Chapter 2

Forest, Climate and Mountain Pine Beetle Outbreak Dynamics in Western Canada

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Abstract

Mountain pine beetle (*Dendroctonus ponderosae* Hopk. [Coleoptera: Scolytidae]) outbreaks have been observed in all pine species in western Canada. However, they have occurred principally in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. latifolia) in the southern half of British Columbia and the extreme south-western portion of Alberta, with one outbreak recorded in the Cypress Hills at the southern junction of the Alberta–Saskatchewan border. At least four large-scale outbreaks have occurred in western Canada in the past 120 years, as documented in forest survey records or detected as growth releases in tree rings. The Chilcotin Plateau in central interior British Columbia has sustained the most years of outbreak. Dendrochronological evidence suggests an outbreak periodicity of about 40 years in this region.

The size of mountain pine beetle infestations varies with short-term changes in weather and long-term changes in host availability. Retrospective modelling suggests that both the amount of susceptible mature lodgepole pine and the area with favourable climate have increased during the past century. An age-class projection model using contemporary forest inventory data in combination with wildfire and harvesting statistics suggests that during the early 1900s, approximately 17% of pine stands were in age-classes susceptible to mountain pine beetle attack. Forest age-class structure is controlled by the disturbance regime. In unmanaged lodgepole pine forests, wildfire was the primary disturbance agent. With fire-return cycles of 40 - 200 years, the long-term average susceptibility to mountain pine beetle would be about 17% - 25% over large areas. However, during the past 80 years the amount of area burned by wildfire in pine forests in British Columbia has significantly decreased. While harvesting has also increased during this same period, the net disturbance rate is believed to have decreased. The reduction in disturbance rate has resulted in an increase in the average age of pine stands such that approximately 55% of pine forests are presently in age-classes considered susceptible to mountain pine beetle. Analysis and modelling of the historical distribution of a climatic suitability index and of outbreaks suggests that over the past 40 years the range of mountain pine beetle has expanded, as has the area that is climatically favourable for it. Thus, an increase in both the amount of susceptible-aged host and range expansion due to a more favourable climate have created ideal conditions for the development of an extensive mountain pine beetle epidemic. A better understanding of the effect of forest dynamics and climatic variation on mountain pine beetle populations and outbreak development will allow for management of lodgepole pine with regard to disturbance risk.

Résumé

Bien que le dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopk. [Coleoptera: Scolytidae]) s'attaque à toutes les espèces de pins dans l'Ouest canadien, le pin tordu latifolié (*Pinus contorta* Dougl. ex Loud. var. latifolia) est sa cible de prédilection dans la moitié méridionale de la Colombie-Britannique et l'extrême sud-ouest de l'Alberta. Une infestation a également été signalée dans les collines Cypress, à la jonction sud de la frontière Alberta-Saskatchewan. Les données d'inventaires forestiers ou les anneaux de croissance des arbres indiquent que l'Ouest canadien a connu au moins quatre graves infestations au cours des 120 dernières années. La région des plateaux Chilcotin, située dans l'Intérieur centre de la Colombie-Britannique, a pour sa part subi le plus grand nombre d'années d'infestation. Les données dendrochronologiques indiquent que les infestations se répètent environ tous les 40 ans dans la région.

L'ampleur des infestations varie en fonction des fluctuations à court terme des conditions météorologiques et de la variation à long terme de la disponibilité des hôtes. Des modèles rétrospectifs donnent à penser que le nombre de pins tordus latifoliés mûrs vulnérables et la superficie du territoire exposé à des conditions climatiques favorables ont augmenté au cours du siècle dernier. Selon un modèle de projection structuré en fonction des classes d'âge fondé sur des données d'inventaires forestiers contemporaines ainsi que des statistiques sur les incendies de forêt et l'exploitation forestière, la proportion de pinèdes appartenant à des classes d'âge vulnérables au dendroctone du pin ponderosa s'établissait à environ 17 % au début des années 1900. La structure des classes d'âge des forêts est déterminée par le régime des perturbations. Dans les forêts de pins tordus latifoliés non aménagées, le feu était le principal agent de perturbation. En présence d'intervalles de récurrence des feux de 40 à 200 ans, la vulnérabilité moyenne à long terme au dendroctone du pin ponderosa à l'échelle de vastes territoires s'établirait à environ 17 à 25 %. La superficie brûlée, dans les pinèdes, a cependant considérablement diminué en Colombie-Britannique au cours des 80 dernières années. Même si l'exploitation forestière s'est intensifiée durant cette même période, il semble que le taux net de perturbation ait diminué. Cette réduction s'est traduite par une augmentation de l'âge moyen des peuplements de pins, de telle sorte qu'environ 55 % des forêts de pins appartiennent aujourd'hui à des classes d'âge vulnérables au ravageur. L'analyse et la modélisation de la répartition historique des régions présentant des conditions climatiques favorables ainsi que des infestations laissent penser qu'au cours des 40 dernières années, l'aire de répartition du dendroctone du pin ponderosa s'est accrue, tout comme la superficie du territoire où le climat lui est favorable. L'augmentation du nombre d'hôtes appartenant à des classes d'âge vulnérables et l'expansion de l'aire du ravageur résultant de conditions climatiques plus favorables ont donc engendré des conditions idéales pour qu'une épidémie majeure se déclenche. Une meilleure compréhension des effets de la dynamique des forêts ainsi que des variations climatiques sur les populations de dendroctones du pin ponderosa et le déclenchement des infestations permettra d'aménager les peuplements de pins tordus latifoliés en fonction du risque lié aux perturbations.

Introduction

Mountain pine beetle *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) infestations have been documented in western Canada for over 85 years. The first Dominion of Canada entomologist, J.M. Swaine, observed mountain pine beetle and other bark beetle outbreaks during field surveys in western Canada in the early 1900s (Swaine 1918). Following the establishment of the Dominion Forest Biology Lab in Vernon, British Columbia in 1919, significant outbreaks occurring in the southern part of the province continued to be recorded. From 1959 to 1996, the Canadian Forest Service, Forest Insect and Disease Survey (FIDS), in cooperation with provincial agencies, conducted annual systematic province-wide aerial overview surveys of forest insect outbreaks. During these surveys, boundaries of infestations were recorded on topographic maps and infestations were classified into "low", "moderate" and "high" severity classes corresponding to <10%, 10%-30% and >30% attacked (i.e., red) trees, respectively (for details see Van Sickle et al. 2001). Photographs of spot (i.e., low), moderate, and high severity infestations are shown in Figure 1. After 1996, provincial governments took over insect and disease surveys in western Canada. The British Columbia Ministry of Forests has carried out annual overview forest health surveys since 1999. Powell (1966), and Wood and Unger (1996), reviewed the historical distribution of outbreaks in British Columbia from insect survey records. However, recent digitization of the historic insect outbreak maps has allowed for new spatial analyses of outbreak dynamics.

Tree rings maintain a record of the canopy disturbance history for a locality, and therefore have been used to determine past outbreaks of bark beetles (Stuart et al. 1989; Heath and Alfaro 1990; Veblen et al. 1991a, 1991b; Zhang et al. 1999; Eisenhart and Veblen 2000) and defoliating insects (e.g., Swetnam and Lynch 1993; Zhang and Alfaro 2002, 2003). Because mountain pine beetle outbreaks do not normally kill all trees in a stand, non-host and surviving host trees experience extended periods of increased growth that is visible in tree ring series. Thus, release from competition can be used as a proxy for canopy disturbance by mountain pine beetle. However, the release is not precisely simultaneous among all trees in the stand because not all host trees are attacked nor die in the same year (Eisenhart and Veblen 2000). Therefore, the method relies on stand averages to date an outbreak. Partial or unsuccessful attacks by mountain pine beetles often leave lesions on surviving trees (Fig. 2). These scars can be dated with dendrochronological methods and provide further confirmation of beetle infestations. Although partial or unsuccessful attacks are most prevalent during outbreaks, they may also occur at sub-outbreak levels. These investigations are providing new insights into temporal outbreak patterns predating the survey period.

In this chapter we review the history of mountain pine beetle infestations in western Canada, and examine the effects of forest age dynamics and climate on these outbreaks. A better understanding of the influence of forest dynamics and climatic variation on the development of mountain pine beetle outbreaks may help to direct longer-term management strategies.

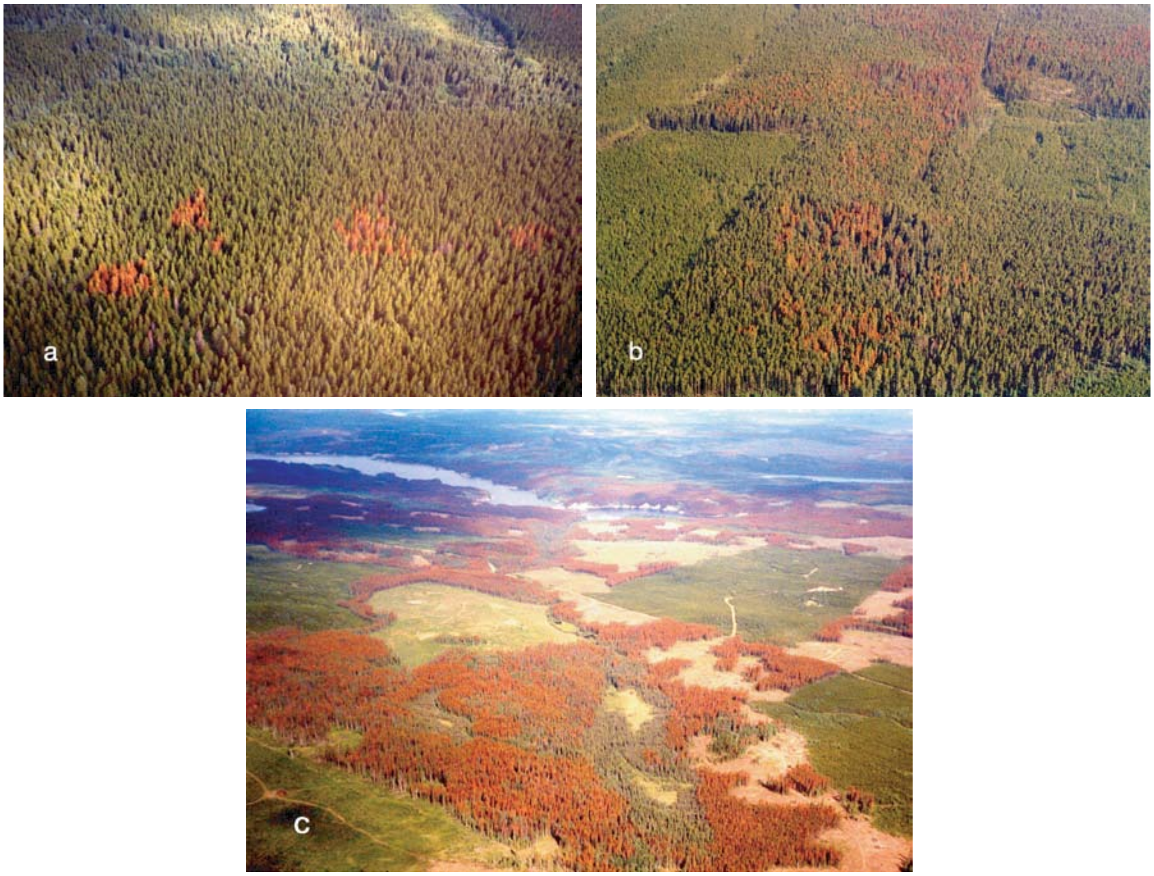


Figure 1. Examples of a. spot (i.e., low), b. moderate and c. severe mountain pine beetle infestations (Photos: J. Westfall).

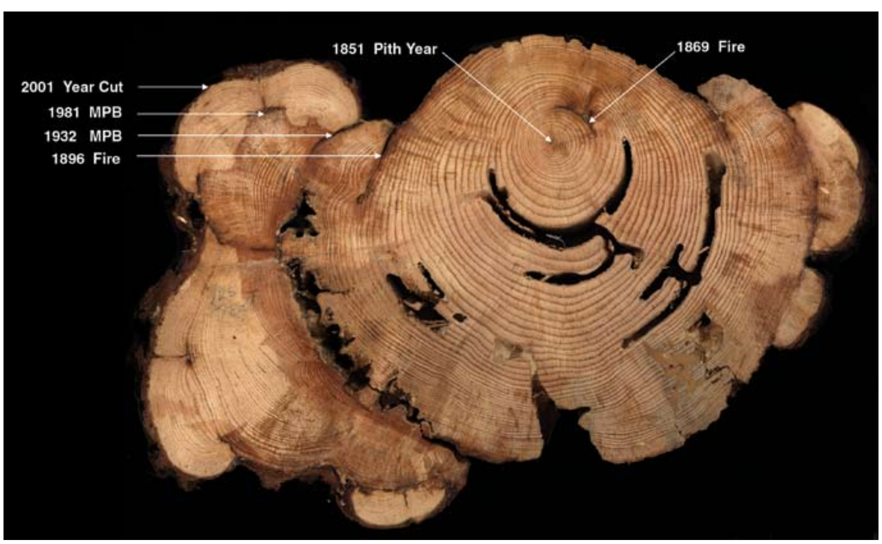


Figure 2. Tree disc showing presumed fire (1869, 1896) and mountain beetle (1932, 1981) scarring cut from a lodgepole pine stand on the Chilcotin Plateau in 2001.

Mountain pine beetle infestations in western Canada

The geographic and elevational range of mountain pine beetle, as with many bark beetles, is determined by the distribution of suitable host trees and by climate (Swaine 1925). Mountain pine beetle occurs in most native and exotic pine species in western North America (McCambridge et al. 1979). Of these, lodgepole, western white, whitebark and limber pine occur in Canada. Occasionally, non-host trees such as Engelmann spruce (*Picea engelmannii* Parry) are attacked, but beetle populations do not persist in these occasional hosts (Unger 1993). In western North America, despite the broad host range of mountain pine beetle, lodgepole pine is considered the main host species.

The mountain pine beetle occurs from northern Mexico (latitude 30°N), north through 12 American states, and into central British Columbia (latitude 56°N); from the Pacific Ocean in the west, to North Dakota; and from sea level to over 2000 m in elevation (Safranyik 2001). In Canada, mountain pine beetle occurs principally in the southern half of British Columbia and the extreme southwestern portion of Alberta with one outbreak recorded in the Cypress Hills at the southern junction of the Alberta – Saskatchewan border. The range of mountain pine beetle appears to be limited mainly by the occurrence of -40° C temperatures within the distribution of host species (Safranyik et al. 1975), temperatures at which all life stages of the beetle suffer extensive mortality (Safranyik and Linton 1998; see Chapter 1 of this book).

Recently, digitization of historical insect survey maps has allowed for re-analysis of mountain pine beetle outbreak patterns in British Columbia. The cumulative area infested by mountain pine beetle by decade since 1920 is plotted in Figure 3 over the distribution of forest stands in which pine species predominate (derived from the 1994 Forest, Range, and Recreation Resource Analysis [British Columbia Ministry of Forests 1995]). Significant outbreaks in lodgepole and ponderosa pine in the 1920s were recorded around Aspen Grove and in the Kettle Valley (Fig. 3a). In the 1930s, a large outbreak was examined in the Chilcotin in west-central British Columbia (Fig. 3b). During the 1940s, significant mountain pine beetle-caused mortality was recorded in Kootenay and Banff National Parks (Fig. 3c); smaller infestations were recorded in western white pine in the Shuswap region and in coastal British Columbia. During the 1950s and 1960s, one of the longest duration outbreaks ever recorded (18 years) was observed around Babine Lake and Stuart Lake in north-central British Columbia (Figs. 3d and 3e). A smaller infestation was observed on shore pine and western white pine on Vancouver Island and the Sunshine Coast during the 1960s. Major infestations developed in the 1970s and 1980s on the Chilcotin plateau and in southeastern British Columbia (Figs. 3f and 3g). Small infestations were also noted in southwestern Alberta and in the Cypress Hills of Alberta and Saskatchewan during the 1980s. The present outbreak began to develop in north central British Columbia during the 1990s, and is the largest recorded outbreak to date (Fig. 3h). The cumulative area affected is shown in Figure 4.

The sum of the annual areas infested by mountain pine beetle (between 1960-2004) was approximately 16.8 million hectares. Of this, 52%, 24%, and 23% of the infested area fell in low, moderate, and high severity classes, respectively. However, the cumulative area infested between 1959 and 2004 was about 9.8 million hectares (Fig. 4). There appears to be a higher proportion of low and moderate severity area affected in the current (1995-2004) outbreak than in the previous (1970s-1980s) major outbreak, possibly because more mixed stands of pine and spruce are being affected in the current outbreak (Fig. 5a).

The digital outbreak maps were intersected with forest inventory records to determine the historical distribution of outbreaks by stand type in British Columbia (Fig. 5b). Between 1959-2002, of the approximately 6 million ha of outbreak for which inventory records were available, 63% of outbreaks occurred in pine-dominated stands (>50% pine species by volume), which represents about 22% of the approximately 14 million ha of pine-dominated forests in British Columbia (British Columbia Ministry of Forests 1995). Pine-dominated stand types sustained the majority of high-severity outbreaks. However, about 70% of affected forests (i.e., all attack severities) had a significant component of non-host tree species, principally white (*Picea glauca*) or Engelmann spruce, Douglas-fir (*Pseudotsuga menziesii*), trembling aspen (*Populus tremuloides*), western larch (*Larix occidentalis*) or subalpine fir (*Abies lasiocarpa*) (Fig. 5b).

The distribution of mountain pine beetle outbreaks was also examined across biogeoclimatic zones (Meidinger and Pojar 1991) in British Columbia. Lodgepole pine is ubiquitous in British Columbia, occurring in all biogeoclimatic zones from sea level to alpine tundra and from rainforest to semi-desert. The majority of mountain pine beetle outbreaks occurred in the Sub Boreal Spruce (SBS) zone, followed by the Sub-Boreal Pine Spruce (SBPS), Interior Douglas-Fir (IDF), and Engelmann Spruce Subalpine Fir (ESSF), Montane Spruce (MS), and Interior Cedar Hemlock (ICH) zones (Table 1 and Fig. 5c). Minor outbreaks have occurred in other zones. Outbreaks in mixed stands of pine and spruce have predominated in the SBS and ESSF zones and in mixed stands of pine and Douglas-fir in the IDF zone. Lodgepole pine is a seral species in these zones and mountain pine beetle outbreaks in mixed stands hasten the successional process to non-host species. Outbreaks in pure lodgepole pine stands have occurred predominantly in the SBS and MS zones. Lodgepole pine is considered a persistent fire-climax species in the SBPS zone, and succession to spruce would be very slow (Steen and Demarchi 1991) because there is little spruce in the understory or as a seed source. The residual stand following mountain pine beetle outbreaks in the SBPS is primarily smaller diameter lodgepole pine. Outbreaks have not occurred to any great extent in the Boreal White and Black Spruce (BWBS) and Spruce Willow Birch (SWB) zones in northern British Columbia despite a relative abundance of host because these zones experience extreme winter temperatures.

The majority of mountain pine beetle outbreaks have occurred between 800 and 1400 m in elevation (Fig. 5d) in British Columbia, with the mean elevation decreasing from about 1400 m at 49° to 1000 m at 55° N. Outbreak severity appears to have been less at lower elevations (400-800 m), possibly because of a higher prevalence of mixed stands of Douglas-fir and lodgepole pine. There also appears to be a higher proportion of low- and moderate-severity outbreaks north from 53° N, possibly because of a higher proportion of mixed stands of lodgepole pine, spruce and subalpine fir.

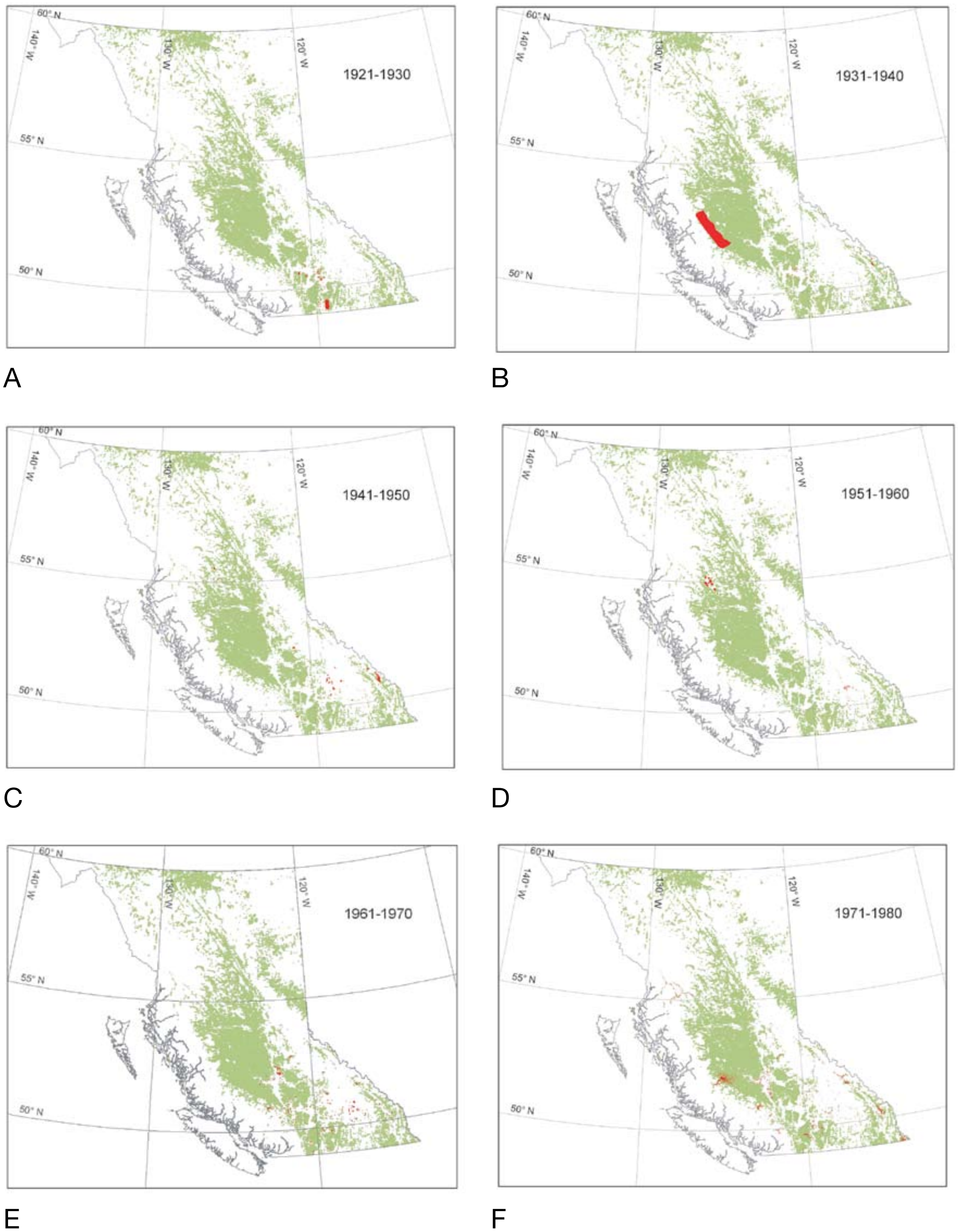
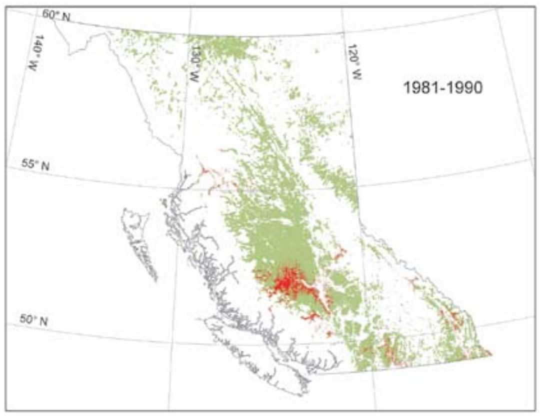


Figure 3. Distribution of mountain pine beetle outbreaks (red) by decade and the distribution of pine-leading stands (green) in British Columbia for 1920-2004. (See following page for Figures G, H, and I.)



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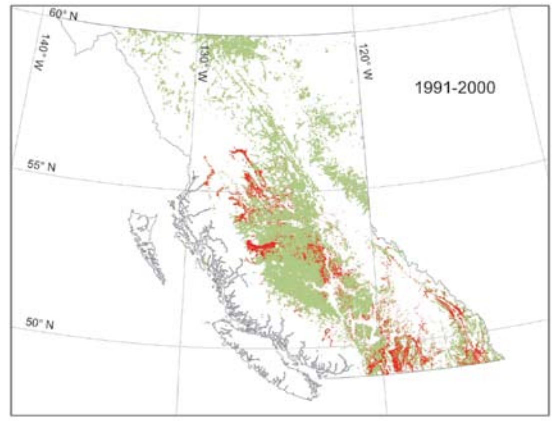

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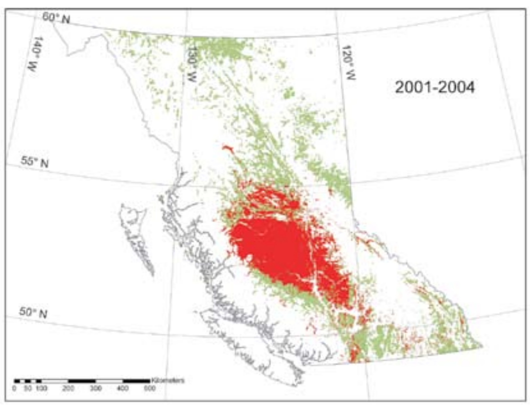

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Figure 3. Distribution of mountain pine beetle outbreaks (red) by decade and the distribution of pine-leading stands (green) in British Columbia for 1920-2004. (See previous page for Figures A to F.)

The Chilcotin Plateau in south-central British Columbia (SBPS zone) sustained the most years of consecutive outbreaks (approximately 52° N, 124° W - see Fig. 4) during 1920-2004. Alfaro et al. (2004) used dendrochronological methods to further investigate the history of canopy disturbances indicative of potential past mountain beetle outbreaks at 15 locations in this area. An example of a standardized chronology for one of the stands showing two periods of release from competition is shown in Figure 6. Of the 15 chronologies, 30% of the stands showed release periods in the 1890s, and 75% showed release in the 1940s and the 1980s (Fig. 7). Each of the three release periods lasted, on average, 13.8 years (Range 5–23) and recurred every 42 years (Range 28–53), counted from the start of one release to the start of the next release. The dendrochronology record still does not show potential release due to the current outbreak (ongoing in 2006). The releases in the 1940s and 1980s are consistent with insect outbreak survey records, but the occurrence in the 1890s predates the surveys. Because of a delay in tree growth response to thinning, the release is not precisely simultaneous (Eisenhart and Veblen 2000). Heath and Alfaro (1990) indicated that the thinning response of lodgepole pine, expressed as a significant increase in ring growth, began 2 to 6 years after the start of a severe beetle outbreak and peaked 5 to 9 years after. Therefore, the outbreak episodes indicated by the dendrochronological assessment may have began nearly a decade earlier (i.e., 1880s, 1930s, 1970s), a premise supported by the survey records of the latter two outbreaks (see Figs. 3 and 5).

Table 1. Distribution of pine-leading stands and mountain pine beetle (MPB) outbreaks by biogeoclimatic zone in British Columbia

Biogeoclimatic zone	Elevation (m) 1	Mean annual temp. (°C)[1]	Mean annual precip. (mm)[1]	Area of lodgepole pine - leading stands (ha)[2]				Cumulative 1960-2002 MPB outbreak area (ha)[3]
				< 80 years	80 - 140 years	140 + years	Total	
AT - Alpine tundra	1000 + 2250+	-4 -0	700 -3000	17 840	36 839	26 284	80 964	38 138
BG - Bunchgrass	-1000	-	-	17	120	44	181	2 178
BWBS - Boreal White and Black Spruce	230 -1300	- 2 -9 - 2.0	330 - 570	1 131 427	1 365 306	110 239	2 606 973	3 221
CDF - Coastal Douglas-Fir	0 - 150	9.2 - 10.5	647 -1263	319	171	0	490	0
CWH - Coastal Western Hemlock	0 -900	5.2 - 10.5	1000 -4400	29 717	48 918	149 625	228 260	67 472
ESSF - Engelmann Spruce Subalpine Fir	900 - 2300	-2.0 - 2.0	400 - 2200	679 045	1 119 162	376 275	2 174 482	670 880
ICH - Interior Cedar Hemlock	400 - 1500	2.0 - 8.7	500 - 1200	322 297	235 449	9 769	567 516	342 949
IDF - Interior Douglas-Fir	350 - 1450	1.6 - 9.5	300 - 750	400 828	534 547	55 348	990 723	1 077 803
MH - Mountain Hemlock	400 -1800	0.0 - 5.0	1700 - 5000	262	1380	2 681	4323	8 674
MS - Montane Spruce	1100 - 1500	0.5 - 4.7	380 - 900	620 785	866 169	271 538	1 758 492	531 732
PP - Ponderosa Pine	335 - 900	4.8 - 10.0	280 - 500	490	536	0	1 026	4 258
SBPS - SubBoreal Pine Spruce	850 - 1300	0.3 - 2.7	335 - 580	567 610	984 488	187 917	1 740 015	1 354 126
SBS - SubBoreal Spruce	1100 - 1300	1.7 - 5.0	440 - 900	1 166 322	2 154 913	483 587	3 804 822	1 846 115
SWB - Spruce Willow Birch	900 -1700	-0.7 - 3.0	46 - 700	281 388	434 431	130 691	846 511	1
Total				5 218 349	7 782 430	1803 998	14 804 777	5 947 547

[1] Meidinger and Pojar (1991)
[2] Adapted from B.C. Seamless Forest Inventory - does not include private land, national parks, some provincial parks, and some tree farm licences.
[3] Canadian Forest Service and British Columbia Ministry of Forests insect survey records.

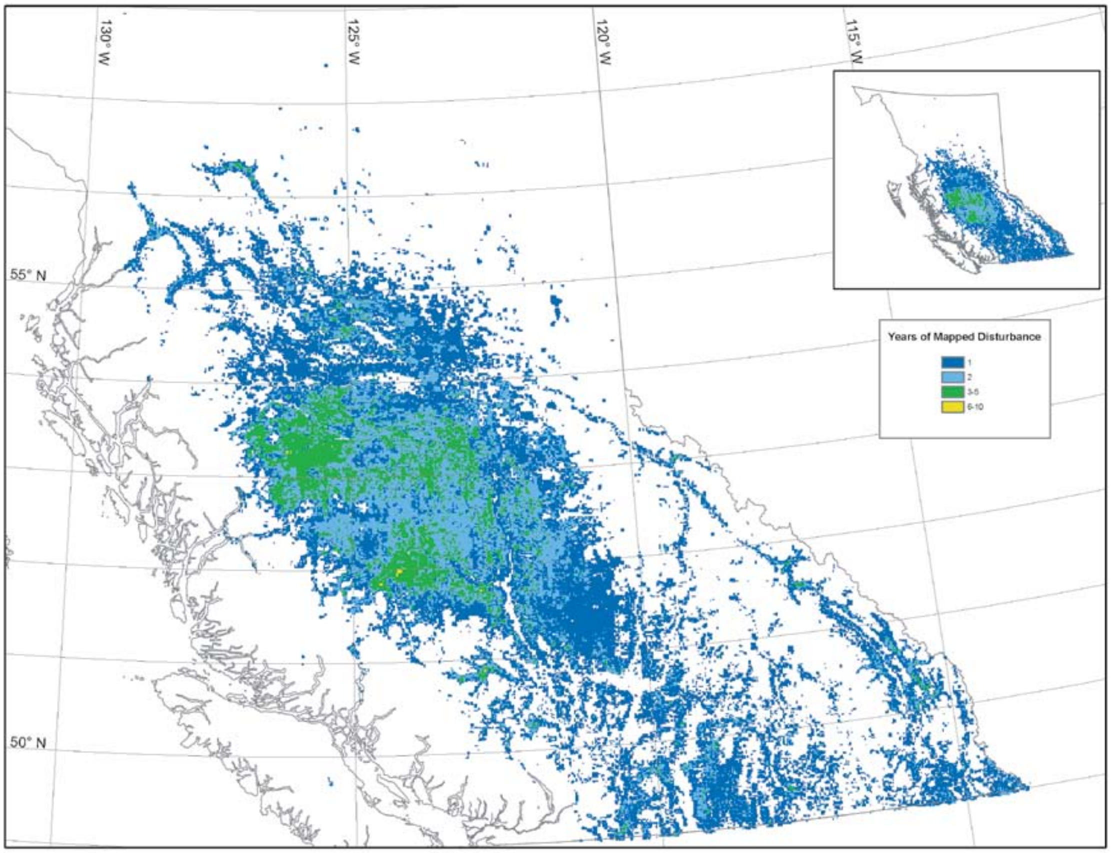

Figure 4. Cumulative area of mountain pine beetle outbreak in British Columbia during 1920-2004 showing number of years of attack.

The combined forest insect survey and dendrochronological records indicate that there have been four significant outbreak periods in British Columbia during the last 120 years and that outbreaks may recur in some areas as surviving trees in the residual stand grow to susceptible size. The records also suggest that outbreak size has been increasing over time. However, infestations have not yet occurred throughout the full range of the beetle's primary host—lodgepole pine (see Fig. 1). 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—lodgepole pine extends north into the southern Yukon and Northwest Territories, and east across much of Alberta, beyond the contemporary range of mountain pine beetle.

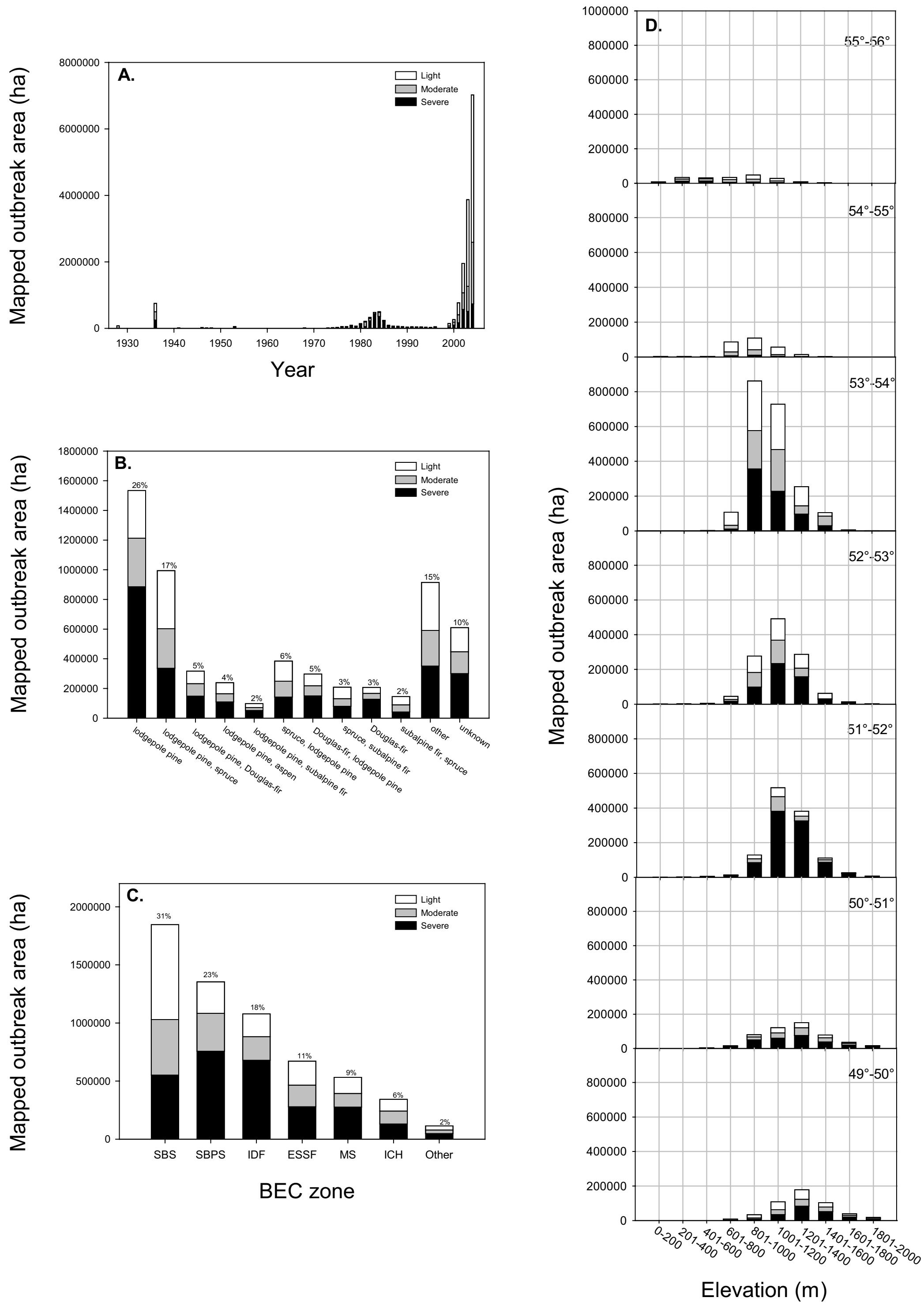

Figure 5. A. Distribution of mountain pine beetle outbreaks in British Columbia during 1959-2004 by severity class. B. Distribution of mountain pine beetle outbreaks in British Columbia during 1959-2002 by forest inventory type group and severity class. C. Distribution of mountain pine beetle outbreaks in British Columbia during 1959-2002 by biogeoclimatic zone and forest type. D. Distribution of mountain pine beetle outbreaks in British Columbia during 1959-2002 by elevation, latitude and severity class.

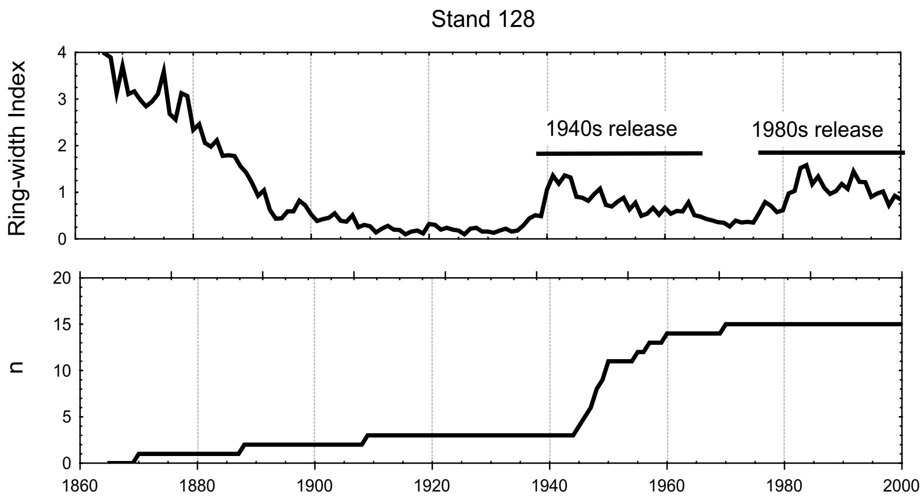

Figure 6. Example of tree ring chronology (top) and sample size for the chronology (bottom). Ring width indices for this stand clearly show two release periods (1940s and 1980s) attributable to canopy disturbances consistent with outbreaks of the mountain pine beetle beginning in the 1930s and 1970s.

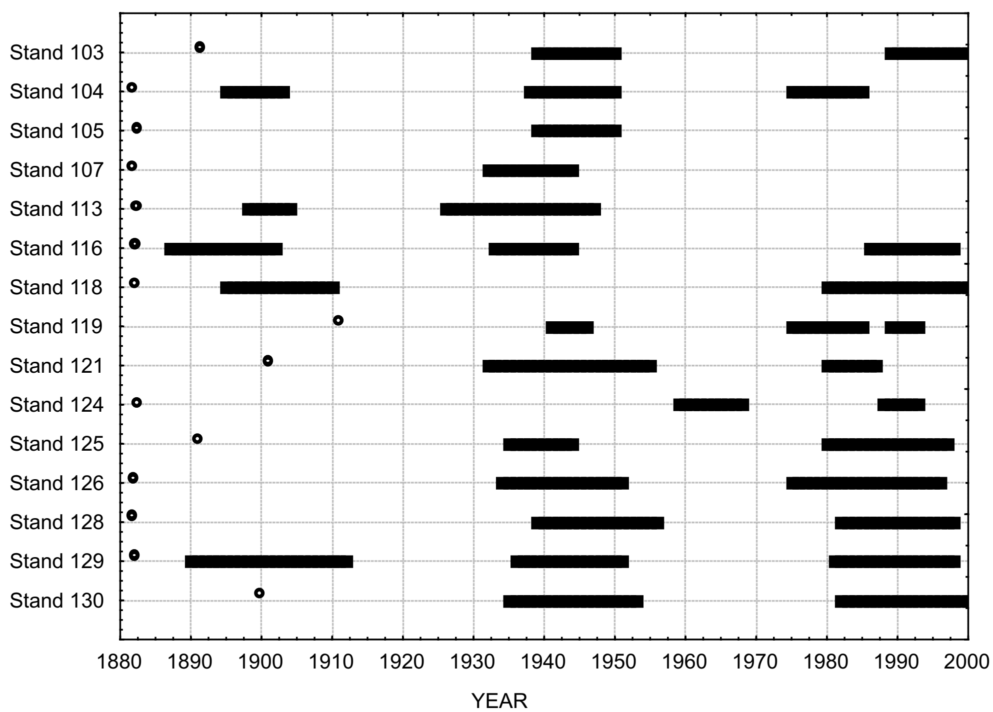

Figure 7. Release periods attributable to mountain pine beetle outbreaks in Chilcotin Plateau of British Columbia inferred from tree ring chronologies. Dot indicates start year for the chronology.

Mountain pine beetle outbreak requirements

For a mountain pine beetle outbreak to develop, two conditions must be satisfied. The first is an abundance of susceptible host trees (Safranyik 1978). Since mountain pine beetle larvae develop within the phloem of their hosts, large-diameter trees with thick phloem are the optimal resource for the beetle (e.g., Amman 1972). Senescing or suppressed trees tend to have thinner phloem and are thereby less suitable to mountain pine beetle (Berryman 1982). Accordingly, mountain pine beetle outbreaks generally occur in stands that are more than 80 years old, containing many trees of large diameter (Safranyik et al. 1974; Shore and Safranyik 1992). Thus, forest composition and age-class structure are the primary factors influencing host susceptibility and outbreak severity. The second condition comprises a sustained period of favourable weather over several years (Safranyik 1978). Insect development and activity are dependent upon temperature and seasonal weather conditions. Specifically, summer heat accumulation must be sufficient to allow development and reproduction followed by winter minimum temperatures that do not fall below thresholds that cause significant mortality (Carroll et al. 2004). Weather conditions during the dispersal period and water deficit have been found to influence mountain pine beetle populations directly through impacting survival of beetle adults, and/or indirectly through influencing host-tree resistance (Safranyik et al. 1975; Carroll et al. 2004). The following sections address these outbreak requirements with regard to the history of mountain pine beetle epidemics.

Lodgepole pine forest dynamics

Lodgepole pine is considered a fire dependent species (Lotan et al. 1985), and most first-growth lodgpepole pine stands are of fire origin. During the heat of crown fires (when the majority of trees are killed), seeds are released from serotinous cones resulting in the re-establishment of virtually even-aged pine stands within a few years. The average frequency of fires at a particular location varies throughout the range of lodgepole pine from less than 100 years to over 500 years (Brown 1975). Based on an analysis of forest inventory data, Smith (1981) suggested that the natural fire-cycle in lodgepole pine forests in British Columbia was about 60 years.

In forests originating from stand-replacing disturbance processes such as wildfire, the rate of disturbance is the key determinant of forest age dynamics. Where fires occur randomly in space at a more or less constant rate, and all stands have an equal probability of burning irrespective of age and location, forest age structure will reach a steady state approximated by the negative exponential distribution (Van Wagner 1978; Li and Barclay 2001) where the average stand age is approximately equal to the fire cycle length. Before fire and timber management were applied in western North America, lodgepole pine forest age dynamics, and so their susceptibility to mountain pine beetle, would have been largely influenced by the forest fire regime, principally the fire cycle length, including the influence of burning by aboriginal peoples.

Taylor and Carroll (2004) examined the landscape-level age-related susceptibility to mountain pine beetle associated with negative exponential age distributions resulting from fire cycle lengths between 40 and 240 years and susceptibility in "normal" fully-regulated forests[1] with rotation lengths between 40 and 240 years, assuming that 80 – 160 year-old stands were most susceptible. They found that the proportion of the landscape susceptible to mountain pine beetle varied in a narrow range between about 12% – 25% for fire cycles of 40 – 240 years; susceptibility increased with fire cycle length to a maximum of 25% with a 120-year fire-return cycle, and then gradually declined (Fig. 8). In the "normal" forest, susceptiblity increased with rotation length to a maximum of 50% at 160 years (Fig. 8b). Examples of age distributions for 60- and 100-year fire-return cycles and a "normal" fully regulated forest with a 100-year rotation length are shown in Figure 9. The proportion of susceptible stands may vary through a greater range on a regional basis where there is deviation from the negative exponential age-class distribution because of spatial and temporal auto-correlation in wildfire occurrence (Boychuk and Perara 1997), or if older stands are susceptible. Where the rate of burning varies in space and time, variation in susceptibility will be greater in increasingly smaller landscapes as the ratio between average fire size and landscape size increases. However, in general, there are more younger stands than older stands in crown fire-dominated landscapes.

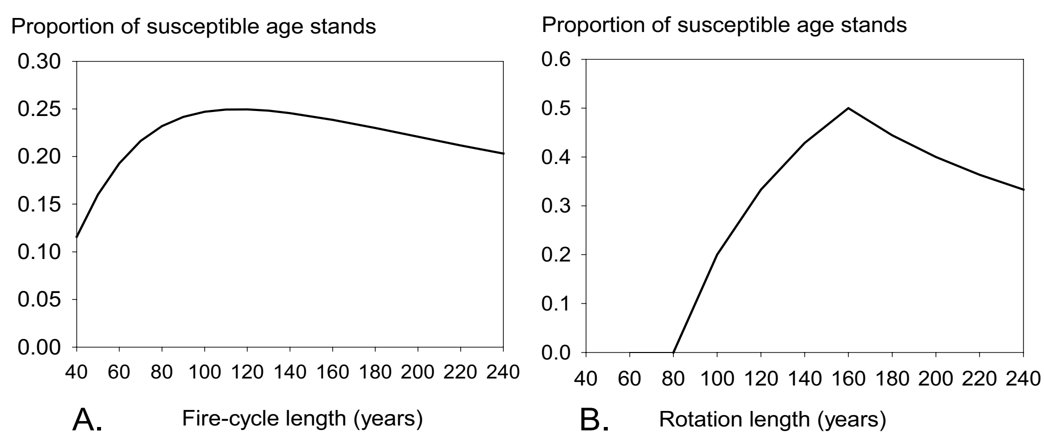

Figure 8. A.) Relationship between fire-cycle length and the proportion of stands susceptible to mountain pine beetle in forests with a negative exponential age-class distribution. B.) Relationship between rotation length and the proportion of stands susceptible to mountain pine beetle in forests with a uniform rectangular distribution.

[1]The "normal" forest is one with an equal amount of area by age class to a fixed rotation age, that is, a rectangular distribution. While rarely achieved, it is the most simple and fully regulated condition and a useful model for comparison.

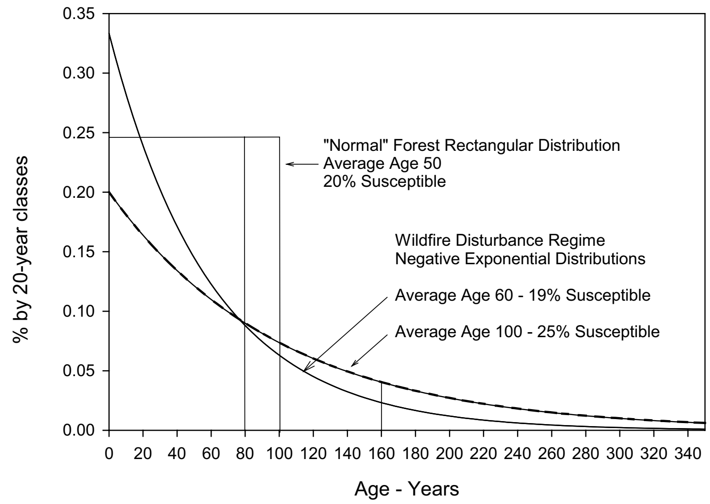

Figure 9. Theoretical distribution of age-classes susceptible to mountain pine beetle in a normal forest with a 100-year rotation, and in forests with 60- and 100-year fire cycles.

Barclay et al. (2005) used the term traversability to describe the presence of a spanning cluster of susceptible host stands that would provide a continuous path for mountain pine beetle to spread across a forested landscape, which they suggest is important to incipient mountain pine beetle outbreak development. The probability of such spanning clusters occurring depends on the proportion of susceptible aged/sized stands as well as patch size distribution. In a wildfire-dominated disturbance regime, patchiness is related to fire size distribution as well as fire cycle length. Using simulation modelling, Barclay et al. (2005) found that landscape traversability decreased as fire (patch) size increased. Barclay et al. (2005) also examined traversability of pine stands across British Columbia using contemporary forest inventory data. They found that traversability was highest in west-central British Columbia, in an area roughly coincident with the extent of the current outbreak. Presumably, this is because of a high proportion of lodgepole pine in these forests, as well as the development of relatively homogenous landscape patterns created by large fires in the region in the late 1800s and early 1900s.

Forest fire suppression began in western Canada approximately 100 years ago. The effectiveness of fire suppression has steadily increased, especially with greater availability of aircraft since the 1950s. This effectiveness is evident in the decreasing trend of area burned in pine-dominated forests in British Columbia between 1920 and 2002 (Taylor and Carroll 2004) (Fig. 10). While logging of lodgepole pine for railway ties also began about 100 years ago, large-scale exploitation of lodgepole pine for lumber and pulp did not occur until the 1960s. Consequently, the stand replacing disturbance rate across the vast pine forests of western Canada was, until recently, greatly reduced from the pre-management level. Using proxy 20-year age-class data from the British Columbia provincial forest inventory, Taylor and Carroll (2004) estimated that the total stand-replacement disturbance rate declined by two-thirds from about 1% during 1911-1930 to 0.31% during 1971-1991.

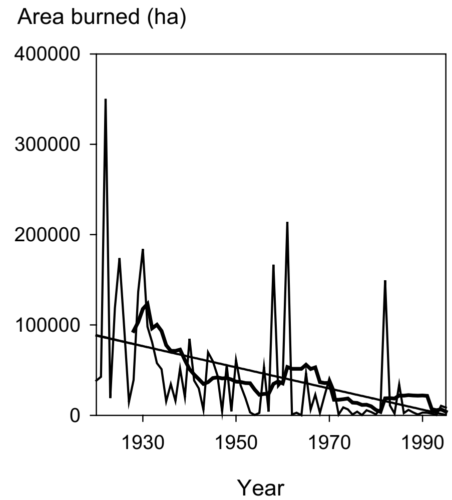

Figure 10. Area burned by forest fires during 1920-1995 in pine-dominated forests in British Columbia. Annual area burned (solid line), ten-year running average (bold line) and linear regression model (straight line).

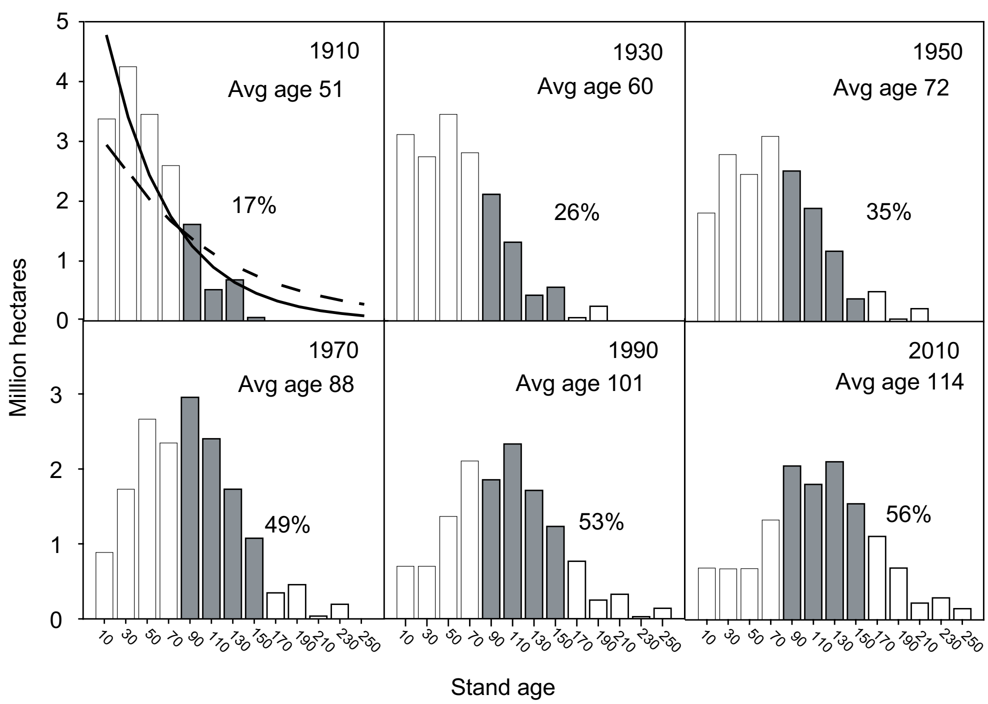

Figure 11. Age-class distribution of pine forests in British Columbia projected from 1990 inventory data. Age-classes susceptible to mountain pine beetle are shaded (percentage of total provided). The theoretical age distribution resulting from a 60-(solid line) and 100-year (dashed line) fire cycle is shown in the 1910 plot.

Combining disturbance data with provincial scale forest inventory data in a simple age-class projection model, Taylor and Carroll (2004) also reconstructed the area of pine by age-class in British Columbia during 1911-1991. Their results suggest that a large pine age cohort originated around 1880-1920, in an amount consistent with a 60-year fire-cycle. The burn rate may have been higher than would be predicted by a 60-year fire-cycle in this period due to fires resulting from mining exploration, land clearing, and railway activity (e.g., Leavitt 1915). With the introduction of fire management, a large proportion of the stands which regenerated after these fires have matured and entered the susceptible age-class for mountain pine beetle. The result is a threefold increase in the area of pine susceptible to mountain pine beetle during the 20th century (Fig. 11). Plotting the annual mountain pine beetle outbreak area alongside the area of susceptible pine by year suggests that the area increase of mountain pine beetle outbreaks since the 1970s are related to an increasing amount of susceptible pine (Fig. 12), although the outbreak area was apparently not limited by host availability on a provincial scale.

According to Clutter et al. (1983), if the rate of harvest in a fully-regulated forest is changed to a new level there are three possible outcomes: the forest structure will reach a new steady state, the forest will be totally depleted, or the forest will become unmanaged (the amount of timber lost to natural mortality exceeding harvesting). The same possible outcomes can be expected as a result of changing disturbance rates in forests that were historically regulated by natural disturbance. Currently, forest depletions by mountain pine beetle in British Columbia are greatly exceeding depletions by harvesting, making management of forest age structure through harvest regulation challenging.

Climatic Influences

Safranyik et al. (1975) developed a model of the influence of climate on the establishment and persistence of mountain pine beetle populations. They used an analysis of climatic variables measured at 42 locations for the period 1950 to 1971. The model combines six climatic variables believed to be important to beetle survival, attack, brood development, and host tree susceptibility (Table 1). The locations were chosen to represent the historic range of mountain pine beetle in British Columbia. The six variables were combined in an index of climatic suitability for mountain pine beetle (F):

$$F = P_i \overline{)X_1 \times X_2} \qquad [1]$$

where: P_i is the number of years with the joint occurrence of variables P_1 through P_4 in runs of ≥2 consecutive years divided by the total number of years (see Table 2). The values of F range from 0 to 1. Climatic suitability classes (CSCs; Table 3) were created by comparing index values with the frequency of mountain pine beetle infestations across its historic range (Powell 1966). The climatic suitability index provides a means of examining the effect of temporal and spatial variation in climatic suitability on outbreaks.

Table 2. Description of climatic variables utilized to construct a model of climatic suitability of habitats to mountain pine beetle (MPB) 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 MPB survival (Logan and Powell 2001). Minimum heat requirement from peak flight to 50% egg hatch is 305 degree-days, 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 MPB flight is ≈18.3°C (McCambridge 1971). It is assumed that when the frequency of maximum daily temperatures is ≥18.3°C and ≤5% during August, the peak of MPB emergence and flight will be protracted and mass attack success reduced.
P_4	Total precipitation Apr. to Jun. < long-term average	Significant increases in MPB 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 MPB, 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 3. 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+

Carroll et al. (2004) used historic weather and digital terrain data to model climatic suitability across British Columbia for the period 1930-2000. They found that during the latter half of the 20th century, there was a substantial shift in climatically benign habitats for mountain pine beetle northward and toward higher elevations. Areas suitable for mountain pine beetle (i.e., high and extreme CSCs) have expanded dramatically in south-central and south-eastern British Columbia (Fig. 13). The distribution of susceptible age pine by climatic suitability class is shown in Figure 14. As with climate suitability alone, there was an increase in the amount of susceptible age pine in moderate and high suitability classes in central British Columbia during 1950-1990. Furthermore, there was an increase in the amount of susceptible age pine in all climatic suitability classes since 1950 (Fig. 14b).

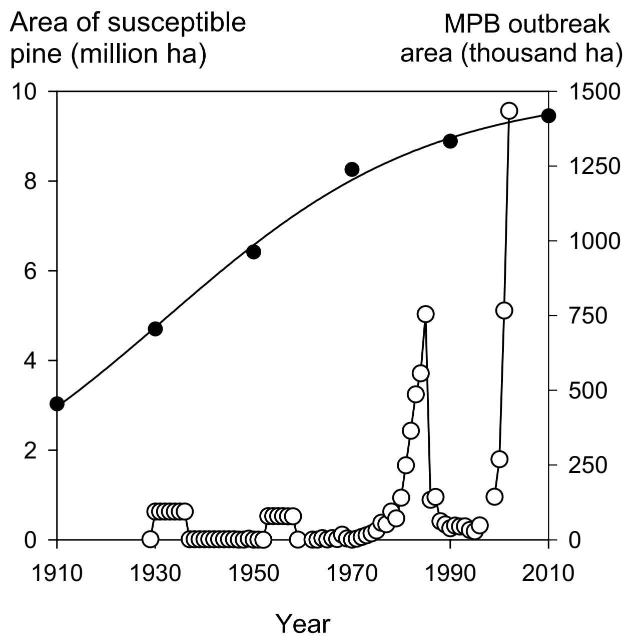

Figure 12. Estimated area of susceptible-aged pine (solid circles = million ha) and of mountain pine beetle (MPB) outbreaks (empty circles = thousand ha) in British Columbia during 1910-2010.

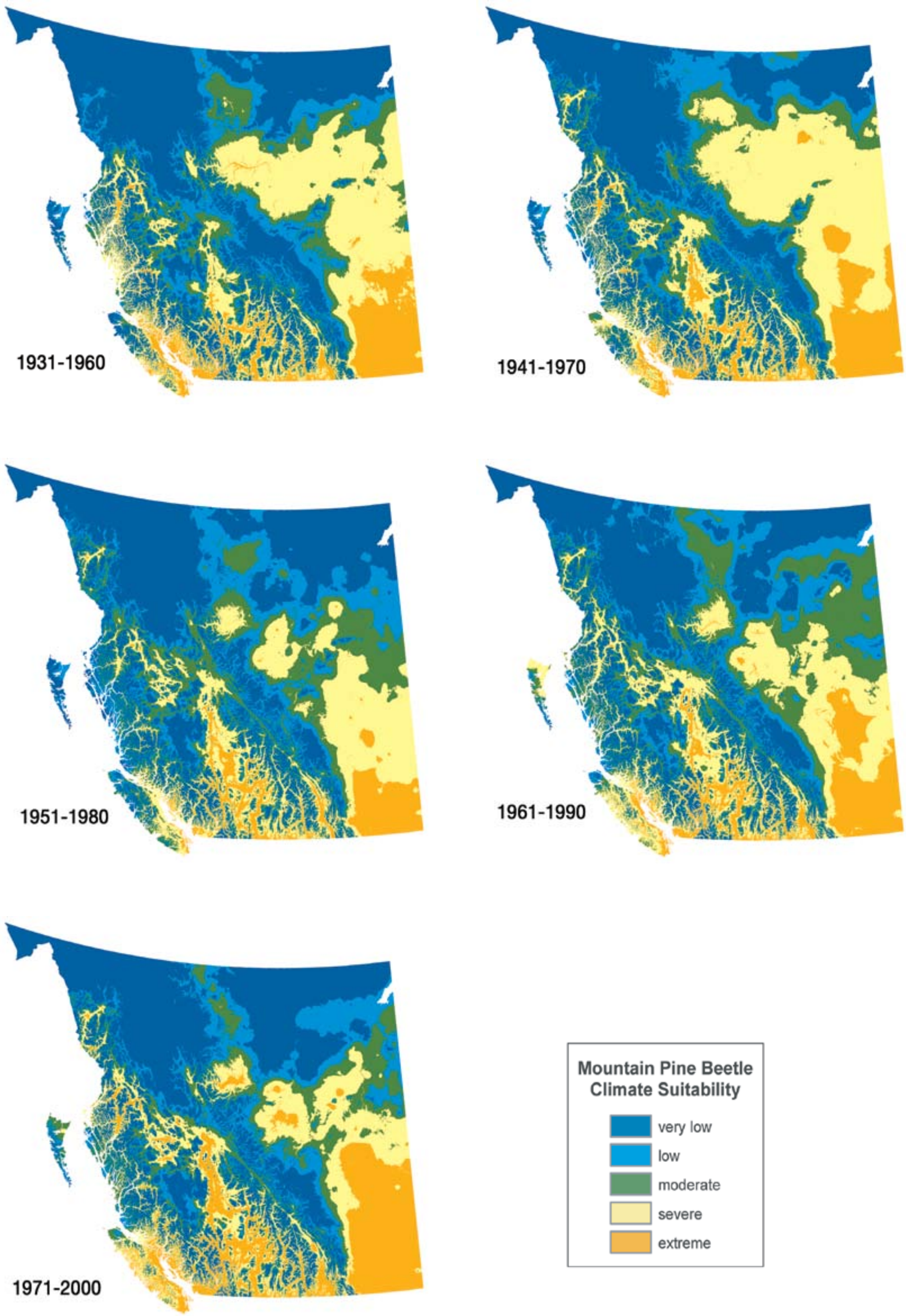

Figure 13. Historic distributions of climatic suitability classes (CSCs) derived from climate normals (30-year monthly means and extreme minima and maxima) for the mountain pine beetle in British Columbia and Alberta. “Very low” CSCs are habitats with climatic conditions unsuitable for mountain pine beetle whereas “extreme” CSCs are those considered climatically optimal.

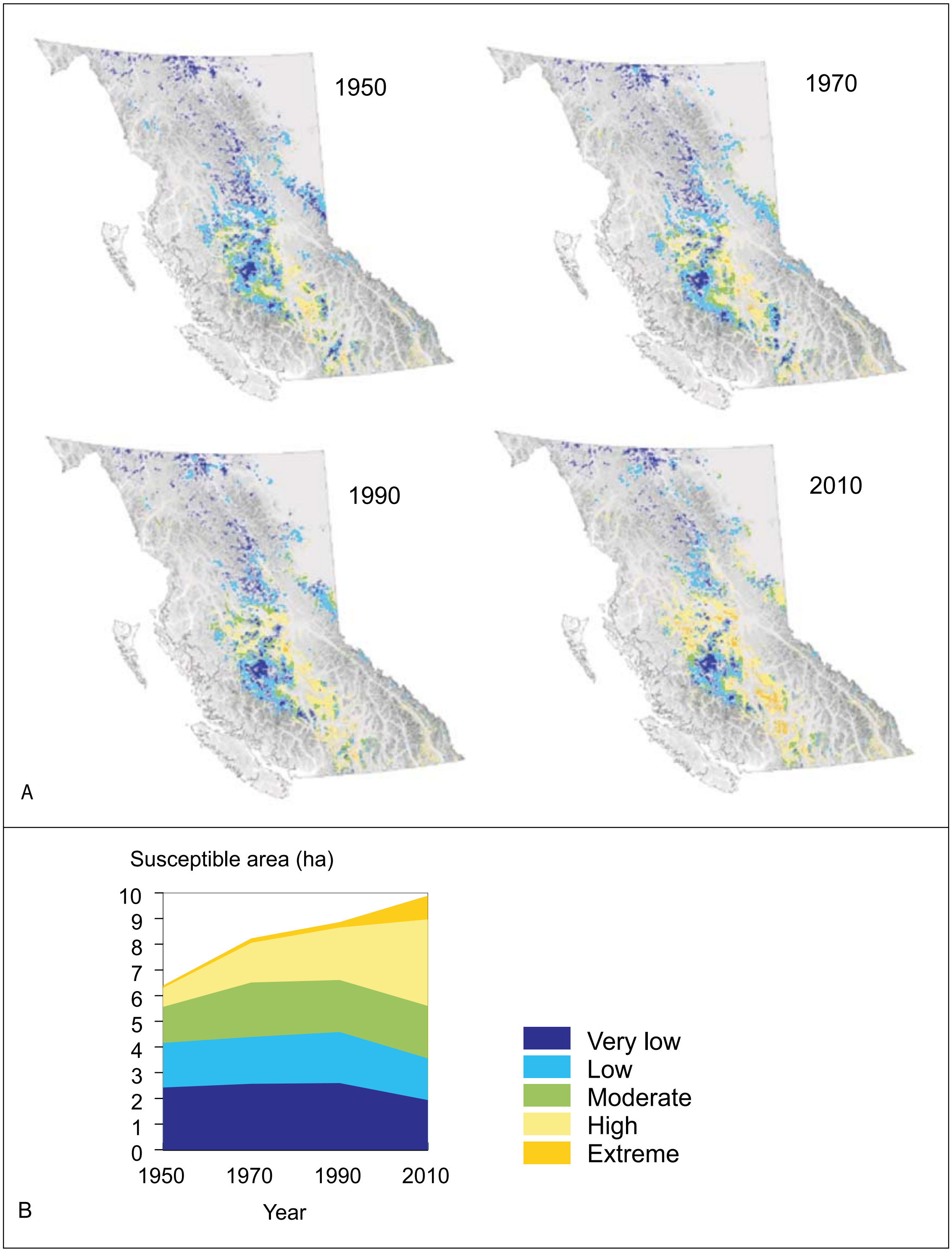

Figure 14. A. Historic and projected distribution of pine of susceptible age by mountain pine beetle climatic suitability class in British Columbia between 1950-2010. B. Area of pine of susceptible age by mountain pine beetle climatic suitability class (million ha) in British Columbia between 1950 - 2010.

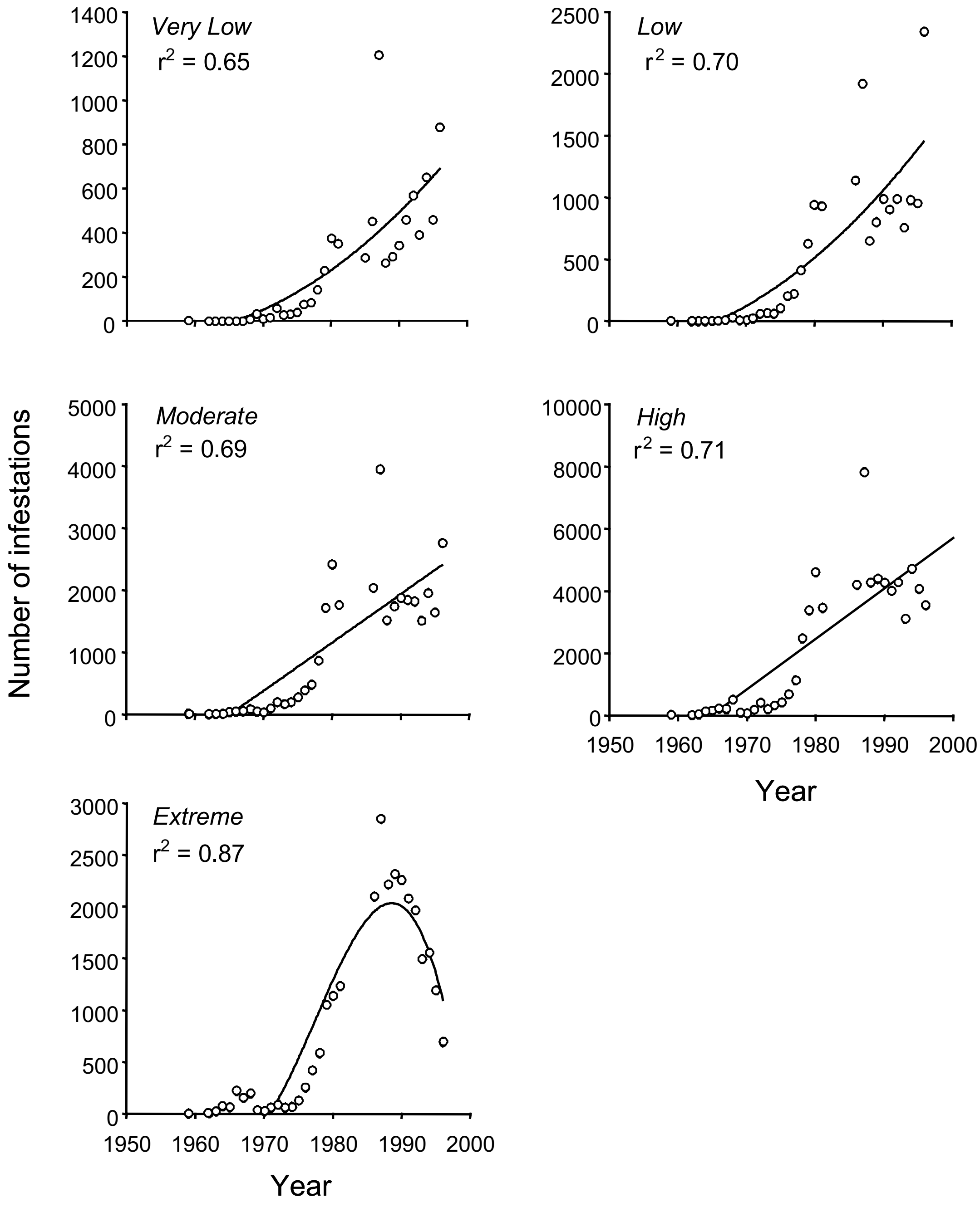

Fig. 15. Mountain pine beetle infestations (all severity classes) from 1998 to 2002 in areas of different climatic suitability classes in British Columbia. "Very low" CSCs are habitats with climatic conditions unsuitable for mountain pine beetle whereas "extreme" CSCs are those considered climatically optimal.

Carroll et al. (2004) also examined the distribution of mountain pine beetle outbreaks in British Columbia from historical survey data in relation to the CSCs. Mountain pine beetle populations have followed the apparent shift in climatically suitable habitats during the past three decades. Prior to 1968, no infestations had been recorded in areas with very low to low

CSCs (Safranyik et al. 1975). Since then, the increase (at an increasing rate) in the number of infestations in these areas of historically very low and low CSCs (Fig. 15) indicates that climate change in these habitats has allowed the establishment and persistence of mountain pine beetle populations in these formerly climatically unsuitable areas. 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, successful establishment of a beetle population is precluded unless the climatic conditions outlined in the climatic suitability model are met within a mature pine stand (Safranyik et al. 1975; Safranyik 1978).

By the mid-1980s, the number of infestations in habitats that were previously most suitable to mountain pine beetle (i.e., extreme CSC) declined dramatically (Fig. 15). There are at least two potential explanations for a decrease in the number of infestations in the formerly extreme CSC: (i) a reduction in the amount of susceptible pine in these habitat types due to previous disturbance (i.e., harvesting, fire, past mountain pine beetle outbreaks), or (ii) adverse effects of warmer temperatures on beetle populations. However, because there has been an apparent increase in the amount of pine in the extreme CSC (see Fig. 14b), the decline in infestations is most likely due to the adverse effects of warming 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 multivoltinism (segments of the population having more than one generation per year) which will cause cold-susceptible stages (eggs, pupae, adults) to overwinter and interrupt flight synchrony, reducing mass attack success in the following year.

Historically, mountain pine beetle outbreaks in Canada have been most common in southern British Columbia. Non-forested prairies, the high elevations of the Rocky Mountains, and the extreme continental climate to the north and east have contributed to confining its range. However, it is hypothesized that as a consequence of global warming, environments that are climatically hostile to the mountain pine beetle will become climatically benign and allow a shift in the beetle's geographical distribution and changes in population behaviour (Logan and Powell 2001). Rapid ecological and genetic adaptation by insects in response to global warming has already been documented in Europe (Thomas et al. 2001). 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 beetle. 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 British Columbia and Alberta at approximately 55° N – areas in which the beetle has not been previously recorded (Alberta Sustainable Resource Development 2003). These beetle populations are now in close proximity to the western range of jack pine, *Pinus banksiana* Lamb., a susceptible species (Cerezke 1995). In the absence of an unusual weather event (i.e., an unseasonable cold period or an extreme winter), expansion by the beetle into new habitats will provide it with a continual supply of mature pine, thereby maintaining populations at above-normal levels for decades into the future.

At the same time, areas with formerly extreme CSCs at southern and low-elevation regions may become less suitable for resident mountain pine beetle populations if further warming results in partial multivoltinism. If this was the case, the net effect would simply be a displacement of mountain pine beetle disturbance northward and areas of former suitability would be, in the future, less suitable. Unfortunately, a recent study (Bentz et al. 2001) has found a genetically-based latitudinal gradient in development rates for mountain pine beetle suggesting that there may be sufficient genetic variability in contiguous mountain pine beetle populations to match changes in the climatic environment within the present range of the species.

Summary

Mountain pine beetle outbreak development is influenced by host susceptibility, climatic suitability for mountain pine beetle, and forest management practices. Host susceptibility may in turn be influenced by the age, species composition, and contiguity of mature stands in the landscape, and by the occurrence of past outbreaks that degrade habitat quality for mountain pine beetle. Past disturbances, including harvesting, wildfire, wildfire suppression, and previous mountain pine beetle outbreaks, can have a profound influence on host susceptibility. Thus, where host susceptibility is age/size-dependent and trees are long-lived, and because it takes a number of years for smaller trees surviving an outbreak to reach a susceptible size, landscapes previously unaffected by outbreaks may be more susceptible than landscapes that have sustained relatively recent attacks.

In the lodgepole pine forests of western Canada, the disturbance regime is changing on a vast scale from an unmanaged state influenced by various natural disturbances to a managed condition in which natural disturbances are suppressed where possible, and forest harvesting is the predominant disturbance. Due to a reduction in the disturbance rate, a large cohort of lodgepole pine has reached an age/size susceptible to mountain pine beetle. This, combined with an increasingly favourable climate allowing for range expansion into previously unaffected forests, has created ideal conditions for an unprecedented mountain pine beetle outbreak. However, this susceptible pine cohort is a transitional phenomena - it is unlikely that such a large amount of susceptible pine will be seen again.

Safranyik (2004) suggested that, in the long-term, our focus should be on management of lodgepole pine, not on management of the mountain pine beetle. However, while management strategies should consider reducing landscape-scale susceptibility, it would take decades to hundreds of years to influence forest composition and age structure over the extensive pine forests in western Canada because large-scale disturbances impart an "ecological memory" to landscape patterns (Peterson 2002). In the short term, a better understanding of the effect of forest dynamics and climatic variation on mountain pine beetle outbreaks will allow for management of lodgepole pine forests with regard to disturbance risk.

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