

**INFLUENCES OF MOUNTAIN PINE BEETLE (*DENDROCTONUS
PONDEROSEA*), FIRE, AND UNGULATE BROWSING ON FOREST STAND
STRUCTURE IN THE SOUTHERN CANADIAN ROCKY MOUNTAINS**

by

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ABSTRACT

Forests in the montane and lower subalpine ecoregions of the southern Canadian Rocky Mountains may have been more open and structurally diverse at the beginning of the 20th century than today. Today, mature *Pinus contorta* var. *latifolia* Dougl. (lodgepole pine) causing mountain pine beetle (MPB, *Dendroctonus ponderosae*) infestations, infrequent high severity fires, and herbivory appear to have increased in Banff and Kootenay National Parks. Based on a review of the literature it was hypothesised that

1. MPB infestations increase forest stand structural diversity;
2. Browsing intensity decreases with increasing amounts of coarse woody debris; and
3. Disturbances such as MPB infestation and low severity fire lead to decreased MPB stand susceptibility.

Stand structure parameters were investigated in mesic montane and lower subalpine stands 15, 25, and 65 years after MPB outbreaks. Parameters measured were tree density, diameter, height class, species, and age distributions as well as coarse woody debris mass. Also, influences of fire frequency, time since fire and fire severity on the current stand structure were analysed. A MPB susceptibility index was calculated for stands with different MPB and fire disturbance histories. The Shannon-Wiener index indicated higher stand structural diversity on plots 15 years but not 25 and 65 years after MPB infestations. Influences of fire on stand structure were limited to increasing tree density with increasing time since the stand initiation fire, and higher proportions of understory vegetation at lower fire severities. Also, there was an indication that high amounts of coarse woody debris resulted in reduced browsing intensity. Finally, the MPB susceptibility index was significantly lower on stands with previous MPB infestations. The MPB susceptibility index also tended to be lower with increasing number of fires. Consequently, none of the above hypothesis could be rejected. Low intensity fires and a reduction of herbivory might be crucial to promote other early successional species such as *Populus tremuloides* (trembling aspen). Management strategies allowing for MPB and fire disturbances would benefit the ecosystems in the study area.

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CHAPTER 1

INTRODUCTION - DISTURBANCES AND STAND STRUCTURE

1.1 GENERAL INTRODUCTION

The current state of the ecosystems of the montane and lower subalpine ecoregions in the southern Canadian Rocky Mountains (Section 2.5) has been of rising concern. Research indicates that, historically, open forests and grasslands dominated by frequent fire cycles were most prevalent in the montane ecoregion of the Rocky Mountains (Tande 1979; White et al. 1998). Today, there is evidence that uniform *Pinus contorta* var. *latifolia* Dougl. (P1¹, lodgepole pine) forests have become increasingly common, while other tree species have declined (Stohlgren et al. 1998, Kay 1997; White et al. 1998). Mountain pine beetle (MPB) infestations in dense *Pinus contorta* forests have been observed west of the Rocky Mountain divide, with tendencies to spread east (BC Ministry of Environment, Lands and Parks 2001). Additionally, fire regimes and herbivory effects appear to have changed with time in the southern Canadian Rocky Mountain national parks. Frequent low severity fires appear to have become less common (Rhemtulla et al. 2002). Locally, high herbivory, especially by elk (*Cervus elaphus*), has been recorded (Binkley et al. 2003).

The montane and lower subalpine ecoregions are of great ecological significance. Not only are they wintering habitat for migrating animal populations (Heitzmann 2001), they are also of major economic importance for the tourism sector and for human settlement (Banff-Bow Valley Study 1996; Kay et al. 1994).

¹ All abbreviations for tree species in the present study follow BC Ministry of Sustainable Resource Management (2003)

Current national park management strategy aims are to maintain or restore ecological integrity, a condition that is characteristic of its natural region and likely to persist. This includes abiotic components, and the composition and abundance of native species and biological communities, and their associated rates of change and supporting processes. "Maintenance or restoration of ecological integrity, through the protection of natural resources and natural processes, shall be the first priority of the Minister when considering all aspects of the management of parks" (Canada National Parks Act 2000). Today, national parks management aims to reduce MPB impacts (Banff National Park 2004) and to convert montane vegetation back to states of pre-Columbian times with more diverse and open forests (Parks Canada 2004a; Kay and White 2001; Kay et al. 1994). However, this approach needs to consider the role that MPB may have in these ecosystems, since Parks Canada Agency (2000) states that "an ecosystem has integrity when it is deemed characteristic for its natural region, including the composition and abundance of native species and biological communities, rates of change, and supporting processes."

The overall objective of the present study was to investigate the influence of MPB on stand structure at 15, 25, and 65 years after a previous infestation. Because of the importance of fire as a disturbance agent, the influence of fire on selected stand structure parameters was also tested. Since high herbivory is thought to impact regenerating trees, correlations between browsing intensity and coarse woody debris (CWD) amounts, potentially caused by previous MPB infestations or fire, was also studied. Finally, the influence of time since the last MPB infestation, as well as fire frequency and severity, on current stand susceptibility to MPB infestations was determined.

1.2 EFFECTS OF DISTURBANCES ON STAND STRUCTURE

Stand structure parameters and stand characteristics allow a description of the current stand, which is a result of its past disturbance history. Many parameters influence stand structure and only a limited number could be captured and their potential effects described in the present study (Figure 1).

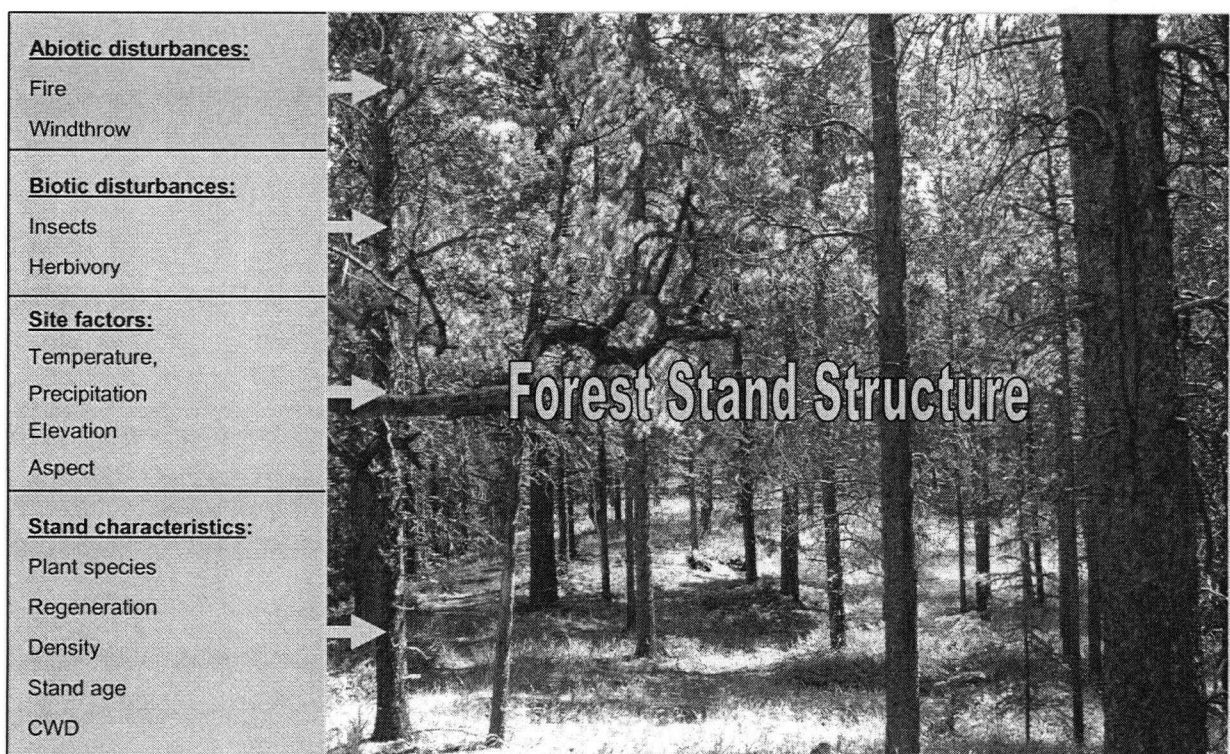


Figure 1 Some of the factors influencing stand structure

Several of the factors given in Figure 1 interact to varying extents, but for clarity these interactions were omitted. In the present study the primary focus was on measuring the influence of mountain pine beetle disturbances, while aiming to consider potential contributions of other factors to stand structure.

1.2.1 Mountain pine beetle and stand structure

The MPB is a temperate pine forest insect with a range extending from Mexico to central BC. The eastern edge of the beetle's distribution lies along the southern Canadian Rocky Mountains near the Alberta-British Columbia border (Alberta Sustainable Resource Development 2002). Mountain pine beetle outbreaks have been recorded within BC since 1910 (Van Sickle 1988). In the southern Canadian Rocky Mountains, particularly large infestations occurred in Kootenay, Yoho and Banff National Parks between 1930 and 1943 (Van Sickle 1988). Another province-wide outbreak throughout BC started in the early 1970's culminating in 1984, affecting about 482,000 ha (Van Sickle 1988). In 2004, MPB affected about seven million ha of forests in BC. Alberta has experienced only two outbreaks in its recent history, which were near the borders of BC and Montana (USA). From 1985 until 1997, no sustained beetle populations had been detected. The first infestation since then was detected in 1997 in Banff National Park, with exponentially increasing numbers of trees infested in the subsequent years. In 2002, the MPB populations in Banff National Park (BNP) appeared to have reached epidemic proportions (Alberta Sustainable Resource Development 2002). For the first time during the current outbreak, mountain pine beetle-infestation had spread over from Banff National Park and killed about 700 trees in the Canmore area east of the park. However, new infestations were less in Alberta in 2003 and 2004, supposedly due to successful application of fall-and-burn (Alberta Sustainable Resource Development 2004).

MPB is the most damaging forest insect in the southern Canadian Rocky Mountains (Mountain Pine Beetle Initiative 2004, Alberta Sustainable Resource Development 2002, Van Sickle 1988). Mature *Pinus contorta* are the most commonly killed tree species, followed by western white pine (*Pinus monticola*), occasionally ponderosa pine (*Pinus ponderosa*), and other pines. Most susceptible trees appear to be between the ages of 80 and 100 years (Van Sickle 1988, Shore et al. 2000, The Mountain Pine Beetle Initiative 2004). Shore et al. (2000) suggested diameters of the most susceptible

trees were > 15 cm, while Whitehead (2001) reported an average of >20cm diameter. However, a substantial proportion of attacked trees might be >25cm diameter at breast height (Whitehead 2001, The Mountain Pine Beetle Initiative 2004).

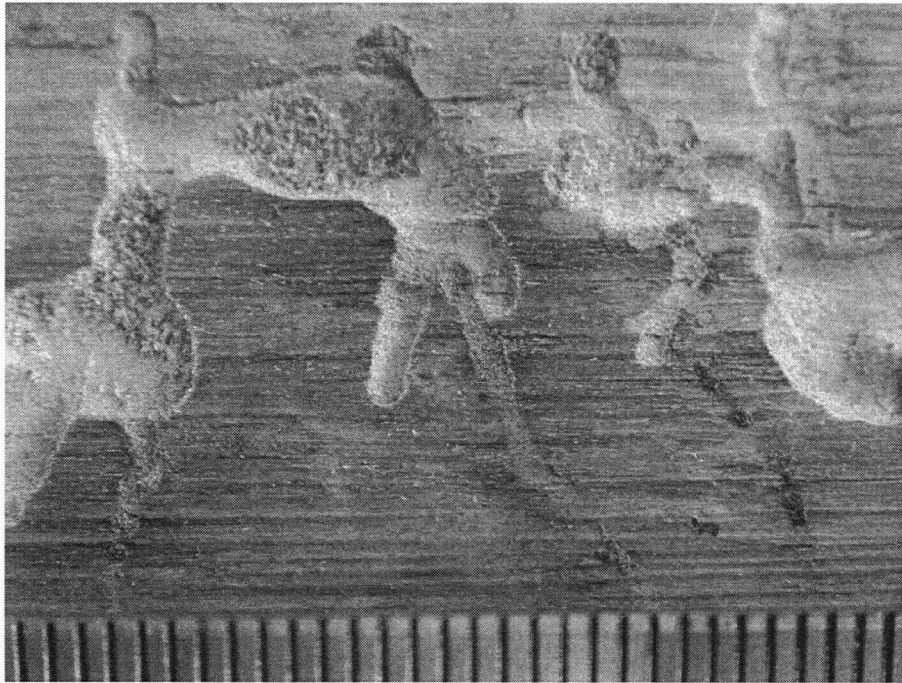


Figure 2 Pattern in the wood of *Pinus contorta* caused by MPB maturation feeding (Agnes Li 2004, unpublished)

The normal life cycle of the MPB takes one year. The female MPB bores through the bark to the cambium region to construct egg galleries and brood in the phloem. The broods usually overwinter as larvae. They resume feeding in April until the completion of their development in June. The larvae turn into pupae and become adults shortly afterwards in mid-summer. The young adults briefly feed under the bark (maturation feeding, Figure 2) and become inoculated with blue stain fungi (mostly *Ophiostoma* species, Figure 3). Afterwards they bore through the bark and emerge as mature adults. Adult beetles fly and attack mature pine trees in mid to late summer (Shore et al. 2000, The Mountain Pine Beetle Initiative 2004). If summers are warmer than average, parent MPB may re-emerge and establish another brood in the same year. On the other hand,

when summers are cooler or elevations are higher, broods may need up to two years to mature (The Mountain Pine Beetle Initiative 2004).



Figure 3 Blue stain fungus on a tree cross- section (Natural Resources Canada 2002, modified)

Trees that have been attacked fill the galleries made by the beetle with resin to “pitch out” (Figure 4) the beetles (Smith and Fischer 1997, Whitehead et al. 2001). If the defence mechanism of the attacked tree is overcome by the beetles, the blue stain fungi carried by the beetle are introduced to the host during gallery excavation (Shore et al. 2000).

The pathogenic blue-stain fungi associated with the mountain pine beetle assist the beetles in exhausting the tree defences (Solheim and Krokene 1998). The relative importance of the beetles and the fungi in killing the trees is still unclear (Solheim and Krokene 1998), but a few weeks after attack, the fungi have colonized the rays and tracheids in the sapwood, disrupted water transport to the crown (Solheim and Krokene 1998, The Mountain Pine Beetle Initiative 2004) and reduced the trees' pitch flow (The Mountain Pine Beetle Initiative 2004). Aging of trees is associated with declining tree vigour which affects individual tree resistance to inoculation by the blue-stain fungus (Whitehead et al. 2001). The combination of pheromone induced mass attack and fungal growth may eventually kill the tree (Shore et al. 2000). The first damage symptoms are reddish boring dust at the base of the trees and a soft, white or reddish pitch tube around each bore hole (Figure 4). Often bark removal by feeding woodpeckers can be observed.



Figure 4 Tree “pitching out” a beetle (Natural Resources Canada 2002, modified)

The foliage of attacked trees turns yellow and then red (red attack) by the spring of the year following the initial MPB attack. After two years, most of the needles have dropped from the tree, leaving a grey snag (grey attack). Trees that survive MPB attacks may show evidence of MPB activity by old galleries and scars (Kulakowski et al. 2003). Several years after a successful brood, visible signs on decaying trees may be reduced to marks made by maturation feeding of the new adults (Figure 2; McLean 2004, personal communication).

Brood success of MPB is directly proportional to the thickness of the inner bark (Safranyik 1988; Edmonds et al. 2000), which is the primary feeding and breeding tissue of the tree for the beetle. It has been suggested that old and even-aged *Pinus contorta* stands are more prone to larger scale infestations (Van Sickle 1988, Amman et al. 1977) based on the assumption that diameter is related to phloem thickness. However, this relationship was not found by other researchers (Katovich and Lavigne 1986; Shrimpton and Thomson 1985). Tree susceptibility appears to decline as *Pinus contorta* ages beyond 120 years (Shore and Safranyik. 1992), potentially due to an increase, peak and subsequent decline in phloem thickness during the tree aging process (B. Hawkes, Canadian Forest Service, pers.com. 2004). There is a general agreement that stands are less susceptible to MPB at lower tree densities (Mata et al. 2003), because tree vigour is greater, allowing for a better resistance to MPB attacks (Shore et al. 2000, Whitehead et al. 2001). Vigorous trees produce more resin than less vigorous ones and thus may successfully "pitch out" attacking beetles (Whitehead et al. 2001). Also, due to a different microclimate, open stands are less susceptible to MPB than dense stands (Whitehead et al. 2001). In open stands, horizontal and vertical wind speeds are higher, wind directions change (Schmid et al. 1992, Bartos and Amman 1989), and light intensities and temperature fluctuations are greater (Bartos and Amman 1989, Schmid et al, 1995). Because these factors affect the success of bark beetle dispersal, attack, or brood development, increased light levels, bark temperatures, and winds result in stands less favourable for MPB (Whitehead et al. 2001). Consequently, below a certain threshold, low tree densities lead to a decline in MPB stand susceptibility (Shore et al. 2000).

Another factor affecting forest stand susceptibility to MPB infestations is tree species diversity. The more species diverse a forest is, the less its susceptibility to MPB infestations (Shore et al. 2000). However, as Shore et al. (2000) pointed out, this is solely due to a lower proportion of *Pinus contorta* (Section 1.2). Consequently, although the *Pinus contorta* component of a species-diverse stand may be attacked by the mountain pine beetle, the stand would be rated as low susceptibility if *Pinus contorta* represents only a minor component of the stand (Shore et al. 2002). Turner et al. (1999) found that stands in Yellowstone National Park (YNP) with severe mountain pine beetle infestations had extensive areas with dead *Pinus contorta*, creating gaps which stimulated understory growth. This indicates that regenerating trees could then lead to a more structurally and diverse forest. This is supported by Armour (1982), who found in a study in north-western Montana that overstory dominance of *Pinus* was replaced by *Picea* species after MPB infestations. Shrimpton (1994) also found in KNP fifty years after a MPB outbreak stands developing towards *Picea* dominance.

As outlined in Section 2.5, in addition to *Pinus contorta*, typical tree species of the montane and lower subalpine in BNP and Kootenay National Park (KNP) include *Pseudotsuga menziesii* (Fd, Douglas-fir), *Picea glauca* (Sw, white spruce), *Populus balsamifera* (Act, black cottonwood) and *Populus tremuloides* (At, trembling aspen), with *Abies lasiocarpa* (Bl, subalpine fir) and *Picea engelmannii* (Se, Engelmann spruce) at higher elevations. It is widely believed that prescribed burning can generate more diverse forest structures and "short of very extensive logging, high-intensity prescribed fire is the one tool that could be effective in slowing the spread of the mountain pine beetle" (Banff National Park of Canada 2004). Consequently, active MPB management, such as fall- and-burn programs, as well as proactive prescribed burning are sought in BNP to prevent MPB infestations from spreading (Banff National Park of Canada 2004).

Prescribed burning has potential for thinning uneven-aged stands of trees, but for thinning the dense coniferous forests that are commonly found in the study area (Kay et al. 1994), burning does not show promise (Wright and Bailey 1982). For those stands, high fuel loads may lead to high intensity and severity fires. Since high intensity fires are generally thought to generate dense *Pinus contorta* stands, such fires may reinitiate

similar forest structures as formed at the turn of the 19th century, leading again to stands highly susceptible to MPB infestations. Thus, a high severity prescribed fire approach may maintain ecosystems in an atypical species composition, while open forest types with young age classes and fewer old trees, grass- and shrublands and aspen communities, which are assumed to be typical for most of the montane valleys in the southern Canadian Rocky Mountains (Kay et al. 1994), are prevented from being re-established.

Since MPB kill only *Pinus contorta* in a forest (Shore et al. 2000), they may actually facilitate development of more structurally diverse forests. It was reported that in the absence of fire, consecutive mountain pine beetle infestations may convert even-aged to uneven-aged forests (Roe and Amman 1970). Thus, MPB may act as a disturbance agent that accelerates transition from human caused homogenous to more structurally diverse forests. However, with an absence of fire and atypical high MPB populations, this may not represent ecological integrity in the study area.

1.2.2 Fire and stand structure

Typically, the montane and lower subalpine ecoregions are dominated by a mixed fire regime, with a tendency of fires burning more frequent in low elevation forests (White 1985a, White et al. 2004). However, generally warm and dry forests have shorter fire intervals than mesic and riparian forests in the montane and cool moist forest types in the lower subalpine (White et al. 2004). Generally, mixed fire regimes are a combination of frequently recurring, low-intensity and severity fires, and less commonly, medium to high intensity fires, creating patchworks of several age-classes over short distances (Heitzmann 2001).

High intensity crown fires¹ generally kill all the mature trees in a stand. In fire dominated ecosystems, stand age equals the time since the last stand-replacing fire (Kipfmüller and Baker, 1998). Following a stand-replacing disturbance, newly regenerating trees compete with other plants also regenerating after the disturbance. Following a minor disturbance, such as low severity fires, newly regenerating trees also compete for growing space with previously established, large trees, as well as understory vegetation that survived the disturbance, and other trees regenerating after the disturbance (Oliver and Larson 1996). Low to moderate severity fires are important in regulating seedling composition and distribution, and reducing the concentration of fuels on the forest floor (Barnes et al. 1980). The proportion of tree mortality in a stand depends on the characteristics of the fire as well as the tree species (Oliver and Larson 1996), including tree age, bark characteristics and the rooting habit (Barnes et al. 1980). "Lingering fires on lee sides of thin-barked species can heat and kill the cambium" (Oliver and Larson 1996). Thin-barked trees such as *Pinus contorta* (Parish et al. 1996) are susceptible to being scarred or killed by fires (Turner et al. 1999, Oliver and Larson 1996). Other species, such as *Pseudotsuga menziesii* (F.d., Douglas-fir), have thicker bark which insulates and protects the cambium from fire when the trees are large (Oliver and Larson 1996). Consequently, high intensity fires will kill most of the *Pinus contorta* in a stand. However, *Pinus contorta* forests are reinitiated from seeds, which are often derived from serotinous cones that release seeds after fire (Schmidt 1988, Oliver and Larson 1996). After an intense fire in mixed conifer forests, *Pinus contorta* may be the only successful conifer regenerating in the first years following the fire (Crane et al. 1983). Therefore, high intensity fires may lead to a higher proportion of *Pinus contorta* in stands following these fires. *Pinus contorta* is shade intolerant and seedlings which may become established under the forest canopy seldom grow to maturity if they are not released. Thus, most of these *Pinus contorta* forests are relatively even-aged and homogeneous (Schmidt 1988) if they are not thinned by disturbances such as insect

¹ Different definitions for several technical terms exist in the literature. Definitions used in this thesis are given in Appendix VI

infestations, windthrow, or low intensity surface fires which allow other tree species to come in.

With fire exclusion, Day (1972) suggested a shift in tree species dominance from *Pinus contorta* over *Picea*¹-*Abies*² to dense *Abies-Picea* climax forests for Rocky Mountain forest in Alberta. Franklin and Laven (1991) reported that surface fires may initiate alternate successional sequences and delayed achievement of *Picea-Abies* climax forests.

Reports about fires in the southern Canadian Rocky Mountains are somewhat contradictory. Past fire regimes in the Athabasca Valley around Jasper have been studied by Tande (1979), who found that fires created a mosaic of age classes in the *Pinus contorta* dominated forests between 1669 and 1913. Those forest structures might have been strongly influenced by aboriginal burning (Kay et al. 1994).

Widespread forest fires in the Rocky Mountains occurred also during the railroad construction and settlement era between the late 1800s and 1900s (Kay et al. 1994).

These fires appear to have initiated widespread dense *Pinus contorta* stands.

Heitzmann (2001) suggested, by quoting Tande (1979), that due to fire control, no significant new age classes appear to have been established since 1913. White (1985a) agreed, but pointed out that there was no evidence for increased burning in the settlement era compared with pre-1800 conditions in BNP. White (1985a) suggested that burning by First Nations had previously contributed significantly to more frequent fires, and that lack of human caused fires, rather than fire fighting, is the cause for infrequent fires today. However, past fires appear to have initiated dense stands of *Pinus contorta* that are now mature and of an age susceptible to mountain pine beetle infestations. This is consistent with reports about general trends in forests in British Columbia. More than half of the *Pinus contorta* stands are older than 80 years and more than three quarters are more than 60 years old (Figure 5).

¹ *Picea* will be used instead of *Picea glauca* (Sw, white spruce) and *Picea engelmannii* (Se, Engelmann spruce)

² *Abies* will be used instead of *Abies lasiocarpa* (Subalpine fir)

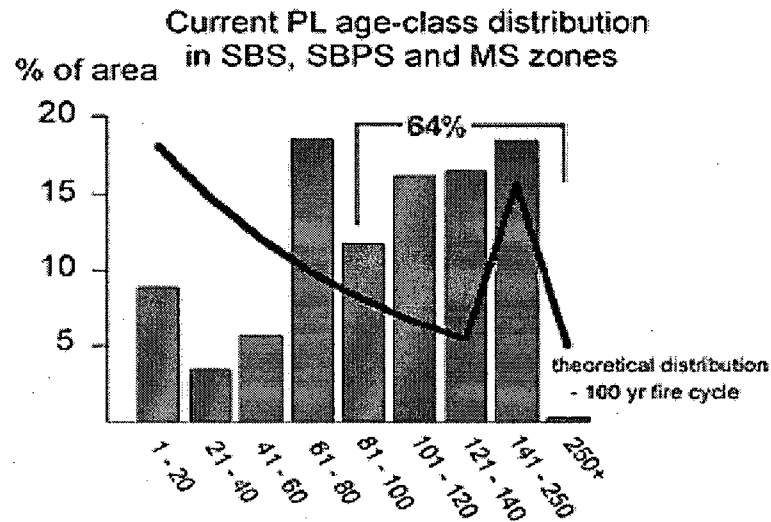


Figure 5 Current age class distribution of *Pinus contorta* in BC (Hawkes and Taylor 2002)

Historical *Pinus contorta* stands with fire cycles less than 100 years would have had a significantly lower proportion of old *Pinus contorta*, and more young age classes which were more evenly distributed (Figure 6) and potentially less susceptible to MPB outbreaks.

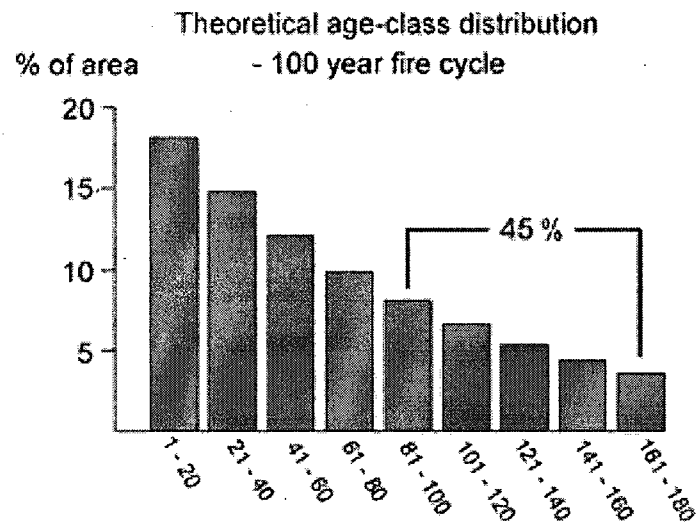


Figure 6 Theoretical age class distribution of *Pinus contorta* in BC (Hawkes and Taylor 2002)

Kay et al. (1994), White et al. (2003) and others suggest that frequent, low intensity fires played a significant role in maintaining stand structures, and open *Pseudotsuga menziesii* and *Pinus contorta* forests or regenerating *Populus tremuloides*, depending on the moisture regime of the site. *Populus tremuloides* is associated with moist, well drained soils at low elevations (Achuff et al. 1984; White et al. 1998; Flook 1962). The *Populus tremuloides* stands in the southern Canadian Rocky Mountains are usually clones. They are long-lived and were regenerated in the past by frequent fires (White and Feller 2001; Hessel 2002). Longer fire cycles allow conifers to invade *Populus tremuloides* stands and reduce *Populus* densities (Hessel 2002; Bartos 2001). In 1996, the Banff-Bow Valley Study (1996) stressed that "Based on vegetation research and effects of fire on wildlife habitat, it is readily apparent that fire needs to be restored to a more natural role in the Banff Bow Valley and adjacent regions." In order to restore the ecological role of fire and to promote more open and structurally diverse forest, Parks Canada uses a program of prescribed burning (Parks Canada 2004a). However, as stated above, although prescribed burning has potential for thinning uneven-aged stands, it is not suitable for thinning dense, even-aged stands (Wright and Bailey 1982). Consequently, using fire in order to create more open stands with younger age classes and few old trees may not be possible if stands are too dense. Smith et al. (1997) pointed out that "it is very difficult to strike the right balance between fires that kill too much and those that kill nothing." Additionally, in restoring fire to the montane and subalpine ecoregions, aspects such as public safety, property protection, neighbouring jurisdictions, tourism, and protection of special features, cannot be neglected (Banff-Bow Valley Study 1996). White et al. (2004) compared predicted to observed prescribed fire patterns in BNP for the period 1983 to 2003, and found that restoration led to fewer trees killed by prescribed fires than what was predicted from model predictions of historic fire intensity/severity. Thus, programs of reintroducing prescribed fires to BNP appear to have managed safety constraints successfully. The evidence shows that the frequency and number of prescribed fires could be intensified in the future.

1.2.3 Ungulate browsing and stand structure

Herbivory in the southern Canadian Rocky Mountain national parks prior to European settlement may have differed from today. This may be due to the extirpation of bison (*Bison bison*), and the reduction of predators of large ungulates such as bears (*Ursus americanus* and *Ursus arctos*) and wolves (*Canis lupus*), a situation induced by increasing human utilization of these areas.

According to Kay and White (2001) bison were historically abundant in the montane with the exception of southern British Columbia, where no evidence was found that modern bison ever inhabited those areas. Bighorn sheep (*Ovis canadensis*), caribou (*Rangifer tarandus*), mountain goat (*Oreamnos americanus*) and moose (*Alces alces*) populations have severely declined (Poll et al. 1994). By contrast, mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) populations appear to be fairly abundant (BC Ministry of Environment, Lands and Parks 2000).

Kay et al. (1994) found indication in repeat photographs, aspen ecology, historical observations and archaeological data that elk populations may once have been relatively low in the southern Canadian Rocky Mountains. Between 1918 and 1920, releases of elk from Yellowstone Park were made in Banff and Jasper National Park, which increased elk populations (Flook 1962). The reintroduction of elk, the establishment of national parks, the lack of hunting pressure, and the reduction of predators have all been contributing factors to the currently high elk populations in many areas (Kay and White 1995; White et al. 2001).

Top predators, such as wolves, are generally thought to be very important in controlling herbivore populations (Primack 2000). Predators are scarce in the southern Canadian Rocky Mountains, especially where human activities are high. Elk concentrate in these high population areas (Kay and White 1995). Additionally, elk migratory behaviour from the montane to higher elevations that could lead to a recovery of the vegetation in lower

elevations, appears to be less important than historically (E. Merrill, pers. com., 2004). Therefore, herbivory predominantly by elk is likely to be locally accelerated.

Generally, high ungulate populations can lead to overgrazing and overbrowsing, with varying outcomes depending on the area and the intensity, such as loss of plant cover, loss of associated insect species and soil erosion (Primack 2000). Thus, ungulate browsing can influence stand structure. Differences in browsing intensity will produce different outcomes. Intensive grazing can lead to deforestation and prevent regeneration of shrubs and trees, thus leading to extensive grasslands. This is of major importance in dry areas with naturally low vegetation growth and densities (Gossow 1976), and in areas heavily overstocked with cattle or wildlife (Hofman 1998). On mesic sites in the montane and lower subalpine in BNP and KNP, however, herbivory is assumed to be more selective. Although ungulate densities are high, their impact is supposedly considerably different from that of high densities of cattle. Certain plant species may be promoted that are less favourable browse, while others are depleted, leading to changes in plant species composition. An intermediate grazing intensity by ungulates may reduce the biomass and density of understory grasses and sedges, which could otherwise outcompete or inhibit tree seedling growth.

Where grazing pressure does not exceed a certain threshold, tree recruitment of less favourable browse species, such as spruce (Fraser et al. 2001), may not be significantly influenced. However, proportions of preferred species, such as *Populus tremuloides* or *Populus balsamifera*, may seriously decline. Past research found that browsing by ungulates, mainly elk, may have contributed to a decline in *Populus tremuloides* in the southern Canadian Rocky Mountains (Kay et al. 1994; White et al. 1998; Kilpatrick and Abendroth 2001; Hessler 2002; Kay 2001; White and Feller 2001). This may result in an increase in more shade tolerant shrubs and trees (Heitzmann 2001). As more trees invade, available light and water decrease, reducing habitat suitability for herbs and grasses. Fewer herbs and grasses also reduce forage quality for ungulates (Heitzmann 2001), favouring ungulates that require lower quality forage, such as elk (White et al. 2001; Flook 1962). This may influence the proportion of different ungulate species present in a given area.

The reduction of fine fuels through herbivory can lead to a decrease in low intensity fires (Van Auken 2000) by reducing the chances of low severity fires to occur. Consequently, these fire-herbivory interactions may promote simple structured, species poor, denser forests in place of former open and park-like coniferous forests (Belsky and Blumenthal 1997). These uniform forests tend to be less fire adapted (Belsky and Blumenthal 1997), examples of which are many of BNP's and KNP's present dense coniferous forests (Kay et al. 1994 and references therein).

The interaction between fire and elk browsing was investigated in Yellowstone National Park by Ripple and Larsen (2001), who focused on the role of coarse woody debris as a mechanism for assisting *Populus tremuloides* regeneration. It was hypothesized that fallen conifers killed in the 1988 YNP fires would provide refuge for *Populus tremuloides* regeneration under heavy ungulate browsing. It was shown that *Populus tremuloides* suckers protected by fallen conifer barriers were over two times the height of adjacent unprotected suckers. These results were also supported by Romme et al. (1995). Based on these studies, regeneration of *Populus tremuloides* and other tree species may actually benefit from woody debris following MPB infestations. Downed trees following MPB infestations may provide shelter for regeneration by hindering easy access by large ungulates. However, it is recognised that besides being created by MPB (Armour 1982) and fire (Wright and Bailey 1982, Oliver and Larson 1996, Ripple and Larsen 2001), CWD can also be a result of windthrow (Oliver and Larson 1996). Thus, in an area with previous MPB infestations, the origin of CWD might not necessarily be solely due to the beetle. That coarse woody debris amounts, following MPB infestations, vary with time needs to be considered. Shortly after an infestation fuel loads remain unchanged, then rapidly increase and level off (Armour 1982). Consequently, the role of large woody debris in sheltering regeneration would last only for a certain period after a disturbance.

1.3 HYPOTHESES

Management of national park ecosystems for ecological integrity requires an understanding of their characteristic disturbances and their dynamics. However, as outlined above, there is still a lack of knowledge about the interacting effects of mountain pine beetle, fire and herbivores on forest stand structure. Consequently, the present study focused on investigating stand structure following MPB infestations compared to stands without records of MPB infestations, while considering the potential influence of past fires on those stands. Since ungulate browsing has the potential to impede or alter regenerating trees (Burschel and Huss 1997) and thus influence stand structure, it is considered as well.

It was hypothesised that

1. MPB infestations increase forest stand structural diversity of forest stands in the southern Canadian Rocky Mountains;
2. Browsing intensity decreases with increasing amounts of coarse woody debris; and
3. Disturbances such as MPB infestation and low severity fire lead to decreased susceptibility of forest stands to MPB in the southern Canadian Rocky Mountains.

CHAPTER 2

THE STUDY AREA

Banff and Kootenay National Parks include many ecosystems. As recognized by the Ecological Land Classification of the Canadian National Parks Service, ecoregions range from montane, through subalpine, to alpine (Poll et al. 1994). The ecoregion classification mainly reflects changes in environmental conditions due to altitude and aspect (Holland and Coen 1982). In British Columbia, the ecosystem classification differs from the one used in the national parks by Parks Canada. The lower part of the montane ecoregion corresponds to the IDF (Interior Douglas-fir) biogeoclimatic zone of the Biogeoclimatic Ecosystem Classification System. Patchy distributions of ICH (Interior Cedar-Hemlock) zone also occur. The upper part of the montane is equivalent to the lower part of the Montane Spruce (MS) zone. The lower part of the lower subalpine ecoregion corresponds to the upper part of the Montane Spruce zone. The upper part of the lower subalpine ecoregion corresponds to the ESSF (Engelmann Spruce – Subalpine Fir zone) (Holland and Coen 1983; Achuff et al. 1984; Meidinger and Pojar 1991; Poll et al. 1994). The study area, however, was limited to the montane and lower subalpine ecoregions of Banff and Kootenay National Parks. The ecoregions are further subdivided into ecosections, which are based on broad differences according to their landform features. Ecosections are again separated into ecosites, on which the plot selections was based (Section 3.1). Ecosites are based on differences in physiognomy, soil parameters and floristic attributes.

2.1 BANFF NATIONAL PARK

Banff National Park was established in 1885 and is located in Alberta (Figure 7). It covers an area of approximately 6,830 km² and extends along the main and front ranges of the eastern side of the Continental Divide. The montane ecoregion occupies

around 3% of the total land area in BNP. The subalpine ecoregion occupies 53.3%, and the alpine ecoregion 24% (Lastra 2001). The climate of BNP is frequently influenced by warm west winds (Chinooks) from the Pacific, which interrupt the more continental climatic conditions. Banff (1397m) has mean daily temperatures ranging between 25.5°C in July and -14.9°C in January, and a mean annual precipitation of 476 mm. Topography and elevation can cause climatic variation with elevation changes less than 100m (Holland and Coen 1982).



Figure 7 Locations of Banff and Kootenay National Parks (BC Rockies Information Portal 2002)

All stands investigated were located in the Bow River Valley watershed from Castle Junction, over Brewster Creek to Lake Minnewanka (approximately from 51°15'N and 115°54'W to 51°12'N and 116°55'W). Ninety plots were established in BNP at elevations ranging between 1410 m and 1650 m. An overview of plot locations in BNP according to ecosites can be found in Appendix III.

2.2 KOOTENAY NATIONAL PARK

Kootenay National Park was established in 1920 and is located in the Rocky Mountains, in south-eastern British Columbia (Figure 7). It is located along the western side of the Continental Divide, which forms the boundary between KNP and BNP. KNP covers an area of about 1,406 km². The montane ecoregion occupies around 30% of the total land area, the subalpine 48.9% and the alpine 18% (Lastra 2001).

The climate of KNP is influenced by warm and moist Pacific air. Kootenay Crossing (1170m) has mean temperatures ranging between 24.1°C in July and -18.1°C in January and a mean annual precipitation of 505 mm (Achuff et al. 1984).

All stands investigated were located in the Upper Kootenay River Valley watershed, from Settlers Road over McLeod Meadows to Dog Lake (approximately from 50°40'N and 115°52'W to 50°46'N and 115°55'W) at elevations ranging between 1140 m to 1300 m. Sixty five plots were established in KNP. An overview of plot locations in KNP according to ecosites can be found in Appendix III.

2.3 PHYSIOGRAPHY

The southern Canadian Rocky Mountains are built of folded and faulted sedimentary rock. The topography reflects the structural control of the bedrock. Colluvial landforms are common (Meidinger and Pojar 1991). Previous glacial events have given the main valleys in BNP and KNP a U-shaped appearance. In the Rocky Mountains, tilted beds may extend for long distances. The general topography exhibits a strong linear character with trellis pattern streams (Achuff et al. 1984)

2.4 SOILS

Soils in BNP and KNP vary greatly because of the complex topographic and climatic conditions. The majority of the soils in the sample plots in BNP and KNP belong to the Brunisolic order, followed by Luvisols and Regosols. Brunisols are normally immature soils, and found under forests, tundra and alpine vegetation (Achuff et al. 1984). In these soils relatively low rates of weathering have resulted in moderate development from the original parent material (Meidinger and Pojar 1991). In the parks, Brunisols occur under moist *Picea – Pseudotsuga menziesii* - mixed deciduous forests on stable slopes (Achuff et al. 1984). Eluvial (Ae) horizons are common in BNP (Holland and Coen 1983), but little or no eluvial horizon is found in these soils in KNP (Achuff et al. 1984). Luvisols usually occur on flat or gently sloping sites. They occur in association with Brunisols throughout much of the montane (Holland and Coen 1983). In some areas, the clay Bt horizon may restrict penetration by roots, air and water (Meidinger and Pojar 1991). Luvisols are moderately well drained and commonly develop on calcareous glacial and glaciolacustrine material (Holland and Coen 1983). Forests dominated by *Populus tremuloides* most commonly occur on Luvisols, but deciduous and coniferous forests also occur on this soil type. Holland and Coen (1983) found that Luvisols usually underlie *Pinus contorta* forests in Banff National Park.

Regosols occur on a variety of calcareous and noncalcareous geomorphic materials, slopes and different vegetation types. Under drier conditions, they are most often intermixed with Brunisolic soils (Holland and Coen 1983). They may also occur in harsh environments with low rates of chemical weathering and microbial activity (Meidinger and Pojar 1991; Holland and Coen 1983). Soil orders for each ecosite in which the plots were located can be found in Appendix II.

2.5 VEGETATION

Sample plot selection in the present study was limited to mesic sites in the montane and lower subalpine ecoregions. Sample areas were chosen according to ecosites in mixed species forests with *Pinus contorta* trees (Section 3.1). Open forests and grasslands are typical of the lower elevations in the southern Canadian Rocky Mountains. Forested areas are generally between 1200m and 1800m, and sample plots were all located between approximately 1100m to 1650m. Typical tree species in the study area included *Pinus contorta*, *Pseudotsuga menziesii*, *Picea glauca*, *Populus balsamifera* (black cottonwood) and *Populus tremuloides*. *Larix occidentalis* (Lw, western larch)) was also occasionally found in the plots within KNP. At higher elevations *Abies lasiocarpa* and *Picea engelmannii* were more common. *Picea glauca* and *Picea engelmannii* frequently hybridize. Less common species were *Betula* (birch) species. A classification of the dominant vegetation according to ecosites in which the plots were located can be found in Appendix II.

2.6 IMPORTANT DISTURBANCES IN BANFF AND KOOTENAY NATIONAL PARKS

Fire and mountain pine beetles have been two of the dominant disturbance agents in BNP and KNP. Although the focus of the present study is on the influence of MPB on stand structure, the fire history and its influences on stand structure could not be neglected, due to the importance of fire in the study area. The montane and lower subalpine ecoregions in the study area are reported to have typically been dominated by a mixed fire regime, with a tendency for fires to burn more in the montane than in the subalpine ecoregion in BNP (White (1985a). Past fire cycles have been relatively short (less than 50 years) with low intensities at low montane elevations (Tande 1979, White 1985a) and becoming generally less frequent with increasing elevations (White et al.

2004). There has been a decline in fire occurrence since the settlement era (Section 1.2). Heathcott (1999) and White (1985a) stated that periods between fires, have now increased. It is assumed that fire cycles have been similar in BNP and KNP, but KNP was reported to be characterized by more severe fire conditions (Heathcott 1999, Miyanishi et al. 2000). Day (1972) suggested that without frequent fires *Pinus contorta* dominated stands (*Pinus* phase) are replaced by *Picea* with *Abies* (*Picea-Abies* phase) and finally, in the climax state, by *Abies* with *Picea* forests (*Abies-Picea* phase). MPB have been frequent in KNP and have also been spreading recently in BNP (Section 1.2). Browsing is generally reported to be high (Section 1.2), but may vary to a large extent, depending on locally varying ungulate densities.

CHAPTER 3

METHODOLOGY

3.1 GENERAL APPROACH

In order to test the hypotheses (Section 1.3) it was necessary to collect stand structure data in areas that did and did not have records of previous MPB infestations.

It is recognized that stand dynamics after disturbances such as fire and MPB infestations are likely to follow a certain trajectory with time (Section 1.2). This is the case for tree growth, which is accelerated shortly after the disturbance (Oliver and Larson 1996) and later levels off (Burschel and Huss 1997), when the remaining and new trees have filled the gaps created by the disturbance. Site characteristics can also have a strong influence on tree growth (Burschel and Huss 1997), and consequently may influence MPB infestations and herbivory (Section 1.2).

To examine MPB and fire effects on stand dynamics an ideal study design would have compared -

- An equal number of stands at different times after MPB infestations,
- An equal number of stands with and without MPB disturbance history originating from the same stand-replacing high severity fire and experiencing the same subsequent low severity fire regime,
- Stands with and without MPB disturbance history from the same ecosite with similar physical features.

However, outbreaks only from the 1940's and 1980's in BNP, and from the 1980's and 1990's in KNP, could be located. Since it was possible to sample only a limited number of plots with records of previous MPB infestations, only a narrow time frame could be captured. It was also not feasible to sample stands with and without MPB in close

proximity that experienced the same stand replacing and subsequent stand maintaining fires. Consequently, the present study is a snap-shot restricted to certain points in time and to the ecosites investigated, both of which limit the generalizations that can be made.

In order to consider varying influences of site factors on stand structure, plots were established and distributed over a range of elevations and different ecosites as much as possible. However, study site selection was predetermined by past MPB incidence, therefore limiting the range of ecosites sampled. Plots in forest stands with records of past MPB infestations were sampled in BNP as well as in KNP. In order to pair KNP MPB plots with similar plots without MPB records, the latter plots were located in BNP due to a lack of suitable areas in KNP. The underlying reason was that past MPB infestations had generally killed all trees of a susceptible age in a sampling area. Consequently stands with records of MPB infestations were paired with stands in the same age class on equivalent ecosites in a different area which had no records of past MPB infestations. Due to different ecosite classifications in BNP and KNP with slightly varying vegetation, ecosites in both parks were compared and matched as closely as possible according to the dominant vegetation (Table 1).

Table 1 **Equivalent ecosites sampled in BNP and KNP**

Group/Ecosites	BNP Ecosites	KNP Ecosites
A	NY1	DG6, WY1
B	PT1	DR7
C	PT3	DR2, DR3, DR8
D	AL1	not sampled
E	BK6	not sampled
F	GA1	not sampled
G	PR1	not sampled
H	PR2	not sampled
I	PR4	not sampled
J	PR6	not sampled

Stand ages were stratified into 3 classes (50-99, 100-149, and ≥ 150 years). Location of stands in those age classes was done using the Ecological Land Classification and

GIS data by Parks Canada. However, sampling those stands occasionally resulted in different stand ages than what was indicated by the GIS data. Consequently, it was rarely possible, for a given ecosite and age class, to sample the same numbers of plots in both MPB and control forests (more detailed descriptions of the ecosites as well as their distribution and numbers of plots are found in Appendix II and III).

3.2 PLOT SELECTION

Plot locations involved the use of Ecosystem Classification Maps for KNP and BNP, a hand drawn map by Hopping and Mathers (1945), and archived documents of Banff National Park. Records of MPB infestations were gained from GIS data by Parks Canada and the Canadian Forest Service (CFS).

Banff National Park

1. Plots in areas **with MPB** records that had been sampled in previous years were re-sampled by using given UTM (Universal Transverse Mercator) coordinates. These plots were all about 100m apart and at least 2 tree lengths away from the nearest road.
2. Plots in areas **with MPB** records that had not been sampled previously were at least 2 tree lengths away from the nearest road and at least 2 tree lengths apart. An Ecosystem Classification Map for BNP was used to ensure that sampling occurred within the selected ecosite. As many plots per area as possible, but at least 2, were sampled.

Kootenay National Park

1. Plots in areas **with MPB** records that had been sampled previously were re-sampled by using given UTM coordinates and permanently marked centre points. These plots were all about 100m apart and at least 2 tree lengths away from the nearest road.
2. Plots in areas **with MPB** records not previously sampled were at least 2 tree lengths away from the nearest road and at least 2 tree lengths apart. An Ecosystem Classification Map for KNP was used to ensure that sampling occurred within the selected ecosite.

Banff and Kootenay National Parks

Plots in areas **without MPB** records were at least 2 tree lengths away from the nearest road on ecosites corresponding to previously sampled plots in areas with MPB records. Ecosystem Classification Maps were used as mentioned above. Prior to sampling it was visually estimated whether or not the trees were actually infested by MPB. With the exception of one site in KNP, corresponding plots without MPB records were located in BNP due to a lack of suitable areas in KNP.

Sampled stands from 1940 MPB infestations were subjected to an extensive fall-and-burn program in the 1940's (Hopping and Mathers 1945); consequently the CWD from the MPB killed trees was not present. There was only limited information about the location of the 1940's infestation (e.g. a hand drawn map from Hopping and Mathers 1945). The identification of areas that were potentially infested was done by searching and relocating old stumps, which originated (according to their appearance and state of decay) presumably from the 1940's.

Using UTM coordinates, it was possible to relocate the approximate locations of previously sampled plots (by Parks Canada) from the 1980's MPB infestations. The identification of areas that had been infested with MPB was assisted by relocating snags and logs, which originated presumably from the 1980's. The plots from the 1940's and 1980's MPB infestations were distributed over several ecosites and two ecoregions (the montane and the lower subalpine, Table 1, Appendix II).

In KNP, plots infested by MPB and sampled in 1993 by Terry Shore had been previously relocated, re-sampled and permanently marked in 2003 by the CFS (Canadian Forestry Service). Thus, it was possible to relocate exactly the centre points and resample those plots for the present study. The CFS plots were solely located in the montane ecoregion and limited to one group of similar ecosites (Appendix III).

3.3 HYPOTHESIS 1 - MOUNTAIN PINE BEETLE AND STAND STRUCTURE

In order to test hypothesis 1, "MPB infestations increase forest stand structural diversity of forest stands in the southern Canadian Rocky Mountains", structural diversity was measured in stands with different disturbance histories. The effects of MPB on stand structure were measured by comparing stands with and without previous MPB infestations on corresponding ecosites. To consider potential influences of fires, plots with different fire histories were compared considering different numbers of fires since stand initiation, different times since fire, and different levels of fire severity and fire frequency.

Horizontal stand structure:

expressed as tree species composition, condition (live or dead), tree density (number of trees per ha), diameter class distribution (DBH, cm), basal area (m²/ha), and vegetation cover (%)

Vertical stand structure:

expressed as proportions of tree species in different height classes

Stand characteristics:

species age class distribution, and dead and down woody fuels

Structural diversity (DBH and height class distribution as well as tree species distribution) was evaluated by using the Shannon-Wiener index:

$$H' = -\sum_{i=1}^S p_i \ln p_i$$

where s = number of species in the sample plots,

where p_i = the proportion of individuals in the i^{th} species, and

where \ln = the natural logarithm.

In the present study p_i is -

- 1) the proportion of trees found in each DBH and height class, and
- 2) the proportion of tree species in each sample set.

This index was chosen over others due to its wide acceptance in the scientific community and its simple application. The Shannon-Wiener index describes species richness and evenness. However, it is especially powerful as an index of richness (Magurran 1988).

3.3.1 Sample plot design

From the centre of a sample plot, 3 sub-plots with a radius of 15m, 7.1m, and 3.9m were established (Figure 8).

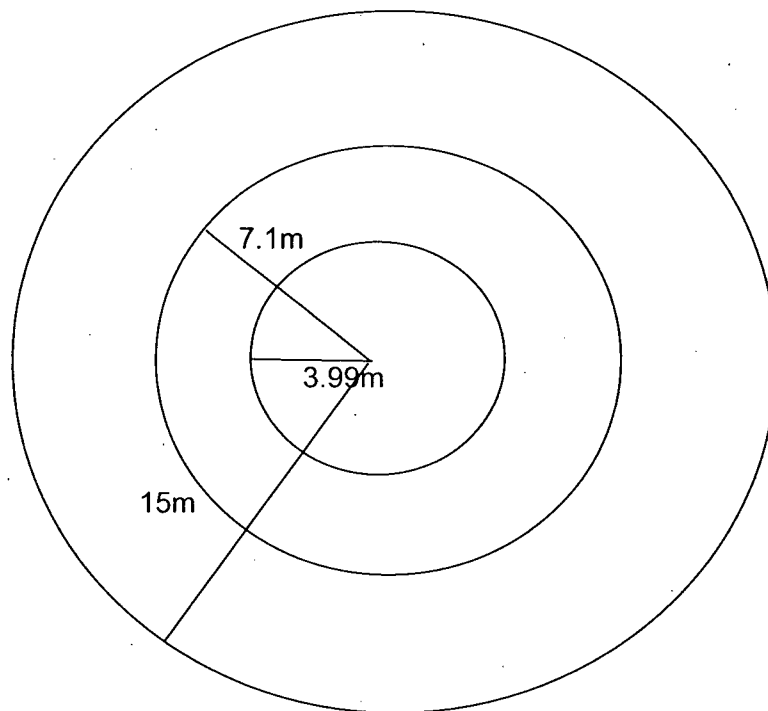


Figure 8 Arrangements and corresponding diameters of sub-plots within a main plot

Trees were measured as follows:

15m radius:

diameters of all trees with DBH $\geq 30\text{cm}$

7.1m radius:

diameters of all trees with heights $\geq 1.3\text{m}$

3.99m radius:

heights of all trees with heights $> 1.3\text{m}$ high

3.3.2 Field sampling

On all plots the vegetation was visually stratified into six vertical height classes (Lastra 2001):

A1: tree canopy $> 10\text{m}$

A2: tree upper subcanopy 5-10m

B1: tree lower subcanopy 2-5m

B2: tree saplings and shrubs 0.5-2m

C: shrub cover $< 0.5\text{m}$

CW: herb cover

- Percent cover was estimated for each of the 6 vegetation strata. Cover estimates were to the nearest 5% (low cover values were recorded as $< 5\%$, 1% , or $< 1\%$).
- DBH (diameter at breast height (cm), 1.3 m) was measured for all trees to the nearest mm
- Tree heights were determined using a clinometer and recorded to the nearest dm
- Increment cores were taken from trees of the same species, but with different diameters, and annual rings were counted to estimate the stand age class distribution. At least two trees per species (one large, one small) were cored at

each plot. These trees were cored as close to the ground and to the pith as possible to get the best estimate of the tree age. It is recognized that the "true" age of each tree is greater than the age from the coring height. Age to the coring height varies depending on the individual microsite conditions (competition, browsing, climatic influences, soils, etc...) and the angle of the slope (the steeper a slope, the closer to the base of a tree a core can be taken). However, to facilitate the analyses due to time constraints, tree age was reported as age at coring height. After counting the annual rings, the increment cores were placed into straws, sealed with masking tape and frozen until rings were counted again in the laboratory.

- Stem counts were made for all seedlings (3.9m radius plot), saplings (7.1m radius plot), and mature trees (7.1m and 15m plots).
- Dead and down woody debris mass was visually estimated using a "photo guide for appraising downed woody fuels for lodgepole pine, and Engelmann spruce – subalpine fir cover types", derived from similar forest types in Montana, U.S.A. (Fischer 1981).
- For identification of MPB plots, every indication of MPB activity (Blue stain within tree disc /stumps, green-, red-, or grey attack, pitch tubes and galleries) was recorded for each tree.
- For each plot, physical environmental factors were recorded, including slope, soil moisture regime, aspect, topographic position, elevation, and UTM coordinates. Vegetation type, based on the dominant vegetation and soil moisture regime, was also visually estimated.

Fire severity and frequency since the last stand replacing fire

While methods of describing a fire regime based on fire scars alone may be appropriate for systems which are characterized mainly by low-severity fires, these methods are less applicable in ecosystems that are also shaped by stand-replacing fires (Kulakowski et al. 2003), such as the ecosystems in the study area (Section 2.6). The relative severity of fires that occurred in a stand was assessed at each plot on a scale of 0-5 (Table 2) by assessing the age distribution of early and late successional tree species present. It was assumed that all the individuals of the fire-adapted pioneer species, *Pinus contorta*, of the same age established after the same disturbance, namely fire. Uneven-aged cohorts of *Pinus contorta* may have resulted from MPB.

Table 2 **Fire severity in relation to tree mortality**

Fire severity class	Tree mortality
0	100% tree mortality
1	95-99% tree mortality
2	50-95% tree mortality
3	5-49% tree mortality
4	Less than 5% tree mortality/understory only
5	no fire since stand initiation

Thus, the age distribution of *Pinus contorta* was used as an indicator of previous fire disturbances. For the present study, errors of recorded ages of ± 10 years were assumed possible, since the individual coring height varied and regeneration after disturbance may have undergone a time lag. For stand-replacing fires the stand age (which, for the present study, equals the age of the oldest trees) was an indicator of the

time since the last stand-replacing fire (Kipfmuehler and Baker, 1998), while fire scars were an indication of subsequent less intense fires. However, regeneration of later successional species, such as *Abies* and *Picea*, was not assumed to be triggered by fire. Older, late successional species were assumed to be survivors of low severity fires.

3.3.3 Laboratory work

Standard procedures were used to process increment core samples. There were four different datasets (Table 6, Section 4.1), encompassing different times of the 2004 field season as well as different people sampling those cores. A random selection of increment cores, which were collected to estimate the stand age class distribution, had their rings counted under a microscope in order to check the accurateness of the field counts.

3.3.4 Data analysis

The statistical analyses (Principal Components Analysis, ANOVA, linear regression, simple correlation, and t-test) and plotting of graphs and figures of the results was done by using SYSTAT 9.0 (1998) and Microsoft[®] Excel 2000. Outliers were removed. For the ANOVA the assumptions were considered to be met. The study is repeatable and the population distribution treated as normal, since several studies have shown that lack of normality in the dependent variable Y does not seriously affect the analysis when the number of observations per treatment is the same for all treatments" (Hicks 1993). This was the case in the present study when ANOVA was used. Additionally, Box (1953) suggested that when little is known of the parent distribution, the practice of testing for homogeneity of variances before making an ANOVA, may as well lead to more wrong conclusions than if the preliminary test (e.g. F-max, Bartlett's test, and others) was omitted. A Bonferroni multiple comparison test based on Student's t statistic was chosen as a post hoc test to determine which pairs of means differed significantly. For a small number of pairs, Bonferroni is relatively powerful compared to other post hoc tests

(SYSTAT 1998). A PCA (Principal Component Analysis) was used to analyse how much of the variation in the stand structure data could be explained by environmental factors such as slope, ecoregion, ecosite, vegetation type, aspect, and elevation, as well as by disturbances such as MPB and fire. The subsequent data analysis and stratification was done according to the outcomes of the PCA. The datasets were stratified according to time since MPB infestation and ecosite (Table 3), as well as number of fires since stand initiation, time since fire, and fire severity (Section 4.1.3).

Table 3 **Sample stratification of MPB and corresponding control plots**

Stand type	Ecosite groups ¹
Control 1990	C
MPB1990	C
Control 1980	B,D,F,G,H
MPB1980	B,D,E ² ,F,G,H
Control 1940	A, C, D, F, H, I, J
MPB1940	A, C, D, F, H, I, J

¹ Key to ecosites in Appendix II

² For this ecosite group no corresponding control plots exist in the sample Control 1980

The stratified datasets (Table 3) were compared with regard to:

- total number of trees/ha
- average age of dominant and co-dominant pine (Height class A1)
- basal area (m²/ha) of all tree species with DBH ≥ 7.5 cm
- basal area (m²/ha) of *Pinus contorta* with DBH ≥ 15cm
- Coarse woody debris amount (kg/m²)
- Regeneration density/ha
- Number of dead trees (Snags)/ha

- Diameter (cm) and height (m) class distribution
- Tree species distribution
- Age class distribution per species and height class (years)
- Percent ground cover per height class

Tree ages were only sampled for the A1, A2 and B1 height classes. Due to scarce data in the A2 and B1 layer and to the fact that both belong to the suppressed / intermediate tree layer; they were combined in the IT-layer. If more than one tree in the same species and height class was cored the average was taken. Broadleaved trees could not be aged, due to technical difficulties (trees were often decayed and increment borers often got jammed). The types of basal areas used were chosen according to the variables used to calculate the MPB susceptibility index (Section 3.5.1). The analysis of fire influences on stand structure was done with a reduced data set, which included only control plots (n=83). This decision was based on the fact that MPB influences stand structure by reducing the proportion of *Pinus contorta* in a stand, thus influencing stand structure. Since the study had been focused on comparing stand structure parameters according to previous MPB infestations, a post field sampling stratification according to number of fires since stand initiation, time since fire, fire severity (taking into account the influences of different ecosites) did not result in a satisfactory number of plots. Thus, the analyses of fire effects were unable to adequately consider the potential influences of ecosites. Consequently, the plots were stratified considering only the number of fires since stand initiation, time since fire (Section 4.1.3), and fire severity (Table 4). Due to a low number of fires following a stand initiating fire, groupings of only 0 fires, one fire and more than 2 fires since stand initiation were investigated. For the stratification of plots with different fire severities it was necessary to group plots into low severity fires and high severity fires (Table 4).

Table 4**Sample stratification according to fire severity**

Fire Group	Fire severity
1	1 to 2 (high)
2	3 to 4 (low)
3	5 (no fire)

High severity fires were considered to be those of class 1-2, while low severity fires were considered to be those of class 3-4. If more than one fire occurred on a given plot, it was stratified into the highest fire severity class (Table 2, Section 3.3.2).

The datasets stratified according to number of fires, time since fire and fire severity were compared with regard to:

- Percent ground cover per height class
- total number of trees / ha
- basal area (m^2 / ha) of all tree species with DBH ≥ 7.5 cm
- basal area (m^2 / ha) of *Pinus contorta* with DBH ≥ 15 cm
- Coarse woody debris amount (kg/m^2)

3.4 HYPOTHESIS 2 - BROWSING AND COARSE WOODY DEBRIS

In order to test hypothesis 2, that "browsing intensity decreases with increasing amounts of coarse woody debris", correlations among current browsing intensity, large woody debris mass and regenerating tree density (all species) in the plots sampled with previous MPB infestations in the 1990's were carried out. Since windthrow and past fires may have also contributed to the mass of CWD, the analysis of hypothesis 2 was limited to those 1990 MPB plots because this was the most extensive and

homogeneous data set for MPB plots (n=50). This data set had the highest amounts of coarse woody debris (kg/m²) and involved plots that were relatively close to one another. Thus, influences of other factors, such as varying ungulate populations, different times since disturbance, climate and ecosites, were minimized.

3.4.1 Sample plot design and field sampling

Sample plot design was the same as described for hypothesis 1 (Section 3.3). The following parameters were recorded in plots with a 3.9m radius:

- Number of trees of each species regenerating (trees with heights < than 1.3m, as described in Section 3.3.2)
- Total height of every regenerating tree

In plots with a 15m radius the following parameters were recorded:

- Browsing intensity, estimated using a 5-point ordinal scale (1=no browsing, to 5=severe browsing) (Table 5)
- Dead and down woody debris (kg/m²), estimated as described in Section 3.3.2
- Descriptive information and fire severity and frequency, recorded as described in Section 3.3.2

Table 5 Browsing intensity classification

Browsing intensity	Proportion of Plant browsed (%)
1	no browsing
2	1 - 25% of leaves browsed
3	26 - 50% of leaves browsed
4	51 - 75% of leaves browsed
5	76 - 100% of leaves browsed

3.4.2 Data analysis

The statistical analyses were done as described in Section 3.3.4. Average numbers of regenerating trees and CWD amounts (kg/m^2) were computed (Section 4.2) for each plot. For the analysis, the plots were stratified according to the different browsing intensities (Table 5), and compared in terms of numbers of regenerating trees and CWD amounts.

3.5 HYPOTHESIS 3 - MOUNTAIN PINE BEETLE STAND SUSCEPTIBILITY

In order to test hypothesis 3, that “disturbances such as MPB infestation and low severity fire lead to decreased susceptibility of forest stands to MPB in the southern Canadian Rocky Mountains”, the influence of disturbances on susceptibility of stands to MPB infestations was studied by applying a MPB susceptibility rating system to stands that had different fire and disturbance histories. The current susceptibility of the stands to MPB infestations was determined by using the susceptibility rating system of Shore and Safranyik (1992). This hazard rating system is used by the Canadian Forestry Service. The susceptibility-rating system provides a short-term index of the likelihood of a MPB infestation occurring and causing significant losses to the stand. According to Shore et al. (2000), this system has been widely used throughout British Columbia and appears to work satisfactorily based on the observed correlation between the stand susceptibility rating and tree mortality caused by mountain pine beetle. In this study it was used to determine the current average MPB susceptibility of stands for groups of stands with different disturbance histories.

3.5.1 The MPB susceptibility index

The Shore and Safranyik (1992) susceptibility index (S) for a given stand is the product of four variables:

$$S = P \times A \times D \times L$$

where $P = 100 \times \text{BA PI} / \text{BA total}$

P is the basal area of *Pinus contorta* (PI) greater or equal to 15cm DBH, expressed as a percentage of the total basal area of all species in the stand greater than or equal to 7.5cm DBH.

where **A** = Age Factor

A is a factor for the average age of dominant and co-dominant pine in the stand (Figure 9).

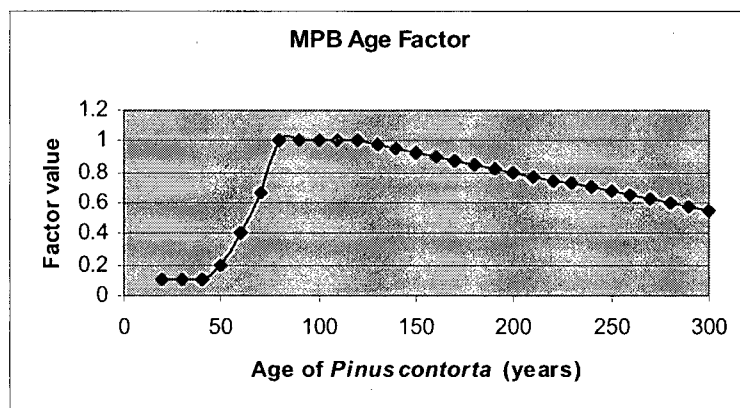


Figure 9 Age factor value, based on age of *Pinus contorta* (Shore et al., in press)

where **D** = Density Factor

D is a density factor for the number of stems per hectare of all trees greater than or equal to 7.5 cm DBH (Figure 10).

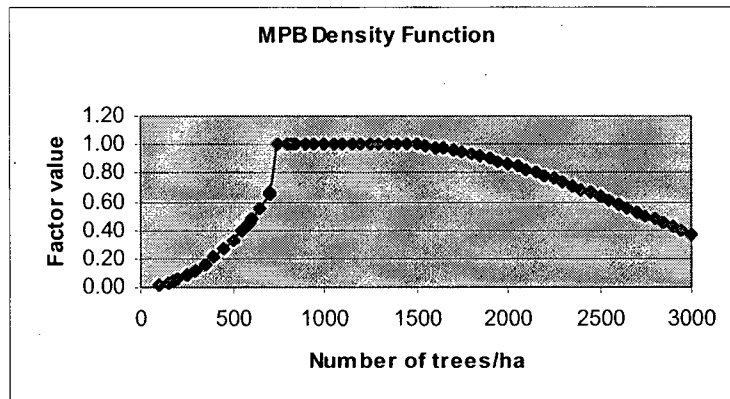


Figure 10 **Tree density factor value, based on tree density (Shore et al., in press)**

where **L** = Latitude / Longitude factor

L is a location factor determined by inserting the longitude, latitude, and elevation of the stand into the following equation and calculating the variable **Y**.

$$Y = (24.4 \times \text{longitude (degrees)}) - (121.9 \times \text{latitude (degrees)}) - (\text{elevation (m)}) + 4545.1$$

which is then used to calculate **L**:

If **Y** > 0, **L** = 1.0

If **Y** = -500 < **Y** < 0, **L** = 0.7

If **Y** < -500, **L** = 0.3

Susceptibility indices range from 0-100, with 0 being the least and 100 being the highest susceptibility to MPB infestations (Shore and Safranyik 1992).

To calculate values of **P**, stand basal area was determined (Section 4.1.2.1). According to Shore et al. (2000), this variable is considered important to determine MPB susceptibility on a stand-level, since it indicates the proportion of larger diameter pine in relation to the rest of the stand. Shore and Safranyik (1992) chose a DBH of 15 cm as a threshold level for the susceptible *Pinus contorta* component, because smaller diameter

trees are rarely attacked. If they are attacked, brood survival of MPB is generally not high due to insufficient phloem thickness in trees with small diameters (Section 1.2). For all species, a DBH threshold of 7.5 cm was chosen, according to the minimum diameter included in most inventory surveys in British Columbia (Shore and Safranyik 1992). Since MPB usually attacks older trees (Section 1.2), this is taken into account using the variable A. D takes into account the observation that stands with low densities are less likely to be attacked due to increased tree vigour and alteration of microclimate, while very dense stands over a certain threshold are again less susceptible to MPB (Section 1.2).

In order to get the values for the density-factor (D) and the age-factor, smoothing functions (Shore et al., in press) which are an update of the step values formerly used (Shore and Safranyik 1992), were used (Figure 9 and Figure 10).

3.5.2 Sample plot design and field sampling

As described above for hypothesis 1 (Section 3.3.2), DBH (cm) measurements, age determinations for *Pinus contorta* (from increment cores), and stem counts for mature trees were conducted on 15m and 7.1m radius plots. Plot description, fire severity and frequency were recorded as described in Section 3.3.2.

3.5.3 Laboratory work and data analysis

Tree ages were determined by counting annual rings in increment core samples extracted from trees within each plot as described above for hypothesis 1 (Section 3.3.3). For each plot the following parameters were computed and used to calculate the individual MPB susceptibility index (previous Section)

- average age of dominant and co-dominant pine (Height class A1) derived from increment core samples

- basal area (m^2 / ha) of pine with $\text{DBH} \geq 15\text{cm}$
- basal area (m^2 / ha) of all tree species with $\text{DBH} \geq 7.5 \text{ cm}$
- tree density/ha of all trees greater than or equal to 7.5 cm DBH

The plots were stratified into MPB and control plots (Table 3). Additional analyses were conducted on plots stratified into groups according to number of fires, time since fire and fire severity (Section 3.3.3). The statistical analyses were done as described in Section 3.3.4.

CHAPTER 4

RESULTS AND DISCUSSION

4.1 HYPOTHESIS 1: MOUNTAIN PINE BEETLE AND STAND STRUCTURE

In order to test if MPB infestations increase forest stand structural diversity of forest stands in the southern Canadian Rocky Mountains, stand structure data were collected from both MPB and non-MPB (control) affected stands. First, the overall influences of environmental parameters, MPB and fire were tested using a principal component analysis. Second, average stand structure characteristics for each stand type were then compared using an ANOVA. Finally, the influence of fire on selected stand structure parameters was also tested using ANOVA. Details of ANOVA tests are given in Appendix IV. Increment cores, which were collected to estimate the stand age class distribution, had their rings counted under a microscope in order to check the accuracy of the field counts (Table 6). It was found that field counts differed up to 7 years on average from the lab counts (Table 6). Field counts generally underestimated the number of annual rings compared to the counts under the microscope.

Table 6 **Difference in annual ring counts in the field and under a microscope¹**

Datasets²	Average difference (yrs)	Total no. of cores collected	Recounted cores (n)	%
Control 1990	7.3 (0.9)	262	71	27
MPB 1990	3.8 (0.7)	381	70	18
Control 1980	6.4 (2.2)	45	10	22
MPB/Control 1940 and 1980	1.1 (0.4)	23	11	48

¹ Standard errors are given in parentheses

² The year following the plot type indicates the year of the MPB infestation. For reasons of identification, the corresponding control plots have the same year attached.

4.1.1 Influences of environmental parameters

In order to quantify influences of environmental parameters, including disturbances, on stand structure, a PCA was run (n=155). First, a data set of stand structure parameters (Table 7) was analysed. The object of the Principal Components Analysis (PCA) was to take p variables (X_1, X_2, \dots, X_p) and find combinations of these to produce principal component indices (Z_1, Z_2, \dots, Z_p) that are uncorrelated (Table 7). Thus, the indices are measuring different dimensions in the data. Z_1 displays the largest amount of variation, Z_2 displays the second largest amount of variation, and so on (Manly 1994).

Table 7 Stand structure parameters¹ analysed in the PCA

Component loadings (n=155)					
Factors (X)	1	2	3	4	5
Cover A1	0.7	-0.4	0.03	-0.2	-0.09
Cover A2	0.1	-0.4	0.4	0.6	0.2
Cover B1	-0.3	-0.5	0.3	0.03	-0.6
Cover B2	-0.3	0.09	0.5	0.4	0.3
Cover Shrubs(CC)	-0.6	0.04	-0.1	0.3	0.09
Cover Ground (CW)	-0.6	0.4	0.02	-0.3	0.1
Stand age	0.2	0.2	-0.5	0.5	0.4
Trees/ha	0.8	-0.3	0.08	0.1	0.09
Regeneration/ha	0.2	0.2	-0.4	0.3	-0.5
Regeneration height	0.3	0.4	-0.3	0.3	-0.3
B2/ha	0.1	0.4	0.4	0.3	-0.5
Total basal area/ha	0.8	0.07	-0.05	-0.2	0.2
Basal area of PI/ha	0.5	0.6	0.3	-0.2	0.1
CWD(kg/m²)	-0.3	-0.5	-0.6	-0.05	-0.06
Eigenvalues (Z)	3.2	1.8	1.4	1.3	1.2
Total variance explained (%)	23.2	12.6	10.3	8.9	8.4

¹ Key for height classes is in Section 3.3

The first PCA axis (Z1) was found to explain 23% of the variation within the stand structure data, while the second axis (Z2) explained 12% (Table 7). The principal component factors had strongly decreasing eigenvalues - 3.2 for Z1 and 1.8 for Z2. Consequently, only the first 2 factors were considered in the following analysis (Table 7).

Table 8 Principal component factors merged with environmental and disturbance parameters¹

Parameters (n=155)	FACTOR(1)	FACTOR(2)
Aspect ²	-0.2	0.2
Slope	0.1	0.09
Elevation	0.6	0.4
Time since MPB	-0.3	0.2
Time since fire	0.2	-0.006
Number of fires	0.03	0.3
Fire severity 1	-0.03	0.3
Fire severity 2	0.009	0.2
Fire severity 3	0.06	0.1

¹ Significant correlations are shown in bold letters ($r > 0.2$)

² Aspects were considered as cool (-316° to 135°) or warm (-136° to 315°).

Merging the PCA file with environmental plot data, correlations were found between the stand structure data (Table 7), expressed by the principal component factors, elevation and time since the last MPB infestation (Table 8). The strong influence of elevation, however, is likely due to the location of 50 of the 1990 MPB plots at the lowest elevations and all on one ecosite class (Label C, Figure 11), because those were all found at the lowest elevations of all sample plots in KNP.

Although the second PCA axis suggests that number of fires and severity of the first fire (Fire severity 1) are related to stand structure, this axis explained only 12 % of the variation of the data. Thus the relationship here is not very strong.

The outcomes of the PCA justified further data analysis, concentrating on stratification of the datasets according to time since MPB infestations and ecosites. Further stratification would have reduced the limited number of MPB plot samples to such a low

number that statistical analysis would not have been possible. Also this did not appear to be necessary based on the low influence of the remaining parameters.

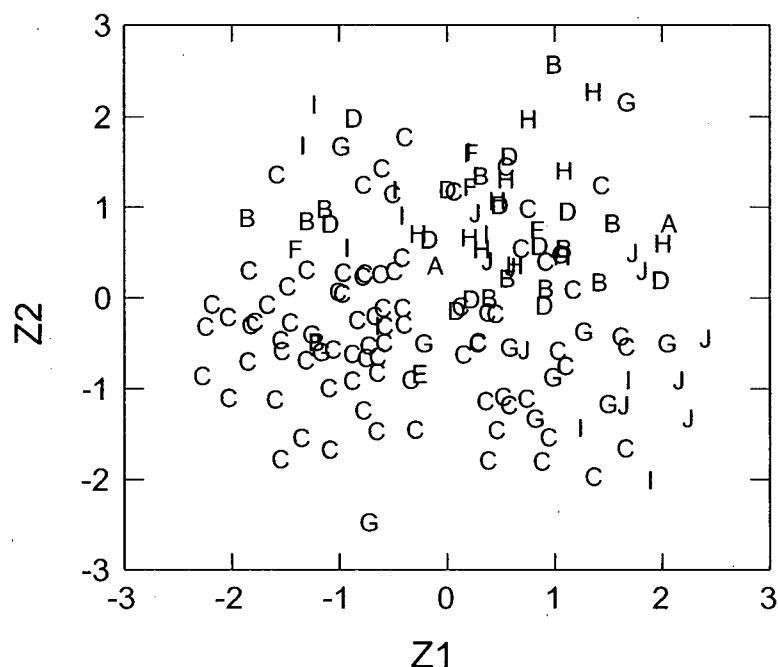


Figure 11 Plots stratified according to ecosites¹ in relation to the first and second PCA axis

4.1.2 Mountain Pine Beetle plots and stand structure

In order to analyse influences of MPB on stand structure parameters the data were stratified by the time since the last MPB infestation and paired with controls on corresponding ecosites (Table 3, Section 3.3.3). Since stand age might have a significant influence on stand structure parameters, the plots stratified according to the time since the MPB infestations (Table 9) were tested for significant differences between the average stand ages. All ages were compared with each other. An ANOVA showed that the average stand age differed significantly among stand types ($P < 0.004$, Table 9).

¹ For key to ecosites see Appendix II

Table 9**Mean stand ages of MPB and control plots**

Origin (year)	Stand type	Plots (n)	Average stand age
1990	Control	28	100 (4.6) ^B
	MPB	50	109 (3.9) ^{AB}
1980	Control	36	124 (6.7) ^A
	MPB	11	128 (10.0) ^{AB}
1940	Control	66	109 (3.0) ^{AB}
	MPB	11	121 (3.6) ^{AB}

Means followed by different superscripts are significantly different at $p < 0.05$, standard errors are given in parentheses. Due to the distribution of the ecosites, several control plots were for more than one MPB type.

A post-hoc Bonferroni's multi comparison test revealed that stand age was not significantly different between the MPB and the corresponding control plots, with the exception of 1990 and 1980 control plots ($p < 0.05$). Thus, comparisons of stand structure between MPB groups (and corresponding controls) were slightly limited due to (besides the influence of different ecosites) an underlying influence of stand age on stand structure. It has to be considered however, that the determination of stand age in the field was based on the oldest trees found in a plot. Consequently, in plots with past MPB infestation, it was not possible to determine the age of the trees that were previously killed by MPB. Thus the stand age may be underestimated. The error is potentially lower in plots with more recent infestations, but may be higher in the 1940 MPB plots.

4.1.2.1 Selected stand structure parameters

It was found for each sample set (MPB and corresponding control) that the number of trees per hectare with a DBH over 7.5 cm was significantly lower in plots with a previous MPB infestation. This is consistent with Hawkes et al. (2003) who reported that density of trees > 7 cm DBH decreased after MPB infestations. However, there appeared to be a trend of increasing numbers of trees with increasing time since the infestation. Hawkes et al. (2003) also found that stand volume decreased 10-19 years after re-measuring

stands with previous MPB infestations, which indicated that mortality occurred not only among numerous trees but also in the higher diameter classes, as found elsewhere (Shore et al. 2000, Whitehead 2001, The Mountain Pine Beetle Initiative 2004). In the present study similar trends were found 15 years after a MPB infestation (Table 10), based on a significantly lower basal area after a MPB infestation in 1990 MPB plots (Table 10). A significantly lower tree density for the 1980 and 1940 infestations, but a similar total basal area compared to the corresponding control plots, suggests that trees remaining after the disturbance might have experienced accelerated growth, increasing total basal area (Table 10).

The basal area of *Pinus contorta* trees with a DBH larger than 15cm was significantly lower on the MPB than on the corresponding control plots (Table 10). These trends are consistent with Armour (1982), who found that the basal area of *Pinus contorta* after MPB infestations in north-western Montana was in a similar range (3.7-9.2m²/ha) to that found in the present study, and was significantly lower from 3 to 80 years after MPB infestations. The lack of a consistent trend in proportion of *Pinus contorta* with time since disturbance may be due to the variety of ecosites or stand age classes (Table 9). Coarse woody debris mass was higher in MPB plots than in control plots for the 1990's, but not for the 1980's and 1940's infestations (Table 10). In the 1990 MPB plots, windthrow of MPB killed *Pinus contorta* has lead to locally high mass of coarse woody debris (a high proportion of those plots were located on ridges). A lower difference in CWD mass between 1980 MPB plots and the corresponding controls might be due to relatively less blow-down of MPB-killed trees. This is supported by a greater number of standing dead trees in the 1980 than in the 1990 MPB plots (Table 11). Coarse woody debris mass in the 1940 MPB plots was (insignificantly) lower than on the corresponding control plots, possibly influenced by the fall-and-burn practices in the 1940's (Hopping and Mathers 1945). However, without removal of CWD, a decline would also be expected: Armour (1982) found in Douglas-fir/pinegrass ecosystems in north-western Montana, an initial increase in CWD after MPB infestation was followed by a gradual decline. In spruce/queen's cup habitat types, however, the initial increase in CWD was followed by a plateau.

Table 10 Mean values of stand structure parameters in MPB and control plots

Origin (year)	Stand type	Plots (n)	Trees/ha DBH>7.5 ¹ cm	BA (m ² /ha) DBH>=7.5cm ²	PI BA (m ² /ha) DBH>=15cm ³	CWD (kg/m ²)	Regeneration /ha
1990	Control	28	1335 ^A (111.4)	34.8 ^A (2.4)	23.7 ^A (2.3)	2.8 ^B (0.3)	1535 ^A (347.0)
	MPB	50	496 ^B (46.0)	24.3 ^B (2.2)	8.1 ^B (1.4)	4.2 ^A (0.2)	824 ^A (178.4)
1980	Control	36	1423 ^A (115.4)	32.0 ^A (2.0)	20.0 ^A (2.0)	2.0 ^A (0.2)	1472 ^A (295.7)
	MPB	11	689 ^B (161.2)	32.6 ^A (4.1)	6.5 ^B (2.6)	3.0 ^A (0.7)	3658 ^A (1172.8)
1940	Control	66	1405 ^A (106.6)	33.6 ^A (1.6)	20.6 ^A (1.5)	2.1 ^A (0.2)	1712 ^A (266.0)
	MPB	11	883 ^B (139.0)	31.6 ^A (7.5)	6.9 ^B (3.8)	1.6 ^A (0.3)	762 ^B (241.6)

Means for a given year of origin followed by different superscripts are significantly different at $p < 0.05$, standard errors are given in parentheses

¹ The 7.5cm cut-off was chosen due in order to avoid counting regeneration and suppressed trees, since these might substantially alter results for this variable and due to its use in the MPB susceptibility index (Shore and Safranyik 1992)

² The 7.5cm cut-off was chosen in order to relate results to the number of trees/ha

³ The 15cm cut-off was chosen due to an increased susceptibility of lodgepole pine >15m DBH to MPB infestations (Shore and Safranyik 1992).

There was no significant difference in the density of regenerating trees between MPB and the corresponding controls with the exception of plots with previous MPB infestations in the 1940's. On those plots, significantly less regeneration density was found in MPB than in control plots. This might be due to lower CWD in 1940 MPB plots, which might have sheltered regeneration from browsing (Ripple and Larson 1992). However, the higher crown closure in those plots could also have inhibited extensive growth of regeneration in recent years (Oliver and Larson 1996).

4.1.2.2 Snags

Small snags, which were most likely killed by competition, were separated from larger diameter ones, which were potentially killed by MPB, using a cut-off DBH of 15cm (Shore and Safranyik 1992). For larger diameter snags that had died due to old age or previous fires, the next DBH cut off was 30cm. Larger diameter *Pinus contorta* tend to be older, often about 120 years, and are less susceptible to MPB than trees aged 80-120 years (Figure 9, Section 3.5.1).

Table 11 Mean densities of snags/ha in MPB and control plots

Origin (year)	Stand type	Plots (n)	Snags/ha for snags with DBH =		
			0-15cm	15-30cm	>30cm
1990	Control	28	801 ^A (188.2)	106 ^A (22.7)	4 ^B (1.4)
	MPB	50	126 ^B (25.1)	143 ^A (35.5)	29 ^A (6.3)
1980	Control	36	1014 ^A (138.7)	54 ^B (11.3)	4 ^A (1.7)
	MPB	11	350 ^B (59.2)	247 ^A (32.4)	38 ^A (19.9)
1940	Control	66	837 ^A (115.7)	85 ^A (12.5)	0 ^{id}
	MPB	11	237 ^B (63.0)	21 ^B (8.6)	1 ^{id} (1.3)

Means for a given year of origin followed by different superscripts are significantly different at $p < 0.05$, standard errors are given in parentheses, id = insufficient data

Significantly fewer smaller diameter snags (DBH 0-15cm) were found in MPB plots compared to control plots (Table 11), most likely because of a lower tree density (Table 10) and thus less competition by other trees in MPB plots. Dense stands contain higher numbers of suppressed trees, which die after a certain period depending on the shade tolerance of the species (Oliver and Larson 1996). Thus, small diameter trees in MPB plots may have had a higher chance of survival than in the more dense control plots. More open stands may also have led to significantly lower 15-30cm DHB snag density in the 1940 MPB plots. Similar trends, with lower densities of larger snags might be observed in the future on 1980 and 1990 MPB plots after MPB killed trees have collapsed.

Dead standing trees with 15-30cm DBH were significantly more abundant in the 1980 MPB plots only, possibly due to a higher density of MPB killed *Pinus contorta* trees. A high proportion of MPB killed trees were windthrown in the 1990 MPB plots, which might explain similar numbers of 15-30cm DBH snags as in the control. However, the proportion of large diameter snags was highest in plots in 1990 and decreased with time since infestation (Figure 12). This was also found by Armour (1982), and is possibly the result of collapsing MPB killed *Pinus contorta*.

Larger snags (>30cm DBH) were significantly more abundant in 1990 MPB plots compared to the control, despite the observed windthrow. One reason might be that very large diameter trees are often solitary, and although dead, might have developed previously a structure that is more resistant to windthrow. Also, these snags might have belonged to tree species with root systems less susceptible to windthrow (Burschel and Huss 1997). The densities of snags in the 1980 and 1990 MPB plots were similar to those of Hawkes et al. (2003), who found 10-19 years after an MPB outbreak in BC and Alberta Rocky Mountain forests that MPB killed tree densities ranged between 120 to 273 trees/ha. A study in an BC ESSF forest reported about 830 snags/ha in stands with ages ranging between 100 and 120 years (Kopra 2001), which resembles the numbers of snags found in the control plots of the present study (Table 11).

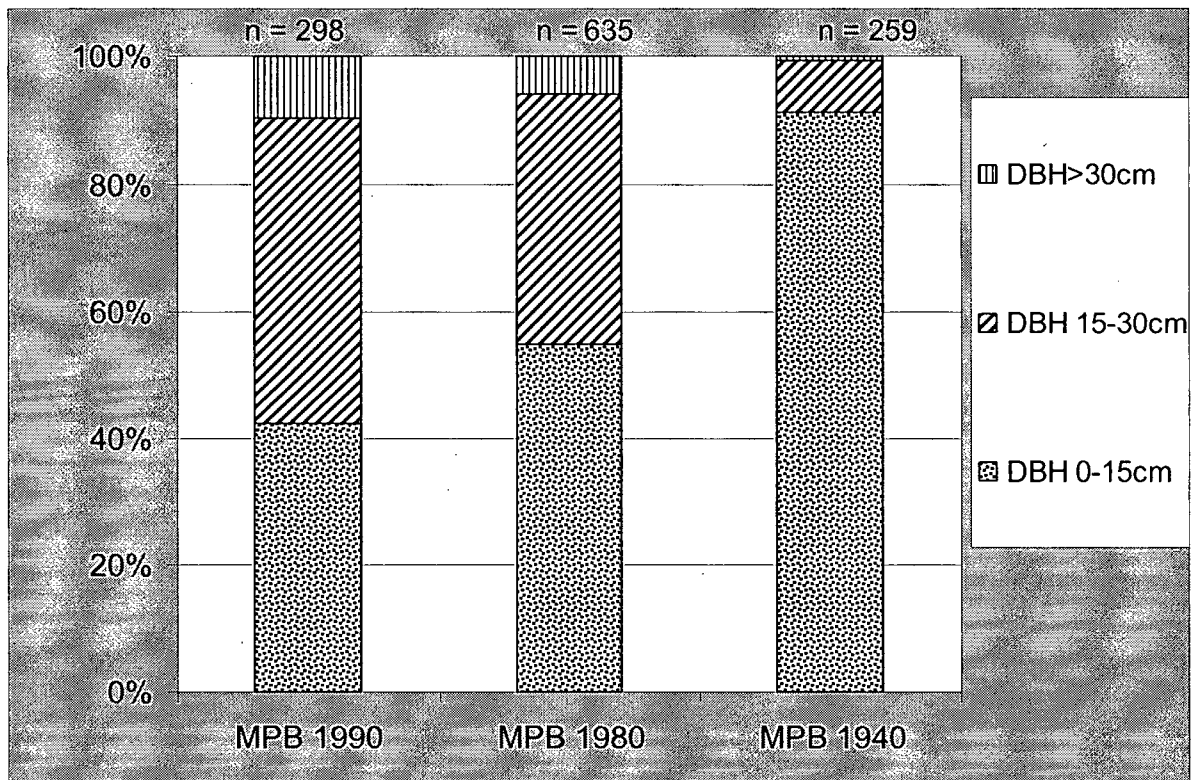


Figure 12 Proportions of snags with different DBH's in MPB plots from the three different MPB infestations

4.1.2.3 DBH and height class distribution

Although comparisons between the MPB plots was limited due to differences in stand age and ecosites, there tended to be fewer medium diameter trees in the dominant tree layer (A1) 15 and 25 years after an infestation (1980 MPB and 1990 MPB)(Table 12). In those plots, the smallest height and diameter class trees were most abundant, presumably because tree regeneration was stimulated by the MPB outbreak. In 1940 MPB plots, however, the situation appeared to be reversed, with most trees occurring in the dominant layer, and few regenerating trees. Overall, the Shannon-Wiener index indicated a higher structural diversity in 1990 MPB than control plots. Indices did not differ significantly following the 1940 and 1980 infestations. Structural diversity indices in 1940 as well as 1980 MPB plots were almost similar to the corresponding control plots (Table 12). Although the Shannon-Wiener index did not indicate any significant

differences between MPB and control plots for the 1980 and 1940 infestations, when based on the averages of individual plot indices, when calculated for the average stand composition per sample set the values differed from those in Table 12:

- **1990 plots**
 - Control = 1.38
 - MPB = 1.74
- **1980 plots**
 - Control = 1.55
 - MPB = 1.73
- **1940 plots**
 - Control = 1.56
 - MPB = 1.47

This suggests that the “average” MPB stand was more structurally diverse than the “average” control stand, for both the 1980 and the 1990 MPB infestations.

Table 12 Mean tree density (stems/ha)¹ and structural diversity of MPB and control plots according to tree DBH and height class

Origin (year)	Stand type	Plots (n)	A1 <15cm	A1 15-30cm	A1 >30cm	A2 <15cm	A2 15-30cm	B1 <15cm	B2 <15cm	Shannon-Wiener Index for structural diversity
1990	Control	28	396 ^A (96.7)	663 ^A (59.5)	78 ^A (15.3)	257 ^A (44.0)	7 ^A (3.8)	60 ^A (13.8)	20 ^B (6.2)	1.07 ^B (0.06)
	MPB	50	66 ^B (12.5)	241 ^B (29.2)	81 ^A (7.9)	106 ^B (22.3)	15 ^A (6.6)	87 ^A (15.3)	87 ^A (19.6)	1.27 ^A (0.05)
1980	Control	36	535 ^A (86.8)	644 ^A (57.8)	53 ^A (12.1)	365 ^A (89.9)	0 ^{id}	263 ^A (49.7)	93 ^B (20.4)	1.19 ^A (0.06)
	MPB	11	121 ^B (40.3)	281 ^B (104.4)	90 ^A (43.7)	212 ^A (73.8)	23 ^{id} (17.6)	379 ^A (158.4)	132 ^A (50.0)	1.20 ^A (0.15)
1940	Control	66	562 ^A (94.6)	619 ^A (37.9)	68 ^A (9.6)	319 ^A (55.5)	7 ^A (2.8)	225 ^A (34.2)	90 ^A (17.1)	1.16 ^A (0.04)
	MPB	11	73 ^B (30.6)	580 ^A (103.9)	82 ^A (23.9)	146 ^B (50.2)	31 ^A (15.4)	123 ^B (32.4)	48 ^A (15.8)	1.17 ^A (0.1)

Means for a given year of origin, DBH and height class followed by different superscripts are significantly different at $p < 0.05$, standard errors are given in parentheses, id = insufficient data for comparisons

¹ Numbers vary from those found in Table 10, because in the above table all diameters of trees with heights $> 1.3\text{m}$ were included.

1990 MPB – Control

Small diameter trees (DBH<15cm) in the dominant tree layer were less common in MPB plots than in the controls (Table 12). After the 1990 MPB infestation, these trees potentially grew into larger diameter classes, because MPB mortality reduced the *Pinus contorta* overstory. This would explain the higher number of trees in the A1 15-30cm DBH class than in the <15cm DBH class (Table 12), even though previous MPB infestation would have killed large *Pinus contorta*. This is supported by the significantly lower basal area of *Pinus contorta* with diameters >15cm on MPB compared to control plots (Table 10, Section 4.1.2.1)).

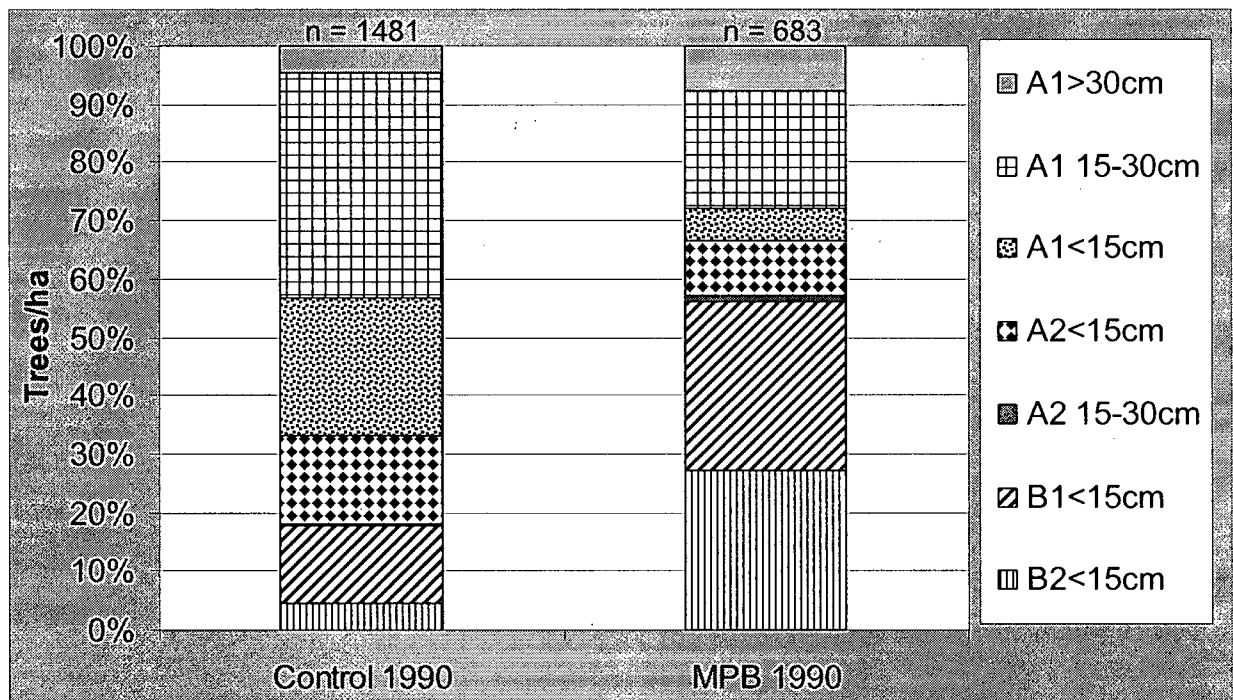


Figure 13 Height and DBH class distribution after MPB infestations in the 1990's

The number of trees in larger diameter classes (>30cm DBH) did not differ significantly between the 1990 MPB and the control plots. A higher number of trees in the A2 tree layer in plots unaffected by MPB might have been due to a higher amount of suppressed trees resulting from competition, since overall tree numbers on those plots are higher (Table 10). Remaining trees on the 1990 MPB plots may have grown faster and into a higher height class due to release. This would explain why the average

number of trees in the A2 class with <15cm DBH of the control plots is similar to the number of trees of the A1 class with 15-30cm DBH of the MPB plots.

Significantly more trees in the smallest height and DBH class (B2) in 1990 MPB plots (Figure 13) indicated that the growth of regeneration might have been triggered by the MPB killed *Pinus contorta* overstory. Overall, stands in 1990 MPB had the highest proportion of small trees (B1 and B2), probably regeneration, and fewer intermediate and large trees than the control plots (Figure 13).

1980 MPB – Control

The same trends as discussed for the 1990 MPB and corresponding control plots (above) were apparent for the 1980 MPB plots. Trees with diameters up to 30cm DBH were lower in 1980 MPB plots than in the corresponding controls (Table 12).

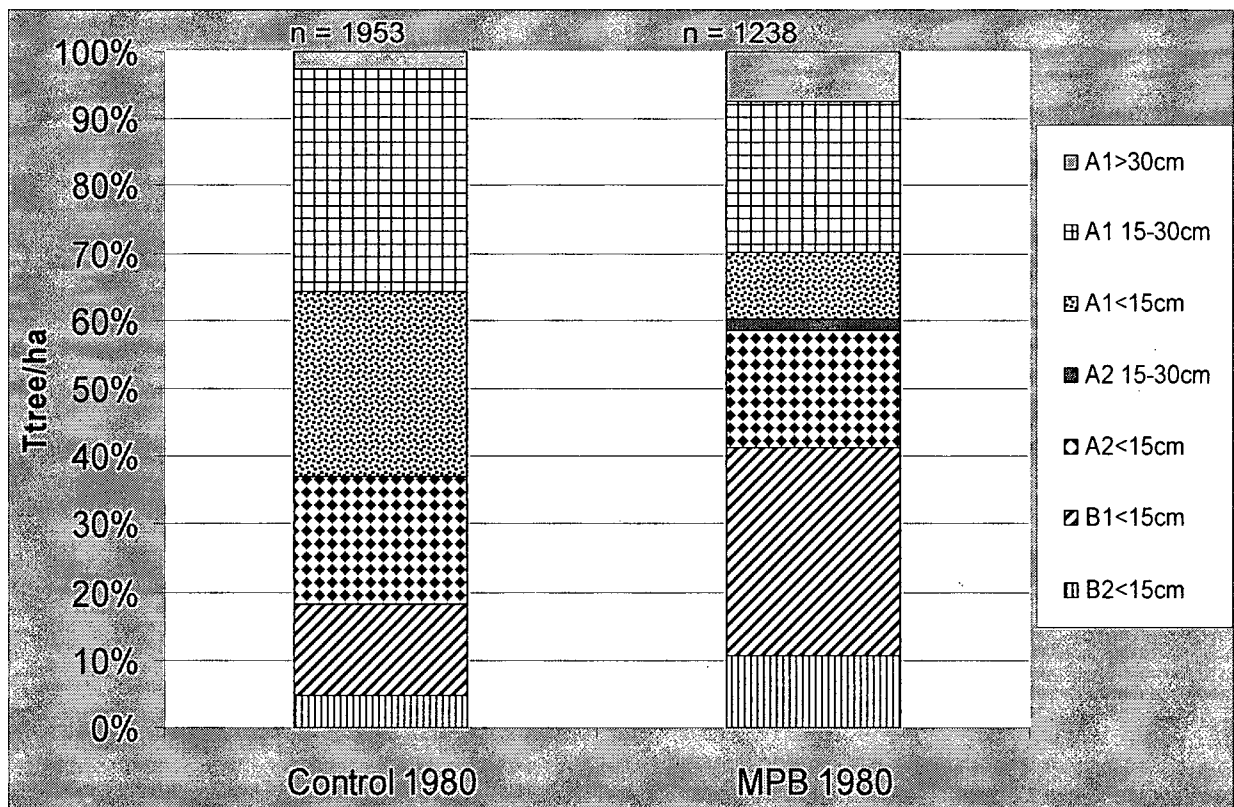


Figure 14 Height and DBH class distribution after MPB infestations in the 1980's

More trees per hectare in the largest diameter class of the MPB plots might have been caused by an increased growth of the remaining trees after release in 1980. Although not statistically significant, there were higher numbers of smaller diameter (<15cm DBH) trees in the A2 height class in the control plots. On the corresponding 1980 MPB plots a proportion of these trees may have grown already into higher height and DBH classes due to release. Significantly more trees in the smallest height and DBH class (B2, Figure 14) indicate that the growth of regeneration might have been triggered by the previous death of overstory *Pinus contorta* trees. Overall, stands in 1980 MPB plots were dominated by, and had a higher proportion of, small trees (B1 and B2), probably regeneration, as well as very large diameter trees (>30cm DBH) than the control plots (Figure 14).

1940 MPB – Control

Most of the remaining trees after the MPB infestation in the 1940's appeared to have grown into the largest height class with diameters between 15-30cm. This would be expected since 65 years after an infestation the remaining trees in the understory or new seedlings would have had time to grow to maturity. Thus, the total numbers of trees in this class is similar on both MPB and control plots (Table 12). Due to lower total numbers of trees on the 1940 MPB plots a higher proportion (%) of trees in 1940 MPB plots is in the A1 height class with diameters between 15-30cm than on the control plots (Figure 15).

4.1.2.4 Tree species distribution

It appeared that the proportion of *Pinus contorta* increased and that of *Picea* decreased with increasing time since MPB infestation (Figure 16). A trend to canopy dominance of *Picea* species after disturbances as observed by Armour (1982) and Antos and Parish (2002) was only obvious in the present study in the 1990 MPB plots (Figure 16) and was certainly solely due to the low numbers of *Pinus contorta*, since densities of *Picea* were similar in 1990 MPB and control plots (Table 13).

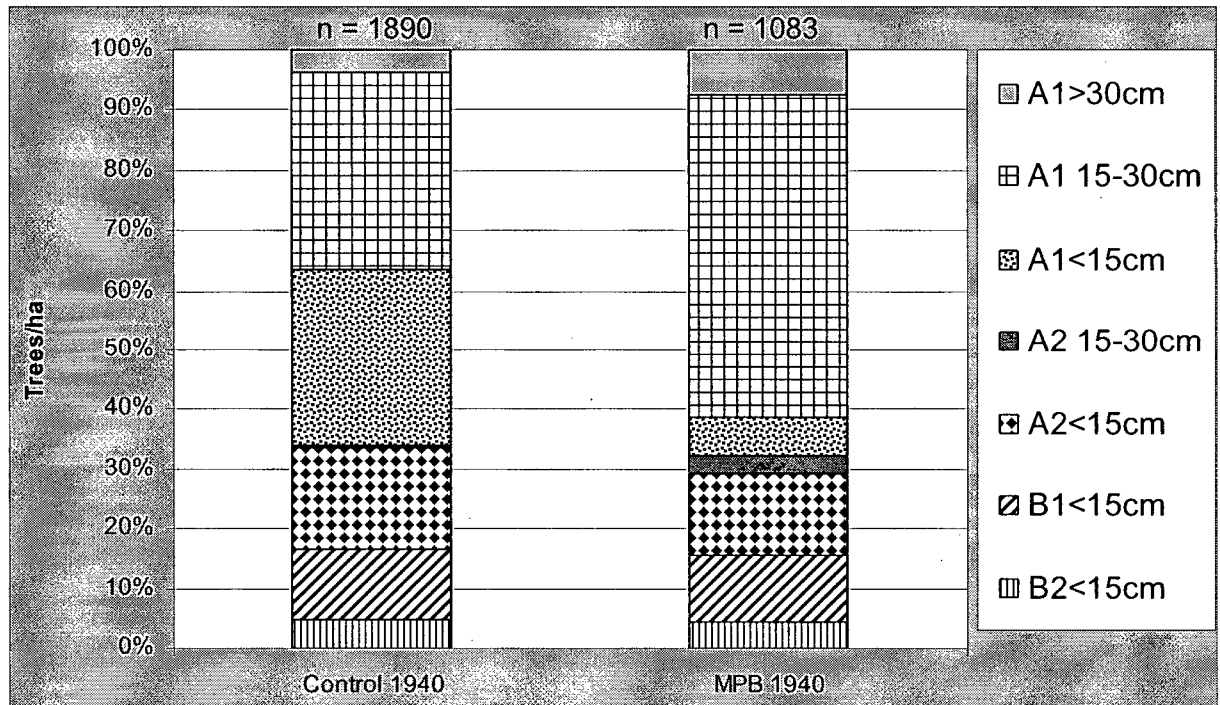


Figure 15 Height and DBH class distribution after 1940 MPB infestations

In the present study, however, on the 1940 MPB plots there was even a trend to a higher proportion of *Pinus contorta* compared to the corresponding control plots with significantly less *Picea*. Regeneration density on those plots, however, was significantly lower than on the corresponding controls (Table 10; Section 4.1.2.1), which may suggest that some time since their establishment had past.

Fewer trees per ha in MPB plots (Table 10, Section 4.1.2.1) might actually promote the growth of the shade intolerant pioneer *Pinus contorta* after a disturbance by MPB, or delay the succession towards a late successional forest with *Abies-Picea* dominance as suggested by Day (1972) and Franklin and Laven (1991) in the face of fire exclusion. However, since the 1980 MPB plots had a significantly higher proportion of *Abies*, compared to the control, the low numbers *Picea* as well as *Abies* in the 1940 MPB plots might have been due to subsequent very low severity fires. Five out of eleven post stand initiation low severity fires were sampled on those 1940 MPB plots.

Table 13 Mean density (stems/ha)¹ for different tree species and species diversity of MPB and control plots

Origin (year)	Stand type	Plots (n)	Act/At	Fd	Bl	Lw	Pl	Se/Sw	Shannon-Wiener Index of species diversity
1990	Control	28	201 ^A (74.2)	157 ^A (38.3)	2 ^A (2.3)	17 ^A (10.4)	750 ^A (133.1)	506 ^A (89.1)	0.76 ^A (0.07)
	MPB	50	345 ^A (93.4)	152 ^A (34.7)	9 ^A (3.6)	4 ^A (2.8)	93 ^B (17.1)	528 ^A (75.4)	0.75 ^A (0.05)
1980	Control	36	16 ^A (7.3)	2 ^A (1.8)	21 ^A (8.3)	0 ^{id}	1174 ^A (106.9)	745 ^A (153.5)	0.51 ^A (0.04)
	MPB	11	202 ^A (182.3)	34 ^A (24.6)	230 ^A (154.2)	12 ^{id} (11.5)	390 ^B (144.5)	289 ^B (122.8)	0.50 ^A (0.1)
1940	Control	66	91 ^{id} (33.4)	70 ^A (18.7)	52 ^A (20.5)	7 ^{id} (4.5)	998 ^A (114.4)	646 ^A (108.0)	0.59 ^A (0.04)
	MPB	11	0 ^{id}	80 ^A (68.2)	33 ^A (17.3)	0 ^{id}	820 ^A (122)	220 ^B (63.4)	0.55 ^A (0.1)

Means for a given year of origin and tree species followed by different superscripts are significantly different at $p < 0.05$, standard errors are given in parentheses, id = insufficient data for comparison

¹ Total numbers for sample sets differ from those in Sections 4.1.2.1 and 4.1.2.3 due to stratification of parameters investigated

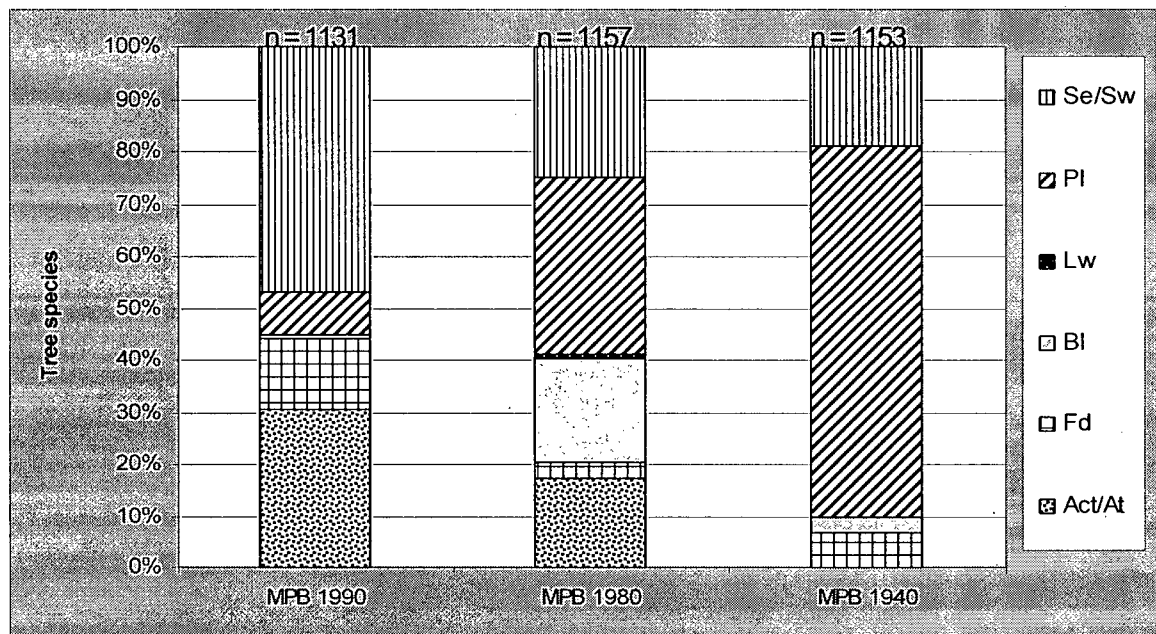


Figure 16 Tree species distribution in MPB plots

However, since it is known that those plots were subject to a fall and burn program, such burns may have been the fires sampled. Nevertheless, post MPB infestation removal of the infested trees and subsequent low intensity burns might have promoted the more open, early *Pinus contorta* dominated forests, since *Pinus* densities are almost equal on the 1940 MPB and control plots. However, other early successional species such as *Populus tremuloides* did not appear to be promoted. Browsing might have prevented regeneration of broadleaved trees, *Pseudotsuga menziesii* or *Abies* from gaining higher proportions in MPB plots, since shoots and other palatable parts of those species are known to be browsed. As *Picea* species are known for their low palatability throughout the year, browsing was not likely to account for the significantly low density of *Picea* in 1940 and 1980 MPB plots (Fraser et al. 2001). On the other hand, numerous other influences, such as available seed sources, weather following the disturbance, and other insect disturbances, might have influenced the species distribution. For example, Antos and Parish (2002), found that although many *Abies* owe their canopy position to release after disturbance, few canopy *Abies* established in response to either

the stand-initiating event or subsequent partial disturbances, pointing out the importance of seedling banks.

Overall, MPB appear not to have increased the tree species diversity significantly as indicated by the Shannon-Wiener index (Table 13). The slightly lower index in the 1940 MPB plots compared to the controls, was most likely due to a lack of *Larix occidentalis* since those MPB plots were exclusively located in BNP. *Larix occidentalis* is not present in BNP (Parks Canada 2004). This shows the limitations of comparisons between plots from different areas. However, *Larix occidentalis* was not abundant on any of the sample plots (Table 13). Low densities of this species might be a reason for overall low values for the Shannon-Wiener indices (Magurran 1988). Also, in plots with only one tree species the Shannon-Wiener index had a value of zero, which had resulted in overall low average values. This is inconsistent with Magurran (1988), who suggested that typically the Shannon-Wiener index ranges from 1.5-3.5.

A cause for similar values between sample sets might be that the index is a good measure for species richness, but not so much for species evenness (Magurran 1988). Consequently, the index might have not accounted sufficiently for the distribution of trees within a sample. For example, the proportions of tree species in the 1940 and 1980 MPB plots are very different (Figure 16), but these Shannon-Wiener indices are very similar (Table 13). Although the Shannon-Wiener index did not indicate any significant differences based on the averages of individual plots, when calculated for the average stand composition per sample set the values differed from those in Table 13. These latter values are -

- **1990 plots**
 - Control = 1.26
 - MPB = 1.25
- **1980 plots**
 - Control = 0.77

- MPB = 1.49
- **1940 plots**
 - Control = 1.09
 - MPB = 0.85

This would suggest that the 1980 MPB plots were more species diverse than the control plots, as indicated by Figure 16.

4.1.2.5 Tree species age distribution

There were some significant age differences for a given tree species between the 1990 MPB and corresponding control plots. On both the 1990 MPB and the control plots the tree species of the A1 height class could be considered to be almost the same age, considering sampling errors due to different coring heights. However, *Picea* trees were significantly younger in 1990 MPB than in control plots (Table 14). This might be due to a sampling error, but is unlikely considering the relatively high number of samples for this species.

Pseudotsuga menziesii and *Picea* were significantly younger in the intermediate canopy layers in the 1990 MPB than in the control plots. This could either be due to a higher amount of younger trees, which have grown into these height classes after the MPB infestation in 1990 if a seed source for this species was close by, or older individuals of these species have grown into the A1 height class, promoted by more light due to less overstory, after MPB infestations.

No significant age differences between MPB and control plots for each of the different species were found for the 1980's infestation (Table 15), although direct comparisons were possible only for *Pinus contorta* and *Picea*, due to a lack of data for the 1980 control plots. However, in 1980 MPB plots *Pseudotsuga menziesii* appeared to be much younger than the other tree species based on the annual ring counts. Since this species

is moderately shade tolerant, the growth of established trees prior to the disturbance might have been promoted by an increase in light caused by MPB killed *Pinus contorta* in the 1980's. However, the data for tree species distribution does not support such a growth promotion, because densities of *Picea* were significantly lower in the 1980 MPB compared to the control plots (Table 13).

In the 1940 MPB plots *Pseudotsuga menziesii* trees in the A1 layer were significantly older than on the 1940 control plots (Table 16) This might suggest that trees in 1940 MPB plots were older than in control plots, consistent with average stand ages (Table 9, Section 4.1.2). Due to a lack of data for the control plots, direct comparisons for other tree species were not possible. Also, no significant age differences in the intermediate canopy layer were obvious between 1940 MPB and corresponding control plots for *Pseudotsuga*, *Pinus*, or *Picea* trees. Due to a lack of data, comparisons for other tree species were not possible in this data set.

For each of the above MPB and control sample sets, the underlying data for the age class distribution were too scarce and had too much variation to allow definitive conclusions to be made. Although there appeared to be a trend towards a larger proportion of later successional tree species such as *Picea* and *Abies*, a few decades after the MPB infestation, age differences for each tree species between MPB and control plots appeared to be less obvious with increasing time since the MPB disturbance. This might suggest that MPB infestations have an ephemeral effect on stand structure. However, this would contradict the findings of Armour (1982) who found a trend to increasing cover by young late successional species with increasing time since the MPB disturbance. Due to missing data on many plots in the present study, conclusions can be only tentative. However, with increasing time since the MPB infestation, MPB do not appear to have had a major or lasting influence on the average stand age structure of the investigated plots. On all plots, ages for *Pinus contorta* did not differ significantly between MPB stands and controls. Assuming regeneration of *Pinus contorta* occurred dominantly after fire, similar ages for this species support the assumption that fire regimes and the recent fire history since stand initiation on MPB plots might have been more or less similar to those on control plots.

Table 14 **Mean ages of different tree species in 1990 MPB and control plots**

Height class	Stand type	Fd			Bl			Lw			Pl			Se/Sw		
		Plots (n)	Age	Age range	Plots (n)	Age	Age range	Plots (n)	Age	Age range	Plots (n)	Age	Age range	Plots (n)	Age	Age range
A1	Control 1990	17	75 ^A (6.0)	23-114	id	id	id	4	73 ^{id} (4.7)	62-85	28	83 ^A (3.5)	46-111	21	84 ^A (4.4)	60-124
	MPB 1990	27	82 ^A (3.9)	20-118	id	id	id	id	id	id	50	90 ^A (3.9)	23-175	39	73 ^B (3.0)	37-106
IT	Control 1990	3	69 ^A (3.1)	65-75	id	id	id	id	id	id	3	69 ^A (14.0)	43-91	7	62 ^A (6.3)	43-84
	MPB 1990	9	49 ^B (5.4)	20-68	2	37 ^{id} (0.5)	36-37	id	id	id	8	53 ^A (7.7)	23-85	27	44 ^B (3.9)	12-80

Means for a given year of origin, species and height class followed by different superscripts are significantly different at $p < 0.05$, standard errors are given in parentheses, id = insufficient data, IT = intermediate height classes (A2 and B1)

Table 15 **Mean ages of different tree species in 1980 MPB and control plots**

		Fd			BI			Lw			PI			Se/Sw		
Height class	Stand type	Plots (n)	Age	Age range	Plots (n)	Age	Age range	Plots (n)	Age	Age range	Plots (n)	Age	Age range	Plots (n)	Age	Age range
A1	Control 1980	id	id		id	id		id	id		36	100 (3.7)	50-149	27	91 (5.0)	51-148
	MPB 1980	2	70 ^{id} (24.5)	45-94	2	108 ^{id} (12.5)	95-120	103 ^{id}	1	9	107 (11.6)	67-161	8	104 (23.4)	24-207	
IT	Control 1980	id	id		id	id		id	id		11	81 (6.5)	50-127	14	73 (9.7)	26-144
	MPB 1980	1	49 ^{id}		2	89 ^{id} (11.5)	77-100	id	id	2	59 (9.0)	50-68	5	69 (22.6)	20-140	

Means were calculated for a given year of origin species and height class. Superscript Id = insufficient data for comparisons, standard errors are given in parentheses, IT = intermediate height classes (A2 and B1)

Table 16 **Mean ages¹ of different tree species in 1940 MPB and control plots**

Height class	Stand type	Fd			BI			Lw			PI			Se/Sw		
		Plots (n)	Age	Age range	Plots (n)	Age	Age range	Plots (n)	Age	Age range	Plots (n)	Age	Age range	Plots (n)	Age	Age range
A1	Control 1940	18	80 ^B (7.3)	23-156	id	id		4	73 (4.7)	62-85	66	96 ^A (3.3)	18-169	45	90 ^A (3.5)	51-148
	MPB 1940	2	97 ^A (3.0)	94-100	id	id		id	id		11	108 ^A (5.4)	70-133	6	94 ^A (10.1)	52-123
IT	Control 1940	3	69 (3.1)	65-75	id	id		id	id		13	78 ^A (6.6)	38-110	20	64 ^A (6.3)	25-121
	MPB 1940	1	69 ^{id}		id	id		id	id		5	75 ^A 11.6)	49-108	6	87 ^A (15.8)	50-153

Means for a given year of origin, species, and height class followed by different superscripts are significantly different at $p < 0.05$, standard errors are given in parentheses, id = insufficient data for comparison, IT = intermediate height classes (A2 and B1)

4.1.3 Fire history and stand structure

In order to test potential influences of fire history on stand structure in the sample plots, a few selected stand structure parameters, such as number of trees/ha, basal area, percent cover of different crown layers, and CWD were chosen. Although the outcomes of the PCA did not indicate that fire had a strong influence on the stand structure parameters investigated, the second PCA axis (Z2) suggested a potential influence on stand structure of the number of fires since stand initiation and fire severity parameters (Section 4.1.1). The following analysis of the investigated variables was done on the basis of their plot averages. (Detailed results for the ANOVA are given in Appendix IV)

4.1.3.1 Number of fires since stand initiation

Due to low sample numbers of plots with more than one fire, plots with 2 and 3 fires since stand initiation were added into a single group. ANOVA (Appendix IV) indicated that the number of fires had no significant influence on any of the stand structure variables measured (Table 17). This differs from Kay et al. (1994) whose findings that a historical higher fire frequency in BNP resulted in more open forests would have suggested declining crown cover and declining number of trees with increasing numbers of fires. As Wright et al. (2002) found that CWD was higher in forests with infrequent (stand-replacing) fires than in landscapes with a moderately frequent (mixed-severity) fire regime, CWD would have been expected to decrease with increasing number of fires. However, there may be trends towards fewer trees per hectare, less A1 tree cover (%) and declining total basal area (m^2) with increasing numbers of fires. CWD may be less in stands with 2-3 post stand initiation fires (Table 17). A lack of statistically significant differences might be due to an insufficient number of stands that were sampled. Also, the locations of the plots on different ecosites (the field sampling had only aimed for matching past MPB infestations with corresponding control plots, not different fire regimes) may also have contributed to high variability and an inability to detect significant trends.

Table 17

Mean values of % cover and stand structure parameters as related to number of fires since stand initiation

Number of fires	Plots (n)	Percent Cover ¹						Trees/ha	BA (m ² /ha) DBH ≥ 7.5cm	PI BA (m ² /ha) DBH ≥ 15cm	CWD (Kg/m ²)
		A1	A2	B1	B2	C	Cw				
0	52	50 (2.8)	10 (1.6)	9 (1.2)	27 (3.5)	14 (2.2)	35 (4.0)	1604 (122.6)	35.7 (1.7)	22.0 (1.7)	2.0 (0.2)
1	26	46 (2.7)	10 (1.5)	7 (1.0)	27 (4.1)	10 (1.7)	38 (5.5)	1278 (115.0)	32.0 (2.5)	20.3 (2.3)	2.4 (0.4)
2-3	5	46 (7.3)	7 (2.4)	3 (1.8)	17 (4.0)	8 (2.0)	44 (12.4)	1162 (523.0)	31.9 (4.9)	19.7 (5.0)	2.1 (0.3)

Mean values without superscripts are not significantly different at $p < 0.05$, standard errors are given in parentheses

¹ Percent cover does not add up to 100% do to existence of layers under one another (shade tolerance)

4.1.3.2 Time since last fire

Since fire appears to be the only disturbance that triggers higher numbers of *Pinus contorta* regeneration (Section 1.2) in the sample plots, the time since the last disturbance was assumed to equal the youngest distinct age class of *Pinus* on a plot. ANOVA indicated that the time since fire had no significant influence on the stand structure variables measured except for the number of trees/ha. A post-hoc Bonferroni test indicated significant differences between the time since fire groups >50-100 and 101-150 years after the last fire. The low sample number for plots 0-50 years since the last fire was most likely the reason for the inability to detect significant trends (Table 18).

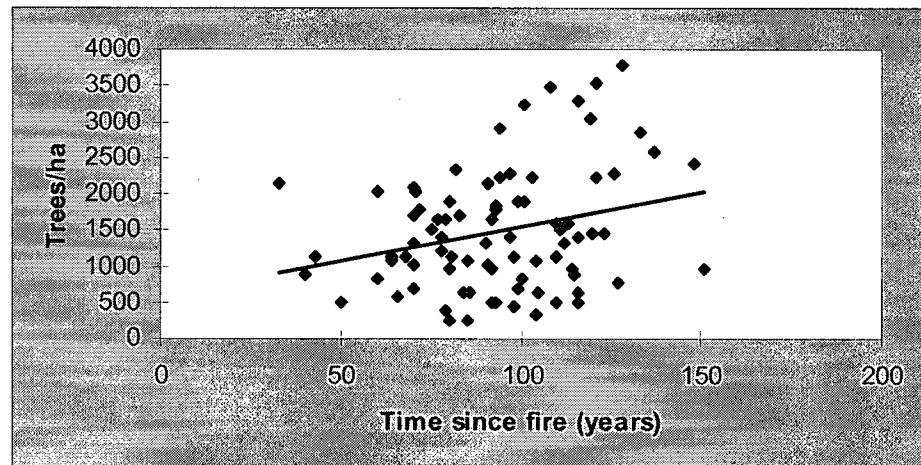


Figure 17 Number of trees per ha as a function of time since fire

A linear regression ($R^2=0.076$) indicated a weak but significant relationship ($p<0.05$) between tree density and time since fire (Figure 17). Linear regressions with time since fire and the remaining stand structure parameters also did not lead to any significant results. Basal area for all species including *Pinus contorta* appeared to be higher in the youngest time since fire group, then declined in the intermediate, and increased again in the oldest group (Table 18), however, these trends might also be related to stand age. The increase in numbers of trees/ha with increasing time since fire might as well be due to an increasing stand age, since the "frequency of disturbances relative to the life spans of component trees also determines the age distribution" (Oliver and Larson 1996).

Table 18

Mean values of % cover and stand structure parameters as related to time since fire

Time since fire (yrs.)	Average (yrs.)	Plots (n)	Percent Cover ¹						Trees/ha	BA (m ² /ha) DBH ≥ 7.5c m	PI BA (m ² /ha) DBH ≥ 15c m	CWD (Kg/m ²)
			A1	A2	B1	B2	C	Cw				
0-50	42	4	40 (2.0)	11 (3.2)	9 (4.0)	40 (7.1)	7 (2.2)	55 (13.4)	1168 ^{AB} (351.1)	42.3 (6.6)	23.9 (4.8)	1.9 (0.4)
51-100	82	47	50 (2.6)	8 (0.9)	9 (1.3)	28 (3.5)	12 (1.8)	38 (4.2)	1307 ^B (91.9)	31.8 (1.8)	20.3 (1.8)	2.3 (0.2)
101-150	117	32	47 (3.4)	11 (2.5)	8 (1.0)	22 (3.8)	14 (2.8)	32 (4.8)	1760 ^A (180.4)	36.9 (2.1)	22.5 (2.0)	2.0 (0.2)

Mean values followed by different superscripts are significantly different at $p < 0.05$, standard errors are given in parentheses data for comparison

¹ Percent cover do not add up to 100% do to existence of layers under one another (shade tolerance)

Thus, the greater the time since disturbance, the higher the chance that trees are older. In British Columbia, *Pinus contorta* stands that are older than 120 years (and all other interior forests older than 140 years) were considered as old-growth (MacKinnon and Vold 1998). In the old-growth stage overstory trees start to die and understory trees and regeneration start to grow (Oliver and Larson 1996), which might have contributed to significantly higher numbers of trees with increased time since fire. Consequently, it would have been expected to find the CWD increasing as well. The amount of coarse woody debris following a disturbance was described by Feller (2003) as a U-shaped curve resulting from an initial large input of CWD that follows disturbance events such as fire. Feller (2003) and others (Muraro 1971, Oliver and Larson 1996) have suggested that this CWD decreases over time as decomposition occurs, and increases again in the old-growth phase as old trees collapse. However, Feller (2003) also pointed out that if "the initial post-disturbance inputs are relatively low, as a result of a severe fire, slow collapse of snags, or low pre-disturbance tree biomass, CWD may not display a U-shaped curve with forest age". An inverse U-shaped curve might occur, if tree mortality is particularly high during the mid-life period of a forest, as a result of high tree densities, or disturbances such as insects, disease, or windthrow (Feller 2003). However, as indicated in the literature, generally the trend of CWD mass will follow a U-shaped curve with forest age (Muraro 1971), with departures from this trend (Feller 2003), according to stand dynamics and the nature of the individual disturbance.

4.1.3.3 Fire Severity

Similar to the influence of numbers of fires and time since fire, the influence of past fire severity on the stand structure parameters investigated appeared to be low. There was an overall trend to less cover in the dominating height classes, declining number of trees/ha, and a significantly higher proportion of ground cover ($p=0.043$) with lower severity fires (Table 19).

Table 19 Mean values of % cover and stand structure parameters as related to fire severity

Fire Group ¹	Plots (n)	Percent Cover ²						Trees/ha	BA (m ² /ha) DBH ≥ 7.5cm	PI BA (m ² /ha) DBH ≥ 15cm	CWD (Kg/m ²)
		A1	A2	B1	B2	C	Cw				
1	17	49 (3.8)	10 (1.9)	7 (1.3)	19 (3.6)	9 (1.3)	28 ^B (4.9)	1397 (175.9)	34.2 (2.4)	19.8 (2.8)	2.8 (0.5)
2	14	43 (3.0)	8 (2.0)	6 (1.3)	33 (6.0)	12 (2.9)	53 ^A (8.0)	1092 (165.5)	29.3 (3.8)	19.3 (3.1)	1.8 (0.2)
3	52	50 (2.8)	10 (1.6)	9 (1.2)	27 (3.5)	14 (2.2)	35 ^{AB} (4.0)	1604 (122.6)	35.7 (1.7)	22.0 (1.7)	2.0 (0.2)

Mean values followed by different superscripts are significantly different at $p < 0.05$, standard errors are given in parentheses

¹ Fire groups: 1 = high severity (1-2), 2 = low severity (3-4), 3 = no fire since stand initiation (5) (see also section 3.3.2)

² Percent cover do not add up to 100% do to existence of layers under one another (shade tolerance)

These trends are consistent with studies finding that 1) increasing fire severity can reduce vegetation cover (Thomas and Wein 1985), and 2) that intense burning could kill small and fire susceptible trees and reduce surface fuels and canopy cover as well (Fulé et al. 2004). Oliver and Larson (1996) suggested that low severity and high frequency fires create open and “park-like” forest stand structures. Wright et al. (2002) found that CWD was higher in forests with infrequent stand-replacing fires than in landscapes with a mixed-severity fire regime with fires moderately frequent, so it would have been expected to find less CWD in fire group 2 (low severity fire plots). CWD quantities were lowest in this fire group, but not significantly so (Table 19)

4.1.3.4 The influence of fire on stand structure

Fire did not appear to have strong influences on the stand structure parameters analysed in the present study. However, as outlined above, some general trends (although mostly not statistically significant) are consistent with the results of other studies. A lack of significant differences in terms of the influences of fire on the stand structure parameters investigated might be due to the sampling methods, in addition to a relatively low number of sample plots and the high variability in some fire groups. Percent covers and the number and severity of past fires were estimated rather than measured precisely. Estimating parameters can rarely be as exact as measurements due to the subjectivity involved, and in the present study this error might have been greater as estimates were made by several people. Different crown densities, which vary between species, for example, could have resulted in biased estimates (BC Ministry of Environment, Lands, and Parks and BC Ministry of Forests 1998). For the estimation of the occurrence of past fires, *Pinus contorta* might have regenerated following disturbances other than fire (e.g. windthrow or insects). Another source of error might have been the effect of different ecosites on stand structure, which could not be excluded for this sample set, as the field sampling focused on MPB infestations rather than distribution of fires on different ecosites. A finer scale of estimating fire severity might have also lead to more significant results. Thus, Francis et al. (2002)

described fire severity on the stand level on a scale of 1-11, which is greater than the 5 category scale used in the present study (Section 3.3). Fire attributes are also likely to vary according to aspect, elevation, slope and other conditions (White 1985), parameters which were not considered in this analysis and thus potential sources of errors. Nevertheless, it might also be possible that the relatively low number of subsequent fires after stand initiation and the decades past since those disturbances, resulted in relatively low impact on stand structure being observed during the present study. Although the structure of young stands can depend on the initiating disturbance, the effects of the disturbance can fade with time. With time stand structure can become more controlled by factors other than the initiating disturbance, as proposed by Antos and Paris (2002) for an ESSF forest in southern BC.

4.1.4 Test of Hypothesis 1

It was found that MPB infestations had a varying influence on the stand structure parameters investigated. Some parameters appeared to have undergone lasting changes, while others changed solely for a certain period after an infestation, and some might not have changed substantially at all. Although it is recognized that the comparison between the different MPB plots is limited due to differences in stand age and ecosites, some of the obvious trends in the data are considered to allow a tentative comparison.

The number of trees per hectare and the basal area of *Pinus contorta* trees were significantly lower on all investigated MPB than on control plots. Total basal area however, increased with time past the MPB infestation. Coarse woody debris mass was significantly higher in plots with previous MPB infestations in the 1990's. The lack of CWD in 1980 MPB plots was assumed to be due to a high proportion of the MPB killed trees still remaining standing. In 1940 MPB plots, however, possibly due to fall-and-burn of MPB infested trees in the 1940's relatively little CWD was observed. Those plots had also the lowest regeneration densities compared to other MPB and control sample sets.

Armour (1982) found in north-western Montana 30 years after MPB infestations for Douglas-fir/pine grass habitat types, total fuel amounts of 8 kg/m². For *Picea*/Queenscup habitat types amounts of CWD as high as 19.8 kg/m² were recorded. From this perspective the CWD amounts recorded in the present study were comparatively low. Moreover, White (1985) found for mesic montane forests in Banff that were mostly unaffected by MPB, total CWD about 4.9 kg/m². Similar forest stands in the present study without MPB infestations yielded only between 2 to 3 kg/m², which suggests that the sampling technique for the present study using photo-guides might have lead to an underestimation of CWD amounts, since Armour (1982) and White (1985) both measured CWD loads. However, Hanel (2000), using a line intersect method to determine CWD loads, found in IDF old-growth forest types, including one sample plot in BNP, very similar fuel loads to the control plots of the present study, ranging between 0.2 to 3.7 kg/m² (average 1.7 kg/m²). Since MPB infestations can increase fuel loads, the comparatively low amounts in stands with previous MPB infestations in the 1980's and 1990's, might increase in the near future, since Armour (1982) indicated that in north-western Montana CWD amounts rapidly increased 25 years after a MPB attack. Having observed a large quantity of standing dead *Pinus contorta* on those plots (Table 11), it can be expected that a CWD increase is yet to come. Further research on those plots would be helpful to detect further trends in CWD amounts in future years.

Although the regeneration density was not significantly higher on any of the plots with previous MPB infestations, the proportion of regenerating broadleaved trees appeared to be higher shortly after an infestation. However, no statistically significant changes in the overall species composition were found in plots 65 years after the infestation, except for significantly lower numbers of *Picea*. It was also found that with increasing time since the MPB infestation, MPB do not appear to have had a major or lasting influence on the average stand age structure of the investigated plots. Although the number of dead large diameter trees was significantly higher several decades after a MPB infestation, probably due to MPB killed *Pinus contorta*, the number of smaller diameter trees (probably suppressed trees) was significantly lower on all MPB plots. On a long-term basis MPB infestations do not appear to have promoted a higher proportion

of any other species nor reduced the proportion of *Pinus contorta* in the investigated forest stands. However, other, unrecognized factors, such as grazing, insect infestations other than MPB or environmental factors might have inhibited the successful growth of the regeneration, thus preventing any changes in species composition. On the other hand, low numbers of *Larix occidentalis* and homogenous ages of this species in plots in KNP (Section 4.1.2.5), support the trends apparent in the data that the stands investigated had a long term lack of fires. *Larix occidentalis* is very shade intolerant, and grows usually only in even-aged stands or as large individuals which survived fires (Parish et al. 1996), so that this species depends on fire for regeneration in the ecosystems investigated. (Peterson 1999) reported similar trends in Glacier National Park with declining earlier successional species due to fire suppression.

The Shannon-Wiener index indicated statistically significant higher structural diversity solely for MPB plots 15 years after the infestation (Table 12). According to the Shannon-Wiener index, tree species diversity was not higher at any time after the MPB disturbance (Table 14). However, the hypothesis that MPB infestations increase forest stand structural diversity of forest stands in the southern Canadian Rocky Mountains could not be rejected considering the significant impact of 1990 MPB infestations on stand structure.

4.2 HYPOTHESIS 2: BROWSING AND COARSE WOODY DEBRIS

Testing of hypothesis 2, "browsing intensity decreases with increasing amounts of coarse woody debris" was based on the 1990 MPB data set (Table 9), 1) because this was the only data set with reasonably high CWD and 2) in order to decrease the influence of potentially confounding factors such as varying ungulate populations, different times since disturbance, climate and ecosites.

4.2.1 Browsing intensity and CWD

A statistical evaluation of plots with maximum browsing intensity of 5 was not possible, due to the small sample size, so plots with browsing intensity 5 were combined with browsing intensity 4 plots (high browsing intensities). Likewise, browsing intensity 1 plots were combined with browsing intensity 2 plots (low browsing intensities). Detailed results for the ANOVA tests used in this section are found in Appendix IV.

Although the numbers of plots for the individual browsing intensities were relatively low (Table 20), an ANOVA test ($p=0.018$) showed significant differences between the CWD means. A post-hoc Bonferroni's test showed significant differences ($p=0.021$) between the highest and the lowest CWD mass analysed (Table 20). The relationship between CWD and browsing intensity appears not to have been addressed in previous studies in North American coniferous forests.

Table 20 Mean coarse woody debris quantities on plots with different browsing intensities

Browsing intensity	Plots (n)	CWD (kg/m ²)
1-2	6	5.5 ^A (0.4)
3	14	4.5 ^{AB} (0.5)
4-5	30	3.8 ^B (0.2)

Mean values followed by different superscripts are significantly different at $p<0.05$, standard errors are given in parentheses

Although the analysis of the relationship between browsing intensity and CWD indicated that browsing might be reduced in plots with high amounts of coarse woody debris, it was considered to be important to investigate if CWD actually promotes regeneration. To rule out the possibility that browsing intensity was simply reduced on those plots due to a lack of regeneration, the relationship between coarse woody debris and the regeneration density was assessed. Regeneration density was not related to CWD ($R^2=0.048$, $p>0.05$). Also, further data analysis (using simple linear regression and

ANOVA) did not find any statistically significant relationship between either coarse woody debris amounts and browsing intensity and

- regeneration density,
- average heights of regeneration (m), or
- accumulated heights of the regeneration (m) (Appendix IV and V).

Average regeneration heights increased significantly with CWD after fires in Yellowstone National Park (Ripple and Larson 1992). However, their methodology differed from the one used for the present study, as they actively searched for "jackstraw piles" where fallen conifers sheltered *Populus tremuloides* from ungulate browsing. Regeneration heights in those piles were compared to those in adjacent open areas.

4.2.2 Test of Hypothesis 2

Relationships between the height of the regeneration and CWD as reported by Ripple and Larson (1992) (Section 1.2), were not found in the present study. However, both the present study and Ripple and Larsen (1992) indicated that fallen conifers may provide refuge from ungulate browsing. The tree regeneration was limited to *Populus tremuloides* in YNP (Ripple and Larsen (1992), while in the present study species of regenerating trees were not quantified. This may make general conclusions more difficult as palatability varies between tree species. Thus, some species might be preferred browse while others are neglected. Also, areas that are more open due to a previous disturbance might attract ungulates due to the presence of more preferred browse species. Thus, areas with higher CWD amounts might be more open (due to less overstory trees) and have more favourable browse species, which are browsed more heavily than areas with a denser overstory and thus less browse species. If coarse woody debris does not exceed a certain amount it might not be an obstacle for ungulates. The arrangement and diameters of CWD in a stand might also play an

important role, by reducing access for ungulates to browse species. A statistically stronger relationship between browsing intensity, regeneration density and CWD might be gained by sampling a higher number of plots, especially with higher amounts of coarse woody debris found in other areas (Section 4.1.4). Since the extent of browsing may depend on the number of herbivores present and the influence of climate on vegetation growth, the dataset may reflect only the time of sampling 2004, particularly since CWD amounts change with time (Armour 1982, Feller 2003 and others). Consequently, the ability of CWD to shelter regeneration would last only for a certain period after the CWD accumulated. Additionally, varying browsing intensities in years prior to data collection might have influenced the abundance of preferred plant or tree species, while promoting less preferred or browsing adapted species (Schütz et al. 2002). Browsing of one species may also have been severe in previous years resulting in reduced growth, but was less in the year of the data collection. Both situations would have resulted in an incorrect impression of the browsing situation on a particular site. Longer-term studies would thus assist in assessing the above relationships.

As the analysis indicated a significant relationship between CWD and browsing intensity, hypothesis 2, Browsing intensity decreases with increasing amounts of coarse woody debris, could not be rejected.

4.3 HYPOTHESIS 3: SUSCEPTIBILITY OF STANDS TO MOUNTAIN PINE BEETLE

4.2.3 Current stand susceptibility to MPB after previous MPB infestations

For testing Hypothesis 3, “disturbances such as MPB infestation and low severity fire lead to decreased susceptibility of forest stands to MPB in the southern Canadian Rocky Mountains”, the MPB susceptibility index was calculated for every plot sampled. In order to test if the MPB susceptibility index differed with increasing time since the

infestation, an ANOVA and Bonferroni test were applied. The tests indicated that the MPB stand susceptibility index was significantly lower after MPB infestations (Table 21).

Table 21 **Mean MPB stand susceptibility indices for different groups of MPB and control stands**

Origin	Stand type	Plots (n)	Mean MPB susceptibility index
1990	Control	28	40.9 ^A (5.1)
	MPB	50	12.4 ^C (3.0)
1980	Control	36	32.1 ^{AB} (3.7)
	MPB	11	7.6 ^C (6.1)
1940	Control	66	32.7 ^A (3.2)
	MPB	11	10.0 ^{BC} (4.6)

Mean values followed by different superscripts are significantly different at $p < 0.05$, standard errors are given in parentheses

Low indices for MPB plots were due to low tree densities and low basal areas of *Pinus contorta* on all plots with previous MPB infestations. Detailed results for the ANOVA tests used in this section are found in Appendix IV.

4.2.4 Current stand susceptibility to MPB infestation after fire

The current susceptibility to MPB infestations was calculated for every plot in the sample. Although no significant differences in the mean MPB susceptibility index were found between stands, between different numbers of fires, different times since fire, or different fire severities (Table 22), there was a trend to less stand susceptibility to MPB infestations with an increasing number of fires. The index was also low for stands 0-50 year after fire, increased between 51-100 years and decreased again at times between

101-150 years since fire. Considering fire severity, the MPB susceptibility index was lowest when fire severity was low, too (Table 22). The lack of statistically significant trends may be due to a low number of plots and variability resulting from data being collected from different ecosites.

Since most of the last fires in the plots investigated occurred more than 50 years ago (Table 22), most of the *Pinus contorta* which were influenced by fire, would have since matured. The trends apparent (Table 22) are consistent with those found in other studies. They suggest that more frequent fires reduce uniformity of *Pinus* stands. (Heitzmann (2001), Kay et al. (1994), White et al. (2003), and others) and lower the susceptibility to MPB (Keane et al. 2002). Consequently, infrequent high severity fires would promote *Pinus contorta* and thus eventually MPB infestations, (Section 1.2.2).

Table 22 Mean MPB stand susceptibility indices for plots with different numbers of fires, times since fire, and fire severity

No of fires since stand initiation	Plots (n)	Mean MPB susceptibility index
0	52	33.2 (3.5)
1	26	32.3 (5.1)
2-3	5	20.3 (10.1)
Time since fire (years)	Plots (n)	Mean MPB susceptibility index
0-50	4	11.0 (3.4)
51-100	47	36.8 (3.7)
101-150	32	27.9 (4.3)
Fire severity groups ¹	Plots (n)	Mean MPB susceptibility index
1	17	32.7 (6.5)
2	14	27.5 (6.5)
3	52	33.2 (3.5)

Standard errors are given in parentheses

¹ Fire groups: 1 = high severity (1-2), 2 = low severity (3-4), 3 = no fire since stand initiation (5)

4.2.5 Test of Hypothesis 3

The MPB susceptibility index (Shore and Safranyik 1992) suggested that the current susceptibility to MPB infestations of the stands investigated was significantly lower for a considerable time after previous MPB infestations. Important agents of the MPB susceptibility index (Section 3.5) are the tree density, the total basal area and the basal area of *Pinus contorta* trees. Thus, low values for these parameters on plots with previous MPB infestations resulted in low indices for MPB plots. Tree density and basal area were not significantly different (with the exception of time since fire and tree density) between different numbers of fires, times since fire, or fire severity (Section 4.1.3). A trend to lower indices with an increasing number of fires, a low index 0-50 years since fire, and a lower index with low severity fires than with high severity or no fires since stand initiation was present. Consequently, concluding that fire does not influence stand susceptibility to MPB, while MPB infestations result in significant and lasting reductions of stand susceptibility would be false. A direct comparison between the effects of MPB and fire in this case can not be justified. This is because of different times since the MPB and fire disturbance events, no evidence of subsequent fires since stand initiation on most of the study plots, and only relatively few plots with more than one fire (Table 22).

Considering the MPB susceptibility index is on a scale of 0-100, even the highest values in the plots investigated do not appear to indicate an extreme MPB susceptibility. The MPB susceptibility index is widely used throughout BC and was chosen due to its accommodation of age, stand density, diameter and location parameters, which are known to be most important in determining stand susceptibility to MPB (Section 1.2). However, in this approach the distance to the closest MPB outbreak was not considered. Thus, a stand can be highly susceptible to MPB but might not be attacked by MPB due to low MPB populations nearby. On the other hand, in stands with a low susceptibility index even small diameter *Pinus contorta* might be killed if there are large numbers of MPB nearby. In this context Shore et al. (2000) pointed out that the index

considers only the *Pinus* component of a stand. Consequently, if this component is low, the susceptibility index will be low as well, although the *Pinus* itself might be highly susceptible.

Alternative MPB stand susceptibility rating systems were found to have a lower accuracy (Shore et al. 2000). For example Schenk et al. (1980) developed a stand hazard rating model (SHR), which is a function of a crown competition factor and percent lodgepole pine basal area. Anhold and Jenkins (1987) based their stand density index (SDI) on tree densities. Neither includes all the parameters considered in the index developed by Shore and Safranyik (1992).

Hypothesis 3 - Disturbances such as MPB infestation and low severity fire lead to decreased MPB stand susceptibility - can not be rejected by the data collected. The data suggested that low severity fires reduce forest susceptibility to MPB infestations (Table 22).

CHAPTER 5

INTEGRATION AND FINAL CONCLUSIONS

In spite of fire exclusion and/or several decades after the last fires and previous MPB infestations in the investigated stands, a species shift in most of the plots was not obvious. The lack of species shift after MPB infestation, unlike that in North-western Montana, where overstory dominance shifted from *Pinus contorta* to *Picea* species (Armour 1982), and a significantly low tree density, even 65 years after a MPB infestation, indicated, that another factor might inhibit subsequent growth of the regeneration. Many factors are possible, including unsuitable climate for seedling growth (Sirois et al. 1994), or the lack of good seed production years (Greene et al. 1999). It might also be possible that the light availability in spite of previous MPB infestations resulting in more open forest stands, is still not always sufficient for shade intolerant species, such as *Populus tremuloides* or *Betula*, which may regenerate under relatively closed forest canopy, but do not survive for a long time (Messier 1999). However, the growth and long-term survival of more shade tolerant species such as *Picea*, and especially *Abies* (Parish et al. 1996) is possible under closed canopies (Messier et al. 1999). Consequently, this gives shade tolerant tree species a potential advantage in establishing canopy dominance after disturbances such as windthrow or insect outbreaks such as MPB (Messier 1999). Consequently, changes in species composition towards higher proportions of *Picea* and *Abies* would have been expected as a long-term outcome of previous MPB infestations such as in the 1940's. Since it was reported that browsing intensity in the montane and lower subalpine of BNP and KNP is high (Section 1.2), growth of those species might be inhibited by browsing and rubbing. This was reported in a post-MPB study of stand structure, where the growth potential of *Abies lasiocarpa* was severely limited by moose browsing in north-western Montana (Armour 1982). Thus, if creation of open forest is a management objective, high browsing pressure following fall-and-burn treated MPB infested areas, might even be beneficial in certain areas. However, on the other hand a potential overall species

loss of browsing sensitive species such as *Populus tremuloides*, might be undesirable. Thus, severe browsing should be reduced by further promotion of predators of larger ungulates. Without fall-and burn, CWD amounts following MPB infestations might promote long term survival of the regenerating trees such as *Populus tremuloides* but might also lead to a long-term species shift towards later successional species in the overstory, if no low severity fires occur to promote earlier successional species. However, the CWD-browsing relationship needs to be further evaluated in future research, since the present study could only detect a promotion of regeneration in MPB plots from infestations in the 1990's.

The low current susceptibility to MPB on all plots with previous MPB infestations indicated that less concern for those stands in terms of repeated infestations is necessary. However, as observed by others, in the face of a mass outbreak, it is expected that those stands are also subject to MPB kill. It is certainly not feasible to rely solely on MPB infestations to open up the denser forest in BNP and KNP, especially due to the previously outlined different effects of MPB infestations and fire on stand structure. "Unlike surface fires which thin a forest from the bottom up, beetles thin from the top down" (Hawkes 2003). Thus, the ecological roles of fire and MPB might be considered as quite different in the southern Canadian Rocky Mountain ecosystems.

The lack of fire on most of the plots and the long period since the last fires in the plots investigated might eventually lead to a decline in early successional tree species (Antos and Parish 2002, Peterson 1999). Although MPB infestations open up the stand and promote regeneration, very shade intolerant pioneer species that rapidly germinate and grow on fire-blackened soils depend on higher severity fires (Parish et al. 1996), and are not likely to find optimal growing conditions and be as able to compete with shade tolerant species, such as *Abies*, already established under the canopy. Those early successional very shade intolerant species might be potentially endangered if fires are completely excluded (Antos and Parish 2002). A management approach that tolerates MPB infestations, promotes low and high intensity fires and reduces herbivory, would contribute towards more open and diverse stands in the ecosystems of the study area.

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APPENDICES

APPENDIX I

DATA SHEETS FOR THE FIELD SEASON 2004

A. First page of a data sheet

STAND STRUCTURE PLOTS (page 1)																							
Sample Crew: Date: Plot: (ST-Location-04-Plot#) Plot size: Location (descript.): UTM's: Watershed Unit: Ecoregion: Ecosite:(map) Vegetation type:(key) Hygrotope: Aspect:	# of animal trails: # Pelletaccumulation per species: Man disturbance: Stand age (keep cores): fire severity: Woody debris accumulation: Photo #: Browsing intensity (main species and degree): Slope: Elevation:																						
<table style="width: 100%; border-collapse: collapse;"> <thead> <tr style="background-color: #cccccc;"> <th style="text-align: left; width: 40%;">Height class</th> <th style="text-align: center; width: 20%;">% cover</th> <th style="text-align: center; width: 40%;">% cover species</th> </tr> </thead> <tbody> <tr> <td>A1 = Canopy >10m</td> <td></td> <td></td> </tr> <tr> <td>A2 = upper Subcanopy. 5-10m</td> <td></td> <td></td> </tr> <tr> <td>B1 = lower Subcan. 2-5m</td> <td></td> <td></td> </tr> <tr> <td>B2 = Saplings/Shrubs 0.5-2m</td> <td></td> <td></td> </tr> <tr> <td>C = Shrubs <0.5m</td> <td></td> <td></td> </tr> <tr> <td>Cw = Herbs/Grasses</td> <td></td> <td></td> </tr> </tbody> </table>			Height class	% cover	% cover species	A1 = Canopy >10m			A2 = upper Subcanopy. 5-10m			B1 = lower Subcan. 2-5m			B2 = Saplings/Shrubs 0.5-2m			C = Shrubs <0.5m			Cw = Herbs/Grasses		
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<table style="width: 100%; border-collapse: collapse;"> <thead> <tr style="background-color: #cccccc;"> <th style="text-align: left; width: 60%;">Key:</th> <th style="text-align: left; width: 40%;">H:</th> </tr> </thead> <tbody> <tr> <td style="vertical-align: top; padding: 5px;"> Age: core 3 trees per species / 1 per canopy class Browsing intensity: total 1 = -no browsing 2 = 1 - 25% of leaves browsed 3 = 26 - 50% of leaves browsed 4 = 51 - 75% of leaves browsed 5 = 76 - 100% of leaves browsed Condition: S=Snag, L=alive Core #: ST-location-04-# (e.g. ST-B-04-1) %Cover: to the nearest 5% (low cover values <5., 1%, or <1%) Fire severity 0 = 100% tree mortality 1 = 95-99% tree mortality 2 = 50-95% tree mortality 3 = 5-49% tree mortality 4 =less than 5% tree mortality/understory only </td> <td style="vertical-align: top; padding: 5px;"> 3 heights per species/1 per canopy Class MPB-Evidence: E= Exit holes G=Gallery PO=Pitch tubes S=MPB-Scar GreenA = Green Attack RedA = Red Attack GreyA = Grey Attack plot size: (>=15 trees per plot) stand age <10yrs = 3.99m radius stand age 10-25 years = 7.1m radius stand age >25 years = 15m radius </td> </tr> </tbody> </table>			Key:	H:	Age: core 3 trees per species / 1 per canopy class Browsing intensity: total 1 = -no browsing 2 = 1 - 25% of leaves browsed 3 = 26 - 50% of leaves browsed 4 = 51 - 75% of leaves browsed 5 = 76 - 100% of leaves browsed Condition: S =Snag, L =alive Core #: ST-location-04-# (e.g. ST-B-04-1) %Cover: to the nearest 5% (low cover values <5., 1%, or <1%) Fire severity 0 = 100% tree mortality 1 = 95-99% tree mortality 2 = 50-95% tree mortality 3 = 5-49% tree mortality 4 =less than 5% tree mortality/understory only	3 heights per species/1 per canopy Class MPB-Evidence: E = Exit holes G =Gallery PO =Pitch tubes S =MPB-Scar GreenA = Green Attack RedA = Red Attack GreyA = Grey Attack plot size: (>=15 trees per plot) stand age <10yrs = 3.99m radius stand age 10-25 years = 7.1m radius stand age >25 years = 15m radius																	
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General Comments: Bring: GPS, Map, Rope /Measuring tape, DBH-tape, Straws, Maskingtape, Increment borers, Clinometer, Compass, Vegetation Key, Ruler, Camera, Photo Guides Woody Debris, Flagging tape...																							

B. Second page of a data sheet

STAND STRUCTURE PLOTS (page 2)											
Trees / tall Shrubs										Regeneration	
Spec.	Height class	DBH	Cond.	Core#	Age	H(m)	MPB Evidence	Comments	Spec.	Cond.	H(m)

APPENDIX II

KEY TO ECOSITES

A. Ecosites based on the Ecological (Biophysical) Land Classification

	Group	Eco-site	Ecoregion	Landform, Genetic Material	Cal-careous-ness	Textural Group	Soils	Vegetation
BANFF NATIONAL PARK	A	NY1	Montane	morainal	calc	med	Brunisol>Regosol	Douglas-fir, pine/buffaloberry
	B	PT1	Montane	morainal	calc	med	Brunisol, Luvisol	pine/buffaloberry
	C	PT3	Montane	morainal	calc	med	Brunisol (lithic)>Luvisol (lithic)	subxeric pine, pine/buffaloberry
	D	AL1	L.Subalp.	fluvial	calc	strat	Brunisol	pine/buffaloberry
	E	BK6	L.Subalp.	strat drift	calc	var	Brunisol	spruce-fir
	F	GA1	Montane	landslide	calc	med	Bruniso, Regosol	subxeric pine, pine/buffaloberry
	G	PR1	L.Subalp.	morainal	calc	med	Brunisol>Luvisol	mesic pine
	H	PR2	L.Subalp.	morainal	calc	med	Brunisol>Luvisol	pine/buffaloberry
	I	PR4	L.Subalp	strat drift	calc	var	northerly: Brunisol southerly: Brunisol>Luvisol, Regosol	spruce -fir subxeric pine, pine/buffaloberry
	J	PR6	L.Subalp	strat drift	calc	var	Brunisol>Luvisol	pine/buffaloberry, mesic pine
KOOTENAY NATIONAL PARK	A	DG6	Montane	colluvial	calc	med-fine	Brunisol>Regosol	pine/buffaloberry
	A	WY1	Montane	strat drift	calc	var	Brunisol	Douglas-fir
	B	DR7	Montane	strat drift	calc	var	Brunisol>Luvisol	pine/buffaloberry
	C	DR2	Montane	morainal	calc	med	Brunisol>Luvisol	pine/buffaloberry > mesic pine
	C	DR3	Montane	morainal	calc	med	Brunisol>Luvisol	spruce-Douglas-fir, mixedwood
	C	DR8	Montane	strat drift	calc	var	Brunisol>Luvisol	pine/buffaloberry

BNP: taken from Holland and Coen (1982, modified), KNP: taken from Achuff et al. (1984, modified)

B. KEY (taken from Holland and Coen 1982, Achuff et al. 1984, modified)

Ecoregion Column:

The landscape is subdivided into Ecoregions which reflect macroclimate. The three Ecoregions: Montane, Subalpine, and Alpine, with the subdivision of Subalpine into Lower Subalpine (L. Subalp.) and Upper Subalpine.

Landform, Genetic Material Column

Landforms and genetic materials are defined according to the Canadian System of Soil Classification.

strat drift = ice contact stratified drift.

Landslide = rock and soil avalanche.

morainal = the landscape characterized by a pattern of morainal landforms interspersed with lesser amounts of fen landforms

Calcareousness Column

This column indicates the calcareousness of the parent materials associated with each Ecosite

calc = calcareous

Textural Group Column

This column indicates the textural group into which the geologic material (and frequently portions of the solumn falls).

Med = medium textured; 20-60% sand and <20% clay or if <20% sand, %sand>%clay; parts of silt loam, loam, sandy loam.

Fine = fine textured; <40% sand and 20-50% clay or if <20% clay, %clay>%sand; parts of silt, silt loam, loam, silty clay loam, clay loam, silty clay, clay.

Strat = stratified; layered material with vertical textural variability encompassing more than one of the above groups.

Var = variable texture; a given mapped area contains more than one of the above groups in unpredictable distribution

Soils Column

This column indicates the dominant soil orders.

Brunisol>Regosol – the landscape has a pattern dominated by Brunisolic soils with a lesser percentage of Regosolic soils

Brunisol, Luvisol – either Brunisolic or Regosolic soils or both occur in any given map area.

northerly: Brunisol, southerly: Brunisol > Luvisol, Regosol – jointly, this symbolism indicates contrasting but inseparable components on northerly aspects (Brunisols) and southerly aspects (Brunisol > Luvisol, Regosol).

Vegetation Column

This column indicates the common vegetation associated with each Ecosite. Mixtures of species within a layer are indicated by a hyphen and a comma separates layers

pine/buffaloberry, mesic pine: indicates that in a given map area either or both of the two vegetation types occur.

pine/buffaloberry > mesic pine: the landscape is characterized by a pattern dominated by pine/buffaloberry with a lesser percentage of mesic pine

APPENDIX III

PLOT CHARACTERISTICS

A. Summary of all locations and all ecosites sampled during the 2004 field season

Ecosites	Location	MPB evidence	Stand Age		
			50 - 99	100-150	>150
A	BNP	1940 MPB		1	
		Control			2
B	BNP	Control	2	6	
	KNP	1980 MPB	2	2	
	BNP	1940 MPB		2	
C		Control	4	13	
		1990 MPB	19	27	4
	KNP	Control	10		1
		1940 MPB		2	
D	BNP	1980 MPB		1	
		Control	1	7	1
		1980 MPB			1
F	BNP	1980 MPB		1	
		1940 MPB		1	
		Control		2	
G	BNP	1980 MPB		1	2
		Control	2	3	4
		1940 MPB		2	
H	BNP	1980 MPB		1	
		Control	4	4	
		1940 MPB			
I	BNP	Control	4	5	1
		1940 MPB		1	
J	BNP	Control		2	
		1940 MPB	2	6	

B. Ecosites with previous MPB infestations in the 1940's and corresponding controls sampled during the 2004 field season in Banff National Park

Ecosites	Stand Age					
	50-99		100-150		>150	
	MPB	CONTROL	MPB	CONTROL	MPB	CONTROL
A			1			1
C		14	2	13		1
D		1	2	7		1
F			1	2		
H		4	2	4		
I		4	1	5		1
J		2	2	6		

C. Ecosites with previous MPB infestations in the 1980's and corresponding controls sampled during the 2004 field season in Banff and Kootenay National Parks

Ecosites	Stand Age					
	50-99		100-150		>150	
	MPB	CONTROL	MPB	CONTROL	MPB	CONTROL
B	KNP 2	BNP 2	KNP 2	BNP 6		
D		BNP 1	BNP 1	BNP 7		BNP 1
E					BNP 1	
F			BNP 1	BNP 2		
G		BNP 3	BNP 1	BNP 2	BNP 2	BNP 4
H		BNP 4	BNP 1	BNP 4		

D. Ecosites with previous MPB infestations in the 1990's and corresponding controls sampled during the 2004 field season in Banff and Kootenay National Parks

Ecosite	Stand Age					
	50-99		100-150		>150	
	MPB	CONTROL	MPB	CONTROL	MPB	CONTROL
C	KNP 19	BNP 4	KNP 27	BNP 13	KNP 4	KNP 1

In several cases MPB outbreaks were sampled on similar ecosites. Thus, controls may appear more than once in Tables B-D. The total number of plots was n=155. Equivalent ecosites in BNP and KNP were put into a group with the same letter (A to J).

APPENDIX IV

ANOVA RESULTS

Hypothesis 1

A. ANOVA for stand age in relation to time since MPB infestation

Parameters	Source	Df	Sum of Squares	Mean Square	F Value	Pr > F
Stand age	MPB and Control plots	5	14650.0	2929.9	3.7	0.004
	Error (Observations)	196	160920.9	821.0		

B. ANOVA for number of fires and selected stand structure parameters

Parameters	Source	Df	Sum of Squares	Mean Square	F Value	Pr > F
A1 cover (%)	Number of fires	2	262.9	131.5	0.4	0.7
	Error (Observations)	80	26033.5	235.4		
A2 cover (%)	Number of fires	2	30.5	15.2	0.2	0.9
	Error (Observations)	80	8083.6	101.0		
B1 cover (%)	Number of fires	2	227.2	113.6	2.1	0.1
	Error (Observations)	80	4416.5	55.2		
B2 cover (%)	Number of fires	2	396.7	199.3	0.4	0.7
	Error (Observations)	80	43080.2	538.5		
C cover (%)	Number of fires	2	363.0	181.5	1.0	0.4
	Error (Observations)	80	14885.6	186.1		
CW cover (%)	Number of fires	2	479.3	239.6	0.3	0.8
	Error (Observations)	80	65617.1	820		
Trees/ha	Number of fires	2	2371688.5	1185844.3	1.8	0.2
	Error (Observations)	80	5.3925E+07	674156.6		
Total BA (m ²)	Number of fires	2	268.2	134.1	0.9	0.4
	Error (Observations)	80	12389.8	154.9		
PI BA (m ²)	Number of fires	2	61.0	30.5	0.2	0.8
	Error (Observations)	80	11188.5	141.6		
CWD (kg/m ²)	Number of fires	2	2.2	1.1	0.6	0.6
	Error (Observations)	80	160.0	2.0		

C. ANOVA for time since fire and selected stand structure parameters

Parameters	Source	Df	Sum of Squares	Mean Square	F Value	Pr > F
A1 cover (%)	Time since fire	2	545.7	272.9	0.8	0.4
	Error (Observations)	80	25750.7	321.9		
A2 cover (%)	Time since fire	2	199.4	99.7	1.0	0.4
	Error (Observations)	80	7914.7	98.9		
B1 cover (%)	Time since fire	2	13.7	6.86	0.1	0.9
	Error (Observations)	80	4630.0	57.9		
B2 cover (%)	Time since fire	2	1520.6	760.3	1.5	0.2
	Error (Observations)	80	41958.3	524.5		
C cover (%)	Time since fire	2	191.9	95.9	0.5	0.6
	Error (Observations)	80	15056.8	188.2		
CW cover (%)	Time since fire	2	2319.2	1159.6	1.5	0.2
	Error (Observations)	80	63777.2	797.2		
Trees/ha	Time since fire	2	4301524.1	2150762.1	650033.6	0.04
	Error (Observations)	80	5.20027E+0.7			
Total BA (m²)	Time since fire	2	765.8	382.9	2.6	0.08
	Error (Observations)	80	11892.2	148.7		
PI BA (m²)	Time since fire	2	118.4	59.2	0.4	0.7
	Error (Observations)	79	11131.1	140.9		
CWD (kg/m²)	Time since fire	2	1.8	0.9	0.5	0.6
	Error (Observations)	80	160.4	2.0		

D. ANOVA for fire severity and selected stand structure parameters

Parameters	Source	Df	Sum of Squares	Mean Square	F Value	Pr > F
A1 cover (%)	Fire group	2	536.1	268.1	0.8	0.4
	Error (Observations)	80	25760.3	322.0		
A2 cover (%)	Fire group	2	24.6	12.3	0.1	0.9
	Error (Observations)	80	8089.4	101.1		
B1 cover (%)	Fire group	2	170.0	85.0	1.5	0.2
	Error (Observations)	80	4473.7	55.9		
B2 cover (%)	Fire group	2	1489.3	744.6	1.4	0.3
	Error Observations)	80	41989.6	524.9		
C cover (%)	Fire group	2	406.5	203.3	1.1	0.3
	Error (Observations)	80	14842.1	185.5		
CW cover (%)	Fire group	2	5107.7	2553.9	3.4	0.04
	Error (Observations)	80	60988.7	762.4		
Trees/ha	Fire group	2	3030352.1	1515176.1	2.3	0.1
	Error (Observations)	80	5.32739E+07	665923.3		
Total BA (m²)	Fire group	2	454.2	227.1	1.5	0.2
	Error (Observations)	80	12203.8	152.5		
PI BA (m²)	Fire group	2	65.5	32.8	0.2	0.8
	Error (Observations)	80	11184.0	141.6		
CWD (kg/m²)	Fire group	2	8.9	4.4	2.3	0.1
	Error (Observations)	80	153.3	1.9		

Hypothesis 2

A. ANOVA for browsing intensity¹

Parameters	Source	Df	Sum of Squares	Mean Square	F Value	Pr > F
CWD (kg/m²)	Browsing	2	17.6	8.8	4.2	0.02
	Error (Observations)	47	97.4	2.0		
Regeneration/ha	Browsing	2	1568007.2	784003.6	0.5	0.6
	Error (Observations)	47	7.64381E+07	1626341.9		
Height of regeneration (m)	Browsing Intensity	2	0.006	0.003	0.09	0.9
	Error (Observations)	47	1.6	0.035		
Accumulated heights of regeneration (m)	Browsing Intensity	2	254.9	127.5	1.9	0.2
	Error (Observations)	47	3193.6	67.9		

¹ Means for other parameters than CWD see Appendix V

Hypothesis 3

B. ANOVA for the Mountain Pine Beetle susceptibility index

Parameters	Source	Df	Sum of Squares	Mean Square	F Value	Pr > F
MPB index	MPB and control plots	5	26711.6	5342.3	9.7	0.000
	Error (Observations)	198	108924.3	550.1		
MPB index	Number of fires	2	7615	380.8	0.6	0.6
	Error (Observations)	80	50631.1	632.9		
MPB index	Time since fire	2	3387.6	1693.8	2.8	0.07
	Error (Observations)	80	48005.0	600.1		
MPB index	Fire severity	2	369.5	184.7	0.3	0.7
	Error (Observations)	80	51023.1	637.8		

APPENDIX V

STATISTICAL TEST RESULTS FOR ADDITIONAL CALCULATIONS

Hypothesis 2

A. Means for additional parameters tested for browsing intensity

Browsing intensity	Plots (n)	Regeneration/ha	Height of regeneration (m)	Accumulated heights of regeneration (m)
1-2	6	467 (191)	0.2 (0.08)	3.4 (1.4)
3	14	1057 (436)	0.17 (0.04)	2.9 (0.8)
4-5	30	786 (216)	0.17 (0.04)	7.6 (1.9)

APPENDIX VI

GLOSSARY OF TERMS

Ecosite: a subunit of an ecoregion based on soil, landform, and vegetation differences; it is further subdivided in vegetation types which are based on the dominant vegetation of a site (Poll et al. 1994).

Ecological integrity: "a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes." "Maintenance or restoration of ecological integrity, through the protection of natural resources and natural processes, shall be the first priority of the Minister when considering all aspects of the management of parks" (Canada National Parks Act 2000).

Fire frequency: "the return interval or recurrence interval of fire in a given area over a specific time" (US National Park Service 2004)

Fire intensity: "the rate at which fuel is consumed and heat is generated" (US National Park Service 2004). "Fire intensity is "generally expressed as energy released per length of fire front per Unit of time. Intensity is dependent on both rate of spread and weight of fuel consumed" (Oliver and Larson 1996).

Fire regime: "the kind(s) of fire and the prominent immediate effects of fire that characterize an area. A fire regime is typically characterized by the following features: type, frequency, intensity, severity, size, and timing (season of burning). Fire type, frequency, and intensity are the most important. The type of fire, according to the level at which they burn, are ground, surface, and crown fires." (Barnes et al. 1980)

Fire severity: "Denotes the scale at which vegetation and a site are altered or disrupted by fire, from low to high. It is a combination of the degree of fire effects on vegetation and on soil properties" (US National Park Service 2004). For the present study fire severity of a stand was assessed since the last stand-replacing fire.

Mixed fire regime: "combinations of understory and stand-replacing fires" (Barnes et al. 1980).

Prescribed fire: "Any fire ignited by management actions to meet specific objectives" (US National Park Service 2004).

Stand-replacing / stand initiation fire: a fire that kills all the trees in a stand

Stand structure: “the physical and temporal distribution of trees in a stand” (Oliver and Larsen 1990)

Susceptibility: “a measure of stand characteristics associated with successful infestation if a stand is attacked” (Whitehead et al. 2001)