



## Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic

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### ABSTRACT

Since the mid-1990s the forests of central British Columbia have undergone an unprecedented Mountain Pine Beetle (*Dendroctonus ponderosae* Hopkins) (MPB) epidemic that has resulted in extensive mortality of canopy lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.). This study investigated how seed-source availability, seedbed substrate, overstory structure, and time since MPB attack interact to affect post-MPB seedling recruitment of the dominant tree species of these forests. In addition to post-MPB recruitment, these forests may be regenerated by trees established in the understory prior to MPB disturbance. Accordingly, we examined abundance and patterns of all regeneration less than 130 cm tall. We found post-MPB recruitment was sparse. Subalpine fir (*Abies laciocarpa* (Hook.) Nutt.) comprised the majority of the post-MPB recruitment. It increased with local parent tree basal area and increased strongly with proximity to a major seed source. This resulted in a patchy distribution for subalpine fir post-MPB regeneration. Lodgepole pine post-MPB recruitment was limited by overstory shading. Recruitment of pine decreased as the total overstory basal area increased. Interior spruce (*Picea glauca* × *engelmannii*) post-MPB recruitment was similarly limited by total overstory basal area. Seedbed substrates were uniform and dominated by moss. Substrate type distribution did not change as time since MPB disturbance increased. The overall low post-MPB recruitment observed was likely due to a lack of disturbance to the moss-dominated forest floor. Moss is known to be a poor substrate in northern forests. The distribution of all regeneration less than 130 cm tall showed the same trends as the post-MPB regeneration. We believe the post-MPB seedling recruitment dynamics of these forests was not substantially changed from conditions prior to MPB disturbance. There was no pulse of regeneration up to 10 years post-MPB disturbance. Unless this changes, future stand structure will be dominated by the seedling bank established prior to the MPB epidemic. Subalpine fir dominated the seedling bank (68%) and post-MPB recruitment (94%). This suggests that MPB-disturbed forests are undergoing a substantial shift in landscape-level species composition.

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### 1. Introduction

The interior forests of British Columbia, Canada, are currently experiencing a Mountain Pine Beetle (*Dendroctonus ponderosae* Hopkins) (MPB) epidemic of unprecedented proportions. The epidemic started in the mid-1990s, and as of 2007, approximately 10.1 million ha of lodgepole pine- (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) dominated forests have been affected with

green-, red- and grey-attack mortality, estimated at 620 million m<sup>3</sup> of mature lodgepole pine (Westfall and Ebata, 2007; Walton et al., 2008). Large-scale salvage and planting operations have been undertaken in many attacked stands. Extensive areas of beetle-disturbed forest will never be salvaged and it is the fate of these forests we address in this study. For stand dynamics, one of the first critical events after a natural disturbance is the recruitment of new tree seedlings. Understanding the focal processes controlling tree recruitment after disturbance is critical to predicting the future population and community dynamics of these forests (Nathan and Muller-Landau, 2000).

There are two dominant mechanisms for the development of a new tree layer and subsequent canopy recruitment after major canopy mortality events. First, regeneration may develop from a

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pulse of new post-disturbance recruitment, such as occurs after wildfire in northern Canadian forests (Greene et al., 1999; Charron and Greene, 2002; Johnson et al., 2003). Alternatively, regeneration can be from the existing seedling bank that survived the canopy mortality event, such as observed for balsam fir (*Abies balsamea* (L.) Mill.) after insect outbreaks (Morin, 1994; Osawa, 1994). The timing and extent of post-disturbance recruitment from seed and the relative importance of the existing seedling bank is poorly understood in MPB-disturbed forests (Mitchell, 2005). Long-term experiments are virtually nonexistent and there has been a lack of multi-year monitoring plots established in MPB-disturbed stands.

The study of plant dispersal across multiple scales is a rapidly growing field in ecology (Bullock and Nathan, 2008) with ongoing research on how plant fecundity, seed dispersal and recruitment success are affected by spatially heterogeneous environments (Schurr et al., 2008). In MPB-disturbed forests, forest managers are challenged to determine which stands will regenerate naturally and which stands will require restoration or rehabilitation. Consequently, forest managers require knowledge of which processes most affect seedling recruitment in MPB-disturbed forests and models for the prediction of seedling abundance to aid decision making.

Key factors that influence seedling recruitment after disturbance in northern temperate and boreal forests are the availability and favorability of seedbed substrates (e.g. Wright et al., 1998; LePage et al., 2000), mother or parent tree proximity and abundance (Ribbens et al., 1994; LePage et al., 2000; Greene et al., 2004) and overstory structure (Gray and Spies, 1996; Wright et al., 1998; LePage et al., 2000; Coates, 2002). A number of methods have been used to develop seedling recruitment functions in forests (Greene and Calogeropoulos, 2002), of which the inverse modeling approach pioneered by Ribbens et al. (1994) is considered the most economical (Greene et al., 2004). Maximum likelihood methods and inverse modeling are effective for determining which processes control tree establishment in forests and these methods are widely accepted and utilized in studies of recruitment from seed (Tanaka et al., 1998; Clark et al., 1999; LePage et al., 2000; Stoyon and Wagner, 2001).

The primary objective of this study was to use inverse modeling to explore which processes are controlling recruitment from seed in post-MPB disturbed forests. Specifically, we examine the influences of seed-source availability, substrate type, overstory structure and time since MPB attack on post-MPB recruitment. Because the presence of a seedling bank may be important in the regeneration success of these forests, we also examine the relationship between local seed-source availability and overstory structure on the abundance and pattern of the existing seedling bank.

## 2. Field sampling

To tally post-MPB recruitment, we sampled 244 regeneration plots from 36 pine-leading stands in the Sub-Boreal Spruce Zone (SBS) (Meidinger and Pojar, 1991) in central British Columbia. The sampling was designed to characterize seedling recruitment, seed-source availability, substrate composition, and local canopy structure. A sample site was comprised of two components: a “seed-source” stand (a non-pine leading stand type) and a large adjacent pine-leading stand attacked by MPB where regeneration plots were established. Two to twenty regeneration plots were established within each pine-leading stand (average 6.8 plots/stand and a median of 5.5 plots/stand). The minimum inter-plot distance was 25 m within 50 m of the seed-source stand and 50 m for plots further from the seed source. Plots were established along a transect that ran perpendicular to the edge

of the neighbouring seed-source stand which was dominated by either interior spruce [a complex of white spruce (*Picea glauca* (Moench) Voss) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)] or subalpine fir (*Abies laciocarpa* (Hook.) Nutt.). Transect lengths were variable. The seed-source stand was the only major non-pine seed source within 1 km of each regeneration plot. Species-specific parent tree abundance (basal area, m<sup>2</sup>/ha) in the seed-source stand was characterized with three variable radius prism plots (all trees >7.5 cm DBH). The distance between the seed-source stand and all regeneration plots was measured. A prism sweep from the plot centre of each regeneration plot was used to quantify the species-specific local seed-source basal area and to determine total local basal area of the overstory.

Regeneration plots were 3.99 m fixed radius plots. The number of lodgepole pine, interior spruce and subalpine fir seedlings older than one growing season and younger than the MPB-attack (i.e. post-MPB seedlings) were tallied in each plot. The age of an individual seedling was estimated from counts of annual height increments combined with destructive sampling. The substrate upon which seedlings regenerated was tallied by species.

We used infestation maps to determine the primary year of attack of sample stands. We further checked this year of attack against a set of criteria developed in collaboration with local entomologists and tested against stands with known infestation times. The criteria were used to determine the primary year of attack by assessing the MPB-killed pine in the plot neighbourhood. These criteria were: (1) presence and colour of foliage, (2) crown condition and proportion of fine branches retained, (3) presence/absence of MPB adults, pupae or larvae, (4) presence and condition of pitch tubes, (5) bark and under bark (wood) condition, and (6) other insect activity. MPB infestations can occur over several years within a stand (Safranyik and Wilson, 2006). Our intent was to identify the year where mass mortality had occurred. The current high MPB population in northern British Columbia has generally resulted in a pulse of mortality of the majority of canopy pine trees within a stand. This has been repeatedly observed in stands throughout northern BC (observation of authors). Hence, infestation time was determined as the year when a pulse of lodgepole pine had been killed, which ranged from 3 to 9 years prior to our sampling. Regeneration plots were established in stands that covered all years within this range. Plots were not equally distributed across years since MPB attack due to differences in abundance and accessibility. Sample sizes were: 3 years prior = 75; 4 years prior = 67; 5 years prior = 39; 6 years prior = 8; 7 years prior = 8; 8 years = 29; 9 years prior = 18.

Percent cover of 11 pre-defined substrate types was recorded for each plot. The substrate types were: (1) animal disturbance (small patches of mixed organic material and mineral soil associated with squirrel middens and vole dens), (2) forest-floor moss (a well developed, undisturbed, moss carpet dominated by red-stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt.), step moss (*Hylocomium splendens* (Hedw.) Schimp. in BSG) and knight's plume (*Ptilium crista-castrensis* (Hedw.) De Not.)), (3) conifer litter, (4) deciduous litter, (5) fresh logs (a solid intact log or stump from windthrow), (6) lichen, (7) moss-covered logs (partially decomposed logs on the forest floor covered by undisturbed moss), (8) mineral soil (exposed mineral soil), (9) organic material, (10) rotten wood (logs or wood considerably decomposed and incorporated into the forest floor), and (11) nonproductive (rock, water, and tree stems). We visually estimated percent cover of substrates by dividing each plot into quadrants and summing estimates from each quadrant for the whole plot. Estimates were based on two field crew members estimating percent cover independently.

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