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Natural regeneration in partial cuts and mature forests after mountain pine beetle infestation in the west Chilcotin Itcha-Ilgachuz Research Project

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Nola M. Daintith and Michaela J. Waterhouse

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Authors' affiliation

Nola Daintith and Michaela Waterhouse
B.C. Ministry of Forests, Lands and Natural Resource Operations
Cariboo Region, Williams Lake, B.C.

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ABSTRACT

The Itcha-Ilgachuz Research Project was initiated in 1995 in the west Chilcotin region of central British Columbia to test variants of group selection and irregular group shelterwood silvicultural systems for managing lodgepole pine (*Pinus contorta* var. *latifolia*) forests for timber and northern caribou (*Rangifer tarandus caribou* Gmelin, northern ecotype) winter habitat. The density, distribution, and growth of naturally regenerated lodgepole pine was monitored in the small harvested openings and the forested matrix of the silvicultural systems treatments, in forested control units, and in adjacent clearcuts over the course of the mountain pine beetle epidemic (2003–2008) and 5 years after.

Natural regeneration in the very dry, cold Sub-Boreal Pine – Spruce (SBPSxc) biogeoclimatic subzone was sufficient to restock small harvested openings and produce a stocked stand in the understorey of a mature stand that was severely impacted by mountain pine beetle. In this subzone, advance regeneration will play an important role in future stand development, more so than ingress resulting from disturbance. In the higher elevation very dry, very cold Montane Spruce (MSxv) subzone, natural regeneration was not abundant enough to stock harvested openings or mountain pine beetle impacted stands. Post-disturbance ingress will be the predominant component of the understorey in this subzone. Our results suggest that recovery after the beetle outbreak will be a slower process in the MSxv than in the SBPSxc due to reliance on new recruits. Better seedling growth and condition in the MSxv, however, may help mitigate the slower recovery rate. The forest canopy, even with considerable mortality, had a significant impact on seedling growth and condition compared to clearcut conditions. The last assessment, completed 5 years after the outbreak, showed that seedlings in all locations, but particularly in the harvested openings, had improved growth and vigour, which suggests that they are responding to the increased site resources. This study shows that pathways of stand recovery after the mountain pine beetle epidemic in the west Chilcotin will differ depending on biogeoclimatic and pre-epidemic stand conditions.

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INTRODUCTION

The Itcha-Ilgachuz Research Project was initiated in 1995 in the west Chilcotin region of central British Columbia to test different silvicultural systems that have potential for managing lodgepole pine (*Pinus contorta* var. *latifolia*) forests for timber while maintaining important winter habitat for northern caribou (*Rangifer tarandus caribou* Gmelin, northern ecotype) (Armleder and Waterhouse 2008). Compared to clearcutting, the silvicultural systems tested, including variants of group selection and irregular group shelterwood systems, maintain terrestrial and arboreal lichens, which are critical winter forage for the caribou. These systems, however, have been rarely applied to lodgepole pine forests in British Columbia, where natural disturbance regimes, predominantly wildfires, are typically frequent and stand replacing. The group selection system, which removes all trees in patches smaller than 1 ha, is the only silvicultural system, other than clearcutting, where natural or planted lodgepole pine regeneration is likely to meet generally accepted regeneration standards (Alexander 1972; Lotan 1975; Lotan and Perry 1983; Schmidt and Alexander 1985). No studies of natural regeneration in small openings (<1 ha) in lodgepole pine forests have previously been conducted in west–central British Columbia, and due to the uniqueness of the climate in this area, natural regeneration studies cannot be confidently extrapolated from other regions.

Our study is located in two biogeoclimatic subzones that are unique to the west Chilcotin (Steen and Coupé 1997). Lodgepole pine forests in the very dry, cold Sub-Boreal Pine – Spruce (SPBSxc) subzone are largely uneven-aged and similar to those in the dry cool Interior Douglas-fir (IDFdk4) subzone in the Cariboo–Chilcotin (Axelson et al. 2010). In these stands, historic mountain pine beetle (*Dendroctonus ponderosae*) (MPB) outbreaks have played an important role in stand dynamics and composition. Hawkes et al. (2004) determined that a unique multi-age and multi-size stand structure exists as a result of past multiple mountain pine beetle outbreaks and surface fires, and the ability of lodgepole pine to regenerate under its own canopy.

Lodgepole pine forests in the higher elevation very dry, very cold Montane Spruce (MSxv) subzone tend to be even-aged, even-sized, and relatively long-lived due to the long interval between stand replacing wildfires. Stands in the MSxv have historically escaped mountain pine beetle outbreaks due to climatic conditions being less favourable for the beetle. In the most recent outbreak (2003–2008), even stands in the MSxv subzone were subject to high beetle-related mortality, which indicates there has been a substantial shift in climatically benign habitats for mountain pine beetle northward and toward higher elevations in the latter half of the 20th century (Carroll et al. 2004).

Before the mountain pine beetle epidemic in central British Columbia, the original objective of the natural regeneration component of the Itcha-Ilgachuz Research Project was to determine whether small openings (0.02–0.07 ha) created by the two silvicultural systems would be naturally restocked with lodgepole pine within 7 years following harvesting. Seven years is the accepted period of time in British Columbia for achieving natural regeneration after clearcutting and before planting is required. Steen et al. (2007) reported on the density and stocking of natural regeneration that had been assessed annually for 7 years following harvest (1996–2002). In year seven, the density of post-harvest ingress of seedlings ≥1 year old was significantly higher in the small harvested openings on the SBPSxc blocks than on the higher elevation MSxv blocks. Advance regeneration was also a substantial component of the overall density and stocking in the SBPSxc but not in the MSxv. The results indicated that small openings harvested in the SBPSxc could be naturally restocked by lodgepole pine, but openings in the MSxv would need to be planted to ensure full stocking of lodgepole pine within 7 years.

The objective of the research project changed in 2003 due to the mountain pine beetle epidemic, which would kill, on average, 61% of the mature, large diameter trees on the study area over the next 5 years. Mountain pine beetle is the most significant forest insect affecting lodgepole pine forests in western North America (Shore et al. 2006), and the 2003–2008 epidemic was unprecedented over the past approximately 100 years of reliable observations (Kaufmann et al. 2008). The objective of our study is to determine the impact of the pine beetle disturbance on the natural regeneration process, particularly whether the disturbance would result in increased recruitment in the forested control units and the forested matrix of the partial cutting treatments. The study was expanded in 2008 to measure the growth of naturally regenerated seedlings in response to the high levels of mortality and improved growing conditions (increased light availability and reduced below-ground competition). At that time, most of the dead canopy trees retained either red or grey needles.

The results presented in this report are from three assessments that have been completed since the start of the mountain pine beetle outbreak, and are provided in context with the results from the earlier natural regeneration study (Steen et al. 2007). The results provide insight into how successfully the study sites and surrounding forests, which have sustained variable levels of mortality, regenerate naturally. Due to the magnitude of the infestation, it is likely that significant areas of the west Chilcotin will never be salvaged harvested; this study will further our understanding of how these stands regenerate and recover.

METHODS

Study Area

The study is located in the winter range of the Itcha-Ilgachuz caribou herd, about 110 km northwest of Alexis Creek, B.C. (52°28' N, 124°43' E). Five replicated study blocks are located in the SBPSxc and MSxv subzones on the gently rolling, high-elevation Chilcotin plateau (Steen and Coupé 1997). Three blocks are located in the SBPSxc at elevations ranging from approximately 1250 to 1410 m. The two blocks in the MSxv are at elevations between 1500 and 1560 m. The study area is described in detail in Waterhouse et al. (2010). Sagar et al. (2005) and Sagar and Waterhouse (2015) describe the microclimate (air and soil temperature, precipitation, and soil moisture) across subzones and treatments.

Lodgepole pine forests dominate the study area, with main canopy tree heights ranging from 17 m in the SBPSxc to 20 m in the MSxv. These forests were initiated after stand-destroying wildfires that burned 160–220 years ago, based on tree-aging of the dominant canopy. In the SBPSxc, the lodgepole pine stands are relatively open due to dry site conditions and periodic, but low-intensity, pine beetle-related mortality. In contrast, stands in the MSxv are denser and have been less affected by past mountain pine beetle activity. The density of trees with diameter at 1.3 m (dbh) greater than 12.5 cm ranged from about 800 stems per hectare (sph) in the SBPSxc to 1400 sph in the MSxv. Pine seedlings and saplings are common in the understorey of the SBPSxc stands, while in the MSxv, there is little natural pine regeneration in the understorey (Steen et al. 2007). Natural regeneration on the study area is almost exclusively lodgepole pine, but interior spruce (*Picea glauca* x *engelmannii*) and whitebark pine (*Pinus albicaulis*) regeneration also occurs at very low densities.

Understorey vegetation in the SBPSxc is low growing and dominated by kinnikinnick (*Arctostaphylos uva-ursi*), pinegrass (*Calamagrostis rubescens*), and a rich diversity of terrestrial lichens, especially species of *Cladonia* and *Cladina*. In comparison, understorey vegetation in the MSxv is characterized by fewer lichens and a higher moss component, primarily red-stemmed feathermoss (*Pleurozium schreberi*). Kinnikinnick is rare, being replaced largely by crowberry (*Empetrum nigrum*) and grouseberry (*Vaccinium scoparium*). In all blocks, herbs such as northwestern sedge (*Carex concinnoides*) and bunchberry (*Cornus canadensis*) occur in low abundance. Soopalallie (*Sheperdia canadensis*) grows in small patches throughout the study area, while common juniper (*Juniperus communis*) is the most abundant shrub in the SBPSxc.

Study Design and Partial Cutting Treatments

The natural regeneration study was established as a completely randomized split-plot design, where biogeoclimatic subzone was the main-plot factor. Five experimental blocks, ranging in size from 60 to 113 ha, were selected from a number of blocks laid out for operational harvesting. Each block was divided into four experimental units of approximately equal size, and three partial cutting treatments and a forested control were randomly assigned to the units (split-plot factor). The partial cutting treatments were combinations of two silvicultural systems—irregular group shelterwood and group selection—and two harvesting methods—stem-only harvesting (trees were limbed and topped at the stump) and whole-tree harvesting (trees were limbed and topped at the roadside). Trees in the partial cutting treatments were harvested in the winter of 1996, so there was virtually no ground disturbance.

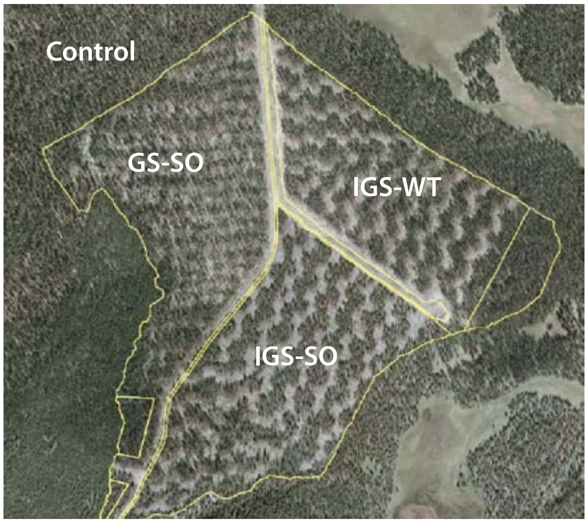

FIGURE 1 *Aerial view of a study block showing the two irregular group shelterwood treatments (IGS-WT and IGS-SO), the group selection treatment (GS-SO), and the forested control.*

The irregular group shelterwood system was tested with stem-only harvesting (IGS-SO) and whole-tree harvesting (IGS-WT). The goal of this silvicultural system is to cut 50% of the area every 70 years. It is considered irregular because the regeneration period has been extended for several decades (Raymond et al. 2009) in this study to maintain stand structure necessary to protect forage lichens. As shown in Figure 1, the irregular group shelterwood treatments created openings that were up to twice the average tree height (approximately 30 m diameter or 0.07 ha), with 39% of the total area being harvested.

The group selection system was tested with stem-only harvesting (GS-SO). Group selection openings were about one tree height, or approximately 15 m, in diameter (0.02 ha). The system was designed to cut 33% of the area on an 80-year cutting cycle, but approximately 28% of the total area was harvested in the first entry.

More details on the silvicultural systems and harvesting methods are provided in Armleder et al. (1996) and Steen et al. (2007).

Natural Regeneration Assessments

Before harvest (1995), 2-m^2 fixed radius permanent plots were established on a 50 × 50 m grid in each treatment unit to monitor the density of lodgepole pine and interior spruce natural regeneration (Figure 2). In total, 900 plots were established across the 20 treatment units (5 blocks × 4 treatments), and pre-harvest density data were collected in all plots. In the annual post-harvest assessments in 1997–2002, density data were collected in plots in the forested control units and in plots that were located wholly in the openings created by the partial cutting treatments (Steen et al. 2007). In these assessments, natural regeneration was counted and classified according to age and height: germinants (<1 year from the current growing season), small (≥1 year to <10 cm tall), and medium (≥10 cm to <1.3 m tall). The distribution of natural regeneration, or stocking, was assessed by tallying the number of plots that were stocked with at least one post-harvest pine seedling that was at least 1 year old (Steen et al. 2007).

Further assessments of natural regeneration density and stocking were completed at the beginning and end of the pine beetle infestation (2004 and 2008, respectively) and 5 years after (2013) using the protocol described in Steen et al. (2007). In the first two assessments, all 900 permanent plots were assessed, including those in the forested matrix of the partial cutting treatment units. Of the original 900 plots, 229 were in the forested control, 451 were in the forested matrix of the partial cutting treatments, and 220 were within the openings created by the partial cutting. In order to capture the taller advance regeneration counted in previous assessments, an additional height class was added in 2008: large (≥1.3 m tall).

FIGURE 2 *A 2-m^2 fixed radius permanent sample plot and the metal hoop used to define the plot for assessing natural regeneration density.*

In 2001, three clearcuts located adjacent to two trial blocks in the SBPSxc and one trial block in the MSxv were added to the study for comparative purposes only. The clearcut blocks were not considered part of the trial design because they were not harvested at the same time as the five trial blocks. Clearcut harvesting was conducted within 18 months so the cutblocks provided a reasonable opportunity to compare natural regeneration patterns after partial disturbance with that following clearcutting. Forty 2-m^2 fixed radius permanent sample plots were established in each clearcut, using the same methodology as in the replicated study. Natural regeneration density data were collected from the clearcut plots in 2005, 2008, and 2014; the first and last assessments were completed one year later than in the replicated trial.

The assessment protocol was further expanded in 2008 to measure the growth of natural regeneration on the trial blocks in response to high levels of overstorey mortality due to the mountain pine beetle. For comparative purposes, the expanded protocol also included an assessment of growth of naturally regenerated pine seedlings in the clearcuts. For this, a 3.99-m radius (50 m^2) plot was established at each density plot centre so that it was completely within the same location as the original 2-m^2 plot; e.g., either in the forested matrix or in harvested openings. In each plot, the two most vigourous pine trees between 30 and 130 cm tall were permanently tagged and measured for total height and ground-level diameter. Seedling height in 2007 and 2006 was estimated by measuring height to the top two whorls of branches. Seedling condition (good, fair, or poor) was evaluated along with leader, stem, and foliage damage.

In 2013, only the density plots and tagged seedlings in the forested control and IGS-SO treatment units of each block were measured. Density and seedling growth assessments were reduced due to limited resources, but the sample size was still sufficient to validate the 2008 results. Tagged seedlings in the clearcuts were further assessed for size, condition, and growth in 2014.

Overstorey mortality directly affects canopy density and light transmittance, which results in increased light availability for regeneration and surviving secondary structure (Amoroso et al. 2013). To quantify the changes in these two variables following the beetle disturbance, hemispherical photographs were taken at the permanent sample plots in the forested control, and in the forested matrix and harvested openings in the IGS-SO treatment in the summer of 2007 and 2013. Analysis of the photography provided estimates of total light availability (MJ/m^2/day) toward the end of the disturbance and 6 years later after significant needle loss and a minor amount of blowdown had occurred.

Statistical Analyses

All data summaries and analyses were performed with SAS (SAS Institute Inc. 2002–2010). Normal analysis of variance (ANOVA) models were fitted with PROC MIXED, and non-normal (negative-binomial and binomial) models were fitted with PROC GLIMMIX. Results were considered significant at $\alpha=0.05$ (Nemec 2014).

Seedling density For regeneration density, the number of stems in the l-th (2 m^2) plot in block k, treatment j (Control, IGS-SO, IGS-WT, GS-SO) and subzone i (MSxv or SBPSxc) was assumed to have a negative binomial distribution with (conditional) mean μ_{ijk} and variance σ_{ijk}^2 given by:

$$\log(\mu_{ijk}) = \alpha_0 + \alpha_i + \tau_j + \alpha\tau_{ik} + \delta_{k\,(i)} + \varepsilon_{jk\,(i)}$$

$$\sigma_{ijk}^2 = \mu_{ijk} + \lambda\mu_{ijk}^2$$

where α_0 is a constant (intercept), α_i is the fixed effect of Subzone i, τ_j is the fixed effect of treatment j, $\alpha\tau_{ik}$ is the fixed interactive effect of treatment and subzone, $\delta_{k\,(i)}$ and $\varepsilon_{jk\,(i)}$ are random effects (nested in subzone) of block and treatment × block interaction, and λ is a constant scale parameter. All (plot) counts and random effects were assumed to be independent, and all random effects were assumed to be normally distributed with mean 0 and homogeneous variances (i.e., variances were assumed to be constant across blocks, treatments, and subzones). Model parameters were estimated by residual pseudo-likelihood estimation, and (Type 3) F tests, with denominator degrees of freedom calculated by Satterthwaite's approximation, were performed to assess the statistical significance of the fixed effects. Least-squares (log) means ($\delta_{k\,(i)} = 0$ and $\varepsilon_{jk\,(i)} = 0$) and (log) mean differences were calculated for all combinations of subzone and treatment. The associated p values were adjusted by Scheffé's method to allow for multiple (unplanned) comparisons. Separate analyses were performed for 2004, 2008, and 2013 for various subsets defined by seedling category and plot location (opening or forested).

Seedling growth For the analyses of seedling height, diameter, and growth, an ANOVA was used to assess subzone, treatment, and location (opening or forested) effects. The following model was fitted:

$$y_{ijklm} = \mu + \alpha_i + \beta_{j(i)} + \tau_k + \alpha\tau_{ik} + \tau\beta_{jk(i)} + \varepsilon_{l(ijk)} + \delta_{m(ijkl)}$$

where y_{ijklm} is the diameter or height response of interest for the m-th tree in the l-th plot in the k-th treatment unit of the j-th block in Subzone i, μ is the overall mean, α_i ($i = 1,2$) is the fixed effect of subzone (MSxv or SBPSxc), τ_k ($k = 1,2,3,4$) is a fixed treatment (Control, IGS-SO, IGS-WT, GS-SO) effect, and $\beta_{j(i)}$, $\tau\beta_{jk(i)}$, $\varepsilon_{l(ijk)}$, and $\delta_{m(ijkl)}$ are respectively the random effects of block, treatment × block (treatment unit), plot within treatment unit, and tree within plot. The random effects were assumed to be independent and normally distributed with mean 0 and homogeneous variances. Scheffé's method was used to compare subzone and treatments combinations. Analyses were conducted for all plots combined and were repeated for the subsample comprising plots in control units and the forested matrix, and the subsample comprising plots in control units and harvested openings.

RESULTS

Overstorey Mortality

Across all study blocks, lodgepole pine canopy mortality caused by the mountain pine beetle increased steadily from 3% in 2003 to 61% in 2008 and then remained at this level until 2013. In 2008, the forested control units and group selection (GS-SO) treatment units had slightly higher levels of mortality (68% and 61%, respectively) than the irregular group shelterwood (IGS-SO and IGS-WT) treatments (approximately 58% for both treatments), although these differences were likely not statistically significant.

Post-disturbance Regeneration Density and Stocking

Natural regeneration on the study area was almost exclusively lodgepole pine, so it is the only species reported. Interior spruce advance regeneration occurred at very low densities pre-harvest, and there was no evidence of spruce recruitment as a result of the mountain pine beetle infestation.

Over the duration of the mountain pine beetle outbreak (2003–2008), natural regeneration densities increased in both subzones, when all treatments and locations were combined (Figure 3). Over the three assessment years, density of the various seedling categories fluctuated depending on seedling growth and mortality. Mean total density was higher in the SBPSxc than in the MSxv over all treatments, but the differences were generally not significant (Table 1). Germinants were recorded at low to very low densities in both subzones in all assessment years, depending on treatment and location (Figure 4).

The ANOVA of the 2004 data, comparing seedling density among subzones and treatments—forested control and the openings of the three partial cutting treatments—showed that the mean density of germinants and small seedlings was significantly higher in the SBPSxc than in the MSxv (Table 1, Figure 3), which suggests that there were higher rates of ingress in the SBPSxc following harvesting. A significant treatment effect was also found where germinants and small seedlings occurred at higher densities in the IGS-WT openings than in the forested control (Figure 4). In 2008 and 2013, there were no significant differences in mean germinant and small seedling density between subzone or treatment.

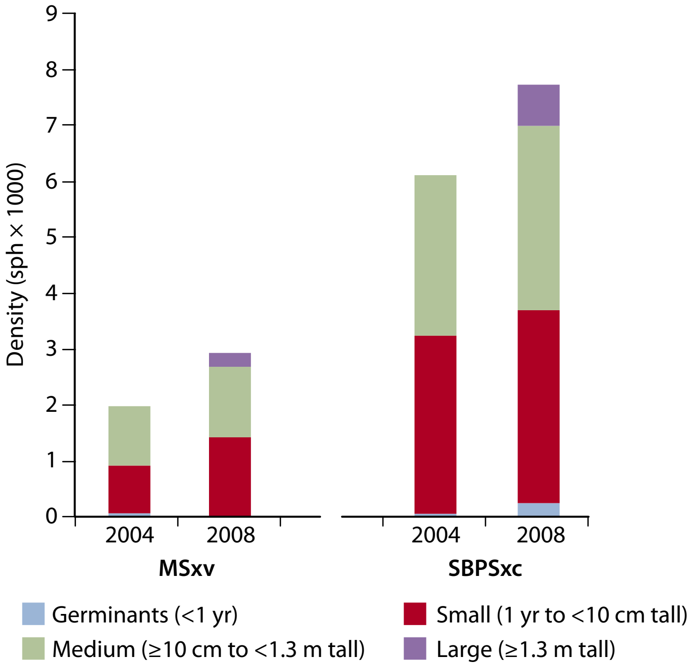

FIGURE 3 *Density (stems per hectare [sph]) of pine natural regeneration in the MSxv and SBPSxc by seedling category and assessment year; all treatments and locations (forested matrix and harvested openings) combined.*

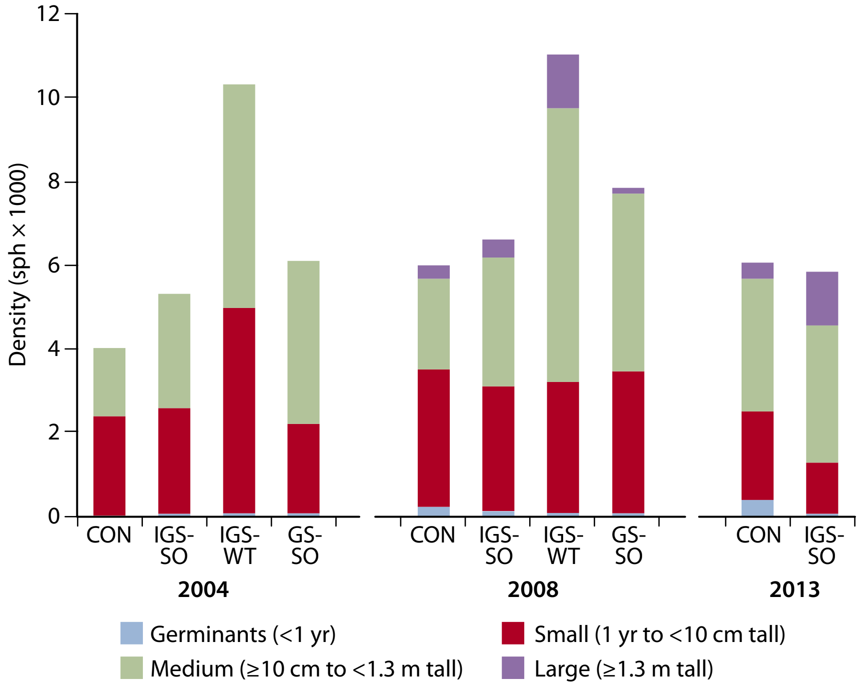

FIGURE 4 *Density (stems per hectare [sph]) of pine natural regeneration in the forested control and harvested openings of the partial cutting treatments by seedling category and assessment year, both subzones combined. In 2013, density was assessed only in the forested control and openings of the IGS-SO treatment.*

TABLE 1 *Seedling density in 2004, 2008, and 20013 as affected by subzone (S), treatment (T), and location (forested control and harvested openings; forested control and forested matrix). Probability estimates in underlined, bold text are significant at a=0.05.*

		2004		2008		2013	
Seedling size category	**Effect**	**Control and openings Prob≥*F***	**Control and forest Prob≥*F***	**Control and openings Prob≥*F***	**Control and forest Prob≥*F***	**Control and openings Prob≥*F***	**Control and forest Prob≥*F***
Germinants (<1 yr)	Subzone (S)	**0.02**	0.16	0.06	0.15	0.15	0.16
	Treatment (T)	**<0.01**	0.44	0.54	0.62	0.50	0.81
	S×T interaction	0.21	**<0.01**	0.15	**<0.01**	0.31	**0.04**
Small (1 yr <10 cm)	Subzone (S)	**0.03**	0.15	0.06	0.17	0.14	0.12
	Treatment (T)	**<0.01**	0.68	0.53	0.73	0.79	0.35
	S×T interaction	0.26	**<0.01**	0.16	**<0.01**	0.24	**0.02**
Medium (10 cm-<1.3 m)	Subzone (S)	0.12	0.31	0.09	0.30	0.41	0.14
	Treatment (T)	**0.04**	0.99	**0.02**	0.61	0.06	0.81
	S×T interaction	0.20	0.26	0.16	0.42	**0.02**	0.88
Large (≥1.3 m)	Subzone (S)			0.08	0.28	0.41	0.13
	Treatment (T)	Not assessed		**0.02**	0.39	**0.03**	0.52
	S×T interaction			0.08	0.26	0.12	0.29
All seedlings	Subzone (S)	0.07	0.22	0.08	0.22	0.25	0.13
	Treatment (T)	**<0.01**	0.57	0.07	0.48	0.13	0.85
	S×T interaction	0.18	**0.04**	0.23	0.14	**0.05**	0.76

Also in 2004, the density of medium seedlings was significantly higher in the IGS-WT openings than in the forested control, an effect that persisted into 2008. When the density of all seedlings was compared in the ANOVA, there was a significant treatment effect in 2004 only, with total seedling density significantly higher in the IGS-WT openings than in the forested control (Figure 4). Large seedlings were not assessed in 2004, but in 2008, densities were significantly higher in IGS-WT openings than in the control. This trend of higher seedling densities in the IGS-WT openings is consistent with the findings of Steen et al. (2007), although their results were not significant. They concluded that densities were higher in this treatment due to higher cone densities on the ground and lower logging slash levels following whole-tree harvesting compared with stem-only harvesting.

In 2013, only the IGS-SO treatment units were assessed; the density of large seedlings in the harvested openings was significantly higher than in the forested control. A significant subzone × treatment (S×T) interaction for the density of medium seedlings and all seedlings combined was noted in 2013 (Table 1). Multiple comparisons using Scheffé's method did not show any significant differences in this data, but in the MSxv, seedling density was higher in the harvested openings than in the forested control, while the opposite trend was evident in the SBPSxc (Table 2).

TABLE 2 *Mean (SE) density and percent stocking of established seedlings (≥1 year old) by subzone, location, and year, all partial cutting treatments included, except where shown. The 1995 data were collected pre-harvest (unpublished data); the 2002 data were reported in Steen et al. (2007). Clearcut densities, measured in 2005, 2008, and 2014, are shown to provide a comparison of natural regeneration after conventional harvesting (MPB = mountain pine beetle).*

			Pre-MPB		**MPB outbreak**		**Post-MPB**
Subzone	**Location**	**Parameter**	**1995**	**2002**	**2004**	**2008**	**2013**
MSxv	All openings	Density (sph)	1067 (427)	2563 (526)	2333 (531)	3133 (683)	
		Stocking	11%	33%	31%	40%	
	IGS-SO openings	Density (sph)			2037 (770)	3519 (1382)	3704 (1547)
		Stocking			35%	45%	45%
	All forest matrix	Density (sph)	1202 (368)	Not assessed	2008 (589)	3182 (706)	
		Stocking	13%	Not assessed	17%	26%	
	IGS-SO forest matrix	Density (sph)			1579 (845)	3289 (1690)	2237 (956)
		Stocking			16%	21%	24%
	Control	Density (sph)	1358 (421)	Not assessed	1419 (514)	2284 (658)	1975 (581)
		Stocking	16%	Not assessed	14%	23%	19%
	Clearcut	Density	Not assessed	Not assessed	25,750 (7047)	22,550 (6131)	24,125(6230)
		Stocking	Not assessed	Not assessed	72%	75%	75%
SBPSxc	All openings	Density (sph)	5522 (834)	10,433 (1476)	9409 (1440)	11,299 (1508)	
		Stocking	50%	67%	55%	64%	
	IGS-SO openings	Density (sph)			7000 (1784)	8100 (1816)	6900 (1362)
		Stocking			54%	56%	58%
	Forest matrix	Density (sph)	4459 (424)	Not assessed	5000 (554)	5820 (521)	
		Stocking	42%	Not assessed	40%	48%	
	IGS-SO forest matrix	Density (sph)			5877 (1010)	6443 (946)	6495 (994)
		Stocking			46%	54%	49%
	Control	Density (sph)	4087 (336)	Not assessed	5439 (776)	7669 (1080)	7669 (1073)
		Stocking	36%	Not assessed	39%	49%	49%
	Clearcut	Density (sph)	Not assessed	Not assessed	16,125 (4296)	15,675 (3918)	16,563 (3853)
		Stocking	Not assessed	Not assessed	52%	51%	58%

In the ANOVA, the comparison of seedling density in the forested control with that in the forested matrix of the partial cutting treatments showed no significant subzone or treatment effects, but there were a number of significant subzone × treatment interactions (Table 1). In all assessment years, there was a significant subzone × treatment interaction for the density of germinants and small seedlings; in the MSxv, they were more abundant in the forested matrix than in the control, while in the SBPSxc, they were more abundant in the control than in the forested matrix. A similar significant subzone × treatment interaction was noted for the density of all seedlings combined, but only in the 2004 data.

Advance Regeneration and Ingress in Harvested Openings

The density of advance regeneration in the SBPSxc partial cutting openings was substantial: approximately 5522 sph pre-harvest (Table 2). The distribution of the advance regeneration, at 50% stocking, indicated that the openings were well stocked before harvest. Seven years after harvest (2002), total density in the openings had almost doubled (10 433 sph) as a result of ingress, and stocking rates had trended upwards to 67%. At the beginning of the mountain pine beetle outbreak 2 years later (2004), both total density and stocking had declined, indicating that seedling recruitment was not replacing seedling mortality. Between 2004 and 2008, density and stocking showed a moderate increase in all openings combined and in the IGS-SO openings due to the pulse of ingress resulting from the mountain pine beetle disturbance (Table 2). By 2013, density had declined in the IGS-SO openings while stocking rates increased slightly (Table 2). In the SBPSxc, natural regeneration appears to ingress at high densities following disturbance, but it is also subject to high rates of mortality.

In contrast, advance regeneration density in the harvested openings in the MSxv was 1067 sph pre-harvest, which was considerably lower than that in the SBPSxc (Table 2). Differences in densities between the subzones pre-harvest were not statistically significant due to high variability in the data. With ingress, total density in the MSxv more than doubled 7 years after harvest, and stocking rates increased three-fold. Density and stocking dropped slightly between 2002 and 2004, followed by an increase over the period of the mountain pine beetle outbreak. Unlike the trend in the SBPSxc, seedling density in the IGS-SO openings continued to increase while stocking remained stable in the 5 years following the outbreak.

Density and Stocking Following Mountain Pine Beetle Disturbance in Forested Locations

Many lodgepole pine stands in the vicinity of the study are not likely to be salvaged after the mountain pine beetle outbreak. Monitoring the density and stocking of natural regeneration in the forested control and forested matrix of the partial cutting treatments will increase our knowledge of how unsalvaged stands regenerate following disturbance. In the SBPSxc blocks, density and stocking in the forested matrix of the partial cutting treatments was relatively stable from pre-harvest to the beginning of the outbreak (Table 2). In the control, there was a slight increase in these two variables over the same period. Over the course of the outbreak, there was a substantial increase in mean density and stocking in the forested matrix and in the forested control units. In both forested locations, stocking increased by approximately 10%, and reached almost 50%. Five years after the outbreak, density and stocking remained stable in the control. In the forested matrix of the IGS-SO treatment, density was constant between 2008 and 2013 while stocking declined. At that time, seedling density in the harvested openings and forested locations was comparable, but stocking rates were approximately 10% higher in the openings, which indicated that natural regeneration under forested conditions was not as uniformly distributed as regeneration in the openings.

In the MSxv blocks, in the 9 years following harvest, density and stocking increased slightly in the forested matrix of the partial cutting treatments but remained relatively stable in the forested control (Table 2). Over the outbreak, density and stocking increased substantially in the both the forested matrix and control units, with stocking increasing by approximately 10%. In the 5 years following the outbreak, density and stocking declined in the forested control. In the forested matrix of the IGS-SO treatment, density declined after the outbreak while stocking rates increased (Table 2).

Density and Stocking in Clearcuts

Mean density and stocking in the MSxv clearcut was substantially higher than that in the SBPSxc clearcuts (Table 2). In both subzones, mean seedling density declined in the clearcuts between 2005 and 2008, but then increased in 2014 (18–20 years after harvest). Stocking in the MSxv clearcut remained stable from 2005 to 2014, while stocking in the SBPSxc clearcut increased notably in 2014. At that time, 2013 stocking in the SBPSxc IGS-SO openings was comparable with 2014 stocking in the clearcuts, even though densities were vastly different (Table 2).

Seedling Growth

Two ANOVA models were used to compare seedling diameter, height, and diameter and height growth between subzones and harvesting treatments in 2008 and 2013. The forested control was compared with the openings in the partial cutting treatments, and then the forested control was compared with the forested matrix of the partial cutting treatments (Table 3).

The ANOVA of the 2008 mean height data showed no subzone or treatment effects in either model. However, the ANOVA of height growth from 2006 to 2008 showed a significant subzone effect and a significant treatment effect among the forested control and harvested openings (Table 3). Mean height growth in the MSxv (19 cm) was significantly higher than that in the SBPSxc (16 cm), even though seedlings in the forested control showed comparable height growth between the two subzones (Figure 5). Mean height growth of seedlings in the forested control (9 cm) was significantly lower than that in the openings of all partial harvesting treatments (20 cm). For comparison, open grown seedlings in the adjacent clearcuts grew an average of 34 cm and 27 cm in the MSxv and SBPSxc, respectively, over the same 2-year period. When comparing seedling height growth in the forested con-

TABLE 3 *Pine regeneration size and growth in 2008 as affected by subzone, partial cutting treatment, and location (forested matrix or openings). Results in underlined, bold text are significant at a=0.05.*

	2008 Height		2006–2008 Height growth		2008 Diameter	
Effect	**Control and openings Prob≥*F***	**Control and forest Prob≥*F***	**Control and openings Prob≥*F***	**Control and forest Prob≥*F***	**Control and openings Prob≥*F***	**Control and forest Prob≥*F***
Subzone (S)	0.75	0.87	**0.04**	0.06	0.08	0.22
Treatment (T)	0.28	0.93	**<0.01**	**0.05**	**0.01**	0.59
S×T interaction	0.16	0.35	0.39	**0.02**	0.32	0.63

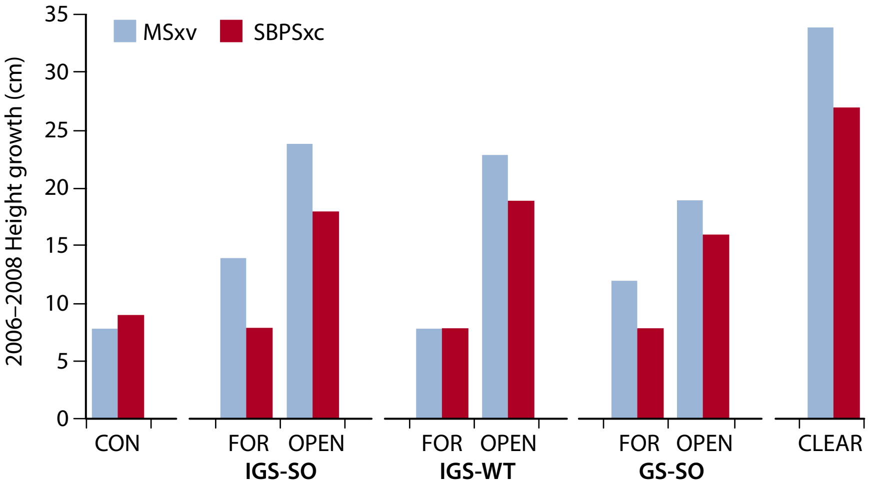

FIGURE 5 *Mean height growth (2006–2008) of seedlings growing in the control (CON), forested matrix (FOR), and harvested openings (OPEN) in each partial cutting treatment (IGO-SO = irregular group shelterwood stem-only harvesting; IGS-WT = irregular group shelterwood whole-tree harvesting; GS-SO = group selection stem-only harvesting). Mean height growth in the clearcuts (CLEAR) is shown for comparison.*

trol to that in the forested matrix of the partial cutting treatments, there was a significant subzone × treatment interaction. Seedlings generally grew better in the forested matrix of the MSxv partial cutting treatments than in the control, while in the SBPSxc, seedlings in the control grew better than those in the forested matrix (Figure 5).

The 2008 ANOVA also showed a significant treatment effect for mean diameter among the forested control and openings of the partial cutting treatments (Table 3). Planned comparisons using Scheffé's method showed that mean diameter in the control (1.4 cm) was significantly smaller than mean diameter in only the IGS-SO openings (1.8 cm). Mean diameter of seedlings growing in the clearcuts in both subzones was 2.2 cm.

The ANOVA comparing the 2013 seedling size and growth data among the forested control and harvested openings showed significant treatment effects ($p<0.01$) for all variables (Table 4). Seedlings were significantly larger in the harvested openings of the IGS-SO treatment than in the forested control: mean seedling height was 143 cm in the openings compared with 97 cm in

TABLE 4 *Pine regeneration size and growth in 2013 as affected by subzone, partial cutting treatment (control and IGS-SO only) and location (forested matrix or openings). Results in underlined, bold text are significant at a=0.05.*

	2013 Height		2011–2013 Height growth		2006–2013 Height growth		2013 Diameter		2008–2013 Diameter growth	
Effect	**Control and opening Prob≥*F***	**Control and forest Prob≥*F***	**Control and opening Prob≥*F***	**Control and forest Prob≥*F***	**Control and opening Prob≥*F***	**Control and forest Prob≥*F***	**Control and opening Prob≥*F***	**Control and forest Prob≥*F***	**Control and opening Prob≥*F***	**Control and forest Prob≥*F***
Subzone (S)	0.20	**0.03**	0.23	**0.01**	0.11	**<0.01**	**0.05**	**0.01**	0.11	**0.02**
Treatment (T)	**<0.01**	0.30	**<0.01**	0.14	**<0.01**	**0.04**	**<0.01**	0.22	**<0.01**	0.25
S×T interaction	0.56	0.35	0.07	0.06	**<0.01**	**<0.01**	0.73	0.25	0.18	0.16

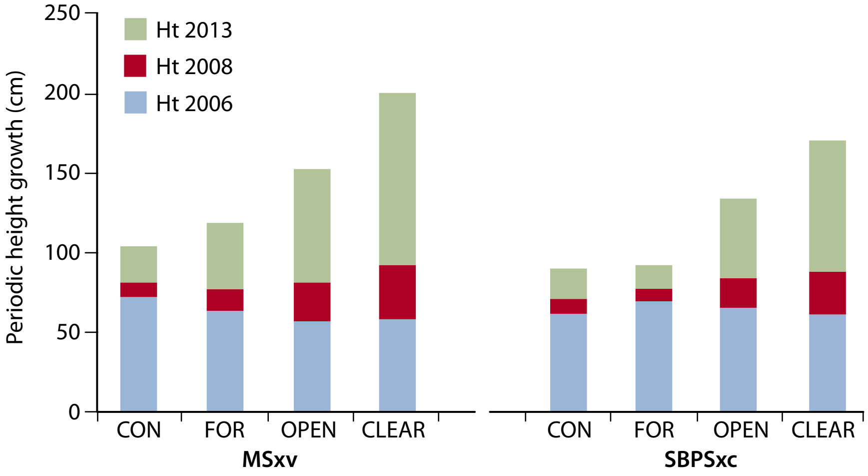

FIGURE 6 *Periodic seedling height growth in the control (CON), forested matrix (FOR), and harvested openings (OPEN) of the irregular group shelterwood stem-only (IGS-SO) treatment. Mean periodic height growth in the clearcuts (CLEAR) is shown for comparison.*

the control (Figure 6). In the clearcuts, mean seedling height in 2013 was 186 cm, approximately double the height of the seedlings in the control (Figure 6). There was a significant subzone × treatment interaction for the longer height growth period (2006–2013) (Table 4), but height growth was still greater in the harvested openings than in the control in both subzones. Only the 2013 diameter showed a significant subzone effect (Table 4): mean diameter in the MSxv (2.7 cm) was significantly larger than that in the SBPSxc (2.3 cm).

The ANOVA of the 2013 seedling size and growth data from the forested control and forested matrix of the IGS-SO treatment showed a significant subzone effect for total height, 2011–2013 height growth, total diameter, and 2008–2013 diameter growth (Table 4). Seedlings in the MSxv were significantly larger and showed significantly better growth than those in the SBPSxc. For example, in the forested locations (control and forested matrix), mean seedling height was 111 cm in the MSxv compared with 90 cm in the SBPSxc. When the 2006–2013 height growth data were compared in the ANOVA, there was a significant subzone × treatment interaction (Table 4). In the MSxv, 7-year seedling height growth was significantly greater in the forested matrix than in the control; in the SBPSxc, the trend was opposite and the differences were not significant (Figure 6). This same trend was seen in the 2006–2008 height growth.

Seedling Condition and Damage

The assessment of seedling condition is subjective, but seedlings rated as good or fair are considered to have the potential to develop into crop trees. In 2008, there were fewer seedlings in good condition in the forested control and forested matrix than in the openings of the three partial cutting treatments (Figure 7). In fact, there were no seedlings in good condition on two forested control units. Overall, 43–64% of seedlings in the forested locations had crop tree potential compared with 85–93% in the openings. Seedlings in the smaller openings in the group selection (GS-SO) treatments were in

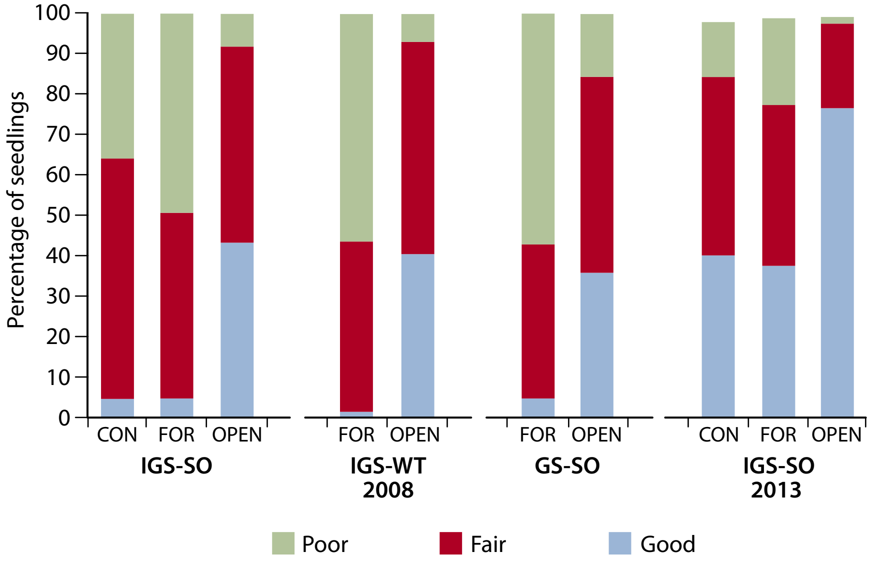

FIGURE 7 *Percentage of sample seedlings reported as being in good, fair, or poor condition in the control (CON), forested matrix (FOR), and harvested areas (OPEN) of the partial cutting treatments in 2008 and 2013, both subzones combined (IGO-SO = irregular group shelterwood stem-only harvesting; IGS-WT = irregular group shelterwood whole-tree harvesting; GS-SO = group selection stem-only harvesting). In 2013, 1–2% of the sample seedlings were dead.*

slightly poorer condition than those in the openings of the two irregular group shelterwood (IGS-WT and IGS-SO) treatments.

Seedlings were in better condition in 2013 than in 2008 in all locations, especially in the forested control and in the forested matrix of the IGS-SO treatment. In the openings of the IGS-SO treatment, the percentage of seedlings with crop tree potential increased slightly from the 2008 assessment, but the percentage in good condition increased from 43 to 76% (Figure 7). In both 2008 and 2013, seedlings growing under forested conditions were in better condition in the MSxv than in the SBPSxc.

In 2008, seedling damage was relatively consistent across all partial cutting treatments. Approximately 15% of seedlings in both subzones had leader damage. Seedlings with foliage damage, primarily sparse foliage, were more common in the SBPSxc (19%) than in the MSxv (6%), and there was a higher incidence in the forested control and forested matrix (19% and 23%, respectively) than in the openings (2%). The incidence of stem damage, primarily bent or forked stems, was 33% in the SBPSxc compared with 26% in the MSxv, and stem damage was more prevalent in forested locations than in harvested openings.

By 2013, the incidence of leader and foliage damage had declined from 2008 levels. In the MSxv, less than 8% of seedlings had foliage or leader damage, regardless of location (forest or openings). In the SBPSxc, approximately 20% of seedlings in forested locations had leader and foliage damage compared with 5% in the openings. Stem damage rates were comparable to those in 2008. Approximately 31% and 28% of all seedlings in the MSxv and SBPSxc, respectively, had stem damage, and the incidence was lower in the openings than in the forested locations.

Light Availability

Total light measured in the forested control, and forested matrix and harvested opening of the IGS-SO treatment increased in all locations between 2007 and 2013 (Figure 8). Levels of total light were higher in the SBPSxc than in the MSxv. The increase in light levels over the 6 years was greatest in the forested control, followed by the forested matrix, and then the harvested openings.

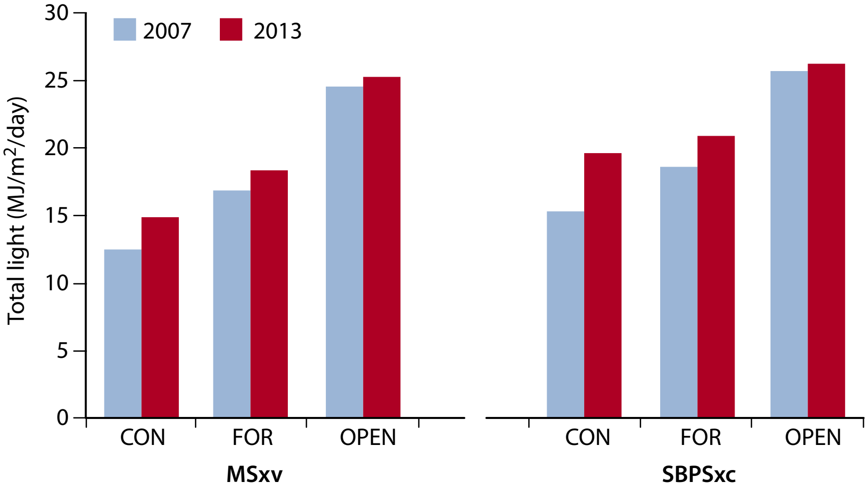

FIGURE 8 *Total light measured at the seedling assessment plots in the control (CON), forested matrix (FOR), and harvested openings (OPEN) of the irregular group shelterwood stem-only (IGS-SO) harvesting treatment.*

DISCUSSION

The Itcha-Ilgachuz Research Project has been monitored over 20 years, including the mountain pine beetle outbreak (2003–2008), which has enabled the study of long-term impacts of tree mortality on such ecological parameters as lichen and vegetation abundance, natural regeneration, microclimate, and tree fall. While we have a good understanding of the development of lodgepole pine forests after clearcut harvesting or wildfire, we know little about how these forests respond to disturbances that remove or kill only a portion of the overstorey (Collins et al. 2011).

Natural regeneration was assessed in two ways in this study. Density provided an estimate of the total number of stems per hectare, while percent stocking provided an estimate of the distribution of seedlings. A lower percent stocking indicates that the distribution of seedlings is less uniform even though densities may appear reasonable. If seedlings were planted on a 2 × 2 m grid over the treatment units, this would yield approximately 2500 sph and 50% stocking. That is, 50% of the 2-m² plots established on a 50 × 50 m grid would contain a planted seedling (Steen et al. 2007).

In both subzones, the density and stocking of natural regeneration increased over the duration of the mountain pine beetle infestation. Seedling ingress occurred during the outbreak and continued in the following 5 years, which indicates that lodgepole pine recruitment can occur for many years following a disturbance, whether it is partial harvesting or mountain pine beetle infestation. Lodgepole pine cones in the study area are predominantly serotinous, but Steen et al. (2007) reported light but consistent annual seedfall over a 5-year period from 1996 to 2001. Seedfall was not monitored in the study area during the mountain pine beetle outbreak, but Teste et al. (2011a) found that seed release from the canopy after mountain pine beetle infestation can be due to a partial loss of cone serotiny after the trees die. Increased cone weathering or heating due to greater exposure to direct sunlight may break down some of the resin bonds that normally keep cone scales closed. Seed release can also occur from a forest floor seed bank (Teste et al. 2011b), which develops from branch breakage shortly after tree death, when branches become dry and brittle. The serotinous cones allow the development of a forest floor seed bank that could enable regeneration after an outbreak, especially as the stands continue to become more open. Teste et al. (2011a) estimated that 6 years after the mountain pine beetle outbreak in northern British Columbia, the number of seeds released reached 45% of the original canopy seedbank as a result of cone fall via branch breakage, increased cone opening due to weathering, and squirrel predation. These three factors could have contributed to the pulse of ingress in our study during and after the pine beetle disturbance. We found that natural regeneration under forested conditions tended to have a clumped distribution, which could indicate that the forest floor seed bank was an important seed source.

Lodgepole pine stands in the SBPSxc in the west Chilcotin have been subject to endemic levels of mountain pine beetle infestation in the past and a moderate outbreak in the early 1980s. This outbreak was part of the same outbreak reported by Axelson et al. (2010) in the IDFdk4 subzone, where multiple tree mortality events were followed by periods of growth release in the canopy and sub-canopy trees, which in turn was followed by establishment of advance regeneration. As a result, these stands were relatively open and supported significant densities of natural regeneration in the understorey.

In our study, advance regeneration was abundant in the partial cutting openings in the SBPSxc before harvest. Recruitment of new seedlings after harvest peaked in year five and remained relatively stable until year seven (Steen et al. 2007). Seedling density had begun to decline by 2004, but it is unknown whether this trend would have continued because the pine beetle disturbance created conditions that resulted in a flush of ingress. By the end of the pine beetle outbreak, mean density was slightly higher than recorded in the year five peak following harvesting. In the IGS-SO openings, mean density increased over the outbreak, but 5 years later density was comparable to that recorded in 2004. Fluctuating seedling densities in the SBPSxc indicate that the flush of regeneration following disturbance is soon subject to early mortality, possibly due to dry site conditions, which generally characterize this subzone and which appear to be exacerbated by partial cutting (Waterhouse et al. 2010). The root systems of first-year lodgepole pine seedlings develop slowly and are relatively weak (Lotan and Perry 1983); if they do not reach mineral soil before the forest floor dries, seedlings may not survive. Openings in the SBPSxc were stocked with advance regeneration at the time of harvest; these established seedlings will likely be the primary source of growing stock in the future.

In the SBPSxc, partial cutting had little impact on seedling density and stocking in the forested locations. The mountain pine beetle disturbance, however, resulted in a modest increase in seedling density in the forested control and the forested matrix, and a substantial increase in stocking to levels comparable to relatively high-density planting. These results indicate that unsalvaged stands in the SBPSxc show good potential to be stocked in the understorey after the mountain pine beetle disturbance and that advance regeneration will control future stand dynamics. That advance regeneration will be the primary source of growing stock after the pine beetle disturbance is consistent with the findings of Astrup et al. (2008) in other forests in the central interior of British Columbia.

In contrast to stands in the SBPSxc, stands in the MSxv experienced very little mountain pine beetle activity until the most recent outbreak. Stands are relatively dense, with lower light levels and cooler temperatures in the understorey. Sagar and Waterhouse (2015) found that snow-free dates were approximately two weeks later at the highest elevation site (MSxv) than at the lowest site (SBPSxc), which resulted in lowered soil temperatures and shortened growing seasons. Forest floors tend to be thicker in the MSxv and support a significant cover of feathermoss compared with SBPSxc sites. The density of advance regeneration in the harvested openings in the MSxv was considerably lower than that reported in the SBPSxc before harvest. Even though post-harvest ingress contributed substantially to the mean density in the harvested openings, density and stocking rates in year seven were such that Steen et al. (2007) concluded that the partial cutting treatments in the MSxv would need to be planted to ensure full stocking within the 7-year regeneration delay. At the start of the outbreak in 2004, stocking rates were unchanged, which indicated that a longer regeneration delay would not necessarily result in improved regeneration success, and further confirmed that planting would be necessary to restock small harvested openings in this subzone. The subsequent pine beetle disturbance resulted in a flush of ingress in the openings that substantially increased mean density and increased stocking to 45%, at which time the openings were adequately stocked.

In the MSxv, the density of advance regeneration in the forested control and forested matrix before harvest was similar to that in the harvested openings. By the end of the pine beetle disturbance, seedling density had more than doubled in the forested environments, which suggests that the new forest will develop from both advance regeneration and new recruits, although new recruits could be more important in this subzone. Nigh et al. (2008) found that some lodgepole pine stands in the Montane Spruce zone in southern British Columbia had adequate advance regeneration to form reasonably well-stocked new stands if most canopy trees died during the outbreak. Other stands had only small amounts of advance regeneration, which indicated that resulting stands would either be understocked or formed from new seedling establishment. In our study, stocking rates increased by approximately 10% over the outbreak period to approximately 25% which suggests that stocking will fall short of that required to consider the stands fully stocked with regeneration following the pine beetle disturbance. Depending on the fate of the surviving overstorey canopy as MSxv stands break up, silvicultural intervention may be required to ensure that unsalvaged stands are fully stocked.

Steen et al. (2007) suggested that the post-harvest density of pine seedlings was consistent with seedbed differences and air and soil temperature differences between the MSxv and SBPSxc, which indicated that thicker forest floor layers and lower temperatures in the MSxv may be impacting natural regeneration success. Astrup et al. (2008) found limited natural regeneration 10 years after the pine beetle attack in central British Columbia, which they attributed to the intact feathermoss-dominated seedbed. Seedbed composition may be a factor contributing to regeneration establishment in our study, since 30–35% of the MSxv understorey is composed of moss cover, predominantly red-stemmed feathermoss (Steen et al. 2007), as compared with the SBPSxc, which has only 1–4% moss cover.

It is clear that advance regeneration will play an important role in stand recovery following disturbance in the SBPSxc but will play a lesser role in the MSxv. Where advance regeneration exists, its growth following mountain pine beetle attack should increase in most stands in response to site resources (light, water, nutrients) becoming more available after canopy death and breakup (Griesbauer and Green 2006). The health and vigour of advance regeneration will directly influence its release potential. Seedlings in the MSxv were in better condition and had a lower incidence of damage than those in the SBPSxc, so they may be better able to respond to improved growing conditions post beetle. When size and growth of the most vigourous seedlings were compared between the two subzones, seedlings were significantly larger and showed significantly better height and diameter growth in the MSxv than in the SBPSxc. While forest floor composition and cooler temperatures may limit germination and seedling establishment in the MSxv, conditions in this subzone, compared with those in the SBPSxc, are more favourable for seedling growth. Planted lodgepole pine also grew significantly better in the MSxv than in the SBPSxc, in spite of the more open canopy and higher light levels in the harvested openings in the SBPSxc (Waterhouse et al. 2010). This difference was partly due to lower precipitation on the SBPSxc sites, which indicates that growth of planted pine was slow due to dry, cool soils in this subzone.

As expected, natural regeneration showed better growth and condition in the partial cutting openings than in forested conditions, in spite of the significant canopy mortality. This can be partly attributed to the increased availability of light in the openings. In the harvested openings in both subzones, annual height growth in 2013, compared with that in previous years, showed a marked improvement, which suggests that regeneration is starting to take advantage of increased site resources as the stands break up. A similar, but smaller, seedling growth response was also noted in seedlings growing under forested conditions.

CONCLUSION

The extent of overstorey lodgepole pine mortality from the pine beetle epidemic has caused concern regarding the future trajectory of beetle-killed forests (Rocca and Romme 2009). It is important to understand the dynamics and growth potential of understorey seedlings and saplings because they may become important components of pine beetle-attacked stands (Amoroso et al. 2013). While we have monitored only natural regeneration recruitment, distribution, and growth response in our study, our results support the following conclusions.

Natural regeneration in the SBPSxc was sufficient to restock small harvested openings and produce a stocked stand in the understorey of a mature stand that was severely impacted by mountain pine beetle disturbance. In this subzone, advance regeneration will play an important role in future stand development, more so than ingress resulting from disturbance. In the MSxv, natural regeneration was not abundant enough to stock harvested openings or mountain pine beetle-impacted stands. Post-disturbance ingress will be the predominant component of the understorey in this subzone. Forest regeneration after mountain pine beetle disturbances, even intense outbreaks such as the one in our study, is a slow process (Axelson et al. 2009), and differences in seedling growth rates and densities will determine the trajectory of stand development in beetle-killed forests (Collins et al. 2011). Our results suggest that recovery after the beetle outbreak will be a slower process in the MSxv than in the SBPSxc due to the reliance on new recruits rather than advance regeneration. The better growth and condition of seedlings in the MSxv may mitigate the slower recovery rate in this subzone.

The forest canopy, even with considerable mortality, had a significant impact on seedling growth and condition. The last assessment, completed 5 years after the outbreak, showed that seedlings in all locations, but particularly in the harvested openings, had improved growth and increased vigour, which suggests that they are responding to increased site resources. McIntosh and Macdonald (2013) stressed the need for future research that monitors recruitment and longer term survival of seedlings in attacked forests as they transition to grey attack and eventually fall to the ground in order to better predict the successional pathway of mountain pine beetle-disturbed stands. Our study shows that pathways of stand recovery in the west Chilcotin will differ depending on biogeoclimatic and pre-epidemic stand conditions (Nigh et al. 2008; Diskin et al. 2010).

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