of Safranyik et al. (1975).

Table 2. Climatic suitability classes (CSCs) for mountain pine beetle derived from an index of climatic suitability (adapted from Safranyik et al. 1975).

Climatic suitability	Range of index (*F*)
Very low	0
Low	0.01 – 0.05
Moderate	0.06 – 0.15
High	0.16 – 0.35
Extreme	0.36+

Climate data

Historic daily weather data (1920 – 2000) for BC were obtained from Environment Canada, Meteorological Services (2002). The number of stations reporting data over the period ranged from 703 in 1920 to 2924 in 1990. To generate a stochastic series of daily values that minimize the effect of short-term weather anomalies and focus on longer-term climatic trends, we first converted the data to monthly normals (30-year means and extreme minima and maxima). We then produced stochastic daily values from the normals using a daily weather generator developed by Régnière and Bolstad (1994).

Landscape-level simulations

We constructed landscape-wide projections of climatically suitable habitats for mountain pine beetles, generated by the climatic suitability model, using BioSIM© software (Régnière et al. 1995; Régnière 1996). BioSIM requires two inputs; digital representations of the terrain and suitable weather data. We extracted a digital elevation model of BC from the US Geological Survey ≈1-km-resolution global coverage. Point sources of weather data (i.e., stations) are usually sparse relative to the spatial resolution required for mapping biological phenomena. Therefore, spatial interpolation methods must be used to obtain air temperature and precipitation information for unsampled points across a landscape from a limited source of geo-referenced weather stations. We used the 'gradient-plus-inverse distance squared' algorithm developed by Nalder and Wein (1998), an approach that combines multiple linear regression and distance-weighting.

We generated a series of maps depicting the distribution of CSCs for mountain pine beetle as a function of climate normals derived from the historic daily weather data in 10-year intervals from 1921-1950 to 1971-2000. Simulations were run for 500 randomly located points in BC. Universal kriging (e.g., Davis 1986) (with elevation as a drift variable) was used for interpolation between simulation points. The map outputs comprise grid coverage of CSC values for ≈1.2 million 64-ha cells.

Range expansion

From 1959 to 1996, the Canadian Forest Service, Forest Insect and Disease Survey (FIDS), in cooperation with the BC Ministry of Forests, conducted annual aerial assessments of forest insect and disease conditions in BC and the Yukon. During these surveys, boundaries of mountain pine beetle infestations were recorded on 1:250,000 NTS topographic maps (for details see Van Sickle et al. 2001). We digitized these maps (≈1000 in total) using ArcInfo® geographic information software (GIS), joined them into annual province-wide coverages (Albers projection, NAD87), and converted them to shape files.

To quantify whether range expansion by mountain pine beetles has occurred during the past 30 years, we chose the map of climatic suitability classes based on the 1941-1970 climate normals to represent the historic distribution of climatically suitable habitats for mountain pine beetles. The gridded map was reclassified to produce an Arc shape file. We overlayed annual mountain pine beetle (MPB) infestation maps using ArcInfo to create new MPB × CSC polygons. Because the climatic suitability grid cells generated by BioSIM are relatively small (64 ha), the intersection process divided many of the large mountain pine beetle infestation polygons into several MPB × CSC polygons. We summarized the number of infestations in each CSC class by year such that only one intersection per MPB × CSC class was counted per infestation polygon.

Range expansion was assessed by regressing the number of mountain pine beetle infestations *versus* year for each of the CSCs derived from the historic distribution of climatically suitable habitats (i.e., based on the 1941-1970 normals). We used polynomial regressions only when they explained significantly more of the variation in the data ($P<0.05$) than simple linear regressions. Since outbreak populations are often forced to briefly occupy sub-optimal habitats prior to their collapse due to the localized depletion of high-quality stands (e.g., Safranyik et al. 1999), data for the peak of the last (i.e., 1983 to 1985, inclusive) and current (i.e., 1997 to present) province-wide outbreaks were not included in the analysis.

Results and Discussion

During the latter half of the last century, there has been a substantial shift in climatically benign habitats for mountain pine beetle northward, and toward higher elevations. Areas most suitable for mountain pine beetles (i.e., high and extreme CSCs) have expanded dramatically in south-central and southeastern BC (Fig. 1).

Interestingly, based upon a comparison of the area affected by the present mountain pine beetle outbreak with the CSC coverage derived from the most recent weather data i.e., 1971-2000 (Fig. 2)], our maps delineate extremely well the areas currently experiencing epidemic populations.

Mountain pine beetle populations have followed the apparent shift in climatically suitable habitats during the past three decades. Prior to 1968, no infestations had ever been recorded in areas with very low and low CSCs (Safranyik et al. 1975). Since then, the increase (at an increasing rate) in the number of infestations over time in the historically very low and low CSCs (Fig. 3) indicates that there has been sufficient change in the climatic conditions in these habitats to have allowed the establishment and persistence of mountain pine beetle populations.

It is important to note that the increase in the occurrence of mountain pine beetles in these formerly climatically unsuitable areas can only be explained by changes in climate. Although temporal changes in the distribution of susceptible hosts (i.e., the amount of mature lodgepole pine) will affect the distribution of mountain pine beetle infestations, unless the climatic conditions outlined in our model are met within a mature pine stand, successful establishment of a beetle population is precluded (Safranyik et al. 1975; Safranyik 1978).

As expected, if climatic conditions have improved in historically unsuitable areas, then conditions should ameliorate, and the number of infestations increase, in the more suitable habitats. This was the case in the historically moderate and high CSCs (Fig. 3). However, by the mid-1980s the number of infestations in the habitats that were previously most suitable to mountain pine beetles (i.e., extreme CSC) declined dramatically (Fig. 3). There are two potential explanations for a decrease in the number of infestations in the formerly extreme CSC: it may be a consequence of

(i) a reduction in the amount of mature pine in these habitat types due to disturbance (i.e., harvesting, fire, past mountain pine beetle outbreaks), or
(ii) adverse effects of warmer temperatures due to climate change.

Taylor and Carroll (2004) have shown that the amount of mature lodgepole pine has increased dramatically in BC during the past century in all habitat types. Therefore, the decline in infestations is most likely due to the adverse effects of changing climate. Studies by Logan and Bentz (1999) and Logan and Powell (2001) have shown that if heat accumulation during summer is sufficiently high, mountain pine beetle populations may be forced into partial multi-voltinism (segments of the population having more than one generation per year) which will cause cold-susceptible stages (eggs, pupae, adults) to overwinter and thus interrupt flight synchrony and mass attack success in the following year.

Given the rapid colonization by mountain pine beetles of formerly climatically unsuitable areas during the past three decades, our results strongly suggest continued range expansion by the beetle with further global warming. At the same time, the apparent degradation of extreme CSCs due to partial multivoltinism because of excessive warming in recent years also suggests that southern and low-elevation regions may become less suitable for resident mountain pine beetle populations. Unfortunately, a recent study (Bentz et al. 2001) has found a genetically based latitudinal gradient in development rates for mountain pine beetles, suggesting that, in the longer term, southern mountain pine beetle populations that are better adapted to warm temperatures may move North.

In the past, large-scale mountain pine beetle outbreaks collapsed due to localized depletion of suitable host trees in combination with the adverse effects of climate (Safranyik 1978). The results of our investigation suggest that in the absence of an unusual weather event (i.e., an unseasonable cold period or

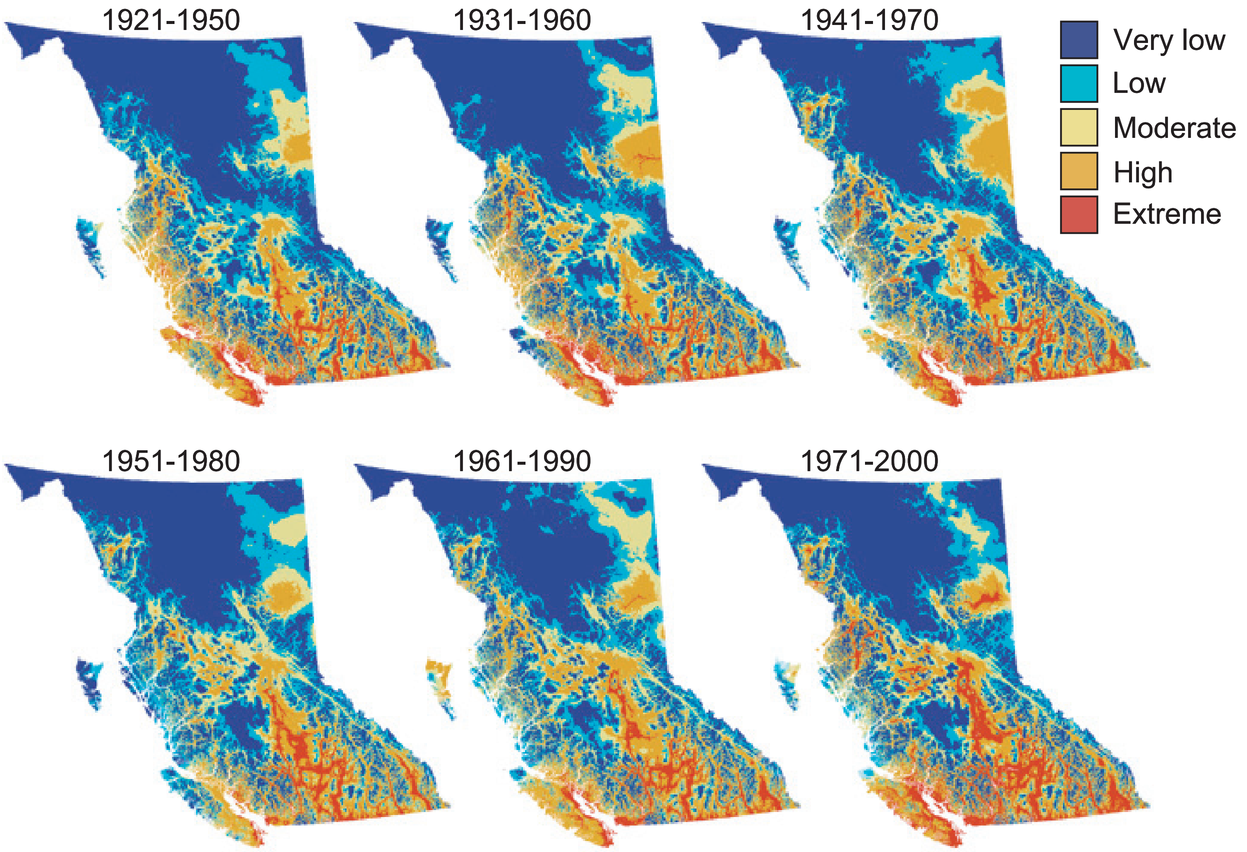

Figure 1. Historic distributions of climatic suitability classes (CSCs) derived from climate normals (30-year monthly means and extreme minima and maxima) for the mountain pine beetle in British Columbia. "Very low" CSCs are habitats with climatic conditions unsuitable for mountain pine beetle, whereas "extreme" CSCs are those considered climatically optimal.

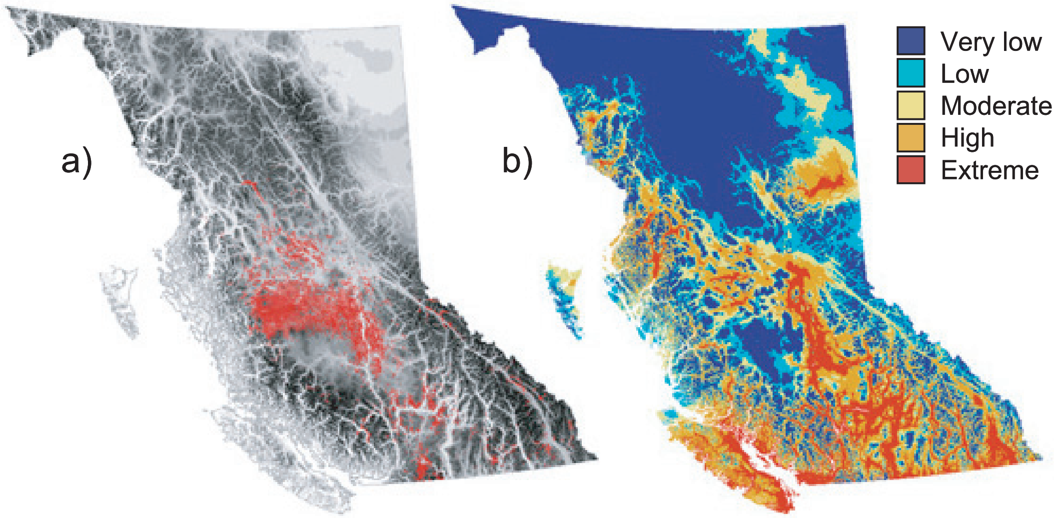

Figure 2. Mountain pine beetle infestations (all severity classes) from 1998 to 2002 (a), and the distribution of climatic suitability classes derived from 1971-2000 climate normals [30-year monthly means and extreme minima and maxima (b)] for the mountain pine beetle in BC. "Very low" CSCs are habitats with climatic conditions unsuitable for mountain pine beetle, whereas "extreme" CSCs are those considered climatically optimal.

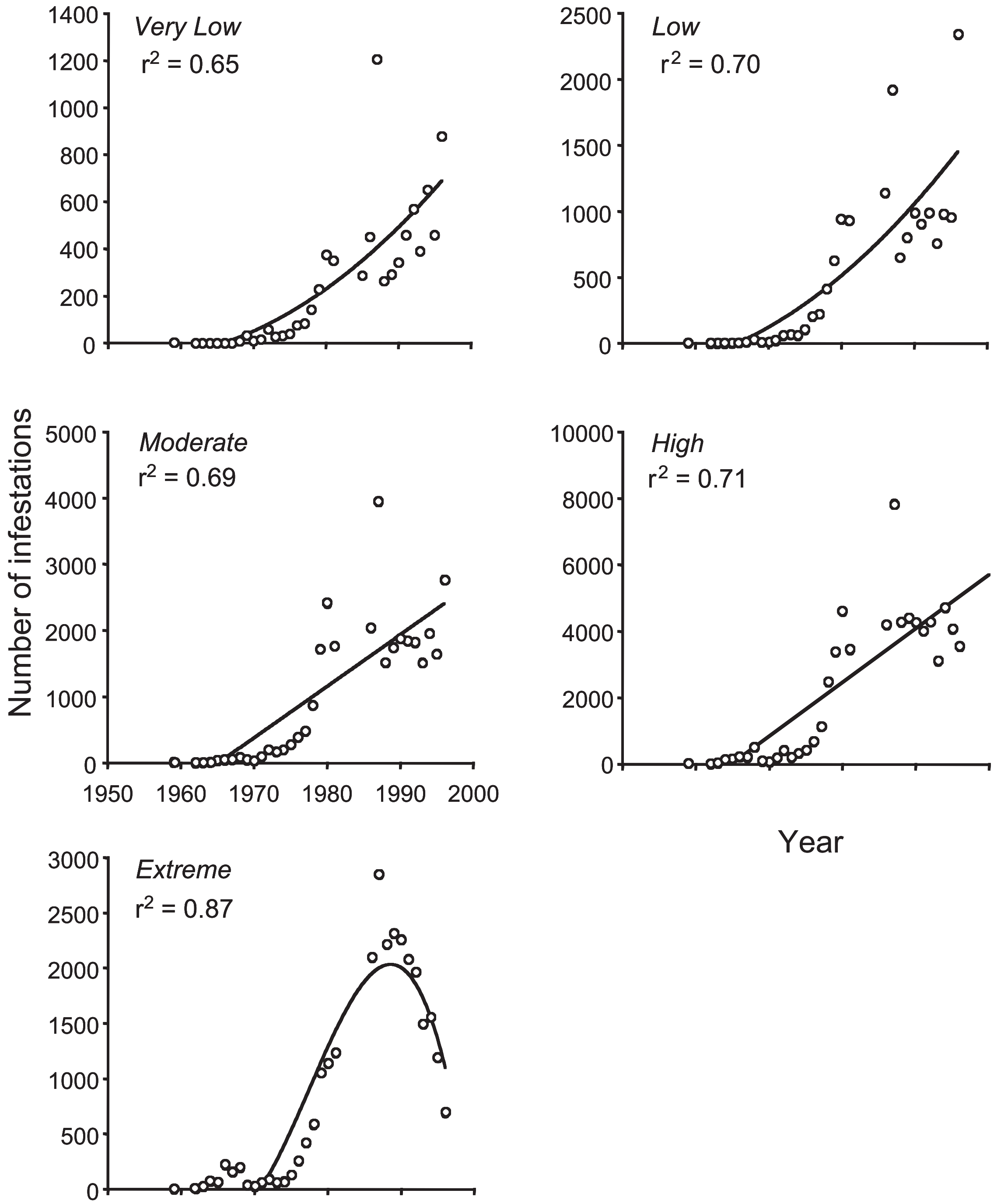

Figure 3. Number of infestations versus year and climatic suitability class derived from 1941-1970 climate normals (30-year monthly means and extreme minima and maxima) for mountain pine beetle in British Columbia. "Very low" CSCs are habitats with climatic conditions unsuitable for mountain pine beetle, whereas "extreme" CSCs are those considered climatically optimal.

an extreme winter), the current outbreak may not entirely collapse as in the past. Expansion by the beetle into new habitats as global warming continues will provide it a small, continual supply of mature pine, thereby maintaining populations at above-normal levels for some decades into the future.

Historically, mountain pine beetle populations have been most common in southern BC. Non-forested prairies and the high elevations of the Rocky Mountains have contributed to confining it to that distribution. With the substantial shift by mountain pine beetle populations into formerly unsuitable habitats during the past 30 years, it is likely that the beetle will soon overcome the natural barrier of high mountains as climate change proceeds. Indeed, with a conservative increase in average global temperature of 2.5 °C associated with a doubling of atmospheric CO_2, as suggested by the Intergovernmental Panel on Climate Change as a plausible global warming scenario (Houghton et al. 1990), Logan and Powell (2001) predict a latitudinal shift of more than 7° N in the distribution of thermally benign habitats for mountain pine beetles. Perhaps as evidence of this shift, in recent years small but persistent mountain pine beetle populations have been detected along the northeastern slopes of the Rockies in Alberta – areas in which the beetle has not been previously recorded (Alberta Sustainable Resource Development 2003). The northern half of Alberta and Saskatchewan is forested by jack pine, *Pinus banksiana* Lamb., a susceptible species (Furniss and Schenk 1969; Safranyik and Linton 1982; Cerezke 1995) that may soon come in contact with mountain pine beetles.

Acknowledgements

G. Thandi, B. Erickson and J. MacDuff provided technical assistance. The cooperation of the BC Ministry of Water, Land and Air Protection, and the BC Ministry of Forests is gratefully acknowledged. This study was supported by a grant from Natural Resources Canada, Canadian Forest Service, Mountain Pine Beetle Initiative.

Allan L. Carroll is a research scientist with the Canadian Forest Service, Pacific Forestry Centre.

Literature Cited

Alberta Sustainable Resource Development. 2003. Alberta Forest Health – Pest Alerts/Moratoriums – Mountain Pine Beetle. [on line] <http://www3.gov.ab.ca/srd/ forests/health/a_mpbeetle.html#pub.

Bentz, B.J.; Logan, J.A.; Vandygriff, J.C. 2001. Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. The Canadian Entomologist 133: 375-387.

Boughner, C.C. 1964. Distribution of growing degree-days in Canada. Canadian Meteorological Memoirs 17. Met. Br., Dept. of Transport. 40 p.

Cerezke, H.F. 1995. Egg gallery, brood production, and adult characteristics of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), in three pine hosts. The Canadian Entomologist 127: 955-965.

Dale, V.H.; Joyce, L.A.; McNulty, S.; Neilson, R.P.; Ayres, M.P.; Flannigan, M.D.; Hanson, P.J.; Irland L.C.; Lugo, A.E.; Peterson, C.J.; Simberloff, D.; Swanson, F.J.; Stocks, B.J.; Wotton, B.M. 2001. Climate change and forest disturbances. BioScience 51: 723-734.

Davis, J.C. 1986. Statistics and data analysis in geology. Second edition. John Wiley and Sons, New York, New York.

Environment Canada. 2002. Canadian daily climatic data 2000, CDCD West CDROM [2000 Canadian daily climate data west]. Environment Canada, Meteorological Services, Downsview, ON.

Furniss, M.M.; Schenk, J.A. 1969. Sustained natural infestation by the mountain pine beetle in seven new *Pinus* and *Picea* hosts. Journal of Economic Entomology 62: 518-519.

Houghton, J.T.; Jenkins, G.J.; Ephraums, J.J., eds. 1990. Climate change: the IPCC scientific assessment. Cambridge University Press, Cambridge, UK.

Logan, J.A.; Bentz, B.J. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. Environmental Entomology 28: 924-934.

Logan, J.A.; Powell, J.A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist 47: 160-173.

Logan, J.A.; Régnière, J.; Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and Environment 1: 130-137.

McCambridge, F.W. 1971. Temperature limits of flight of the mountain pine beetle, *Dendroctonus ponderosae*. Annals of the Entomological Society of America 64: 534-535.

Nalder, I.A.; Wein, R.W. 1998. Spatial interpolation of climatic normals: test of a new method in the Canadian boreal forest. Agriculture and Forest Meteorology 92: 211-225.

National Atlas of Canada. 1970. Department of Energy, Mines, and Natural Resources. Ottawa, Canada.

Powell, J.M. 1966. Distribution and outbreaks of *Dendroctonus ponderosae* in forests of Western Canada. Can. Dept. Forestry, Inf. Rep. A-X-2, Forest Res. Lab., Calgary, AB. 19 p.

Régnière, J. 1996. A generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environmental Entomology 25: 869-881.

Régnière, J.; Bolstad, P. 1994. Statistical simulation of daily air temperature patterns in eastern North America to forecast seasonal events in insect pest management. Environmental Entomology 23: 1368-1380.

Régnière, J.; Cooke, B.; Bergeron, V. 1995. BioSIM: A computer-based decision support tool for seasonal planning of pest management activities. User's Manual. Can. For. Serv. Inf. Rep. LAU-X-116.

Reid, R.W. 1962. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia. I. Life cycle, brood development, and flight periods. The Canadian Entomologist 94: 531-538.

Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. Pages 79-86 *in* D.L. Kibbee, A.A. Berryman, G.D. Amman, and R.W. Stark, eds. Theory and practice of mountain pine beetle management in lodgepole pine forests. Symp. Proc., Univ. Idaho, Moscow, ID.

Safranyik, L.; Shrimpton, D.M.; Whitney, H.S. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Can. For. Serv. Tech. Rep. 1. 24 p.

Safranyik, L.; Shrimpton, D.M.; Whitney, H.S. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. Pages 406-428 *in* D.M. Baumgartner, ed. Management of lodgepole pine ecosystems. Washington State Univ. Coop. Ext. Serv., Pullman, WA.

Safranyik, L; Linton, D.A. 1982. Survival and development of mountain pine beetle broods in jack pine bolts from Ontario. Can. For. Serv. Res. Note 2: 17-18.

Safranyik, L; Linton, D.A. 1998. Mortality of mountain pine beetle larvae, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in logs of lodgepole pine (*Pinus contorta* var. *latifolia*) at constant low temperatures. Journal of the Entomological Society of British Columbia 95: 81-87.

Safranyik, L.; Barclay, H.; Thomson, A.; Riel, W.G. 1999. A population dynamics model for the mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae). Can. For. Serv. Inf. Rep. BC-X-386.

Taylor, S.; Carroll, A. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective. Pages 41-51 *in* T.L. Shore, J.E. Brooks, and J.E. Stone (editors). Mountain Pine Beetle Symposium: Challenges and Solutions. October 30-31, 2003, Kelowna, British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC. 298 p.

Thomas, C.D.; Bodsworth, E.J.; Wilson, R.J.; Simmons, A.D.; Davies, Z.G.; Musche, M.; Conradt, L. 2001. Ecological and evolutionary processes at expanding range margins. Nature 411: 577-581.

Thomson, A.J.; Shrimpton, D.M. 1984. Weather associated with the start of mountain pine beetle outbreaks. Canadian Journal of Forest Research 14: 255-258.

Ung, C-H.; Bernier, P.Y.; Raulier, F.; Fournier, R.A.; Lambert, M-C.; Régnière, J. 2001. Biophysical site indices for shade tolerant and intolerant boreal species. Forest Science 47: 83-95.

Van Sickle A.; Fiddick, R.L.; Wood, C.S. 2001. The forest insect and disease survey in the Pacific Region. Journal of the Entomological Society of British Columbia 98: 169-176.