



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

Rasmus Astrup^{a,*}, K. David Coates^b, Erin Hall^b

^a Bulkley Valley Centre for Natural Resources Research and Management, Box 4274, Smithers, BC V0J 2N0, Canada

^b British Columbia Forest Service, Research Section, Bag 6000, Smithers, BC V0J 2N0, Canada

ARTICLE INFO

Article history:

Received 1 September 2007

Received in revised form 21 July 2008

Accepted 29 July 2008

Keywords:

Advanced regeneration

Inverse modeling

Multiple scales

Recruitment

Regeneration

Seed dispersal

Seedling bank

Spatially heterogeneous environments

Storage dynamics

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.

© 2008 Elsevier B.V. All rights reserved.

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 m³ 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

* Corresponding author. Current address: Norwegian Forest and Landscape Institute, Høgskoleveien 8, Postboks 115, 1431 Ås, Norway.
Tel.: +47 94 97 70; fax: +47 94 29 80.

E-mail address: rasmus.astrup@skogoglandskap.no (R. Astrup).

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, m²/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.

In addition to our count of post-MPB recruitment, we tallied in all 244 plots the total number of seedlings (pre- and post-MPB combined) less than 130 cm tall. We combined our total seedling count data with data from an additional 561 plots located in 99 stands not sampled in our study (Rakochoy, 2005; Cichowski, unpublished data). These additional data were collected in the same general geographic area as our sampling using similar methodologies to count all seedlings less than 130 cm tall and to characterize species-specific basal area of the local overstory trees. A GPS coordinate was recorded for each plot center with a handheld device. Distance to the nearest major seed source from plot center was not recorded. These 561 plots were combined with the 244 plots from our study to create one common dataset ($n = 805$) of total regeneration less than 130 cm tall.

3. Analysis

The analysis was performed with an inverse modeling approach. We developed and tested six species-specific candidate models that represented relationships between post-MPB recruitment or total regeneration and (1) seed-source availability, (2) time since beetle infestation, (3) seedbed substrate, or (4) total local overstory basal area. In effect, the alternate models represent competing hypotheses for the suite of factors that determine recruitment dynamics in forests. For post-MPB recruitment data ($n = 244$) we utilized the average annual recruitment (total number of recruits younger than the attack divided by the number of years post-MPB attack) as the predicted variable (Y). For the total regeneration ($n = 805$), we utilized total seedling count as the predicted variable (Y). All six models were fitted to the post-MPB recruitment dataset. For the total regeneration count data, we did not have data for distance to a non-pine seed source or data on substrate types. Therefore, it was only possible to test a subset of the models (Models 1, 2, and 6; see below) for the total regeneration dataset.

The Null Model (Model 1) assumes that regeneration abundance was controlled by factors not considered in this study and represents a simple mean of the observed data. Models 2 and 3 are nested models where recruitment is dependent on seed-source proximity. In the first seed-source model (Model 2), recruitment is predicted as a function of local basal area of parent trees (BA_{LPT}) measured with the variable radius plot. The second seed-source model (Model 3) includes the effects from Model 2 and an additional term that represents the distance to (dist) and basal area of parent trees in the nearest major non-pine seed-source stand (BA_{SSPT}). In Model 3, it was assumed that the effect of the seed-source stand is negatively proportional to the distance between the regeneration plots (maximum distance = 1000, minimum distance = 0) and the seed-source stand.

Model 4 represents change in recruitment with time since MPB attack (TsMPB). Model 5 predicts recruitment from substrate variability utilizing an equation developed by LePage et al. (2000). In Model 5, J represents one of the 11 measured substrate types (S), C_j is the proportion of substrate type J in a plot (0–1), while F_j is an estimated favorability parameter for substrate J that is limited between 0 and 1. Thus, the summation provides an index of substrate favorability (LePage et al., 2000). The final model (Model 6) assumes decreased recruitment with increased total overstory basal area (BA_{Tot}).

Model 1:

$$Y = \alpha$$

Model 2:

$$Y = \alpha + \beta_1 \times (1 - \exp(-\beta_2 \times BA_{LPT}))$$

Model 3:

$$Y = \alpha + \beta_1 \times (1 - \exp(-\beta_2 \times BA_{LPT} - \beta_3 \times (-0.001 \times \text{dist} + 1) \times BA_{SSPT}))$$

Model 4:

$$Y = \beta_1 \times (1 - \exp(-\beta_2 \times \text{TsMPB}))$$

Model 5:

$$Y = \beta_1 \times \sum_{j=1}^S C_j F_j$$

Model 6:

$$Y = \beta_1 \times \exp(-\lambda_1 \times BA_{Tot})$$

The α parameter represents an intercept. The parameter β_1 can be interpreted as an “optimal recruitment parameter” that is obtained under optimal conditions (the latter part of each equation varies between 0 and 1 and the optimal recruitment estimate is obtained when the latter part of an equation = 1). Parameters β_2 and β_3 determine how seedling recruitment increases with seed-source abundance or time since MPB infestation. Parameter λ_1 determines how seedling recruitment changes with total overstory basal area.

Maximum likelihood estimates (Edwards, 1992) of model parameters were obtained using simulated annealing (a global optimization algorithm) (Goffe et al., 1994). Global optimization methods are appropriate for rough likelihood surfaces which were observed for some of our tested models. We used Akaike's Information Criterion (AIC, Akaike, 1973) corrected for small sample sizes (AIC_c) (Hurvich and Tsai, 1989) for model selection. We used the negative binomial probability density function (PDF) for error distribution in all models. This PDF is well suited for overdispersed count data (e.g. Hilborn and Mangel, 1997) as in the collected dataset. The analysis was implemented in the statistical software R (R Development Core Team, 2006).

The total regeneration dataset contained spatial locations for all plots. We used this information to investigate stand level (less than 1000 m) spatial autocorrelation of total regeneration abundance by calculating Moran's I (e.g. Fortin and Dale, 2005) in distance classes of 100 m for each of the three species. Values of Moran's I close to zero indicate lack of spatial autocorrelation while values around 1 indicate strong positive autocorrelation.

4. Results

There were large variations in composition of the seed-source stands. Basal area averaged 39 m²/ha and varied from 12 and 69 m²/ha (Table 1). Canopy trees in seed-source stands were dominated by interior spruce and subalpine fir. Basal area of the local overstory at the individual recruitment plots varied between 4 and 78 m²/ha with a mean of 39 m²/ha, but was dominated by dead pine (mean of 24 m²/ha) (Table 1).

Post-MPB recruitment was sparse and patchy (Fig. 1A and B); subalpine fir was present in 27 plots (11%), interior spruce in 14 plots (6%), and lodgepole pine in 13 plots (5%). No post-MPB recruitment was observed in the majority of the plots, while a small number of plots had large amounts of recruitment. Subalpine fir post-MPB recruitment (1498 seedlings) was the most prevalent species followed by lodgepole pine (65 seedlings) and interior spruce (37 seedlings). There was little variation in substrate types across the study sites and substrate type distribution did not show

Table 1Species-specific variation in seed-source stand and local overstory parent-tree basal area (BA, m²/ha) of post-MPB disturbance recruitment plots

	Seed-source plots			Local recruitment plots		
	Basal area (m ² /ha)			Basal area (m ² /ha)		
	Mean	Maximum	Minimum	Mean	Maximum	Minimum
All species	39	69	12	39	78	4
Subalpine fir	5	30	0	2	30	0
Interior spruce	19	59	0	3	35	0
Dead lodgepole pine	5	20	0	26	72	0
Live lodgepole pine	1	3	0	6	40	0

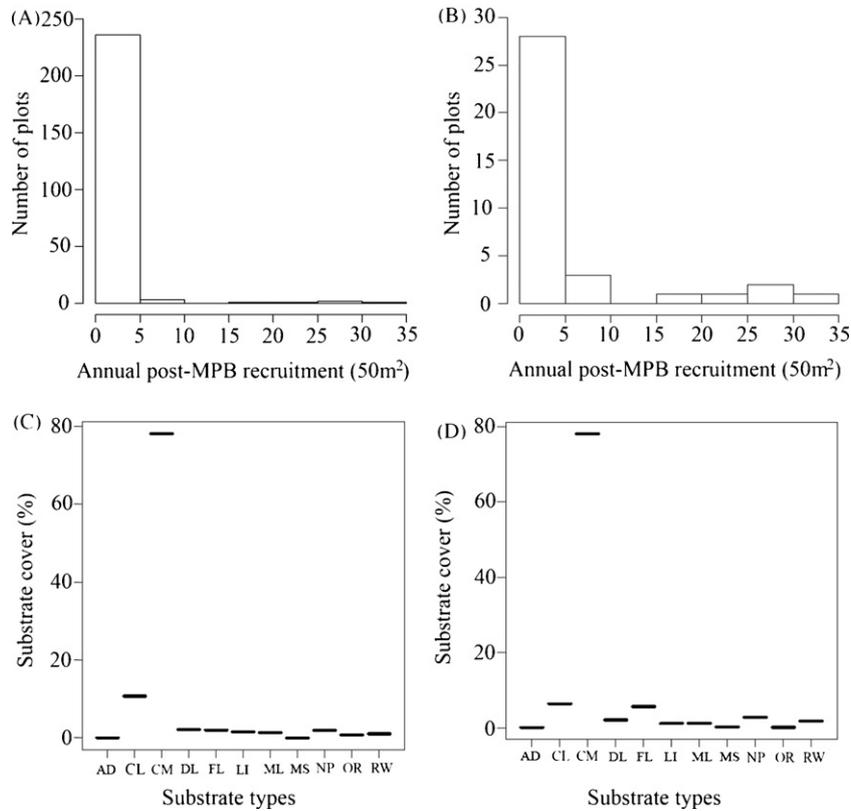


Fig. 1. Post-MPB disturbance seedling recruitment (in 50 m² plots) and substrate type distribution (in 3.99 m² plots). (A) Annual seedling recruitment including zero-observations. (B) Annual seedling recruitment excluding zero-observations. (C) Substrate type distribution in plots 1–4 years post-MPB attack. (D) Substrate type distribution in plots 5–9 years post-MPB attack. A comparison between (A) and (B) illustrates the magnitude of plots without post-MPB seedling recruitment. A comparison between (C) and (D) illustrates little change in substrate type distribution over time. Substrate types are animal disturbance (AD), conifer litter (CL), forest-floor moss (CM), deciduous litter (DL), fresh logs (FL), lichen (LI), moss-covered logs (ML), mineral soil (MS), non-productive (NP), organic material (OM), rotten wood (RW).

any substantial changes as time since MPB disturbance increased (Fig. 1C and D).

Due to the limited post-MPB recruitment observed, our dataset had relatively little information for model fitting and testing of the alternate hypotheses related to the processes controlling recruitment from seed after MPB canopy mortality. Consequently, many of the proposed models were worse approximations of the data than the Null Model (Model 1) (Table 2), however, some trends were evident.

The best model for representing post-MPB subalpine fir recruitment was Model 3, indicating that regeneration was related to seed-source availability (Table 2). Subalpine fir post-MPB recruitment increased strongly with proximity to a major seed source (Fig. 2A) and then increased further as local parent tree basal area increased (Fig. 2B). The estimated subalpine fir parameters in Model 3 with support intervals (upper S.I., lower

S.I.) (Edwards, 1992) were: $\alpha = 0.001$ (−0.000034, 0.013); $\beta_1 = 16.7$ (10.9–33.1); $\beta_2 = 0.00093$ (0.00003, 0.005); $\beta_3 = 0.00602$ (0.0037, 0.361).

Lodgepole pine post-MPB recruitment was best represented by Model 6, suggesting a relationship between total overstory basal area and recruitment. For Model 6, the lodgepole pine parameter estimates with support intervals (upper S.I., lower S.I.) were estimated at: $\beta_1 = 0.354$ (0.16, 0.62) and $\lambda_1 = 0.065$ (0.05, 0.09). Lodgepole pine post-MPB recruitment clearly increased as the total overstory basal area decreased (Fig. 2C).

Interior spruce post-MPB recruitment may also be influenced by total overstory basal area. Model 6, representing total overstory basal area limitations, had the lowest AIC_C but the Null Model (Model 1) had the same level of support as Model 6 (Table 2). Increased overstory basal area had a less severe negative effect on interior spruce post-MPB recruitment than on lodgepole pine

Table 2
Comparison of post-MPB disturbance seedling recruitment models

Model	Interpretation	Subalpinefir	Lodgepolepine	Interiorspruce
Model 1	Null Model	75	5	0.2
Model 2	Local parent trees	79	9	4.3
Model 3	Local parent trees and seed source	0	11	4.4
Model 4	Time since attack	64	3	4.3
Model 5	Substrate	94	21	17
Model 6	Total overstory	76	0	0

Values are ΔAIC_c . Bold values indicate the best approximating models for each tree species.

recruitment (Fig. 2C). Spruce parameter estimates for Model 6 with support intervals (upper S.I., lower S.I.) were: $\beta_1 = 0.119$ (0.046–0.242) and $\lambda_1 = 0.044$ (0.024, 0.073).

The total seedling counts of all regeneration <130 cm tall were much higher (Fig. 3) than the amounts of regeneration established post-MPB attack (Fig. 1A and B). This larger dataset was much better suited to model fitting and testing than the smaller post-MPB recruitment dataset. Interestingly, results from both datasets were similar in terms of factors affecting seedling abundance (Tables 2 and 3). The total seedling count for subalpine fir was best explained by local seed-source availability (Model 2; Table 3) with increased seedling counts as local parent tree basal area increased (Model 2 parameters with support intervals: $\alpha = 2.335$ (1.751, 3.005); $\beta_1 = 9.800$ (5.264, 18.355); $\beta_2 = 0.252$ (0.079, 3000)). Lodgepole pine and interior spruce total seedling counts were found to increase with decreasing total local overstory basal area (Model 6; Table 3) (Model 6 parameters with support intervals: $\beta_{1\text{pine}} = 3.701$ (3.071, 4.446), $\lambda_{1\text{pine}} = 0.0374$ (0.0325, 0.0421), $\beta_{1\text{spruce}} = 2.251$ (1.936, 2.608) and $\lambda_{1\text{spruce}} = 0.012$ (0.008, 0.016).

There was no evidence of spatial autocorrelation at the stand level (Moran's I of approximately zero) in the total seedling count data for interior spruce and lodgepole pine. This suggests spruce and pine seedlings had a fairly regular distribution in the understory of MPB-disturbed forests. In contrast, data for all subalpine fir seedlings had a positive spatial autocorrelation, with values of Moran's I close to one at all distance intervals between 0 and 1000 m. Unlike pine and spruce, subalpine fir was clumped in its distribution. Results from the spatial autocorrelation analysis were consistent with our model fitting analysis where subalpine fir abundance was strongly influenced by proximity and amount of a seed source.

5. Discussion

The mountain pine beetle epidemic in the northern forests of western Canada, although vast in extent, has been a low intensity disturbance in terms of impacts on the forest floor. Our study clearly demonstrated that recruitment of new seedlings after MPB canopy mortality was substantially lower than observed after wildfires in northern forests (e.g. Greene et al., 1999; Charron and Greene, 2002; Johnson et al., 2003). We observed no significant

Table 3
Comparison of models for total seedling counts for all seedlings less than 130 cm tall

Model	Interpretation	Subalpinefir	Lodgepolepine	Interiorspruce
Model 1	Null Model	31	18	2
Model 2	Local parent trees	0	5	2
Model 6	Total overstory	33	0	0

Values are ΔAIC_c and bold values indicate the best approximating model for each tree species.

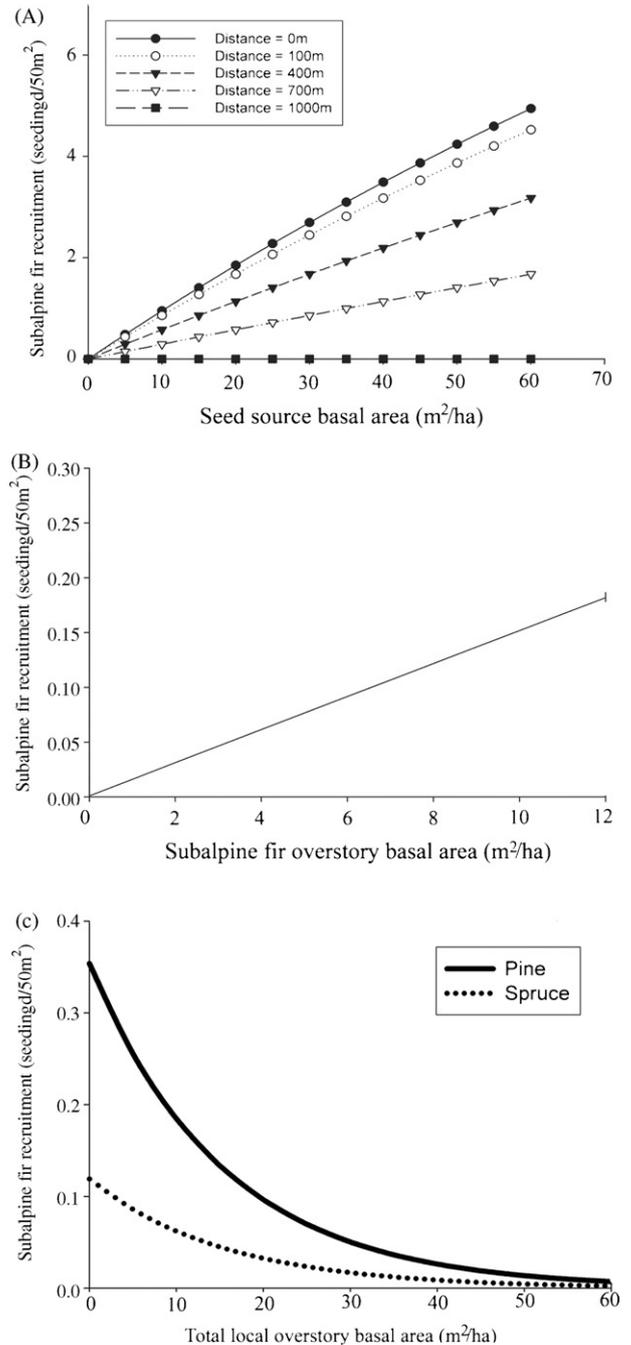


Fig. 2. The predicted effects of seed-source availability on post-MPB seedling recruitment. (A) Recruitment of subalpine fir as a function of seed-source stand basal area and distance to seed-source stand. (B) The effect of local parent-tree basal area on recruitment of subalpine fir. (C) The effect of total (all species) local overstory basal area on recruitment of lodgepole pine and interior spruce. The x-axes vary to cover the approximate range of the observed data.

post-disturbance pulse in regeneration shortly after MPB disturbance as is commonly seen after fire.

A key difference between fire and MPB disturbance for seedling recruitment is the impact on substrate availability and favorability. Our results illustrated that in the first 10-years after beetle disturbance, the substrate distribution undergoes limited change and remains dominated by moss as in an undisturbed forest. The effect of MPB canopy mortality on forest floor conditions is similar to that found in gap-phase dynamics forests (Coates and Burton,

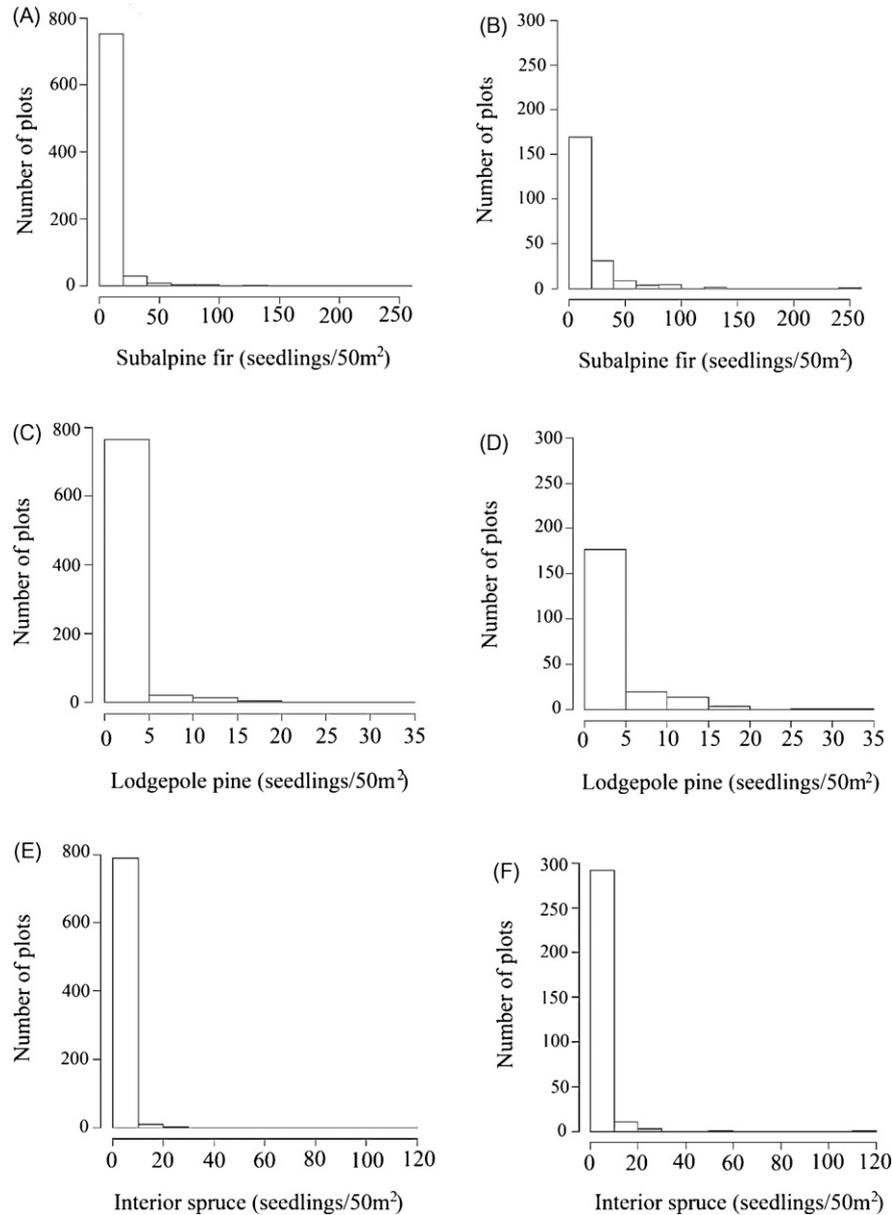


Fig. 3. Histograms of total seedling counts for all seedlings less than 130 cm tall. (A), (C) and (E) contain all observations, including plots with zero observations while (B), (D) and (F) exclude non-zero observations. Comparison of plots A–B, C–D, and E–F illustrate the magnitude of plots without seedlings for subalpine fir, lodgepole pine and interior spruce, respectively. Note that y-axis values change between comparisons.

1997). In contrast, after wildfire, seedbed substrates are generally more variable with a higher proportion of substrate types considered favorable for regeneration establishment (e.g. Miyanishi and Johnson, 2002). This is also the case after logging disturbance such as gap cuts or clear cuts where seedbed substrates are more variable than observed in adjacent undisturbed forests (LePage et al., 2000; Coates, 2002). The importance of substrate type for regeneration in northern forests has been well established (Farmer, 1997; LePage et al., 2000). In our tested models for MPB-disturbed forests, information about seedbed substrates was not found to improve model predictions. Our data contained little inter-plot variation in substrate types and this is likely the major reason for the poor predictive ability of seedbed substrate type in our analysis. Continuous and undisturbed moss-dominated forest floors are relatively unfavorable for establishment of seedlings in northern forests (Wright et al., 1998; LePage et al., 2000; Coates, 2002). The low levels of post-MPB recruitment

observed in the first 10 years after MPB attack are likely due to poor seedbed substrate availability.

Even though post-MPB recruitment was sparse, there were some evident trends in regeneration success. Regeneration abundance varied by species and strong species-specific differences in canopy influences on regeneration success were evident. Subalpine fir post-MPB recruitment was substantially higher than that of lodgepole pine and interior spruce. In part, this can be explained by the superior ability of true fir species, compared to spruce and pine, to regenerate on the moss forest floors that dominated all study sites (Day, 1964; Cui, 1991; Wright et al., 1998; LePage et al., 2000). The large seed size of subalpine fir relative to other species is thought to explain its superior ability to regenerate on moss-dominated substrates (Day, 1964; Cui, 1991; Wright et al., 1998). The post-MPB regeneration of subalpine fir was very patchy and our analysis illustrated that recruitment of subalpine fir was seed-source limited. The dispersal limitations of

subalpine fir may be due to the larger seed size of the species (e.g. Greene et al., 1999). We did not find any evidence of dispersal limitation for post-MPB recruitment of pine and spruce and the abundance of pine was negatively correlated with total canopy basal area above regeneration plots. This was also the case for spruce but the effect was much stronger for pine. The species-specific effects of local overstory on regeneration abundance relate well to common shade-tolerance rankings where subalpine fir is a shade-tolerant species, interior spruce is mid-tolerant species, and lodgepole pine is a shade-intolerant species.

Interestingly, the processes influencing the abundance and distribution of the post-MPB recruitment were the same as those influencing the abundance and distribution of all seedlings less than 130 cm tall. Seedling bank trees can grow very slowly in the undisturbed understory and may have recruited over an extended time period. During the period of this study, there has been little substantial change in the factors that control recruitment in these forests. In the analysis, this can be seen directly from the low level of support for the model that includes time since attack (Table 2). Up to 10 years post-beetle disturbance, the seedbed substrates are still moss-dominated and all seed sources are virtually unchanged. The serotinous cones of lodgepole pine still contain seeds and the other trees species have survived the pine mortality event. The overstory pine snags, which maintain needles for approximately 5 years, still shade the forest floor. It is unknown if seedbed substrate type distribution will substantially change in the future or whether a later major recruitment pulse might still occur. At this time, it appears that the seedling bank established prior to the MPB disturbance is the tree layer most likely to control future stand dynamics of these forests.

In the northern forest of eastern North America, there is a long history of large scale outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.)) that kills overstory balsam fir (e.g. Johnson et al., 2003). After budworm outbreaks, the balsam fir stands often re-establish from well developed seedling banks (e.g. Ghent, 1958; Dechesneau and Morin, 1999; Johnson et al., 2003). In western Canada, the seedling bank is generally less well developed and has a smaller proportion of true firs than in eastern Canada (Messier et al., 1999). Recruitment of new seedlings post-MPB attack has been very slow. The composition and dynamics of MPB-disturbed forests will to a large extent be determined by the species composition, density and size of trees established in the understory prior to the MPB epidemic unless a future regeneration pulse occurs.

Our study has illustrated that both the existing seedling bank and new post-MPB recruitment are patchy in the MPB-disturbed forests of northern British Columbia. This is primarily due to the dominance of subalpine fir in both regeneration categories and the clear seed-source limitation of this species. While subalpine fir dominates the regeneration layers, other species are present in varying amounts resulting in diverse species mixtures. The patchy structure of regeneration and the various species combinations developing in these stands has future forest management implications. For example, stand level means, so commonly used in forestry (Puettmann et al., 2008), may be poor descriptors of stand development after MPB disturbance. Non-spatial single-species growth models will not be able to represent future stand development. Either repeated inventories or spatially explicit mixed-species growth models will be required for prediction of future stand dynamics.

The high proportion of subalpine fir regeneration in the post-MPB recruitment layer and in the seedling bank further suggests a substantial shift in the landscape-level species composition of MPB-disturbed forests. Our results indicate that MPB-disturbed stands that had well developed seedling banks will be much more

likely to rapidly develop into reasonably stocked stands while a substantial regeneration delay can be expected where seedling banks are absent.

Acknowledgements

We thank three anonymous reviewers for their comments and suggestions. We are especially grateful to the guest editor whose thoughtful review greatly improved this manuscript. We thank Jacqueline Prior and Lisa Mahon for their assistance with field data collection. Ken White assisted with developing the criteria used to assess infestation time. We are indebted to Patience Rakochy, UNBC and Debbie Cichowski, Caribou Ecological Consulting, for providing datasets used in this study. We are also grateful to Phil Burton, Canadian Forest Service, Prince George, BC, and his crew for collecting data used in this study. Funding for this project was provided by the British Columbia Forest Science Program through Project Y072148.

References

- Akaike, H., 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov, B.N., Csaki, F. (Eds.), Second International Symposium on Information Theory, Akademiai Kiado.
- Bullock, J.M., Nathan, R., 2008. Plant dispersal across multiple scales: linking models and reality. *Journal of Ecology* 96, 567–568.
- Charron, I., Greene, D.F., 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forests. *Canadian Journal of Forest Research* 32, 1607–1615.
- Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichten, J., McLachlan, J., Mohan, J., Wyckoff, P., 1999. Interpreting recruitment limitations in forests. *American Journal of Botany* 86, 1–16.
- Coates, K.D., 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia. *Forest Ecology and Management* 155, 387–398.
- Coates, K.D., Burton, P.J., 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *Forest Ecology and Management* 99, 337–354.
- Cui, M., 1991. The Ecophysiology of Seedling Establishment in Sub-alpine Conifers of the Central Rocky Mountains. University of Wyoming, USA.
- Day, R.J., 1964. The microenvironments occupied by spruce and fir regeneration in the Rocky Mountains. Canadian Department of Forestry Research Branch Publication Number 1037.
- Dechesneau, R., Morin, H., 1999. Early seedling demography in balsam fir seedling banks. *Canadian Journal of Forest Research* 29, 1502–1509.
- Edwards, A.W.F., 1992. Likelihood. John Hopkins University Press, Baltimore.
- Farmer, R.E., 1997. Seed Ecophysiology of Temperate and Boreal Zone Forest Trees. St. Lucie Press, Delray Beach, Florida, USA.
- Fortin, M.-J., Dale, M., 2005. Spatial Analysis, A Guide for Ecologists. Cambridge University Press, Cambridge.
- Ghent, A.W., 1958. Studies of regeneration in forest stands devastated by the spruce budworm. II. Age, height, growth and related studies of balsam fir seedlings. *Forest Science* 4, 135–146.
- Goffe, W.L., Ferrier, G.D., Rogers, J., 1994. Global optimization of statistical functions with simulated annealing. *Journal of Econometrics* 60, 65–99.
- Gray, A.N., Spies, T., 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *Journal of Ecology* 84, 635–645.
- Greene, D.F., Calogeropoulos, C., 2002. Dispersal of seeds by animals and wind. In: Bullock, J., Kenward, R., Hails, R. (Eds.), *Dispersal Ecology*. Blackwell Press, Oxford, UK, pp. 3–23.
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., Simard, M.J., 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research* 29, 824–839.
- Greene, D.F., Canham, C.D., Coates, K.D., LePage, P.T., 2004. An evaluation of alternative dispersal functions for trees. *Journal of Ecology* 92, 758–766.
- Hilborn, R., Mangel, M., 1997. *The Ecological Detective: Confronting Models With Data*. Princeton University Press, Princeton.
- Hurvich, C.M., Tsai, C.-L., 1989. Regression and time series model selection in small samples. *Biometrika* 76, 297–307.
- Johnson, E.A., Morin, H., Miyanishi, K., Gagnon, R., Greene, D.F., 2003. A process approach to understanding disturbance and forest dynamics for sustainable forestry. In: Burton, P.J., Messier, C., Smith, D.W., Adamowicz, W.L. (Eds.), *Towards Sustainable Management of the Boreal Forest*. National Research Council of Canada. NRC Research Press, Ottawa, pp. 261–306.
- LePage, P.T., Canham, C.D., Coates, K.D., Bartemucci, P., 2000. Seed sources versus substrate limitations of seedling recruitment in interior cedar–hemlock forest of British Columbia. *Canadian Journal of Forest Research* 30, 415–427.
- Meidinger, D., Pojar, J. (Eds.), 1991. *Ecosystems of British Columbia*. Special Report Series No. 6, B.C. Ministry of Forests, Research Branch, Victoria, B.C.

- Messier, C., Doucet, R., Ruel, J.-C., Claveau, Y., Kelly, C., Lechowicz, M.J., 1999. Functional ecology of advanced regeneration in relation to light in boreal forests. *Canadian Journal of Forest Research* 29, 812–823.
- Mitchell, J.M., 2005. Review and Synthesis of Regeneration Methods in Beetle-Killed Stands Following Mountain Pine Beetle (*Dendroctonus ponderosae*) Attack: A Literature Review. Mountain Pine Beetle Initiative, Working Paper 2005-16. Natural Resources Canada, Canadian Forest Service, Victoria, BC, Canada.
- Miyaniishi, K., Johnson, A.D., 2002. Process and patterns of duff consumption in the mixed-wood boreal forest. *Canadian Journal of Forest Research* 32, 1285–1295.
- Morin, H., 1994. Dynamics of balsam fir forest in relation to spruce budworm outbreaks in the boreal zone of Quebec. *Canadian Journal of Forest Research* 24, 730–741.
- Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15, 278–285.
- Osawa, A., 1994. Seedling responses to forest canopy disturbance following a spruce budworm outbreak in Maine. *Canadian Journal of Forest Research* 19, 850–859.
- Puettmann, K.J., Coates, K.D., Messier, C., 2008. A Critique of Silviculture: Managing For Complexity. Island Press, Washington, DC.
- R Development Core Team, 2006. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>.
- Rakochy, P.I., 2005. Lodgepole pine stand dynamics as a result of mountain pine beetle attack in central British Columbia. MSc Thesis. University of Northern British Columbia, Prince George, BC.
- Ribbens, E., Silander Jr., J.A., Pacala, S.W., 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75, 1794–1806.
- Safranyik, L., Wilson, B. (Eds.), 2006. The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC.
- Schurr, F.M., Steinitz, O., Nathan, R., 2008. Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology* 96, 628–641.
- Stoyon, D., Wagner, S., 2001. Estimating the fruit dispersion of anemochorous trees. *Ecological Modelling* 145, 35–47.
- Tanaka, H., Shibata, M., Nakashizuka, T., 1998. A mechanistic approach for evaluating the role of wind dispersal in tree population dynamics. *Journal of Sustainable Forestry* 6, 155–174.
- Walton, A., Hughes, J., Eng, M., Fall, A., Shore, T., Riel, B., Hall, P., 2008. Provincial-level projection of the current mountain pine beetle outbreak: update of the infestation projection based on the 2007 Provincial Aerial Overview of Forest Health and revisions to “the model” (BCMPB.v5). <http://www.for.gov.bc.ca/hre/bcmapb/>.
- Westfall, J., Ebata, T., 2007. Summary of Forest Health Conditions in British Columbia. Pest Management Report Number 15. British Columbia Ministry of Forests and Range, Victoria, BC. http://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial_Overview/2007/Aerial%20OV%202007.pdf.
- Wright, E.F., Coates, K.D., Bartemucci, P., 1998. Regeneration from seed of six tree species in the interior cedar–hemlock forests of British Columbia as affected by substrate and canopy gap position. *Canadian Journal of Forest Research* 28, 1352–1364.