Discussion Paper

BC Journal of Ecosystems and Management

Regeneration and growth following mountain pine beetle attack: A synthesis of knowledge

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Abstract

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) infestation has altered forests of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) to an unprecedented extent in British Columbia. After an MPB outbreak, advance regeneration significantly contributed to form a new canopy and stand; however, the time needed to form a new stand depends on site-specific conditions. Assessment of regeneration and the growth of residual trees in stands after MPB attack are critical for three purposes: (1) forecasting long-term development (yield) of attacked stands; (2) selecting stands for growth-improving silvicultural treatments; and (3) forecasting impacts to ecological attributes such as hydrology, habitat, and vegetation types. This article reviews and synthesizes recent research concerning lodgepole pine stand performance after MPB attack in British Columbia. Species composition, abundance, spatial distribution, and overall stand health are described. This information is important for forest managers or practitioners who make decisions regarding management of MPB-attacked stands. Moreover, a number of key gaps exist in our knowledge about factors affecting advance regeneration and the residual trees of MPB-attacked stands. This article presents a list of knowledge gaps for management information and further research initiatives.

KEYWORDS: *knowledge gap; lodgepole pine; mountain pine beetle; secondary stand structure; spatial distribution; species composition.*

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Dhar, A. and C.D.B. Hawkins. 2011. Regeneration and growth following mountain pine beetle attack: A synthesis of knowledge. *BC Journal of Ecosystems and Management* 12(2):1–16. ***http://jem.forrex.org/index.php/jem/article/view/22/84***

Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) is the most damaging biotic disturbance agent in British Columbia stands of mature lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.). The MPB in combination with associated blue stain fungi usually attacks and often kills less vigorous lodgepole pine (Waring and Pitman 1985). Typically, the MPB attacks larger-diameter (DBH > 20 cm) (Amman et al. 1977) and older trees (> 60 years) (Shore et al. 2006). However, the current MPB infestation is more widespread and severe than past outbreaks. As a result of this severity, the MPB has also attacked younger stands (even < 20 years) if there were no mature ones to attack (Maclauchlan 2006; Runzer et al. 2008). Generally, extended cold weather and the absence of suitable hosts both contribute to beetle mortality, but such cold weather has not occurred in the interior of British Columbia over the past 10 years (Carroll et al. 2004). This scenario, combined with the abundance of mature lodgepole pine, has created ideal conditions for the rapid spread of the MPB (Taylor and Carroll 2004). The current infestation of lodgepole pine by the MPB has been estimated at over 10.1 million ha (Westfall and Ebata 2007), with approximately 630 million m^3 of merchantable mature pine killed in British Columbia to the end of 2009 (Walton 2010). Therefore, MPB is a major factor regulating stand dynamics of lodgepole pine forests throughout the British Columbia interior.

Because of the huge loss of potential timber volume to the MPB, the B.C. Ministry of Forests and Range increased the allowable annual cut (AAC) in 2008 (B.C. Ministry of Forests and Range 2008). However, it was suggested that 200 million m^3 of MPB-attacked timber would remain unsalvaged throughout the province (B.C. Ministry of Forests 2004; Hawkes et al. 2004; Pedersen 2004). The two major reasons for unsalvaged stands are (1) low feasibility for salvage (accessibility, location, management objectives, lack of milling capacity, economic factors); and (2) ecological concerns.

Salvage harvesting activities undermine many ecosystem benefits (Lindenmayer et al. 2004). The major ecological consequences for salvage-harvesting activities include the negative impacts on biological diversity as different biological components benefit from each other's presence, the impairment of ecosystem recovery, and the maladaptation of some species to the interactive effects of two disturbance events (MPB and logging) in rapid succession (Lindenmayer et al. 2004). Moreover, poorly planned and executed large-scale salvage operations have significant negative effects on several forest values, including hydrological regimes at various scales (Foster et al. 1997; Lindenmayer et al. 2004). Therefore, unsalvaged stands are not only important for ecological restoration, but they also provide a unique opportunity to establish permanent sample plots (Griesbauer and Green 2006), which can subsequently reshape our knowledge about the regeneration and stand dynamics under complex conditions following the MPB outbreak.

There is a great amount of completed and ongoing research regarding the management of MPB-attacked stands. However, this information needs to be gathered, synthesized, and presented such that it is widely available to mangers, practitioners, and researchers alike.

Natural regeneration can be valuable as a method of enhancing genetic diversity of new stands. Furthermore, advanced regeneration is the major source of canopy replacement and change of forest structure under natural or unmanaged conditions following MPB attack (Veblen et al. 1989; Morin 1994). It plays an important role in ecological processes, hydrologic recovery, visual quality, and wildlife habitat. However, stands developing from advanced regeneration following MPB attack are quite different from managed forests or forests originating from other types of disturbance (Burton 2006). Therefore, these differences or future forest conditions need to be considered before taking any further management initiatives.

The British Columbia mountain pine beetle (BCMPB) model version 2 projection showed that 50% of mature lodgepole pine would die by the year of 2008 and 80% would be dead by 2013 (Eng et al. 2005). Although salvage operations continue to recover as much wood as possible before it becomes unusable, it has been suggested that 25–40% of MPB-attacked stands may not be salvaged (Pedersen 2004). As a result, a considerable area will need management if it is to contribute to the mid- or long-term timber

supply as well as ecological goods and services. Therefore, estimates of the amount of residual stocking and the rates of growth (release) in stands following MPB attack are important for three main reasons:

1. forecasting the long-term prospects of these stands,
2. selecting stands for silvicultural treatments to improve yield, and
3. forecasting impacts to hydrology, habitat, and vegetation types.

There is a great amount of completed and ongoing research regarding the management of MPB-attacked stands. However, this information needs to be gathered, synthesized, and presented such that it is widely available to mangers, practitioners, and researchers alike. The aims of this article are fourfold:

1. to review and synthesize the results of recent MPB research progress in the central and southern interior of British Columbia;
2. to describe the resultant stand composition after MPB attack, including type of tree species, their health, abundance, and spatial distribution;
3. to review the potential models for projecting stand development; and
4. to list knowledge gaps on regeneration and growth following MPB attack to improve management of MPB-attacked stands.

Regeneration status of lodgepole pine stands

Lodgepole pine has a wide range of ecological amplitude and grows as a dominant seral species throughout British Columbia and Alberta (Pojar 1985; Klinka et al. 2000). It can grow from low to high elevations, in warm to cold sites, in relatively dry to wet conditions, and on almost every soil type (Schmidt 1989). Lodgepole pine is highly shade intolerant and grows rapidly at a young age (Shore et al. 2006), enabling it to compete successfully with other vegetation for space, light, moisture, and nutrients.

The greatest abundance of secondary stand structure (existing seedlings, saplings, poles, and residual trees) following MPB attack probably is found in stands where pine was the seral species (Griesbauer and Green 2006); however, the successional patterns and processes of stand development from new seedling establishment to seral lodgepole pine remain largely unknown, as most previous investigations were based on regeneration, either planted or natural seeding, immediately following a large-scale stand disturbance (e.g., logging or forest fires) (Messier et al. 1999). This gap could be diminished by studying natural succession to a climax stand structure. Interestingly, models developed by Coates et al. (2006) indicated that stands with healthy, vigorous, and well-spaced advanced regeneration may develop rapidly following MPB attack and can contribute harvestable volumes of 200–300 m^3/ha within 25–40 years. Similarly, Pousette's (2010) SORTIE-ND model projections in the Prince George Timber Supply Area (TSA) (Sub-Boreal Spruce [SBS] zone, six subzones) showed that MPB-attacked stands can contribute mid-term merchantable timber within 30 years. In another study by Coates and Hall (2005), SORTIE-ND model projections suggested that, after MPB-induced pine mortality, residual spruce in well-stocked stands with good basal area recovered to pre-attack basal areas within 50 years in two of four experimental stands in British Columbia. With the age structure and dendrochronological technique, Veblen et al. (1991) indicated that subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and Engelmann spruce (*Picea engelmannii* Parry) had basal areas ranging from 20 to 37 m^2/ha 50 years after attack by spruce bark beetle (*Dendroctonus rufipennis* Kirby) in high-elevation stands, whereas in undisturbed stands, basal areas ranged from 42 to 56 m^2/ha. This suggests that some attacked stands have the potential to contribute to mid-term timber supply.

Considerable variation in secondary stand structure exists among different lodgepole pine stands (Coates 2008b; Coates et al. 2009; Vyse et al. 2009). This creates a challenge for forest practitioners and managers: without knowing composition metrics on a stand-by-stand basis, it becomes difficult to set management objectives and predict future yields and harvests.

Growth of secondary stand structure

Secondary structure (Coates et al. 2006) has been shown to display enhanced growth rates after the death of MPB-infested trees as the amount of light increases on the forest floor (Cole and Amman 1980; Waring and Pitman 1985; Stone and Wolfe 1996). The release that occurred with the sudden death of canopy trees, such as observed in MPB outbreaks, showed more rapid and prolonged response compared to those following the slow death of canopy trees, such as death caused by root rot (Thompson et al. 2007). However, the rate of release and subsequent stand dynamics after MPB attack are still poorly understood (Veblen et al. 1991; Stockdale et al. 2004) and inadequately documented. Nevertheless, a dendroecological reconstruction study for MPB outbreaks in the Chilcotin Plateau of British

Columbia showed that in a period of 120 years, three release events occurred in response to beetle attack, with an average duration of 13.8 years and a 42.3-year interval between outbreak events (Alfaro et al. 2004). Pine and non-pine species showed similar release responses.

Factors affecting regeneration

Many factors directly affect the growth and development of regeneration after an MPB outbreak. These include:

- overstorey structure (Wright et al. 1998; LePage et al. 2000; Coates 2002);
- moisture content of the soil (Kobe and Coates 1997; Wright et al. 1998);
- availability of seedbed substrates (Wright et al. 1998; LePage et al. 2000); and
- proximity and abundance of parent seed trees (Greene et al. 1999; LePage et al. 2000).

Among these, light and moisture regimes appear to be the most influential factors for seedling survival and growth (Kobe and Coates 1997; Wright et al. 1998; Gagnon et al. 2004). On the other hand, Burton and Brooks (2008) mentioned that light and moisture did not have a significant effect on regeneration. A negative relationship between advanced regeneration abundance and both overstorey basal area and stand density was reported by Nigh et al. (2008). In another study, low post-MPB recruitment was found to be due to a lack of disturbance of the moss dominating the forest floor, as moss is known to be a poor substrate for seed germination in the forests of central British Columbia (Astrup et al. 2008). There is not enough information to model regeneration capabilities across a variety of ecosystems after MPB attack. Therefore, further investigation on factors influencing the establishment of regeneration is required to meet this gap. Maximum likelihood methods and inverse modelling approaches (Ribbens et al. 1994) could be used to determine different processes that control seedling establishment in forests. These methods have been extensively used in forest science to determine seedling recruitment function (Tanaka et al. 1998; Clark et al. 1999; LePage et al. 2000; Stoyon and Wagner 2001).

Species composition

The regenerative species composition is the basis of future stands following MPB attack. In British Columbia, a stand's tree species composition is generally recorded by the provincial inventory. However, most of the past inventory methods were based only on merchantable components of the stand, resulting in little knowledge about advanced regeneration in lodgepole pine stands (Vyse et al. 2009). Although the recently revised inventory method includes regeneration assessment, such assessment has not yet been extensively carried out. Yet, a well-defined inventory that includes information about regeneration is a prerequisite for sound forest management. As well, forest managers require knowledge concerning the processes of seedling recruitment and species composition in MPB-disturbed stands (LeMay et al. 2007; Astrup et al. 2008).

According to different investigations, the most common shade-tolerant regenerative species after MPB mortality were interior spruce (*Picea glauca* Voss × *P. engelmannii* Parry), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), and Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) (Coates et al. 1994; Kobe and Coates 1997; Shepperd et al. 2004; Mitchell 2005). However, shade-intolerant species such as lodgepole pine, trembling aspen (*Populus tremuloides* Michx.), or paper birch (*Betula papyrifera* Marsh.) may be found in the advanced regeneration cohort in uneven-aged stands on edaphically limiting sites (Stuart et al. 1989; Williams et al. 1999; Kneeshaw and Burton 1997; Hawkes et al. 2004; Daintith et al. 2005). The MPB disturbance enhanced the release of shade-tolerant species, resulting in the rapid conversion of stands from lodgepole pine to shade-tolerant conifers (Griesbauer and Green 2006). This contributes to the conversion of an even-aged stand to an uneven-aged stand (Roe and Amman 1970). Therefore, the landscape-level age-class structure of lodgepole pine can be described as a mosaic of even-aged and uneven-aged patches intermingling in space and time (Agee 1993).

Based on the studies by Coates et al. (2009) and Nigh et al. (2008), species composition varied by ecological zone (i.e., moist versus dry sites). Different results were reported by N. Balliet (Mixedwood Ecology and Management Program, University of Northern British Columbia, pers. comm., March 2010), wherein they found that species composition generally varied at stand and landscape levels, not by dry, mesic, and moist sites. Heath and Alfaro (1990) described stand conditions before and after MPB attack for a mixed stand of lodgepole pine and interior Douglas-fir in the Cariboo Forest Region of British Columbia. They concluded that MPB attack affects species composition more in the overstorey compared to the understorey. According to them, the total overstorey species composition before attack was 80% lodgepole pine, 19% interior Douglas-fir, and 1% white spruce (560 stems per hectare); understorey composition was 90% interior Douglas-fir,

5% lodgepole pine, and 5% white spruce (3190 stems per hectare). The MPB infestation killed 76% of the pines, and after 14 years the understorey layer was 2698 stems per hectare, which consisted of similar composition to that observed before beetle attack (91% interior Douglas-fir, 7% lodgepole pine, and 2% white spruce).

In a recent study of the SBS zone in central British Columbia, Astrup et al. (2008) reported a high proportion of subalpine fir regeneration in the post-MPB recruitment layer and the seedling bank, suggesting a substantial shift in species composition after MPB disturbance. Similar results were observed by Nigh et al. (2008). Based on the Forest Practices Board report (2007), MPB-attacked pine stands created a unique multi-aged and multi-sized stand structure in the Sub-Boreal Pine–Spruce (SBPS) xc, SBPSmk, and SBPSdc biogeoclimatic subzones. Although Statland (2008) reported that the proportion of spruce decreased and broadleaf species increased at the Pantage Creek site (SBSdw2 subzone) after MPB attack, this was not observed at the Takysie Lake site (SBSdk subzone) (Table 1). From the above discussion, it appears that MPB-disturbed forests are undergoing substantial conversion—moving from lodgepole pine to more shade-tolerant species as well as moving toward an uneven-aged stand structure. Therefore, it is critical for forest managers to assess the potential of preferred species to release and achieve satisfactory growth for mid-term timber supply.

Regeneration density and distribution

In several recent inventories, huge amounts of regeneration beneath the tree layer has been found in different stands throughout British Columbia (Table 1) (Coates 2008b; DeLong et al. 2008; Statland 2008; Zumrawi et al. 2008; Vyse et al. 2009). According to Coates et al. (2006), 20–30% of infected stands have enough secondary stand structure and could possibly contribute to a mid-term timber supply if the dead pine is not removed from the stand. An additional 40–45% of stands have secondary structure that can provide future

TABLE 1. Recent investigations on regeneration for MPB-attacked stands in British Columbia

Geographic area and biogeoclimatic zone (when available)	No. of samples	Age sampled	Regeneration species composition	Density	Distribution	Health	Data holder
Northern interior	35	–	Mostly subalpine fir	Less	Patchy	–	Coates (2008b)
Flathead area, southeast British Columbia	22	70	Mostly subalpine fir	Less	Patchy	–	
Pantage Creek (SBSdw2)	12	28	Diverse species	High	Wide	Good	Statland (2008)
Takysie Lake (SBSdk)	15	79	Mostly pine	High	Wide	Good	
SBSdw3, SBSmc3, SBSdk	50	–	Lodgepole pine, white spruce	High	–	–	DeLong et al. (2008)
IDF, SBPS, and SBS zones	56	–	Pine	High	–	–	Zumrawi et al. (2008)
MSxk2, MSdm3, IDFdk1, IDFdk2	167	–	Mostly subalpine fir	Moderate	Clumpy	–	Vyse (2008)
SBSdk, SBSmc, SBSdw, SBSmc	500	80	Mostly non-pine species	Variable	–	–	Burton and Brooks (2008)
MS, Merritt	28	–	Subalpine fir, lodgepole pine, interior spruce, Douglas-fir	High	Clumpy	–	Nigh et al. (2008)
Lakes TSA, SBSdk	302	100+	Lodgepole pine, spruce, subalpine fir	Low	Sparse	Good	Rakochy (2005)
SBS, six subzones, Prince George TSA	525	60–250	Diverse species	Less	Variable	Good	N. Balliet, pers. comm. (2010)

The spatial distribution of advanced regeneration within the stand plays an important role in determining the local environment of each individual and its ability to develop and grow.

timber without any further management intervention. They also reported that almost 40% of sample plots in pine-leading stands across the SBS biogeoclimatic zone exceeded 1000 stems per hectare. These results are supported by Burton and Brooks (2008), who reported that 50% of their sample plots in the SBS zone had more than 1200 stems per hectare (a common, well-spaced regeneration target in silvicultural prescriptions). Nigh et al. (2008) also concluded that over half of the severely MPB-attacked stands in the Montane Spruce (MS) biogeoclimatic zone of the Merritt TSA in south-central British Columbia had adequate advanced regeneration (1000 stems per hectare or more). In another study in the Prince George TSA (SBS, six subzones), Pousette (2010) reported that the mean density of secondary stand structure was 900 stems per hectare. Based on the Vyse et al. (2009) investigation, about 60% of the total sample plots represent a density of 600 stems per hectare in the south-central interior of British Columbia (MSxk2, MSdm3, Interior Douglas-fir [IDF]dk1, and IDFdk2 biogeoclimatic zones) (Table 1). A similar finding (600 stems per hectare) has been reported by Burton (2006), with more than 40% of the stands (or 80% by volume) dominated by lodgepole pine.

A low density of secondary stand structure or no regeneration following MPB attack has also been reported by some investigators (Weetman and Vyse 1990; Puttonen and Vyse 1998; Parish and Antos 2005; Astrup et al. 2008; Coates et al. 2009; Pousette 2010). This suggests those stand types require significant silviculture intervention to ensure adequate recruitment and future productivity. If there is low or no regeneration, then logging-and-planting or thinning-and-planting activities with acceptable species may be recommended to increase the amount of regeneration and subsequent yield.

The spatial distribution of advanced regeneration within the stand plays an important role in determining the local environment of each individual and its ability to develop and grow. Spatial distribution also determines the possibility of establishing seedlings and the renewal capacity of the stand. From different investigations, it was revealed that clumpy distribution of advanced regeneration related to stand and site condition is common in MPB-attacked stands (Weetman and Vyse 1990; Puttonen and Vyse 1998; Parish and Antos 2005; Nigh et al. 2008; Vyse 2008; Hawkins et al. unpublished data), and such distributions may result in low overall site occupancy even though stem densities are high. Moreover, such distributions also diminish release potential due to competitive stress (Oliver and Larson 1996) and reduce future timber yields (Smith 1988). The clumpy distribution could also affect seed production, which leads to future stand regeneration (Daniel et al. 1979). Therefore, knowledge concerning the distribution of the regeneration after MPB attack is essential for the forest manager or practitioner before initiating any kind of management actions. If the management objective is timber production and distribution is clumpy, then thinning may promote crown expansion and rapid release of target species.

Health of regeneration

Health of secondary structure is very important, for it directly influences the release potential of MPB-attacked stands. The health of secondary structure following MPB attack is mainly affected by abiotic factors such as soil moisture content, and falling branches and stems, which can cause injury or mortality. Increased seedling exposure following canopy mortality also increases the potential for radiation frost injury and even mortality (Ruel et al. 2000).

The death of overstorey trees following MPB attack changes the hydrological balance on the site by reducing evapotranspiration and precipitation interception, which can increase the level of soil moisture (Hélie et al. 2005; Rex and Dubé 2006). In moist environments, an anaerobic soil condition may develop that can potentially reduce the vigour of seedlings and increase the chance of regeneration mortality (Kozlowski et al. 1991; Oliver and Larson 1996).

Examining the overall health of regeneration following MPB attack, Statland (2008) reported that the majority of the advanced regeneration at Pantage Creek (SBSdw2) and Takysie Lake (SBSdk) was of good to medium quality, and N. Balliet (Mixedwood Ecology and Management Program, University of Northern British Columbia, pers. comm., March 2010) indicated that much of the regeneration in the investigated plots in central British Columbia was healthy and vigorous at the time of assessment. In another study, Rakochy (2005) reported

that 50% of advanced regeneration was healthy following MPB attack in the Lakes TSA (SBSdk). Similar findings were observed in the IDF zone (Kaipainen et al. 1998). However, other studies reported that some dominant species (e.g., subalpine fir) in the advanced regeneration layer are susceptible to health problems during stand development (Weetman and Vyse 1990; Ruel et al. 2000).

Biotic damage also occurs in advanced regeneration of lodgepole pine, including browsing by animals and mistletoe infestation. Animal browsing can have a direct detrimental influence on advanced regeneration. Ives (1982) indicated that small saplings were considered to be the most vulnerable to hare browsing. Based on another study on secondary structure of MPB-affected pine stands in the Cariboo-Chilcotin, Coates et al. (2009) reported that in understorey pine trees (seedlings and saplings), infestation by mistletoe averaged 3.3% across all ecological units.

Although health and vigour of advanced regeneration is a determining factor for the future commercial value of a stand, knowledge about the effects of abiotic and biotic damage that diminishes the health of secondary structure is limited. This is a major gap in our understanding of the management of MPB-attacked stands.

Application of different models and their limitations

Within sustainable forest management planning models, which can be used to predict forest development over time, one of the most difficult tasks is to predict regeneration dynamics. Although our understanding of the development of overstorey trees is well detailed, many processes of forest regeneration and growth are still poorly understood because it is difficult or even impossible to measure the long list of biotic and abiotic factors that affect regeneration and subsequent growth (Maguire and Forman 1983; Miina and Saksa 2006; Sagnard et al. 2007). In addition, strong, random temporal and spatial processes affect the germination, growth, damage, and mortality of seedlings (Miina et al. 2006).

Models that simulate a wide range of biological processes may help to estimate natural regeneration more precisely (Vanclay 1994). These models may also provide greater control over the simulated environment as well as promote the model for hypothesis generation, extension into new populations, and testing of new management regimes (Robinson and Monserud 2003). Different types of models such as SORTIE-ND, Prognosis^{BC}, and their hybrids are mainly used to predict the regeneration dynamics of MPB-attacked stands.

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SORTIE-ND is a resource-mediated, spatially explicit, mixed-species forest model that forecasts population dynamics for regeneration and adult trees (Coates et al. 2003; Coates et al. 2006; Simard 2008). It has the flexibility to incorporate a wide range of silvicultural strategies such as understorey protection and understorey planting, and different harvest systems such as selective harvesting, shelterwood, single-tree or group selection, and variable retention (Table 2). LeMay et al. (2007) demonstrated promising results with this model for estimating natural regeneration following MPB attack. On the other hand, Sattler (2009) reported that natural regeneration was biased and highly variable at even the finest scales. These results suggest the SORTIE-ND model needs improvement with respect to the interaction of seeds and seedlings with parent trees, substrate availability, soil moisture, and light to obtain more reliable and accurate estimates of regeneration. However, N. Balliet (Mixedwood Ecology and Management Program, University of Northern British Columbia, pers. comm., March 2010) compared actual field data with model projections and found the SORTIE-ND model moderately variable, as it was underestimating the growth of secondary stand structure and, depending on the species, overestimating or underestimating the growth of residual mature trees.

Prognosis^{BC} is a distance-independent stand growth model (Stage 1973; Wykoff et al. 1982) and well suited for use in multi-species, uneven-aged stands. Due to its wide range of silvicultural applicability, this model is a valuable tool for forest practitioners to test different harvesting regimes. The basic Prognosis^{BC} growth and yield model cannot simulate regeneration precisely. Because of this, a regeneration module is

TABLE 2. Three different models used to predict regeneration following MPB attack of lodgepole pine stands

	SORTIE-ND	Prognosis^{BC}	Hybrid
Description	• Processed-based approach • Spatially explicit, light-mediated, mixed-species model for growth and natural recruitment	• Empirically based functions • Single-tree, distance-independent growth model based on permanent sample plot data	• Combination of SORTIE-ND and Prognosis^{BC}
Strengths	• Ability to parameterize sub-models (growth, mortality, recruitment) using field data • Liberty to add predictive equations freely from available sources • Spatially explicit due to the high degree of spatial heterogeneity • Predicting understorey tree growth	• Extensive use of permanent sample plot data to calibrate the growth equations to even-aged and complex stands • Use of site and climate factors (e.g., slope aspect, elevation) to adjust model predictions • Ability to accept a tree list from a variety of inventory formats • Empirical growth models calibrated using permanent sample plots	• Combines the strengths of SORTIE-ND and Prognosis^{BC}
Major limitations	• Physiological approach to modelling growth tends to sacrifice precision • Less clear since many of the model parameters are obtained from outside the study area • Tree lists are not updated to match tree lists in Prognosis^{BC} • Tendency to overestimate the growth	• Natural regeneration sub-model is required in Prognosis^{BC} • No well-suited sub-model for assessment of regeneration • Prognosis^{BC} content tree list longer than SORTIE-ND	• High variability between measured and observed regeneration • Hybrid model could not apply to a wider set of starting stand conditions • Estimated density for smaller regenerated trees generally poor

an essential component of this model. Multivariates nearest neighbour methods are used to predict regeneration in Prognosis^{BC} (LeMay et al. 2007). Using this modelling approach, Hassani et al. (2004) found reasonably accurate results for predicting regeneration in the Kamloops and Cariboo (IDFdk1, IDFdk2, and IDFdk3) forest regions. A similar approach was carried out by LeMay et al. (2007) in the southern and central interior of British Columbia (IDF, SBPS, and MS); they reported a logical, consistent estimation of regeneration by species and size. Although a large variation exists between estimation and observation in some cases, this represents the large variability in seed source availability, seedling success, and site characteristics. They also suggested applying other dynamic approaches to better explain regeneration variation among stands but did not suggest new approaches.

A hybrid model combining Prognosis^{BC} and SORTIE-ND has been developed to predict regeneration dynamics more accurately. Overall, prediction accuracy for the hybrid model was better than the simulation run using SORTIE-ND and Prognosis^{BC} alone (Sattler et al. 2008). The linkage allowed for estimates of natural regeneration to be passed from SORTIE-ND to Prognosis^{BC} after an elapsed forecast time following MPB disturbance. Based on studies of the hybrid model, Sattler (2009) reported that the approach appears to be a promising and useful tool that forest managers could use to aid in the development of mid-term harvest plans for stands that have been disturbed by MPB. Although Zumrawi et al. (2008) observed reasonably good results using the hybrid model for advanced regeneration of pine, spruce, and aspen, poor results were observed at the seedling stage. According to Zumrawi et al. (2008), the major limitations of the hybrid model are bias in predicted regeneration, the high number of regeneration stems per hectare, and high variability between observed and measured regeneration (Table 2). This indicates the necessity of further hybrid model improvement.

Identification of knowledge gaps

Little is known about long-term, post-infestation development and growth of MPB-attacked stands. Therefore, forest managers and researchers need to understand the impact of MPB outbreaks on the growth and yield of surviving residual trees and secondary stand structure. The MPB infestation also has huge impacts on timber supply (AAC), forest health, habitat quantity and quality, hydrological integrity, and many other factors. This information is essential for managers to make better decisions regarding management of MPB-attacked stands. Knowledge of the release response of secondary structure after MPB attack is also fundamental to modelling stand dynamics of non-salvaged MPB stands. Furthermore, to secure a healthy, productive mid-term timber supply, it will be necessary to identify stands that require immediate treatment to bring them back as productive forest land. Appropriate silvicultural activities that are both cost-effective and ecologically sound will also have to be identified.

Different investigations and a workshop concerning regeneration and growth after MPB attack are the main sources that were used to identify the following knowledge gaps. The workshop was held September, 2008, at the University of Northern British Columbia, where several scientists presented their research findings. During a field tour that facilitated discussion of regeneration and growth following MPB attack, all participants significantly contributed to knowledge gap identification. Based on a literature review and expert opinion from the workshop (especially for categories f–i below), the following knowledge gaps have been identified to improve management of MPB-attacked stands.

a) Secondary stand structure

Generate predictions for:

- Seedling to sapling (< 2 cm DBH) mortality levels
- Recruitment of germinates and their survival, growth, and health in both MPB-disturbed and undisturbed stands
  - Identify substrate and abiotic conditions favourable for germination
  - Compare the germination and growth among different biogeoclimatic subzones
- Growth and release of suppressed understorey trees in older stands
- Release of secondary structure and residual trees in MPB-attacked immature stands (age classes 2 and 3)
- Favourable site conditions (subzone, site series) for secondary stand structure
  - To date, the available literature suggests this will be difficult
- Release response of competing, non-crop-tree vegetation in MPB-attacked stands
- Factors that directly influence the survival ability of advanced regeneration following MPB attack
- Growth of under-planted seedlings in a variety of site conditions
- Threshold levels of biotic problems (e.g., pests, diseases) in secondary stand structure that would require management intervention

b) Management

- Set priorities for which stands to target for management activities
- Determine the economic health of secondary stand structure
- Determine different management tools that can be used to enhance the growth of secondary structure and regeneration recruitment
- Establish permanent sample plots in MPB-attacked stand to track changes over time for regeneration, residual trees, and stands in general

c) Modelling

- Develop stand models for prediction of stand dynamics after MPB attack
- Identify limitations of models and modify them for more accurate prediction of stand dynamics and yields
- Incorporate the impact of climate change and health issues into models for better prediction (stand or landscape level) of future AAC
- Incorporate stand dynamics and stand yields into timber supply models to illustrate the utility of secondary stand structure
- Verify models through long-term monitoring of plots

d) Productivity and products

- Develop yield tables and curves for advanced regeneration in the understorey
- Determine the quality of the "new crop," which will be suitable for future products and markets

e) Stocking

- Determine the most effective way to deal with overstocking, clumpiness, and stagnation of the new forest in MPB-infested stands
- Describe the relationship between stand stocking (secondary structure) and future forest condition

f) Sampling

- Develop efficient sampling techniques to assess large areas of MPB-attacked stands
- Develop cost-effective methods to quantify secondary stand structure

g) Economics

- Define yield (economic) thresholds to be used to determine whether attacked stands should be harvested (regardless of product), partially cut, or left for future timber supply
- Define the cost of starting over (log and plant) versus other management options
- Define products that British Columbia should be managing for in the near, medium, and long term

h) Climate change

- Forecast the impact of climate change on MPB-infected stand development (dynamics)
- Determine the impact of climate change on current preferred and acceptable species in MPB-infected stands and whether these will change in the future
- Determine the impact of global warming on MPB survival, virulence, and distribution
- Define preferred and acceptable species that are not currently standard in MPB-attacked stands but potentially are in the "new" forest (e.g., subalpine fir, most broadleaf species)
- Determine the impact of climate change on species' release potential in MPB-affected stands
- Collect different climatic factors that can be used to predict MPB dispersal more accurately

i) Knowledge management

- Determine the effective processes of knowledge transfer from one region to another or from one biogeoclimatic zone to another
- Describe the influence of human intervention on the current MPB outbreak

The mountain pine beetle infestation in British Columbia crosses ecological, social, and economic boundaries, and its management goes beyond insect control.

The mountain pine beetle infestation in British Columbia crosses ecological, social, and economic boundaries, and its management goes beyond insect control. Therefore, it is time to determine how quickly MPB-infested stands can be brought back to productive forests. Forest managers need more training about the management of MPB-killed stands so these stands can potentially contribute to future timber supply. Considering the mid-term timber supplies, productivity of secondary stand structure following MPB attack in British Columbia will be highly variable due to lack of understanding about the complex interactions among primary factors (e.g., species composition, density and distribution, health, and the degree of release after MPB attack) and requires further investigation. However, in some cases, effective management of secondary stand structure is required following MPB attack to attain desired future stand level conditions to maintain ecological processes.

Acknowledgements

This work was funded by the FSP project G095048. The authors would like to thank all participants who shared their presentations during the September, 2008, University of Northern British Columbia workshop and field tour discussion groups, as well as Nicole Balliet, Marian Hasegawa, and Peter Forsythe, for facilitating the workshop and the field tour. Nicole Balliet and John Pousette are acknowledged for their comments on the article. The comments and meaningful suggestions of the anonymous reviewers and the subject editor of the *BC Journal of Ecosystems and Management* helped us to improve the overall manuscript substantially.

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ARTICLE RECEIVED: **May 17, 2010**
ARTICLE ACCEPTED: **April 13, 2011**

Production of this article was funded, in part, by the British Columbia Ministry of Forests, Lands and Natural Resource Operations.

Test Your Knowledge . . .

Regeneration and growth following mountain pine beetle attack: A synthesis of knowledge

How well can you recall some of the main messages in the preceding Discussion Paper?
Test your knowledge by answering the following questions. Answers are at the bottom of the page.

1. Assessment of regeneration and growth of residual trees after MPB attack is critical for:
   A) Forecasting long-term development (yield)
   B) Selecting stands for growth-improving silvicultural treatments
   C) Forecasting impacts to ecological attributes
   D) All of the above

2. Which model can predict regeneration dynamics more accurately?
   A) Prognosis^{BC}
   B) Hybrid model combining Prognosis^{BC} and SORTIE-ND
   C) SORTIE-ND
   D) TIPSY

3. What will happen after a mountain pine beetle attack?
   A) The forest will grow again, and 20–30% of infected stands could possibly contribute to a mid-term timber supply
   B) The forest will not grow again
   C) All lodgepole pine forests will disappear from British Columbia

ANSWERS

1. D 2. B 3. A