

Chapter 3

Effects of the Mountain Pine Beetle on Lodgepole Pine Stand Structure and Dynamics

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Abstract

This chapter reviews the ecology of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) in relation to interactions with fire and the mountain pine beetle (*Dendroctonus ponderosae* Hopk. [Coleoptera: Scolytidae]), with special reference to western Canada. Lodgepole pine has wide ecological amplitude. In western Canada, lodgepole pine is present in the majority of biogeographic zones in its distributional range and has four successional roles ranging from minor seral to climax. Although lodgepole pine can regenerate without fire disturbance, it is principally a fire-maintained species. The mean fire return period and mean fire size are the major determinants of age distribution of lodgepole pine types on the landscape, and hence the spatial and temporal extent of susceptible forests. Epidemics may heavily deplete the large diameter pine components of stands, thereby increasing the non-host overstory component of mixed stands. The surviving host and non-host trees will generally increase in growth. Post-epidemic development of forest types depends on a large number of factors such as fire disturbance, extent of stand depletion, advance regeneration, presence of non-host overstory trees, and biogeographic zone, and may range from pure stands of lodgepole pine to pure stands of non-host species.

Résumé

Le présent chapitre étudie l'écologie du pin tordu latifolié (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) en rapport avec les interactions du feu et du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopk. [Coleoptera: Scolytidae]), principalement dans l'Ouest canadien. Le pin tordu latifolié a une grande amplitude écologique. Dans l'Ouest canadien, il se rencontre dans la majorité des zones biogéographiques comprises dans son aire de répartition et joue quatre rôles dans la succession forestière, depuis le stade de transition jusqu'au stade climacique. Bien que les perturbations occasionnées par le feu ne soient pas indispensables à la régénération du pin tordu latifolié, elles jouent un rôle prédominant dans la pérennité de cette essence. La fréquence et l'ampleur moyennes des incendies sont les principaux déterminants de la répartition par âge des types de pins tordus latifoliés à l'échelle du paysage et, par conséquent, de la répartition des forêts vulnérables dans le temps et dans l'espace. Les épidémies peuvent entraîner une forte réduction des pins de grand diamètre dans les peuplements touchés, ce qui

fait augmenter, par conséquent, l'élément non hôte de l'étage dominant des peuplements mixtes. La croissance des arbres survivants, tant hôtes que non hôtes, va généralement s'intensifier à la suite d'une infestation. L'établissement, après une épidémie, des types forestiers dépend de nombreux facteurs, comme les perturbations liées au feu, l'ampleur de la réduction du peuplement, une régénération préexistante, la présence d'arbres non hôtes dans l'étage dominant et la zone biogéographique. Selon le rôle joué par ces divers facteurs, la formation des nouveaux types forestiers peut aller de peuplements purs de pins tordus latifoliés à des peuplements purs d'essences non hôtes.

Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae), is the most significant biological agent of mortality in mature pines in western North America. Adult beetles attack and cause mortality in most species of pine within the beetle's range. Early epidemics were reported primarily in ponderosa pine (*Pinus ponderosa* P.Laws. ex C.Laws). In recent years, the majority of large epidemics have occurred in lodgepole pine (*P. contorta* Dougl. ex Loud.); therefore, this chapter focuses on this host species.

Multiple-use, sustainable management of forest resources requires a sound understanding of stand dynamics resulting from mountain pine beetle outbreaks. This knowledge is crucial to managing forests in a manner that approximates natural disturbance processes and patterns while reducing future risks from mountain pine beetle attacks. Due to the importance of lodgepole pine to the ecology and economy in Canada and the USA, substantial research efforts have focused on mountain pine beetle. Considering the depth of our knowledge regarding mountain pine beetle biology and the ecology of lodgepole pine forests, very little is known about how the beetle and fire interact in lodgepole pine dominated forest stands, and how mountain pine beetle, lodgepole pine stand dynamics, and fire interact on the landscape to regulate the ecosystem as a whole.

Although a variety of silvicultural tools and management strategies can be used to minimize timber losses to mountain pine beetle (Safranyik et al. 1974; Shore and Safranyik 1992; Maclauchlan and Brooks 1994; McMullen et al. 1986; Whitehead et al. 2001), effective control programs require early detection, rapid implementation, and continuous commitment. Long-term effects of these control strategies on the ecosystem are unknown (Hughes and Drever 2001), and little is known about long-term, post-epidemic development and growth of stands that have not undergone control measures. A sound understanding of the impact of mountain pine beetle outbreaks on growth and yield of surviving trees in residual stands, regeneration, woody debris dynamics, and fire potential is needed for managers to make better decisions regarding stand management in the face of mountain pine beetle infestations.

The mountain pine beetle-blue stain fungi association affects the structure and dynamics of lodgepole pine forests via interactions with individual tree characteristics, stand characteristics, and the distribution of these characteristics on the landscape (see Chapter 1).

In this chapter, we review the current knowledge of mountain pine beetle effects on lodgepole pine stand structure and dynamics. As fire plays an important role in lodgepole pine ecology (Agee 1993), we briefly review the main silvical characteristics of lodgepole pine and the effects of fire on regeneration and age distribution on the landscape. We then describe a sample of predominantly lodgepole pine stands from infestations in British Columbia as they were prior to infestation, just after infestation, and as they are currently. This information provides a foundation to the knowledge base required to manage large areas of beetle-killed forest and illuminates the gaps in knowledge that require further research.

The prevalence of lodgepole pine forests

In Canada, two subspecies of *Pinus contorta* occur: shore pine (*P. contorta* Dougl. ex Loud. var. *contorta*) and lodgepole pine (*P. contorta* var. *latifolia* Engelm.). The former is confined to the coast and islands of British Columbia. Although both varieties can be attacked and killed by the mountain pine beetle, by far the most damage occurs in lodgepole pine.

Lodgepole pine is an important component of the forests of western North America. Its range extends from about 37° to about 64° latitude and from the Pacific coast to the Black Hills of South Dakota (Koch 1996). In the USA it represents about 6 million ha of commercial forest land (Koch 1996). In Canada, the total area of lodgepole pine forest type is about 20 million ha, mostly in British Columbia and Alberta. Lodgepole pine comprises 22% of the total forest in western Canada (Koch 1996). In British Columbia, pine species cover approximately 14 million ha, most of it lodgepole pine (Taylor and Carroll 2004). Prior to the current massive infestation, pine accounted for roughly 25% of the provincial timber supply in British Columbia (Taylor and Carroll, 2004). In Alberta, pine represents approximately 41% of the coniferous forests, or about 7 million ha. The majority of pine in Alberta is lodgepole pine and jack pine (*P. banksiana* Lamb.). Pine forests serve many purposes such as recreation, habitat for wildlife, cover for watersheds, lumber and fibre production.

Silvics of lodgepole pine

Lodgepole pine has large ecological amplitude. For example, in Alberta and British Columbia lodgepole pine grows in all but three of nearly 20 biogeoclimatic zones (Pojar 1985). Lodgepole pine grows from low to high elevations, from warm to cold, and from relatively dry to wet conditions, and it grows on most soil types (Schmidt 1989), but it is most prevalent within an elevation range of 800 to 1400 m. It reproduces best on bare soil. With relatively minor exception, lodgepole pine is a seral species that is highly shade intolerant but grows fast at a young age. This is an important characteristic of a pioneer species that enables it to compete successfully with other vegetation for space and light. As a consequence, most lodgepole pine stands tend to be even-aged, homogeneous in composition and, in the absence of a disturbance event such as fire, succeeded by more shade tolerant species. Commonly,

the succeeding species are Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) and white spruce (*P. glauca* Moech [Voss]). The rate at which succession proceeds varies by site conditions, being relatively fast in low elevation mesic sites and considerably slower in northern and high-elevation forests (Schmidt 1989).

Lodgepole pine has two types of cone habits: open and serotinous. Seeds are released from open cones usually during September and October but serotinous cones require high temperatures in the range of 45° - 50° C to open and release seeds. Ambient temperatures of this magnitude can occur on or near the ground during summer in most stands, at least at lower elevations. However, in areas where lodgepole pine has a predominantly serotinous cone habit, fire events provide the most suitable conditions for a high density of seeds to be released over a short time period. This is sufficient for establishment of even-aged, new stands. The incidence of cone serotiny increases with latitude (Koch 1987) but tends to decrease with elevation. Near the northern limit of mountain pine beetle distribution (latitude 56°N), on average about 80% of mature lodgepole pine trees have serotinous cones. However, the incidence of serotiny can vary considerably among and within stands (Koch 1996). Lodgepole pines 6-10 years old start producing cones that are mainly the open cone type and cone serotiny is set between ages 17 and 60 (Koch 1987).

Four basic successional roles are described for lodgepole pine (Pfister and Daubenmire 1975):

1. *Minor seral*. Lodgepole pine is a minor component in young, even-aged, mixed species stands and is replaced by more shade-tolerant species, often within 50-100 years on more mesic sites.
2. *Dominant seral*. Even-aged lodgepole pine is the dominant cover type that is replaced by an understory of shade-tolerant species in 100-200 years.
3. *Persistent*. This is similar to the Dominant seral condition except that there is little evidence of replacement by shade-tolerant species. This situation usually occurs when there are either inadequate seed sources of shade-tolerant species or the site is poorly suited for other tree species.
4. *Climax*. These are sites where lodgepole pine is the only tree species capable of growing. Consequently, it perpetuates itself usually in uneven-aged stands. This condition is often found on sites where soils hold limited moisture.

Lodgepole pine forest and stand dynamics

The high incidence of serotinous cone habit of lodgepole pine in western Canada is an indication of the important role wildfires played in its ecology under natural conditions. The importance of fire in maintaining lodgepole pine on the landscape is well documented (Agee 1993). Although lodgepole pine produces both serotinous and non-serotinous cones, permitting successful regeneration in either the presence or absence of fire, it is considered to be a fire dependent species (Lotan et al. 1985). The landscape level age-class structure

of lodgepole pine can be described as a mosaic of even-aged and uneven-aged patches intermingling in space and time (Agee 1993). Whether a given patch or stand is even-aged or uneven-aged depends upon the disturbance history of the site: in the absence of fire, consecutive mountain pine beetle attacks in the stand contribute to conversion of an even-aged stand to an uneven-aged stand (Roe and Amman 1970). Non-stand-replacement fires (i.e., surface fires) also lead to creation of uneven-aged stands (Agee 1993). The type of fire regime that operates within a given stand or landscape has significant effects on stand structure. High-intensity stand-replacement fires create even-aged stands, whereas low-intensity surface regime fires contribute to development of uneven-aged stands. Falling dead trees following fire may cause mechanical injury to seedlings or residual overstory and provide entry for fungal infections, which can provide a focal point for endemic level mountain pine beetle infestations (Geiszler et al. 1984).

Lundquist and Negron (2000) developed a conceptual model of stand development in ponderosa pine that linked stand structure with underlying tree-killing disturbances. Disturbance agents could be classified into two basic ecological functions. First, new stands developed as a result of fire, wind, and epidemic populations of mountain pine beetle killing trees over large areas. Second, small-scale canopy gaps influenced stand development and structure due to a wide variety of factors killing small numbers of trees. Due to the complexity of interactions in both space and time between various disturbances, the authors indicated that direct effects of specific agents might be difficult to estimate.

Without fire control, and considering an average fire return period of 100 years and an expected negative exponential age-class distribution (Van Wagner 1978), on average only a relatively small proportion of unmanaged lodgepole pine stands would be susceptible to mountain pine beetle at any one time (Taylor and Carroll, Canadian Forest Service, Victoria, British Columbia, unpublished report). As a consequence of increased success in fire control over the past century, combined with recent (ca 40 years) commercial utilization of lodgepole pine, the area in British Columbia covered by mature lodgepole pine in 2000 was over three times that of 100 years ago (Taylor and Carroll, 2004). In addition to the area occupied by lodgepole pine forests, size distribution of age-classes and their spatial arrangement on the landscape may also have important consequences for the spread of epidemics by dispersing beetles (Li et al. 2005). In a given landscape, in unmanaged natural stands, size distribution and spatial arrangement of age-classes will be dominantly affected by wildfire characteristics.

In the longer term, combinations of fire control, harvesting of commercial stands, type conversion, and use of prescribed fire in non-commercial areas will result in a reduction in the area and contiguity of susceptible stand types. These actions are not likely to reduce the frequency of mountain pine beetle outbreaks, but should certainly reduce their intensity, outbreak size and tree volumes affected. For example, consider a landscape that is dominated by lodgepole pine stand types where lodgepole pine is the preferred species for regeneration. When managed strictly on a sustained-yield basis in the long term, the area occupied by susceptible (mature) age-classes will be roughly of an area that produces a wood volume equal to yearly volume growth. Moreover, these mature stands will be interspersed with younger (less susceptible) stands.

Mountain pine beetle and lodgepole pine forests

Mountain pine beetle is the most significant forest insect affecting lodgepole pine forests in western North America. Historically, in Canada, most of the damage occurred in lodgepole pine forests of the southern interior regions of British Columbia. This insect is responsible for killing large numbers of mature pine trees in western North America each year (Ebata 2004; Gibson 2004). In the USA, the area infested by mountain pine beetle approximately doubled to 0.7 million ha in 2002 (Gibson 2004). In recent years, British Columbia has experienced an unprecedented infestation, with over 8 million hectares of lodgepole pine affected by 2005 (Ebata, T., personal communication, British Columbia Ministry of Forests, Victoria, British Columbia). This current infestation is the worst of a number of infestations that have been documented in British Columbia (Alfaro et al. 2004; Wood and Unger 1996) and has been described as the worst insect infestation ever recorded in a North American forest (British Columbia Ministry of Forests 2003).

During outbreaks, the large diameter components of stands can be heavily depleted over vast areas (Safranyik et al. 1974). Also, during and following mountain pine beetle outbreaks, populations of some secondary bark beetle species such as the pine engraver (*Ips pini* [Say]) can build up simultaneously in parts of killed trees not utilized by mountain pine beetle (Safranyik and Linton 1991). During and following the collapse of mountain pine beetle outbreaks, these secondary species often kill some trees on their own. These infestations, however, are usually short-lived and tree mortality is normally confined to smaller diameter classes (Safranyik and Linton 1991; Wood and VanSickle 1988).

In addition to socioeconomic impacts, in areas of high outbreak hazard, mountain pine beetle infestations affect the structure and dynamics of lodgepole pine stands. The magnitude of tree mortality caused by mountain pine beetle epidemics creates a situation where thousands of stands, of which lodgepole pine is a component, contain a mixture of live and dead trees. The resultant change in stand structure and characteristics has major ramifications on a number of resource issues such as timber production, forest regeneration and growth, hydrology, wildlife and biodiversity.

Effects of mountain pine beetle on lodgepole pine stand structure and dynamics

The epidemiology of mountain pine beetle is discussed in Chapter 1. The following is a brief account of the important characteristics.

Endemic populations mainly exist in unthrifty, often small diameter trees. These trees are often attacked earlier in the season by secondary bark beetle species. Many of the attacked trees are suppressed, diseased, or affected by factors such as senility, fire injury, flooding, or large fluctuations in the water table. The beginning of sustained endemic level mountain pine beetle activity tends to coincide with the attainment of maximum wood volume production per hectare (i.e., attainment of maximum current annual increment [CAI], and maximum

stocking). Some trees suffering from competitive stress during and just following the period of peak wood production will be infested by secondary bark beetle species and, eventually, mountain pine beetle. An important consequence of this relationship is that, in unmanaged stands, stand hygiene plays an important role in the establishment of endemic populations.

Incipient epidemic populations of mountain pine beetle can develop in some stands when, locally, the beetles can overcome the resistance of the average large diameter trees (Safranyik 2004). This will occur either because of a decline in stand resistance due to factors such as drought, favourable conditions for beetle establishment and survival for a number of generations, immigration of beetles from another area, or a combination of these factors (Shore and Safranyik 2004). From this point on, beetles have access to the most productive trees in terms of mountain pine beetle brood, and beetle population size becomes one of the main factors in infestation growth.

Mortality

The beetle's preference for breeding in larger diameter trees results in proportionately more small-diameter trees surviving each year and following the collapse of the infestation. In general, during epidemics the percentage of trees killed is proportional to tree diameter above a minimum diameter of ca 10 cm. Above this minimum tree diameter, observed rate of increase in percentage of trees killed is 1.5% to 4% with each 1 cm increase in tree diameter (Safranyik 2004). This pattern of tree mortality indicates that the density of killed trees in a diameter at breast height (dbh) class above the minimum dbh infested will be proportional to the product of the number of trees in that dbh class and the mid-point of the dbh class. Consequently, post-infestation mean diameter and density of the residual stand will be reduced.

A commonly stated hypothesis is that mountain pine beetle acts as a thinning agent in stands, thereby reducing density and benefiting residual trees (e.g., Peterman 1978). This hypothesis may have some merit in the context of mixed species stands in that the non-host species may benefit. However, in terms of pure lodgepole pine stands, or the lodgepole pine component of mixed stands, mountain pine beetle at the incipient or epidemic level kills the biggest and apparently healthy trees and leaves smaller, possibly genetically inferior trees as residuals (Roe and Amman 1970). The effect of this preference on the genetic makeup of the seed source and subsequent replacement stand is not known.

In the Chilcotin Plateau, the highest proportion of lodgepole pine stems killed by mountain pine beetle was in diameter classes greater than 20 cm (Fig. 1). From 1987 to 2001, standing live tree volume and density was reduced for the 15 stands re-measured in 2001 by 22% and 36% respectively, although there was significant variation due to differences in stand structure (Hawkes et al. 2004a). Despite an increase in growth rates in smaller diameter residual trees, there still was a reduction in standing live volume from 1987 to 2001 due mainly to additional mountain pine beetle-caused mortality (Fig. 1).

In Kootenay National Park, live lodgepole pine density declined by 31% from 1993 to 2003 (219 stems per ha to 151 stems per ha) as a result of snag fall down and additional mountain

pine beetle and other mortality (Brad Hawkes and Terry Shore, Canadian Forest Service, Victoria, British Columbia, unpublished data). Live tree density, for all tree species, declined by 16% from 1993 to 2003 (657 stems per ha to 554 stems per ha). Lodgepole pine was the dominant tree species prior to the mountain pine beetle outbreak, accounting for 47% of the live stems. In 1993, lodgepole pine accounted for 33% of the live stems. In 2003, due to additional mortality since 1993, lodgepole pine accounted for only 27% of live stems.

Reduction in pine density and resulting change in diameter distribution and mean diameter following an outbreak by mountain pine beetle depends on a number of factors such as beetle pressure (population size), diameter distribution, species composition and age of pine component in the original stand, habitat type, and climatic factors. To what extent each of these factors influences severity of stand depletion has not been investigated.

In a limited test, there was a significant correlation between the index of stand susceptibility (SI) (Shore and Safranyik 1992) and pine mortality from mountain pine beetle (Shore et al. 2000). As SI is a measure of the effects of pine age, stand density, susceptible pine basal area, and stand location (climate), these factors in combination affect mortality from mountain pine beetle. However, there was considerable variation in mortality among stands corresponding to fixed values of SI. The effect of mountain pine beetle on SI is to reduce it as susceptible pine basal area is reduced following death of the larger diameter pine component of the stand. In addition, beetle outbreaks reduce stand density. This may contribute to lower susceptibility, although dead trees still affect stand microclimate in ways favourable to beetles for several years (See chapters 7 and 8).

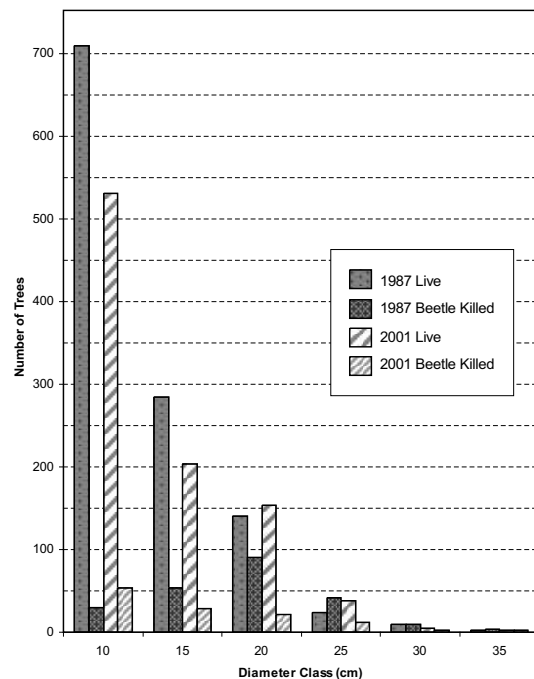


Figure 1. The number of live and beetle-killed lodgepole pines by diameter class on plots in the Chilcotin Plateau area of British Columbia at the end of the outbreak (1987) and fifteen years later.

Mortality caused by mountain pine beetle tends to decline with elevation (Roe and Amman 1970; Amman 1973; Amman et al. 1973) mainly because of prevailing cool climate at higher elevation that negatively affects attack establishment, development rates and brood survival. Stand density affects growth rates of trees and phloem thickness as these two factors are positively correlated. Beetle production is directly related to phloem thickness (Amman 1972). Consequently, beetle production and subsequent tree mortality in dense, unmanaged stands tend to be less than in more open stands (Amman et al. 1977; Shore and Safranyik 1992). On the other hand, there is some evidence that regularly spaced (at least 4 m x 4 m spacing) mature lodgepole pine stands may sustain reduced mortality from mountain pine beetle (e.g., Whitehead et al. 2004).

Habitat types (biogeoclimatic zones in British Columbia) reflect differences in environments. Therefore, it is reasonable to assume that some differences exist among habitat types in severity and size-related mortality caused by mountain pine beetle. Indeed, Roe and Amman (1970) reported some differences in stand-level tree mortality among three habitat types. However, as there was some overlap in elevation of stands belonging to different habitat types, the elevation factor confounded the results. Comparable studies have not been done in Canada.

In British Columbia, the observed range in pine mortality in individual stands is from zero (in mostly young stands) to nearly 100% (in some mature stands growing on good sites in high climatic hazard areas). At the landscape level, however, average pine mortality by number of trees in individual stands will be in the range of 25% - 50%. This concurs with results from applying the range in rate of mortality, discussed earlier, to the usual diameter distribution of mature lodgepole pine types.

Residual stand growth and development

The residual stand following the end of an infestation will be comprised mainly of trees in the suppressed and intermediate crown classes, with some slow growing dominants and co-dominants with thin phloem (Roe and Amman 1970) and in mixed stands, non-host trees in a variety of classes. Residual pine trees may have poor growth response to release, at least on poorer sites. Heath and Alfaro (1990) examined a mixed Douglas-fir/lodgepole pine stand near Williams Lake, British Columbia, where 76% of the pine was killed by mountain pine beetle in the early 1970s. In response to this natural thinning treatment (Peterman 1978), the radial growth rate of residual Douglas-fir was enhanced for 14 years after mountain pine beetle attack with an 11.7% increase in growth rate, whereas surviving lodgepole pine experienced a 5.4% increase. Release of remnant Douglas-fir and spruce post-epidemic was also observed in Wyoming and Idaho by Cole and Amman (1980). Roe and Amman (1970) reported post-epidemic release and increased growth of both residual lodgepole pine and subalpine fir. These observations indicate that residual trees accelerate their growth when beetle-infested trees die, and suggest that stand volume lost by mortality in lodgepole pine might be, at least partially, compensated by increased growth of the residual stand by the time harvest rotation was reached.

Absence of fire in lodgepole pine stands combined with depletion of stands by mountain pine beetle favours the displacement of lodgepole pine. There is strong evidence that the growth of succeeding species is stimulated by mortality from mountain pine beetle through the release of existing reproduction and establishment of new seedlings in stand openings (Roe and Amman 1970). Hence, in the absence of fire, most stands in which lodgepole pine occupies a minor or major seral role will eventually convert to climax species, such as Douglas-fir at the lower elevations, subalpine fir and Engelmann spruce at higher elevations, and white spruce in the central interior regions of British Columbia. Roe and Amman (1970) found that repeated infestations by mountain pine beetle in the absence of fire will convert even-aged (dominant seral) lodgepole pine stands to an uneven-aged condition (and maintain a multi-age condition in climax lodgepole pine stands). However, because pine-dominant stands occur in several biogeoclimatic zones, on different soil and site types that contain differing densities of herbs and shrubs in the understory and different species mixes in the overstory, it is likely that several post-disturbance forest cover types will develop. These post-disturbance forest types may range from pure lodgepole pine to lodgepole pine-hardwood or mixed conifer-hardwood to pure stands of other conifer species (Kimmins et al. 2005).

The importance of accelerated growth as opposed to new seedling establishment following a mountain pine beetle outbreak is a major contrast to what is usually observed following high intensity fires where few trees survive (Veblen 1986, Aplet et al. 1988, Veblen et al. 1991a,b). Stand replacement fires favour regeneration of lodgepole pine and other shade intolerant species that regenerate quickly. However, ecosystem responses following a mountain pine beetle outbreak may be less rapid, because surviving trees may be old and unable to respond, and because mountain pine beetle-killed trees do not immediately drop their foliage (Waring and Pitman 1985). This would partially explain the release of saplings in the Chilcotin Plateau throughout the last thirty years.

Regeneration

Turner et al. (1999) found that lodgepole pine regeneration was more successful in severe-surface burned stands compared to stands experiencing crown fires. Stuart et al. (1989) and Mitchell and Preisler (1998) noted that the structure of lodgepole pine forests in central and southern Oregon was uneven-aged, with distinct episodic pulses pattern of regeneration strongly correlated to mountain pine beetle outbreaks and fire. The magnitude of regeneration pulse was a function of disturbance intensity. DeLong and Kessler (2000) investigated the ecological characteristics of mature forest remnants left by wildfire in sub-boreal landscapes near Prince George, British Columbia, and found some remnants had an uneven-aged, episodic pattern of lodgepole pine regeneration.

On the Chilcotin Plateau, a unique multi-age and size stand structure exists as a result of lodgepole pine being able to regenerate under its own canopy, as well as past multiple mountain pine beetle outbreaks and surface fires (Hawkes et al. 2004a). Lodgepole pine understory tree density averaged 4547 and 3386 seedlings per ha in 1987 and 2001, respectively (Fig. 2).

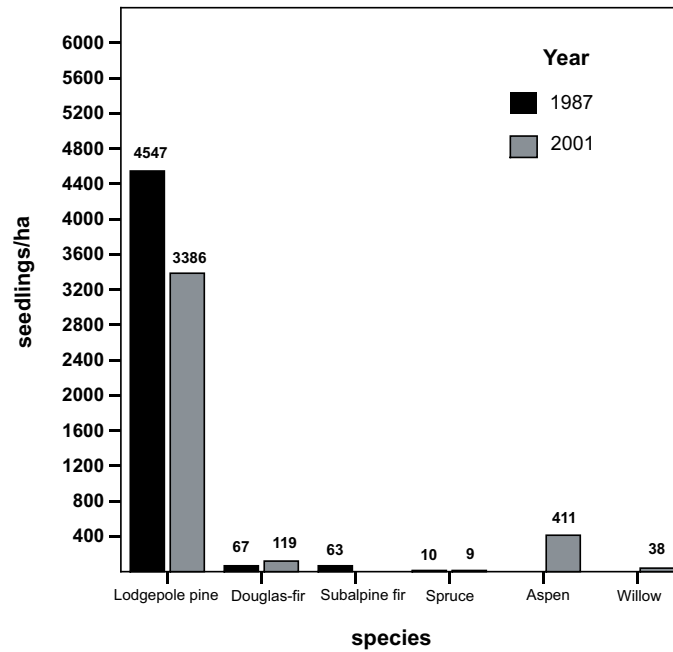


Figure 2. Understory tree density (<1.5 m height) by tree species in 15 stands in the Chilcotin Plateau area of British Columbia in 1987 and 2001.

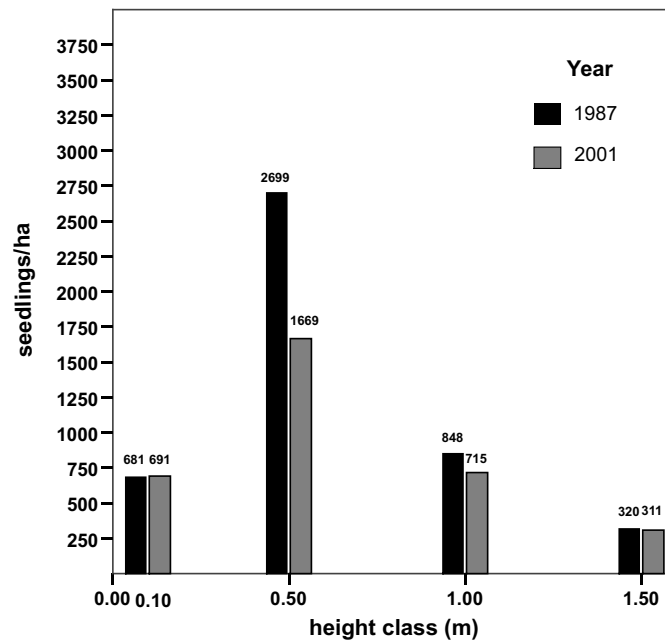


Figure 3. Lodgepole pine understory tree density (<1.5 m height) by height class in 15 stands in the Chilcotin Plateau area of British Columbia in 1987 and 2001.

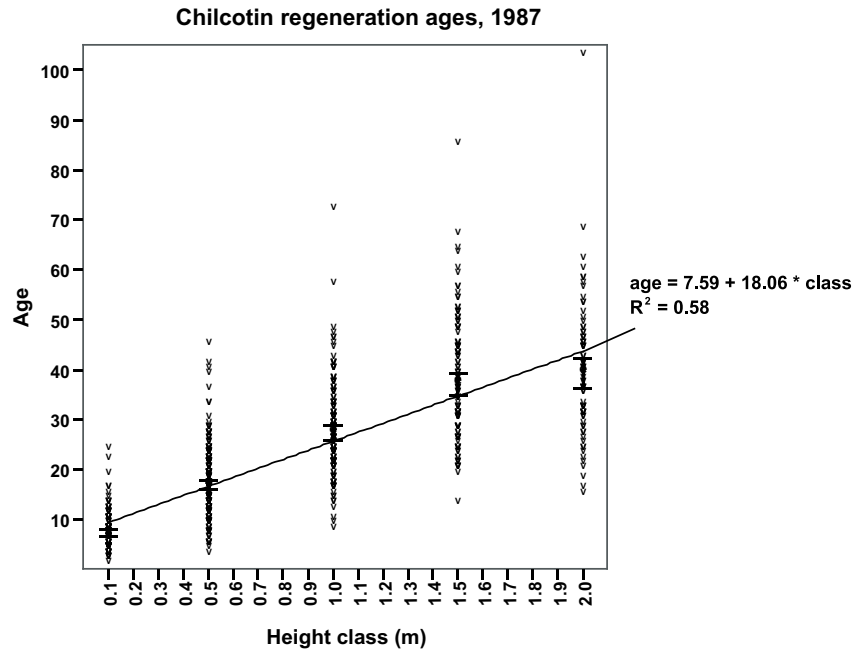


Figure 4. Lodgepole pine understory tree age (<2 m height) by height class in 30 stands in the Chilcotin Plateau area of British Columbia in 1987.

Most lodgepole pine understory trees were between 10 and 50 cm in height (Fig. 3). Lodgepole pine understory tree ages by height class ranged from a few years old at 0.1 m in height to over 100 years at 2 m in height (Fig. 4).

There was a minor amount of Douglas-fir, spruce, and sub-alpine fir in 1987. In 2001, Douglas-fir and spruce understory trees were still present in small numbers, but sub-alpine fir understory trees were no longer present and two new species, trembling aspen (*Populus tremuloides* Michx.) and willow (*Salix sp.*) appeared. Of these two new species, trembling aspen was most abundant at approximately 400 understory trees per hectare (Fig. 2). For comparison, in Kootenay National Park understory tree density averaged 1106 stems per ha. Spruce (536 stems per ha) and Douglas-fir (510 stems per ha) account for the vast majority of understory trees, with small amounts of lodgepole pine (46 stems per ha) and subalpine fir (13 stems per ha) (Brad Hawkes and Terry Shore, Canadian Forest Service, Victoria, British Columbia, unpublished data). Very little regeneration existed under 0.1 m in height. Low numbers of lodgepole pine understory trees may be due to dominance of closed cones and absence of suitable seedbed, because stand replacement fires are the most common type of fire disturbance. Absence of a suitable seedbed without recent large-scale fire disturbance may not be conducive to lodgepole pine regeneration.

Woody debris

Mitchell and Preisler (1998) found that in unthinned lodgepole pine stands in southern Oregon, mountain pine beetle-killed trees began to fall to the forest floor after 5 years, with 50% of trees falling within 9 years, and 90% fallen by 14 years post-attack. Johnson and Greene (1991) found that it is possible to make reasonable post-fire disturbance estimates of tree-fall rates by using equations of decomposition rates of trees already on the ground. Given the mass density of downed trees, rough estimates of actual time of fall could be determined. They did not examine mortality due to mountain pine beetle attack. Depending on the habitat type, beetle-killed trees begin falling within five years of the decline of an infestation (Flint 1924) and may continue 10 - 30 years thereafter. In general, because the decay process is faster under conditions of higher moisture and temperature, trees will deteriorate and fall faster under warm and humid conditions. On the other hand, under dry conditions such as in the Chilcotin Plateau, dead trees tend to dry quickly and caseharden, and a large proportion of the trees may remain standing for two decades or more.

Hawkes et al. (2004b) found that in the Chilcotin Plateau and Kamloops Forest Region standing dead lodgepole pine density in sampled stands 18 years post-attack was reduced by 52% (289 to 140 stems per ha) and 26% (370 to 273 stems per ha), respectively, due to fall down. Only about 10% of the trees had fallen 14 years after the end of an outbreak in Kootenay National Park (Hopping 1943), British Columbia. In the wetter ecosystem of the park, six mixed-species (lodgepole pine, Douglas-fir and white spruce) stands were sampled in 1993 and re-measured in 2003. Lodgepole pine accounted initially for 51% of the volume and 46.8% of the trees in the stand (Brad Hawkes and Terry Shore, Canadian Forest Service, Victoria, British Columbia, unpublished data). Mountain pine beetle-induced mortality reduced stand volume by 21.9% and live stems by 13.6% for all tree species in the stand. In 2003, 23.7% of the trees that had been standing in 1993 had fallen. Most of these trees that had fallen were killed in the 2003 mountain pine beetle epidemic (75.5%), but the balance of fallen trees had been alive at the end of the epidemic, indicating further mountain pine beetle-caused mortality between 1993 and 2003.

Hawkes et al. (2004a, 2005) found, in the early 1980s mountain pine beetle outbreak on British Columbia's Chilcotin Plateau, a link between the mortality rate of trees in lodgepole pine forests and subsequent accumulation of downed coarse woody debris over time. Coarse woody mass, averaging 20 tons per hectare, 60% of which was comprised of dead trees, fell between 1987 and 2001. In another British Columbia study area (the Kamloops Forest Region) lodgepole pine volume loss was similar to that of the Chilcotin Plateau. Coarse woody debris mass in four sampled stands was three times that found for the Chilcotin Plateau. This was because of larger sized lodgepole pine and additional windthrow of other tree species due to some stands being located in riparian leave strips in Kamloops.

Effects of mountain pine beetle on forest fire potential

It is evident that mortality imposed on lodgepole pine stands by mountain pine beetle attacks should influence fire behaviour. Mountain pine beetle kills trees, changing both the quantity and spatial distribution of fuels in the forest. During the first 2-3 years following beetle-kill, while most of the dead needles are retained on the killed trees, there is, presumably, a greater likelihood of a crown fire. This is because foliar moisture content is as low as 7% as compared to live needle moisture content of over 100%. In addition, fine branchwood in tree crowns dries, lowering its previous live fuel moisture to less than 20%, thus allowing more complete combustion during crown fires. After dead lodgepole pine needles drop to the forest floor, usually 2-3 years after trees are killed, more solar radiation reaches the surface forest litter and winds more readily penetrate the open canopy. Both factors have the potential to dry out the litter more than in a live canopy. On the other hand, once most dead needles have fallen, the remaining branchwood in dead crowns, which has lower moisture content than live branchwood, would not support development and spread of a continuous crown fire. This is because needles in crown bulk density play an important role in crown combustion. In theory, once dead trees have fallen, the increased distances among neighbouring residual trees should result in a decrease in the likelihood of a crown fire developing because of breaks in crown fuels. Fallen dead trees will increase surface woody fuel loading, increasing fire intensity and resulting flame length. However, the residual live trees may have high enough temperatures near their crown bases to result in stand-replacing crown fires.

Empirical evidence that supports the theory that there is either greater incidence of fires, greater area burned, or greater fire severity following mountain pine beetle attack is, however, very limited. Using a retrospective approach, Turner et al. (1999) found that high severity mountain pine beetle attacks (>50% of trees killed) increased crown fire probability, but intermediate or light levels of mountain pine beetle severity reduced crown fire probability during the wildfires of 1988 in Yellowstone National Park. These authors also found that once dead trees had fallen, crown fire probability increased in remaining overstory trees.

Experimental work is going on in British Columbia to examine fire behavior in mountain pine beetle affected stands, and historical fire records in mountain pine beetle affected areas. Retrospective studies of fire incidence are confounded with the effects of fire suppression; historical mountain pine beetle outbreaks in Canada occurred mainly in southern interior British Columbia where there has been a decline in area burned associated with fire suppression (Taylor and Carroll 2004).

Research needs

This synthesis points to a number of important gaps in our knowledge. Little is known about the long-term post-epidemic development and growth of stands that have not been subjected to control measures. A sound understanding of the impact of mountain pine beetle outbreaks on growth and yield of surviving trees in residual stands, regeneration, woody debris dynamics, and fire potential is needed for managers to make better decisions regarding stand management in the face of mountain pine beetle attacks. Specifically, the following knowledge gaps need to be addressed:

- Factors affecting variation in stand depletion
- Growth response of residual stands in different habitat types
- Release of advance regeneration and establishment of new regeneration in stands representing different successional stages for lodgepole pine
- Rates of deterioration and falling of beetle-killed trees in different habitat types
- More specific research on effect of mortality caused by mountain pine beetle on fire occurrence and intensity
- Ecological impacts of large outbreaks and management (control) programs on fish and wildlife.

Summary

Lodgepole pine is an important component of the forests of western North America. In Canada, the total area of lodgepole pine forest types is about 20 million ha, mostly in British Columbia and Alberta. Lodgepole pine has large ecological amplitude. In Alberta and British Columbia it occurs in all but three biogeoclimatic zones. With relatively minor exceptions, lodgepole pine is a seral species that is highly shade intolerant and reproduces best on bare soil. It has two types of cone habits: open and serotinous. Serotinous cones require high temperatures in the range of 45° - 50° C to open and release seeds. In areas where lodgepole pine has a predominantly serotinous cone habit, such as most areas in western Canada, lodgepole pine is, under natural conditions, essentially a fire-maintained species. It has four successional roles: minor seral, dominant seral, persistent, and climax. Climax sites are those on which lodgepole pine is the only tree species capable of growing.

At the landscape scale, mosaics of even-aged and uneven-aged patches of lodgepole pine are the norm and reflect disturbance history. Non-stand replacement fires and mountain pine beetle attacks contribute to conversion of even-aged stands to an uneven-aged stand. On the other hand, high intensity fires tend to create even-aged stands. Without fire control, and considering a mean fire return period of 100 years, only a relatively small portion of unmanaged lodgepole pine stands in British Columbia would be of an age susceptible to mountain pine beetle. Over the past century, increased success in fire control combined with the recent commercial utilization of lodgepole pine resulted in a ca threefold increase in the area of lodgepole pine susceptible to the mountain pine beetle.

Existing evidence does not support the popular hypothesis of a pine-beetle-fire cycle by which weakened, mature lodgepole pine give rise to mountain pine beetle epidemics and the resulting dead trees, being highly susceptible to fire, burn and give rise to new stands of lodgepole pine as a result of seeds being released from serotinous cones. Existing evidence is in strong support of outbreak development in mature forests but there is no current evidence in support of increased fire incidence in stands depleted by mountain pine beetle. However, some observations, as well as theoretical considerations, indicate that both fire severity and probability of crown fires may increase following outbreaks due to increased fuel loading and changed fuel characteristics.

In general, endemic mountain pine beetle populations get established in stands near the culmination of current annual increment (CAI), often in trees suffering from competitive stress and other forms of weakening. Incipient populations develop when beetle numbers have grown to a size sufficient to successfully attack the average large diameter trees in the stand. These trees provide the best conditions for brood survival. Under favourable conditions incipient populations develop into landscape level outbreaks in a few years. Epidemics often deplete the large diameter pine component of stands. The level of stand depletion varies with factors such as site quality, species composition, pine age, density, and climatic conditions. The residual stand is mainly composed of non-host species and lodgepole pine in the smaller diameter classes. In general, surviving trees will increase in growth in response to the increased light conditions and reduced competition. The rate of falling of dead trees depends on site conditions; generally the fall rate is greater on warm and moist sites compared with dry and cold sites.

Mortality from mountain pine beetle stimulates growth of successional species. In the absence of fire most stands in which lodgepole pine occupies a minor or dominant seral role will eventually convert to the climax species. Without fire, repeated infestations by mountain pine beetle will convert even-aged, dominant seral stands to an uneven-aged climax condition. However, pine-dominant stands occur in different biogeographic zones, on different soil and site types, with different densities of herbs and shrubs in the understory and different species mixes in the overstory. It is likely, therefore, that combinations of these variables will result in different post-disturbance forest types ranging from pure pine to various mixes of host and non-host species as well as non-host climax forests.

There are a number of important gaps in our knowledge relating to factors affecting variation in stand depletion: rates of deterioration and falling of killed trees, post-outbreak growth and development of surviving overstory trees; succession, regeneration, and effects of tree mortality on fire occurrence and intensity.

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