The Mountain Pine Beetle *Dendroctonus ponderosae* in Western North America: Potential for Area-Wide Integrated Management

A. L. CARROLL

Pacific Forestry Centre, Canadian Forest Service, Victoria BC, Canada V8Z 1M5

ABSTRACT Epidemics of the mountain pine beetle *Dendroctonus ponderosae* Hopkins have occurred within the pine forests of western North America four times during the last century. Considerable resources have been directed toward suppression of populations due to the extensive tree mortality associated with outbreaks. However, management efforts have been largely unsuccessful. A framework for successful control based on simple population processes is proposed and used to evaluate past management efforts. The compounding effects of increasingly susceptible forests due to climate change and the legacy of forest fire suppression are discussed. Due to the increase in the amount of susceptible pine, the mountain pine beetle epidemic that began in the 1990s has spread over nine million hectares. Because of its size, control efforts against the present major outbreak are largely irrelevant. However, a swift and aggressive area-wide control strategy is required to limit the spread of isolated populations east of the Rocky Mountains. This strategy must integrate advances in remote sensing technology that permit the earliest possible detection of small incipient epidemic infestations with novel forms of direct control and aggressive sanitation harvesting. In the long term, mitigation of impacts will only be possible through the area-wide management of the amount of susceptible pine.

KEY WORDS mountain pine beetle, direct control, forest fire suppression, climate change, range expansion, area-wide management

1. Introduction

The mountain pine beetle *Dendroctonus ponderosae* Hopkins. is the most destructive biotic agent of mature pine forests in western North America. Normally it is innocuous, infesting only a few suppressed or damaged trees scattered throughout a forest. However, populations periodically erupt into large-scale epidemics capable of causing the mortality of trees over many thousands of hectares. In Canada, the most extensive outbreaks have occurred in the southern interior regions of British Columbia, while in the USA the largest outbreaks have manifested in the Rocky Mountain states. In addition to extensive timber losses, mountain pine beetle epidemics may increase fuels for wild fires, alter successional patterns of forest growth, affect watershed quality, wildlife composition, and recreational values (Safranyik et al. 1974).

The mountain pine beetle is broadly distributed in western North America from northern Mexico to north-western British Columbia, Canada. Throughout its range, it breeds in virtually all species of native or introduced pine (Furniss and Schenk 1969). However, lodgepole pine *Pinus contorta* var. *latifolia* Engelmann is considered to be the beetles' primary host due to the size, intensity and commercial impact of epidemics in that forest type.

During the past century, four significant mountain pine beetle epidemics have occurred in North America (Taylor and Carroll 2004). Given the extensive tree mortality associated

M.J.B. Vreysen, A.S. Robinson and J. Hendrichs (eds.), Area-Wide Control of Insect Pests, 297–307.

with outbreaks, considerable resources have been directed toward their control. Unfortunately, very few management efforts have achieved population suppression (Klein 1978). The objectives of this paper are to (1) establish a theoretical framework for successful control of the mountain pine beetle derived from simple population processes, (2) utilize this theoretical framework to assess previous efforts at control (insofar as the literature permits), (3) examine the challenges for successful control associated with changing climate and the legacy of past forest management practices, and (4) discuss the relevance of future, area-wide control efforts in the short- and long-term given the current status of mountain pine beetle in North America.

2. A Population-Based Framework for Successful Control

2.1. Mountain Pine Beetle Population Processes

Normally, the mountain pine beetle must kill its host to reproduce successfully. It is a subcortical herbivore that feeds within the phloem (i.e. the vascular tissues between the bark and the sapwood). Mature, large-diameter trees are preferred due to their thicker, more nutritious phloem (Amman 1972). However, these trees are normally the most vigorous and therefore the most resistant to attack within a stand (Safranyik et al. 1974). As attacking beetles bore through the bark of a potential host, the tree responds by producing copious quantities of toxic resin (Berryman 1972). If the density and/or rate of arrival of attacking beetles are low, they may be flushed from the tree or encapsulated in resin-soaked tissues beneath the bark (Safranyik et al. 1975).

The mountain pine beetle has evolved two complex adaptations that facilitate the colonization of often highly resistant trees. First, beetles employ aggregation pheromones to ensure that they arrive and initiate attacks simultaneously (i.e. mass-attack), thereby overwhelming host defences (Raffa and Berryman 1983). Second, the beetles have evolved a mutualistic relationship with phytopathogenic ophiostomoid fungi. Attacking beetles introduce fungal spores that rapidly invade the phloem and sapwood, thereby compromising the expression of tree defences (Safranyik et al. 1975). The combination of larval tunnelling within the phloem, and rapid fungal colonization following mass-attacks invariably cause tree mortality before the onset of winter.

Following successful colonization, mated females oviposit in niches chewed along vertical galleries. Eggs hatch within several days and larvae mine circumferentially around the bole, developing through four instars. The beetles typically overwinter as late-instar larvae, before completing their development during the following spring and early summer (Reid 1962).

There are four distinct phases in the population cycle of the mountain pine beetle: endemic, incipient epidemic, epidemic (i.e. outbreak) and post-epidemic populations (Safranyik and Carroll 2006). The endemic and incipient epidemic phases represent distinct population states regarding interactions of beetles with individual host trees and stands, whereas the latter two population phases mainly represent differences in population size and spatial extent.

Following the collapse of outbreaks during the post-epidemic phase, and before populations increase to incipient epidemics, the mountain pine beetle is considered to be in the endemic phase. An endemic population can be defined as one with insufficient beetles to overcome the resistance of any large-diameter tree within a stand. Beetles are therefore restricted to low-quality host trees with little or no defensive capacity. Natural enemies, weather, inter- and intraspecific competition combine to balance mortality and reproduction rates so annual changes in population and damage levels are minimal. Since female mountain pine beetles produce an average of 60 eggs, and two-thirds of offspring (i.e. 40) are female (Reid 1962), then given that only one female offspring needs to survive to achieve replacement, approximately 97.5% generation mortality (i.e. 39/40) is required to keep endemic populations static (Safranyik and Carroll 2006).

The incipient epidemic phase begins when mountain pine beetle populations have grown to a minimum size sufficient to successfully mass-attack a single large-diameter tree within a stand. The main factors that permit populations to increase to the incipient epidemic phase are those that cause either a decline in tree resistance or an increase in beetle population size. For example, a number of consecutive years of warm and dry weather, favouring beetle survival and compromising tree resistance (through drought), have been associated with sustained increases in beetle populations (Thomson and Shrimpton 1984). Interestingly, only a very small rise in survival is required for populations to increase dramatically. For example, if generation mortality declines from 97.5 to 95.0%, then populations have the potential to double in size (Safranyik and Carroll 2006). Once populations have gained access to large-diameter trees, their potential rate of increase is often extremely high. During the transition from the incipient epidemic to the epidemic phase, local populations often increase more than eight-fold, yearly.

An outbreak forms as incipient epidemic infestations coalesce over the landscape. This involves emigration of mountain pine beetles from localized points of increase into neighbouring stands, thereby facilitating the endemic-incipient epidemic transition of resident populations. If large areas of susceptible host trees coincide with sustained favourable weather conditions for beetle survival, epidemics will spread over vast areas. Due to the sheer number of beetles, epidemic populations can rebound from a large-scale mortality event.

The post-epidemic phase comprises the collapse of outbreaks, generally as a consequence of depletion of the large-diameter trees within stands and/or unseasonably cold weather conditions during the period from late autumn to early spring. In the final stages of the post-epidemic phase, increased mortality from natural enemies and competitors can hasten population collapse (Safranyik and Carroll 2006).

2.2. The Framework

Knowledge of the basic population processes associated with the mountain pine beetle is essential for effective control efforts. In populations where conditions have changed such that reproduction outweighs mortality, unless a sufficient amount of additional mortality is introduced, the infestation will expand. Given that beetles spend the vast majority of their life cycle beneath the bark of trees, the only viable means (to date) of adding mortality involves destroying beetles in infested trees before they can complete their life cycle and disperse to new hosts. More specifically, this entails the treatment of single trees or small groups of trees through felling and burning (or bark removal), removal and processing (where transport to a mill is economical), or the application of a systemic insecticide. Larger groups of trees are felled, transported to a mill and processed; a practice known as sanitation harvesting. The relative success of these tactics is dependent upon the state of the beetle population.

Initially mountain pine beetle populations appear to grow relatively slowly. For example, a stand with one infested tree and a population where the generation mortality has declined slightly to allow it to double each year (i.e. a rate of increase $R = 2$) will have 512 dead trees after ten years. This represents less than 2% of the trees within a 20-hectare stand, and therefore the population may escape detection or concern for a number of years. If the infestation was detected and, in an effort to control it, 37.5% of the infested trees were removed during the 4th year, 194 fewer trees would be killed by year ten, but the population would continue to expand (Fig. 1). From this example, the question arises: what level of mortality must be added and how often, to slow or stop an increasing population?

The general concept is straightforward. To maintain a static population, a proportion of infested trees (*P)* must be removed in each year equivalent to:

$$P = 1\text{-}1/R \qquad (1)$$

where *R* is the yearly rate of increase in the population. In other words, if the population is expected to triple yearly (*R* = 3), then two-thirds of all infested trees would have to be removed and destroyed before the flight period each year. Obviously, if a reduction in the size of the population is the goal, then removal rates must exceed two-thirds. The concept is presented graphically in Fig. 2. For any measured rate of increase, unless sufficient mortality is introduced that equals or exceeds the yearly growth in a population, it will continue to increase.

Figure 1. *Number of trees killed by mountain pine beetle versus age of an incipient epidemic population doubling in size yearly (solid line). The broken line represents the same population with the removal of 37.5% of infested trees in year four.*

With the above framework in mind, control efforts must be considered in light of the population phases described previously. In the endemic situation, population increase is usually constrained to unity. This is the state where management efforts can have their greatest impact. Beetles are restricted to a few weakened or damaged trees within a stand, so relative to the potential rate of increase and the number of trees involved, removal of any of the infested stems would suppress the population (Fig. 2). Thus, provided they can be detected, endemic populations are amenable to virtually any management strategy.

By virtue of their larger size and more obvious impacts, incipient epidemic populations are relatively easy to detect. Because they have gained access through mass-attack to healthy, large-diameter trees, their rates of increase are often between two and four per year. Typically, when these populations are first detected, the number of trees involved is still small (less than 500), and the area they occupy is well defined (Safranyik and Carroll 2006). Yearly rates of increase can be easily assessed through ground and/or aerial surveys of the number of trees or area infested. To limit the potential for increase if *R* = 4, then more than 75% of the infested trees must be treated every year (Fig. 2). If 500 infested trees were found, then at least 375 stems must be treated that season, and a similar proportion in subsequent seasons provided *R* remains constant. If there is ready access to the infestation, it is highly amenable to direct control.

An incipient epidemic population may take only two to three years to develop into an outbreak if left untreated and rates of increase remain high. During an outbreak, the number

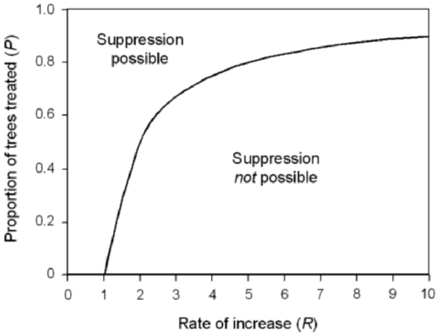

Figure 2. *Graphical representation of the proportion of a mountain pine beetle population (*P*) that must be removed in relation to the yearly rate of increase (*R*) to suppress population growth (*P = *1-1/*R*). The area below the curve represents treatment levels where suppression is not possible; treatment levels above the curve (applied yearly) will suppress populations.*

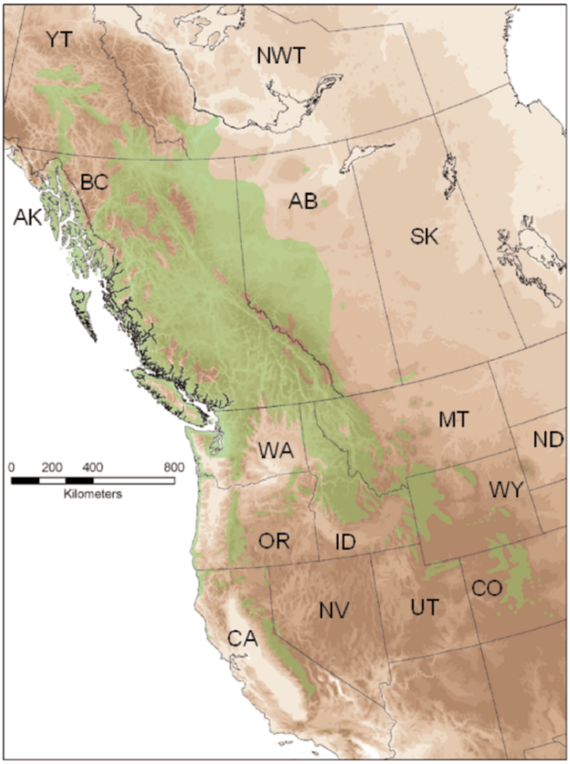

Figure 3. *Distribution of lodgepole pine in North America (adapted from Little 1971).*

of trees killed annually is often in the millions and may encompass hundreds of thousands of hectares. The rate of increase may not be more than that of an incipient epidemic population, but its sheer size renders most management tactics ineffective. As an example, if an outbreak is spread across 300 000 hectares and $R = 2$ (a conservative rate during peak outbreak years), then 150 000 hectares of infested trees must be harvested in each year just to keep the infestation static. Logistically, detection and removal of such a vast number of infested trees is impossible.

3. Trials and Errors: Lessons from the Past

Lodgepole pine forests occur over approximately 160 million hectares of western North America (Fig. 3). The mountain pine beetle is an ubiquitous component of mature stands over much of this area. Despite the vastness of the region in which mountain pine beetle populations exist, epidemics normally initiate and spread from well defined epicentres (Aukema et al. 2006). Therefore, direct control tactics aimed at controlling developing epicentres in the incipient epidemic phase are theoretically amenable to a suppression strategy.

Despite many significant efforts at direct control of mountain pine beetle populations during the previous century, most authors concluded that suppression was seldom if ever achieved and, at best, the rate of tree mortality was reduced only marginally (Craighead et al. 1931, Amman and Baker 1972, Klein 1978, Amman and Logan 1998). A brief examination of historical control activities in light of

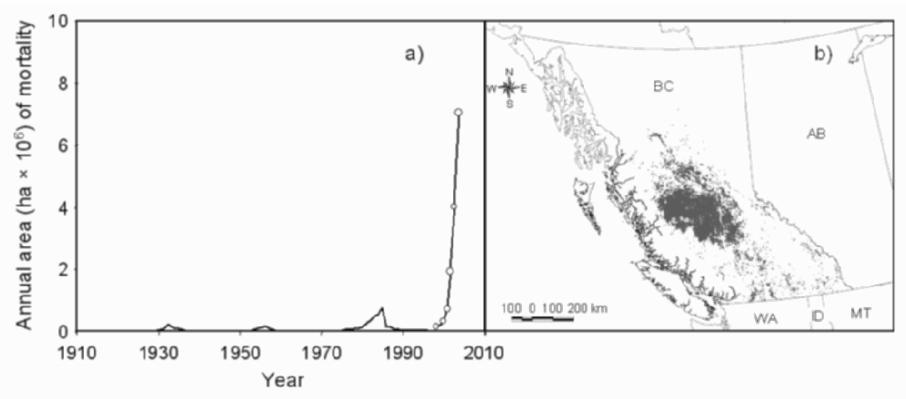

Figure 4. *(a) Historic occurrence of mountain pine beetle epidemics, and (b) cumulative area of mortality from 1992 to 2003 in western Canada.*

the framework proposed above reveals three major shortcomings.

First, most efforts targeted removal of infested trees as either a fixed percentage of the total or of the area involved (Klein 1978). Without assessments of the yearly rate of increase of a population, the treatment levels were most often insufficient. Second, even when a sufficient proportion of a population may have been removed in one year, the efforts frequently did not persist in subsequent years (Craighead et al. 1931). Since incipient epidemic populations often have very high rates of increase, and conditions amenable for increase typically persist for more than one year, then a single aggressive intervention may slow the development of an epidemic, but not prevent it (Fig. 1). Finally, early control programmes suffered from the inability to accurately detect and delimit increasing populations. As a consequence they were often abandoned when populations "erupted" in adjacent unsurveyed jurisdictions (Evenden 1944). In recent years, thorough systematic aerial survey techniques have been developed that provide accurate, real-time quantification of the condition of mountain pine beetle populations over the landscape. In addition, incorporation of these data into geographic information systems (GIS) along with detailed forest "inventory" data (e.g. species composition, stand age, stem density, etc.) have facilitated effective integrated management efforts over large areas (Wulder et al. 2005).

Interestingly, there is one documented example of successful suppression of a mountain pine beetle population. During the early 1940s, an incipient epidemic was detected near Banff, Alberta, Canada. Every tree in the vicinity of the infestation was assessed over two years, and any with evidence of mountain pine beetle attack was felled and burned. During the third year, no beetles could be found (Hopping and Mathers 1945). Although rates of increase were not considered, it is not surprising that such an aggressive and consistent intervention was successful.

4. Changing Rules? Altered Disturbance Regimes and Global Warming

Although mountain pine beetle populations have erupted several times in the past, the latest outbreak that began in the early 1990s has reached levels that are nearly an order of magnitude greater than any previously recorded (Fig. 4a). Its consistent rate of increase quickly outstripped the resources available for its management. Indeed, populations have been doubling each year for the past eight to ten years such that the cumulative area impacted comprises well over nine million hectares of lodgepole pine forests in western Canada alone (Fig. 4b). As outlined above, for an epidemic to occur there must be an abundance of susceptible host trees in combination with a sustained period of favourable weather. Both of these conditions have coincided in recent years in western North America. Moreover, evidence suggests that these conditions have been exacerbated by anthropogenic activities.

Virtually all lodgepole pine forests originate from stand-replacing wild fires (Smith 1981). However, due to aggressive fire suppression, the average yearly area burned in lodgepole pine in western Canada has declined to less than 1% of historic levels during the last five decades (Taylor and Carroll 2004). This dramatic reduction in the rate of disturbance has allowed pine forests to age to the extent that nearly 70% of current stands are more than 80 years old – a significantly greater proportion than that expected from a natural wild-fire regime (Taylor and Carroll 2004). Since mountain pine beetles preferentially attack trees more than 80 years old (Safranyik et al. 1974), fire suppression has dramatically increased the amount of susceptible trees. In fact, it has been estimated that there was 3.3 times more susceptible pine at the start of the present mountain pine beetle epidemic than in 1910 (Taylor and Carroll 2004).

In addition to an abundance of suitable hosts, climatic conditions have steadily improved for mountain pine beetle populations in recent years. Historically, the extent and severity of epidemics have been limited by insufficient summer temperature accumulation and/or minimum winter temperatures below a critical mortality threshold (Carroll et al. 2004). It has recently been shown that during the past three decades relevant climatic conditions have improved for the beetle over large portions of western Canada (Carroll et al. 2004). More importantly, as a consequence of changing climate, populations have expanded into formerly climatically unsuitable habitats, especially toward higher elevations and more northerly latitudes. Indeed, large parts of the current epidemic occur in areas that were climatically unavailable prior to 1970, despite the presence of susceptible host trees (Carroll et al. 2004).

Previous large-scale mountain pine beetle epidemics have collapsed as a consequence of localized depletion of suitable host trees in combination with the adverse effects of climate (Carroll et al. 2004). Given that the occurrence of an adverse weather event sufficiently severe and widespread to affect the epidemic is improbable, the current outbreak in western Canada is projected to continue unabated until 2015 when approximately 80% of susceptible pine could be killed (Eng et al. 2004). Due to the sheer size of the epidemic, efforts to control it have been largely abandoned and redirected toward salvage of dead stands. However, aggressive tactics aimed at slowing the spread of the outbreak at its periphery continue and remain important to minimize the potential spread of the mountain pine beetle into new habitats.

5. Area-Wide Control: Relevance in the Short- and Long-Term

Although the current mountain pine beetle epidemic in western North America renders irrelevant any available control tactic, recent expansion of the epidemic beyond the geo-climatic barrier presented by the Rocky Mountains (Carroll et al. 2004) demands an aggressive area-wide control effort. During 2004, mountain pine beetle infestations were discovered in the Peace River region of north-eastern British Columbia, Canada (Fig. 5); an area that was historically considered climatically unsuitable for mountain pine beetle (Safranyik et al. 1974, Carroll et al. 2004). Assessments of these infestations revealed that they originated in 2002 (i.e. did not increase from local populations), most probably as a consequence of long-distance dispersal from epidemic populations located several hundred kilometres to the south-west, across the Rocky Mountains (Fig. 5). The expansion by the mountain pine beetle into this previous-

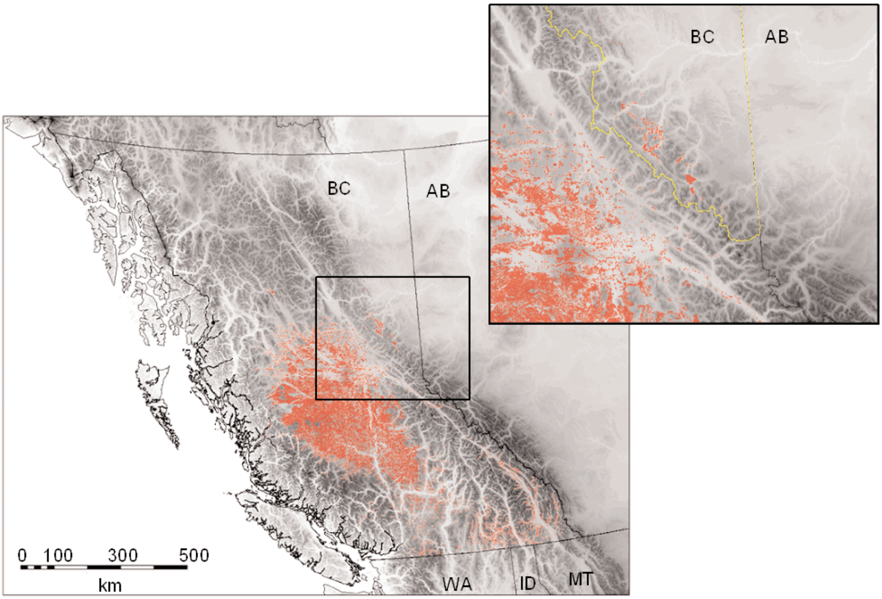

Figure 5. *Distribution of the mountain pine beetle epidemic in western Canada in 2004, and (inset) the isolated population established east of the Rocky Mountains as a consequence of a long-distance dispersal event in 2002.*

ly unoccupied region is a source of considerable concern. Immediately adjacent the Peace River region, lodgepole pine forests intermingle and hybridize with jack pine *Pinus banksiana* Lamb., a species susceptible to mountain pine beetle (Furniss and Schenk 1969), and a major component of the boreal forest that encompasses most of northern North America.

Several aspects of the Peace River population make it amenable to a variety of area-wide control techniques: (1) it is isolated from the epidemic to the west. Although additional inputs of beetles into the region via long-range dispersal are possible, it has not occurred subsequent to the original introduction, and the probability of the occurrence of such an event diminishes yearly as the source population to the west declines due to host depletion, (2) in relative terms the population is small, consisting of scattered incipient epidemic infestations, and confined to an area of approximately 2000 square kilometres along the north-eastern slopes of the Rocky Mountains (Fig. 5), (3) the region is almost entirely comprised of publicly owned land, facilitating an area-wide approach, and (4) the state of the beetle population, its distribution and its rate of increase are extremely well quantified based upon aerial and ground surveys (A.L. Carroll, unpublished). Since this final aspect is critical to successful area-wide management, it is worthy of further examination.

Once mountain pine beetle populations reach the incipient epidemic state, the number of infested trees can be used as a reliable index of beetle population size (Safranyik 1988). Infested trees display several distinct symptoms (Safranyik and Carroll 2006). The most obvious and easiest to detect over large landscapes by standard analogue (i.e. aerial surveys) or digital (i.e. aircraft- or satellite-borne sensor) remote sensing techniques, comprises gradual "fading" of foliage from green through yellow to reddish brown as leaves become chlorotic and die (reviewed by Wulder et al. 2006).

Although quantification of the number of infested trees based on crown fading can provide a simple and accurate indication of the location, size and yearly rate of increase of mountain pine beetle infestations, by itself it has limited value in beetle management programmes due to a significant delay in the onset of crown fading following attacks. Adult beetles disperse, colonize and establish broods in new trees during mid to late summer of each year. However, reliable visible signs of foliage fading do not manifest until early summer of the year after attack, leaving only an 8- to 12-week period following detection within which to plan and apply control tactics before emergence and dispersal of the next beetle generation. This narrow temporal window generally precludes application of effective control tactics, particularly in remote and inaccessible areas such as the Peace River region.

In recent years, significant research efforts have focused on developing techniques to detect infested trees before the onset of visible changes to foliage (reviewed by Wulder et al. 2006), thereby increasing the temporal window for direct control efforts. Unfortunately, reliable differentiation of non-visual stress due to mountain pine beetle attack from other sources of stress has so far been impractical with existing technologies. To maximize the time available to access and treat infested trees, traditional mountain pine beetle management programmes employ a hierarchical approach involving: (1) aerial surveys to ascertain the location of infestations based on visual crowns symptoms, (2) systematic ground surveys around identified infestations to locate newly colonized trees based upon evidence of attack on the bole (Safranyik and Carroll 2006), and (3) prioritization and application of treatments based on an integrated management plan intended to encompass ecological and economical objectives (Hall 2004). Given the significant potential for the Peace River population to expand eastward toward the boreal forest (Carroll et al. 2004), traditional detection and monitoring systems have been applied with unprecedented rigour, thereby providing reliable information on the state of the beetle population and making possible an area-wide control programme.

Although research into novel tactics for direct control continues (Borden 1995), the eruptive nature of mountain pine beetle requires that any intervention against the Peace River population be swift and aggressive. Consequently, in the short term the suite of available area-wide control tactics will be limited to conventional techniques such as aerial and ground surveys to detect infestations, followed by felling and burning, or harvesting and processing. However, to minimize the probability of continued spread toward the boreal forest, management in the near future must integrate existing operational control tactics with emerging techniques for detection/monitoring and novel forms of direct control. For example, advances in remote sensing technology that permit early detection of endemic or small incipient epidemic infestations throughout the region combined with prompt application of fell and burn treatments. Alternatively, if larger incipient epidemic infestations are detected, aggregation and anti-aggregation pheromones should be deployed to concentrate beetles in accessible stands followed by aggressive sanitation harvesting (Borden 1995). In the longer term, management efforts should focus on an area-wide approach to reduce the susceptibility of host trees through silvicultural modification of existing pine stands to increase their vigour and, therefore, resistance to the beetle, and/or harvest planning or prescribed wild fire to create landscapes with a mosaic of age classes or tree species.

In spite of the most aggressive efforts, eradication of the Peace River population using conventional approaches to direct control will be virtually impossible given the challenges associated with detection and treatment of low-density populations in remote forested landscapes. Based on the preponderance of susceptible hosts (Taylor and Carroll 2004) and the potential for continued improvements to climatic conditions due to global warming (Carroll et al. 2004), the mountain pine beetle population will likely persist in this new habitat, and the threat of spread to the boreal forest will remain. If the Peace River mountain pine beetle population can be controlled, and its spread limited in the short term, other tactics may emerge that ultimately facilitate its eradication. For example, sterile insect releases have been successfully employed in the area-wide control of coleopteran species (Setokuchi et al. 2001), although the feasibility of this technique has not been explored against bark beetles.

6. References

Amman, G. D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. Journal of Economic Entomology 65: 138-140.

Amman, G. D., and B. H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. Journal of Forestry 70: 204-209.

Amman, G. D., and J. A. Logan. 1998. Silvicultural control of mountain pine beetle: Prescriptions and the influence of microclimate. American Entomologist 1998 (Fall): 166-177.

Aukema, B. H., A. L. Carroll, J. Zhu, K. F. Raffa, T. Sickley, and S. W. Taylor. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. Ecography 29: 427-441.

Berryman, A. A. 1972. Resistance of conifers to invasion by bark beetle-fungal associations. BioScience 22: 598-602.

Borden, J. H. 1995. Development and use of semiochemicals against bark and timber beetles, pp. 431-449. *In* Armstrong, J. H., and W. G. H. Ives (eds.), Forest insect pests in Canada. Natural Resources Canada, Canadian Forest Service, Science and Sustainable Development Directorate, Ottawa, Canada.

Carroll, A. L., J. Regniere, S. W. Taylor, and L. Safranyik. 2004. Effects of climate change on range expansion by the mountain pine beetle, pp. 223-232. *In* Shore, T. L., J. E. Brooks, and J. E. Stone (eds.), Proceedings: Mountain Pine Beetle Symposium: Challenges and Solutions, 30-31 October 2003, Kelowna, Canada. Canadian Forest Service Information Report BC-X-399, Victoria, Canada.

Craighead, F. C., J. M. Miller, J. C. Evenden, and F. P. Keen. 1931. Control work against bark beetles in western forests and an appraisal of results. Journal of Forestry 29: 1001-1018.

Eng, M., A. Fall, J. Hughes, T. Shore, W. Riel, and P. Hall. 2004. Provincial-level projection of the current mountain pine beetle outbreak. British Columbia Ministry of Forests, Victoria, Canada. http://www.for.gov.bc.ca/hre/bcmpb/ BCMPB_MainReport_2003.pdf

Evenden, J. C. 1944. Montana's thirty-year mountain pine beetle infestation. USDA Forest Insect Laboratory, Bureau of Entomology and Plant Quarantine, Coeur d'Alene, Idaho, USA.

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

Hall, P. M. 2004. Provincial bark beetle strategy: technical implementation guidelines, pp. 67-75. *In* Shore, T. L., J. E. Brooks, and J. E. Stone (eds.), Proceedings: Mountain Pine Beetle Symposium: Challenges and Solutions, 30-31 October 2003, Kelowna, Canada. Canadian Forest Service Information Report BC-X-399, Victoria, Canada.

Hopping, G. R., and W. G. Mathers. 1945. Observations on outbreaks and control of the mountain pine beetle in the lodgepole pine stands of western Canada. The Forestry Chronicle, June 1945: 1-11.

Klein, W. H. 1978. Strategies and tactics for reducing losses in lodgepole pine to the mountain pine beetle by chemical and mechanical means, pp. 54-63. *In* Berryman, A. A., G. D. Amman, R. W. Stark, and D. L.

Kibbee (eds.), Proceedings, Symposium: Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. University of Idaho, Moscow, USA.

Little Jr, E. L. 1971. Atlas of United States trees. Volume 1: conifers and important hardwoods. US Department of Agriculture Miscellaneous Publication 1146. Washington, DC., USA.

Raffa, K. F., and A. A. Berryman. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecological Monographs 53: 27-49.

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. 1988. Estimating attack and brood totals and densities of the mountain pine beetle in individual lodgepole pine trees. The Canadian Entomologist 120: 323-331.

Safranyik, L., and A. L. Carroll. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests, pp. 3-66. *In* Safranyik, L., and B. Wilson (eds.), The mountain pine beetle: a synthesis of its biology and management in lodgepole pine. Natural Resources Canada, Canadian Forest Service, Victoria, BC, Canada.

Safranyik, L., D. M. Shrimpton, and H. S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service, Technical Report No. 1. Victoria, BC, Canada.

Safranyik, L., D. M. Shrimpton, and H. S. Whitney. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada, pp. 406-428. *In* Baumgartner, D. M. (ed.), Management of lodgepole pine ecosystems. Washington State University Cooperative Extension Service, Pullman, USA.

Setokuchi, O., T. Sugimoto, T. Yamaguchi, S. Izumi, T. Tokunaga, K. Kawasoe, T. Tanaka, N. Makino, and Y. Sakuratani. 2001. Efficiency of the sterile insect release method as an eradication method for the sweet potato weevil, *Cylas formicarius* (Fabricius) (Coleoptera: Brentidae) in the field. Applied Entomology and Zoology 36: 161-167.

Smith, J. H. G. 1981. Fire cycles and management alternatives, pp. 511-531. *In* Mooney, H. A., T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners (eds.), Proceedings: Fire Regimes and Ecosystem Properties, 11-15 December 1978, Honolulu, USA. USDA Forest Service General Technical Report WO-26, Washington, DC., USA.

Taylor, S. W., and A. L. Carroll. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: a historical perspective, pp. 41-51. *In* Shore, T. L., J. E. Brooks, and J. E. Stone (eds.), Proceedings, Mountain Pine Beetle Symposium: Challenges and Solutions, 30-31 October 2003, Kelowna, Canada. Canadian Forest Service Information Report BC-X-399, Victoria, Canada.

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

Wulder, M. A., R. S. Skakun, S. E. Franklin, and J. C. White. 2005. Enhancing forest inventories with mountain pine beetle infestation information. The Forestry Chronicle 81: 149-159.

Wulder, M. A., C. C. Dymond, J. C. White, D. G. Leckie, and A. L. Carroll. 2006. Surveying mountain pine beetle damage of forests: a review of remote sensing opportunities. Forest Ecology and Management 221: 27-41.