The effects of harvest intensity and seedbed type on germination and cumulative survivorship of white spruce and balsam fir in northwestern Quebec

C. Calogeropoulos, D.F. Greene, C. Messier, and S. Brais

Abstract: The effects of different harvest intensities, including uncut, 1/3 and 2/3 partial cuts, clearcuts with and without slash, were investigated on the germination and cumulative survivorship of white spruce and balsam fir over 2 consecutive years. We also investigated the regenerative capacity of both species on three different seedbeds across all harvest intensities. The seedbeds included were mineral, humus, and organic soil. At the germination stage, both species were strongly affected by seedbed type ($p < 0.032$). The germination rates of fir seeds in partial cuts were significantly greater than clearcut treatments, but spruce remained unaffected at this stage by harvest intensity. The addition of slash improved the germination rates of fir relative to the clear-cut plots without slash. The germination rates the following year were reduced on mineral soil for spruce. The cumulative survivorship at the end of the third summer still showed a significant seedbed response for both species ($p < 0.007$) and a significant harvest response for fir ($p < 0.005$). The cumulative survivorship of the second fir cohort was no longer affected by either harvest or seedbed type. Spruce, however, was still affected by seedbed type ($p = 0.006$). The data from this study provide us with a more detailed description of the fate of cohorts recruited following a harvest operation. Still, what remains to be studied is the fate of these cohorts over the next 5–10 years.

Résumé : Les effets de différentes intensités de récolte sur la germination et la survie cumulative de l'épinette blanche et du sapin baumier, incluant l'absence de coupe, la coupe partielle d'un tiers ou des deux tiers du peuplement et la coupe totale avec ou sans rémanents, ont été étudiés pendant 2 années consécutives. Nous avons aussi étudié la capacité de régénération des deux espèces sur trois lits de germination à toutes les intensités de récolte. Les trois lits de germination retenus incluaient le sol minéral, l'humus et le sol organique. Au stade de la germination, les deux espèces étaient fortement affectées ($p < 0,032$) par la nature du lit de germination. Le taux de germination des graines de sapin était significativement plus élevé dans les coupes partielles que dans la coupe totale mais à ce stade l'épinette n'était pas affectée par l'intensité de la récolte. L'addition de rémanents a amélioré le taux de germination du sapin comparativement aux parcelles de coupe totale sans rémanents. La deuxième année, le taux de germination de l'épinette chutait sur le sol minéral. Le taux cumulatif de survie à la fin du troisième été était toujours significativement influencé par le lit de germination chez les deux espèces ($p < 0,007$) et par l'intensité de la récolte dans le cas du sapin ($p < 0,005$). Le taux cumulatif de survie de la seconde cohorte de sapin n'était plus affecté ni par le type de récolte ni par la nature du lit de germination ($p = 0,006$). Les résultats de cette étude nous fournissent une description plus détaillée du sort des cohortes recrutées après une opération de récolte. Il reste tout de même à étudier le sort de ces cohortes au cours des 5–10 prochaines années.

[Traduit par la Rédaction]

Introduction

It has been well documented that mineral soil seedbeds, rotten wood, and *Sphagnum* mosses offer the best environments for the germination of small, seeded species (Lees 1963; Alexander 1984; Eis 1965; Jeglum and Kennington 1993; Groot and Adams 1994), especially during periods of prolonged drought (Parker et al. 1997; Oleskog et al. 2000).

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Fibric organic (the Of horizon) seedbeds on upland sites are generally very porous and prone to desiccation, resulting in insufficient moisture to induce germination (Cayford and Dobbs 1967). The rule of thumb for upland boreal sites is that seedbed suitability will decrease as the depth of the organic layer increases (Greene and Johnson 1998; Charron and Greene 2002).

Moreover, we know that germination rates are inversely proportional to light intensity primarily because of seedbed desiccation in high light environments (McLaren and Janke 1996; Wright et al. 1998; Duchesneau and Morin 1999) and not because of a physiological response of seeds to high-radiation environments. Light, however, is not the only abiotic factor governing the high germination rates under closed canopies. In fact, a closed canopy shelters the subcanopy environment from temperature extremes, which can result in desiccation and frost damage. However, light environments conducive to germination are not necessarily the same as those promoting subsequent survival. For example, Duchesneau and Morin (1999) found that regardless of the higher germination rates observed under reduced light, second summer survivorship under a dense canopy was only half of that in environments receiving more light.

In this study, harvesting operations were done in even-aged aspen (*Populus tremuloides* Michx.) stands to create a range of partial canopies. This experimental setup, coupled with the creation of three seedbed types, was used to determine which portion of a canopy cover gradient will yield the highest cumulative survivorship when a range of seedbeds are included in the analyses. The question is cogent because of increasing interest in full and partial harvesting techniques used to emulate natural disturbances (e.g., fire outbreaks, insect epidemics, etc.) (Bergeron et al. 2002; Harvey et al. 2002). Furthermore, ensuring conifer regeneration under an aspen canopy is of special interest in the west, where it is more cost-effective to grow spruce among aspen where graminoid cover (e.g., *Calamagrostis* spp.) is less abundant. While optimum microsites can be inferred perhaps by pooling the existing literature (e.g., Lees 1970; Wurtz and Zasada 2001 (for partial harvests); Alexander 1984; Wurtz and Zasada 2001 (for clearcuts); and Gregory 1966 (for intact forests)), temporal and spatial variation between studies can often bias the results.

Other factors that should influence management decisions with respect to harvest intensity and seedbed preparations are the cumulative survivorship results from cohorts recruited in the years following the disturbance. Seedbeds, such as exposed mineral soil, are expected to deteriorate with time because of the accretion of surface litter converting them back to organic litter seedbeds (Alexander 1984). Harvest operations are also expected to affect the surrounding herbaceous vegetation because of a response to an increase or decrease in light receipt. The cumulative survivorships of these later cohorts are therefore expected to differ from the initially established recruits. What is of interest here is which portion of the canopy gradient will favor recruitment in subsequent years.

The main objective for this study was to determine which seedbed type and harvest intensity provided the best conditions for conifer recruitment beneath even-aged aspen stands. The recruitment potential was investigated at the germination stage and at the end of the third growing season for *Picea glauca* (Moench Voss) (white spruce) and *Abies balsamea* (L.) Mill. (balsam fir). Our second objective was to determine whether seedbed suitability was reduced in the year following seedbed manipulation and to determine the cumulative survivorship of this cohort, across all treatments, at the end of the second year. Finally, based on the results of this study, present the optimal sowing rate under each harvesting regime and seedbed type to successfully obtain adequately stocked stands. The objectives will be addressed separately for white spruce and balsam fir.

Materials and methods

Study area

This study was conducted in a forest dated to a fire in 1923 (Dansereau and Bergeron 1993) at the Lake Duparquet Research and Teaching Forest in Abitibi–Temiscamingue, approximately 45 km northwest of Rouyn-Noranda (48°N, 79°W). The area is part of the northern Clay Belt of Quebec and Ontario, where the soils (Grey Luvisols) are derived from glaciolacustrine clay deposits left from the maximum Holocene extension of the Barlow–Ojibway proglacial lakes (Vincent and Hardy 1977). Soil texture is that of heavy clay (>75% clay), and the forest floor is a thin mor of 2–7 cm.

The mean annual temperature is 0.6 °C, with a mean annual precipitation of 823 mm and a mean frost-free period of 64 days (Environment Canada 1982). Prior to harvesting, the sites were composed mainly of aspen (*Populus tremuloides* (Michx)). There was a sparse subcanopy of *Pinus banksiana* Lamb., *Thuja occidentalis* L., *Abies balsamea*, *Picea mariana* (Mill.) BSP, and *Picea glauca*. The dominant herbaceous species were *Aralia nudicaulis* L. and *Aster macrophyllus* L.

Harvesting treatments

Four levels of forest harvesting were applied during the winter months of 1998–1999 and replicated three times according to a complete block design. Each block included a 1/3 partial cut, a 2/3 partial cut, a clearcut, and a control treatment (where no harvesting was performed) measuring between 1–2.5 ha in size. The 1/3 partial cut removed 30% of the basal area. In the 2/3 treatment, 61% of the basal area was removed. The clearcuts removed all of the standing biomass greater than 1 m, while protecting the short (<1 m tall) advance regeneration. Table 1 shows the pre- and post-harvest basal area ($m^2 \cdot ha^{-1}$) for all three sites, including the controls. Note, however, that for block 2 only the clearcut treatment was used for this study because of a slug infestation in the other three treatments, which consumed all of the organic soil horizons, leaving only exposed mineral soil. Moreover, initial sowing experiments conducted on this site resulted in virtually no germination. The clearcut treatment of block 2 was not affected by the infestation. A much more detailed description of the techniques used for harvesting and forest composition before and after harvest can be found in Brais et al. (2004).

Seedbed treatments

The three seedbeds studied were forest litter organic soil (Of), humus (Oh), and mineral soil. The Of seedbed repre-

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Table 1. Pre- and post-harvest stand basal area ($m^2 \cdot ha^{-1}$) for sites 1, 2, and 3.

Site	Treatment	Preharvest	Postharvest
1	Control	45.1	45.1
	1/3	43.9	32.2
	2/3	39.2	16.5
	Clearcut	46.7	0
2	Clearcut	37.2	0
3	Control	42.4	42.4
	1/3	38.5	29.2
	2/3	39.7	16.8
	Clearcut	48.2	0

sents the top horizon of the normal forest floor (LF) comprised primarily of a layer of aspen and less abundantly of mountain maple (*Acer spicatum* Lamb.) leaf litter. Conifer litter represents a small fraction of the litter layer. The Oh seedbed was created by manually removing the litter layer, exposing the humic material beneath. Finally, the mineral soil was created by removing the Of and Oh layers.

Under each of the harvest experimental units, eight permanent plots (2 m × 2 m) were randomly set up in early May 2000. On each plot, the Of seedbed occupied the northwest (1 m × 1 m) subquadrat. The Oh and mineral seedbeds occupied the southwest (1 m × 1 m) and northeast (1 m × 1 m) subplots, respectively. The southeast subplot was vacant.

Slash treatment

To compare the effects of slash on germination rates and survivorship within the clearcut treatment, we added an additional eight permanent plots per block. Because the clearcut treatment in block 2 was not affected by the slug infestation, this analysis involved three experimental blocks. These plots were then covered with slash debris from the clearcut, covering approximately 70% of the plot. The diameter of the slash ranged between 5 mm (small branches, twigs) and 10 cm (mountain maple shrubs, downed trees). The slash piles also included downed foliage (mainly coniferous, since the harvest was done in the winter). The height of these slash piles were approximately 30–50 cm to ensure uniformity with the surrounding clearcut. These plots are referred to as the clearcuts with slash treatment (CCS) to differentiate from the clear-cut plots without slash treatment (CCNS). To avoid pseudoreplication, we averaged values from seedbed subplots over each harvesting experimental unit leading to one value per combination of harvesting and seedbed experimental units.

The first cohort (coh1) was sown the second week of May 2000. Two hundred seeds of spruce were sown on each of the permanent plots under each harvest treatment. Because of a limited supply of fir seeds, 200 seeds were sown on Of and Oh seedbeds. On mineral soil in the control, 1/3, and 2/3 treatments, a total of only 50 seeds were sown. Mineral soil seedbeds in the clearcut treatments (CCS and CCNS) were sown with 100 seeds. In the CCS treatments, seeds were sown before applying the slash to mimic natural seeding conditions. In 2001, however, seeding was done above the slash piles, again as would occur naturally. Germinant emergence for the 2000 cohort began in mid-June, and the first census was done on June 25, 2000. The plots were revisited on July 20 and September 4, 2000, where newly emerged individuals and mortality were recorded. The total number of seeds germinating (including the fraction that did not survive this first summer) was assessed at the end of the first summer. The germination rate (seedlings germinated per total sown) for this first cohort will be denoted as $S_{g2000.}$ The cumulative survivorship was recorded in May, July, and August of 2001, and again in May and August of 2002. The third year cumulative survivorship data were calculated as the quotient of the total surviving seedlings at the end of the third summer (August 2002) over the total viable portion sown for each of the permanent plots.

The second cohort (coh2) was sown the following spring (2001) after snowmelt. The sowing rate under each harvest intensity was 200 seeds per species for each seedbed type. The germination rate for this second cohort will be denoted as $S_{g2001.}$ The latter was followed throughout the summer of 2001 (June, July, and August). The cumulative survivorship of this cohort was followed until the end of the summer of 2002 (second summer survivorship).

The seeds of both cohorts were provided by the ministère des Resources naturelles du Québec. A viability test was performed in the laboratory on wetted filter paper. For coh1, seed viability was 79% for spruce and 50% for fir, based on a sample size of 200 seeds of each species. The viability for the coh2 seeds were 82% and 51% for spruce and fir, respectively. All germination and survivorship analyses were based on the proportion of viable seeds only.

Litter traps

Within each block for each of the harvest treatments, five (0.5 m^2) litter traps were randomly placed in August 2000, and its contents emptied on May 2001. The litter was subsequently dried in the laboratory, then weighed (in grams), and used as an index of litter accretion across all harvest intensities. Litter accretion beneath the slash seedbeds was not included.

Data analyses

Germination analyses

All statistical analyses involving germination rates were completed using arcsine-transformed data to conform to the assumptions of normality and homoscedasticity. Data analyses were done using GLM and MEANS procedures of the SAS statistical package (SAS Institute Inc. 1988). A split-block analysis was conducted with four harvesting treatments replicated twice and three nonrandomized seedbed treatments within the main harvesting treatments. This analysis is similar to the split-plot with the exception that the subplots are not randomized (Steel and Torrie 1980). This analysis provides three error terms, which is high for the main effects (harvest and seedbed) but relatively low for interactions (Steel and Torrie 1980). Contrasts between treatments were used to answer the three the following a priori questions (Steel and Torrie1980): (*i*) Are the partial cuts different from the unharvested stands? (*ii*) Are the partial cuts different from the clearcuts? (*iii*) Is the 1/3 partial cut treatment different from the 2/3 partial cut treatment? For con-

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trasts involving seedbeds, we asked whether both manipulated soil surfaces (mineral and Oh) differed from the untreated (Of) and if the Oh seedbeds differed from the mineral seedbeds. As we were more interested in tendencies than in the absolute level of probability of the observed differences, a level of significance of 0.1 was retained.

The CCS treatments in this experimental design were randomly set within the main experimental units. To simplify analyses, we considered them in a separate analysis, comparing them to the CCNS treatments using a two-way analysis of variance with three blocks (clearcut units) and two slash treatments (CCS and CCNS).

To determine the effects of time since disturbance, we performed a paired-sample t test between the cohort germinating in 2000 and 2001 (coh2), where the paired units were the individual plots. Separate tests were performed for each of the treatments (i.e., seedbeds, harvests, and species).

Litter accretion analyses

The dry masses were log-transformed and a one-way ANOVA was used to determine if litter accretion differed significantly across the harvest treatments. A post hoc Tukey's test was used to determine which of the harvests significantly differed from one another.

Cumulative survivorship analyses

The analyses performed here aimed to determine survivorship differences as a function of seedbed type and canopy cover within each cohort for each species. For coh1 this was based on the third year survivorship data. Coh2 analyses were on second year survivorship data. An alternative to the split-block analysis was required because of violations of homoscedasticity. For all tests, we employed an extension to the Kruskal–Wallis test (Sokal and Rohlf 1981), which is designed to replace the two-way ANOVA when nonparametric data are used. The data for this test are ranked and a 2-way ANOVA is then performed on the ranked data. Post hoc Tukey's tests were then performed on the ranked data

Results

Seed germination (2000)

Effects harvest and seedbed

Split-block analyses concerning the main effects showed a significant seedbed effect for both species, but failed to show an effect of the harvest treatments (Table 2). Under each harvest intensity, the highest germination rate for both species in 2000 was observed on mineral soil seedbeds. Figure 1a (fir only) indicates that the germination rates on Oh seedbeds were intermediate between mineral and Of seedbeds. Contrast analyses showed that both manipulated soil surfaces (mineral and humus) significantly improved the germinability of seeds relative to untreated seedbeds (Of) (Table 3). The complete removal of the organic matrix (mineral seedbeds) yielded significantly higher germination rates relative to Oh seedbeds for fir but not for spruce (Fig. 2a). A priori contrasts for fir showed a significant difference between the clearcut and partial cut germination rates.

Table 2. Results from split-block analyses for germination data of *Abies balsamea* and *Picea glauca.*

	df	F	$p > F$
A. balsamea			
Block	1	1.68	0.242
Harvest	3	4.59	0.054
Seedbed	2	12.52	0.007
Block × Harvest	3	1.28	0.363
Block × Seedbed	2	0.10	0.903
Harvest × Seedbed	6	0.71	0.655
P. glauca			
Block	1	0.04	0.852
Harvest	3	2.43	0.163
Seedbed	2	6.41	0.032
Block × Harvest	3	2.99	0.118
Block × Seedbed	2	0.34	0.727
Harvest × Seedbed	6	0.34	0.894

Effects of slash

The addition of slash in the clearcut treatments significantly improved the germination rates of fir seeds relative to the CCNS treatments ($p < 0.001$). An investigation of seedbed suitability under the clearcut treatments also revealed a significant seedbed response ($p = 0.004$). For fir, mineral seedbed germination rates significantly differed from the Oh and Of treatments (Tukey's: $p = 0.031$ and 0.003, respectively) (Fig. 1a). The factorial ANOVA showed no significant interaction between the two factors investigated. A significant response to seedbeds and slash addition was also observed for spruce ($p < 0.001$ and 0.03, respectively). A significant interaction between the two factors ($p = 0.004$) was also found (Fig. 2a).

Effects of delayed sowing (S_{g2000} vs. S_{g2001}) and litter accretion across all harvest intensities

Mineral soil receptiveness was strongly affected the year following seedbed manipulation (Figs. 1b and 2b). Under the control, 1/3, and 2/3 partial cuts on mineral soil, we found a general decrease in germination rates in the second year, where the most pronounced decrease was for seeds germinating on mineral soil under the control treatment. The germination rates of spruce seeds on Oh under the three highest canopy cover classes also significantly decreased. With the exception of fir seeds germinating under the CCNS treatment, the germination rates of both species on Of seedbeds did not change in the second year of sowing.

While germination decreased in 2001 for seedbeds in the control, 1/3, and 2/3 treatments, there was an increase in fir germination in 2001 under the CCS and CCNS treatments. The increase was significant for all seedbeds under the CCNS treatment. The germinability of spruce in 2001 in the CCS and CCNS treatments was not significantly affected.

Litter accretion was highest in the control treatment and subsequently declined thereafter as a function of increasing harvest intensity (Fig. 3). The clearcut treatment received significantly less litter than all other treatments (Tukey's: $p < 0.001$).

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Fig. 1. Mean germination rates of fir in (*a*) 2000 (S_{g2000}) and (*b*) 2001 (S_{g2001}) on each seedbed type and harvest intensity. Oh, humus; Of, organic soil; CNT, control; CCS, clearcuts with slash treatment; CCNS, clearcuts without slash treatment. Asterisks denote a significant difference between S_{g2000} and S_{g2001}, where *, $p < 0.05$; **, $p < 0.001$. Error bars represent ±1 SE.

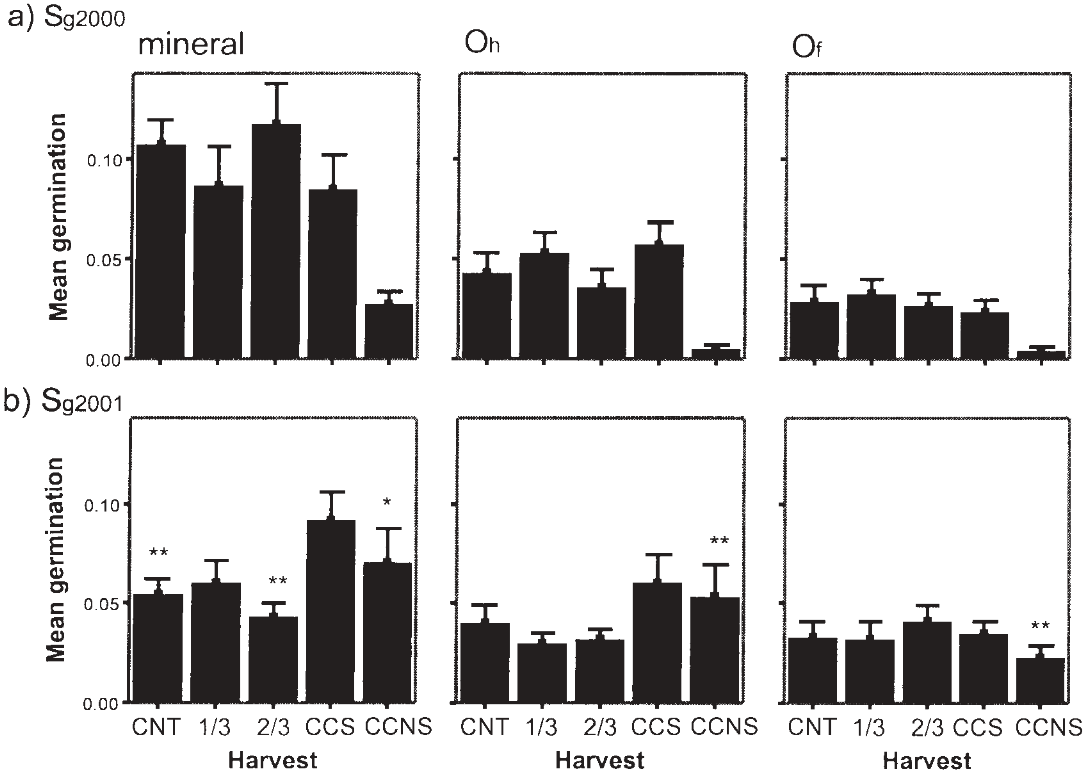

Table 3. Probability and mean square error (MSE) values for simple comparisons of effects of harvesting and seedbed type on the germination values of *Abies balsamea* and *Picea glauca*.

Treatment	Contrast	$p > F$ *A. balsamea*	*P. glauca*
Harvest	Control vs. partial cuts	0.923	0.514
	Clearcut vs. partial cuts	0.055	0.415
	1/3 vs. 2/3	0.910	0.617
	MSE	0.00014	0.0003
Seedbed	Mineral and Oh vs. Of	0.009	0.029
	Mineral vs. Oh	0.007	0.143
	MSE	0.000012	0.000034

Note: Oh, humus; Of, organic soil.

Cumulative Survivorship

Third year cumulative survivorship (coh1)

Effects of harvest and seedbed

The analyses for third year cumulative survivorship for fir and spruce still showed a significant seedbed response ($p < 0.001$ and 0.007, respectively) and a significant harvest response for fir ($p = 0.005$) (Figs. 4 and 5), where post hoc tests showed that both partial cuts were significantly higher than the clearcut (CCNS) ($p < 0.019$). For both species, a significant interaction between the two factors investigated was not observed. Tukey's tests performed on the ranked data showed that mineral soil survivorship for both species was significantly higher than Of ($p < 0.006$). The cumulative survivorship of fir on mineral soil seedbeds was also significantly higher than that on Oh ($p = 0.010$).

Effects of slash

Analyses between the two slash treatments showed a significant effect for fir only ($p = 0.007$) A significant seedbed effect was found for both species ($p = 0.010$), and a significant interaction was still present for spruce ($p = 0.042$). A posteriori tests for fir showed that mineral soil survivorship was significantly higher than that of Of ($p = 0.009$) but not Oh.

Second year cumulative survivorship (coh2)

Effects of harvest and seedbed

The cumulative survivorship of fir at the end of the second year was not significantly affected by either harvest or seedbed type (Fig. 6). The cumulative survivorship of the second spruce cohort showed a significant response to seedbed type ($p = 0.010$) but not to harvest (Fig. 7). A significant interaction between the two factors for spruce was not found. Post hoc tests showed that mineral soil survivorship for spruce was significantly higher than that of Of ($p < 0.009$).

Effects of slash

Analyses concerning the cumulative survivorship of the two slash treatments showed a significant seedbed effect for spruce only ($p = 0.006$) and an absence of interaction between the two factors investigated. Mineral soil receptiveness was significantly higher than that of Of ($p = 0.005$).

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Fig. 2. Mean germination rates of spruce in (*a*) 2000 (S_{g2000}) and (*b*) 2001 (S_{g2001}) on each seedbed type and harvest intensity. Oh, humus; Of, organic soil; CNT, control; CCS, clearcuts with slash treatment; CCNS, clearcuts without slash treatment. Asterisks denote a significant difference between S_{g2000} and S_{g2001}, where *, $p < 0.05$; **, $p < 0.001$. Error bars represent ±1 SE.

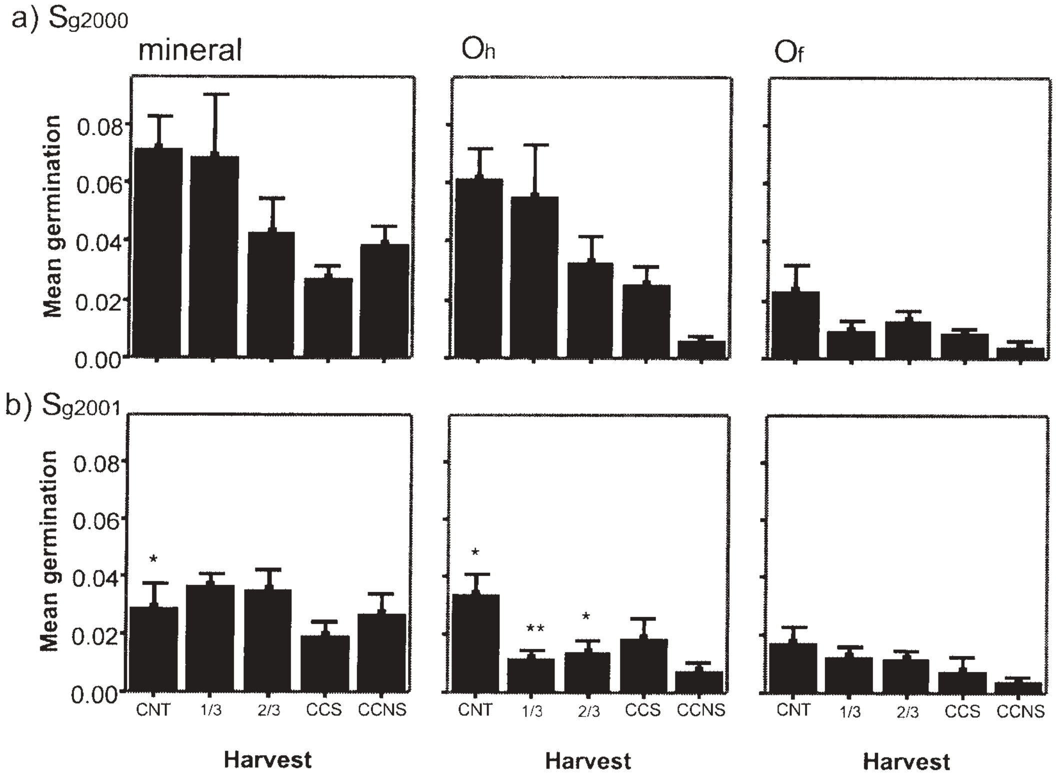


Fig. 3. Mean dry mass (g) of litter from traps placed under each of the harvest intensities in August 2000 and collected in May 2001. CNT, control; CC, clearcut. Error bars indicate ±1 SE.

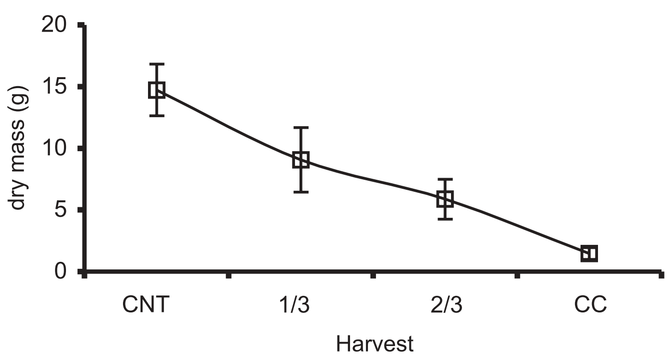
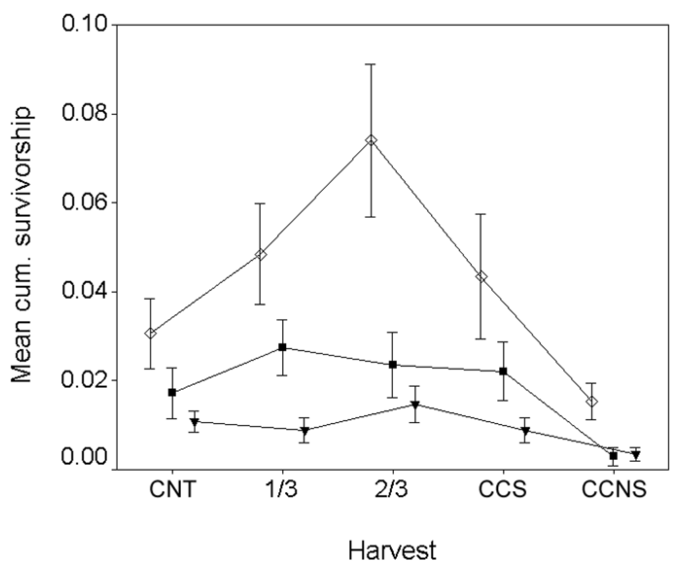


Fig. 4. Mean third year cumulative survivorship of fir on mineral (◇), Oh (■), and Of (▼) across all harvest intensities. CNT, control; CCS, clearcuts with slash treatment; CCNS, clearcuts without slash treatment. Bars represent ±1 SE.



Discussion

Germination

Effects of harvest and seedbed

Similar to other studies (e.g., Lees 1963; Delong et al. 1997; Feller 1998), the germination rates in 2000 for both species were highest on mineral soil substrates, followed by Oh seedbeds, and Of with the poorest regenerative capacity. Interestingly, we found that for spruce, the removal of only the litter layer (Oh) can improve the quality of seedbeds relative to untreated (Of) seedbeds, but that complete removal of the organic matrix will not further improve the germination rates for this species. Fir, however, does significantly benefit by the removal of the Oh layer. This is of interest silviculturaly, primarily because scarification to expose mineral soil is expensive and time consuming, whereas the removal of only the litter layer is less labor intensive and therefore more economical. The data here show that Oh

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Fig. 5. Mean third year cumulative survivorship of spruce on mineral (◇), Oh (■), and Of (▼) across all harvest intensities. CNT, control; CCS, clearcuts with slash treatment; CCNS, clearcuts without slash treatment. Bars represent ±1 SE.

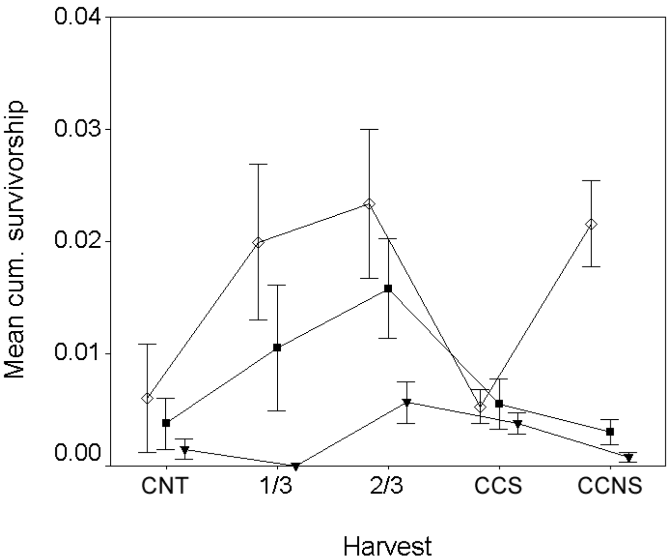


Fig. 6. Mean second year cumulative survivorship of fir on mineral (◇), Oh (■), and Of (▼) across all harvest intensities. CNT, control; CCS, clearcuts with slash treatment; CCNS, clearcuts without slash treatment. Bars represent ±1 SE.

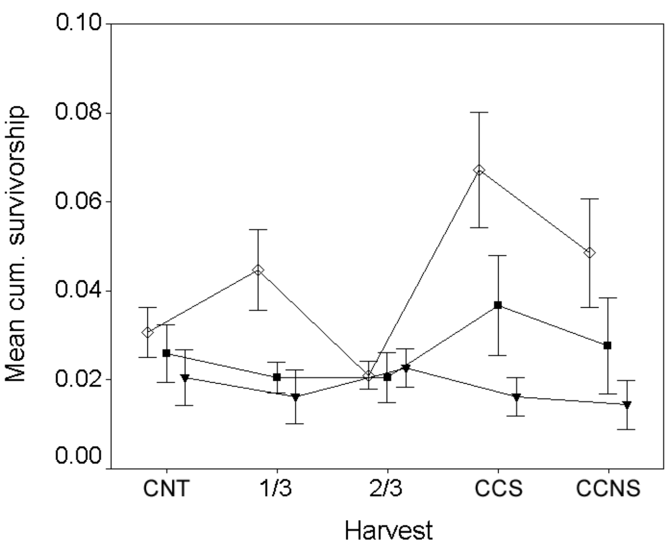
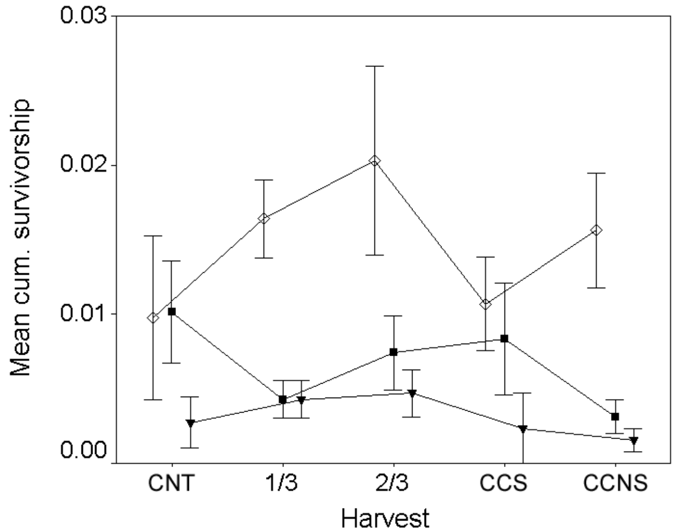


Fig. 7. Mean second year cumulative survivorship of spruce on mineral (◇), Oh (■) and Of (▼) across all harvest intensities. CNT, control; CCS, clearcuts with slash treatment; CCNS, clearcuts without slash treatment. Bars represent ±1 SE.



seedbeds can become a more common practice where the regeneration of spruce is concerned.

The different levels of harvest intensity did not strongly affect the germination rates of either species investigated. The only significant effect of harvest observed in this study was between clearcuts (CCNS) and partial cuts for fir seeds. Previous studies (e.g., McLaren and Janke 1996; Duchesneau and Morin 1999; Wright et al. 1998), however, have shown emergence to increase as a function of canopy cover. We do not conclude here that harvest intensity does not affect germination rates of spruce seeds. In fact, Fig. 2*a* does show a clear decline in germination rates as we move from the unharvested to the clearcut treatment, but our a priori contrasts did not entertain differences between the control and clearcut treatments. The conclusions drawn at this stage are that seedbed effects largely dictate success in establishment at the germination stage for both species and that harvest intensity will only moderately affect the amount of recruitment.

Effects of slash

Germination rates of fir seeds in clearcuts were increased by the addition of slash. This suggests that the amount of light reaching the soil surface was reduced by the addition of slash on clear-cut plots. Light measurements were not taken beneath the slash. Only an estimate of percent cover was made, and thus it cannot be clearly established whether or not seeds were subjected to greater or less light than that in the 1/3 or 2/3 harvest intensities. The benefits of shade in clearcuts have also been noted elsewhere (Fraser and Farrar 1955; Clark 1969). It is unclear, however, why the germination of spruce seeds was improved by the addition of slash on Oh and Of, while the reverse conditions on mineral soil seedbeds were observed. Moreover, this contrasts with Alexander (1984), who showed a twofold increase in the germination rates of *Picea engelmanni* on scarified seedbeds with shade compared with unshaded, scarified plots. This finding merits further investigation, especially since the same pattern was observed in the germination rates of the second cohort (although the effects were not statistically tested).

Effects of delayed sowing

Germination in the year following seedbed manipulation is of theoretical and practical interest but seldom studied. Mineral and Oh seedbeds deteriorated in 2001 for both species. We attribute this finding to the accretion of surface litter under the unharvested and partial canopies (Fig. 3). The loss in seedbed receptiveness reported here is similar to Lees (1970), where white spruce germination rates were reduced

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Table 4. Recommended sowing density (×10³) based on the cumulative survivorship values of the first germinating cohort from this study and from existing literature.

	Seeds/ha (×10³)			
	Mineral	Oh	Of	Sources[a]
Partial cut	400	NA	NA	(third year) Lees (1970); *Picea glauca* on dry site; BA 16.3 $m^2 \cdot ha^{-1}$
	125	NA	NA	(third year) Lees (1970); *P. glauca* on moist site; BA 14.9 $m^2 \cdot ha^{-1}$
	118	NA	NA	(third year) Lees (1970); *P. glauca* on wet site; BA 15.1 $m^2 \cdot ha^{-1}$
	1 000	1 818	∞[b]	(third year) This study *P. glauca*; 1/3 treatment; BA 30.7 $m^2 \cdot ha^{-1}$
	867	1 250	3 333	(third year) This study *P. glauca*; 2/3 treatment; BA 16.7 $m^2 \cdot ha^{-1}$
	417	741	2 222	(third year) This study *Abies balsamea*; 1/3 treatment; BA 30.7 $m^2 \cdot ha^{-1}$
	270	833	1 333	(third year) This study *A. balsamea*; 2/3 treatment; BA 16.7 $m^2 \cdot ha^{-1}$
Clearcut (shaded)	667	NA	2 000	(fifth year) Alexander (1984); *Picea engelmannii*; north aspect
	6 667	NA	6 667	(fifth year) Alexander (1984); *P. engelmannii*; south aspect
	4 000	3 333	5 000	(third year) This study *P. glauca (*CCS treatment)
	465	909	2 222	(third year) This study *A. balsamea* (CCS treatment)
Clearcut (unshaded)	2 000	NA	10 000	(fifth year) Alexander (1984); *P. engelmannii*; north aspect
	∞[b]	NA	∞[b]	(fifth year) Alexander (1984); *P. engelmannii*; south aspect
	909	6 667	28 571	(third year) This study *P. glauca (*CCNS treatment)
	1 333	6 667	6 667	(third year) This study *A. balsamea* (CCNS treatment)
Full-canopy	22 222	NA	NA	(fifth year) Gregory (1966) *P. glauca*
	3 333	5 000	10 000	(third year) This study *P. glauca (*control)
	645	1 176	1 818	(third year) This study *A. balsamea* (control)

Note: The data from the literature include third year cumulative survivorship data (Lees 1970) and fifth year cumulative survivorship data (Alexander 1984; Gregory 1966). NA, not applicable; BA, basal area; CCS, clearcuts with slash treatment; CCNS, clearcuts without slash treatment.

[a]Only studies for which specify canopy cover and seedbed type have been included.

[b]Denotes a cumulative survivorship value of zero.

by 2.4 times in the second year and 2.5 times in the third year of sowing under a partial harvest.

To ensure that temporal variation (e.g., weather, granivore density) did not influence his results, Lees (1970) included the germination data on freshly scarified soil for both years. In this study, this corrective measure was not taken. However, temporal variation in the present study is assumed to be negligible given that the germination rates on Of seedbeds for both species under the control treatment did not change in 2001. Alridge (1967) had repeating sowing data for spruce for 5 consecutive years on mineral soil under partial canopy. By the fourth year, the seedbeds deteriorated to levels typical of Of seedbeds.

The literature, however, only provides us with data for partial canopies and to our knowledge provides no comparative data for fir. This is the first study to show improved germination rates of fir in the year following seedbed manipulation in clear-cut environments. Oleskog et al. (2000) showed that relative humidity levels above 65% will reduce evaporative losses from seeds and thereby improve germination rates. This suggests that the improved germination in the clear-cut environments was the result of increased humidity levels provided by the asexual aspen recruits, which dominated the clearcuts in the 2001 (personal observation).

Cumulative survivorship

Third year cumulative survivorship (coh1)

Effects of harvest and seedbed

For this part, we have taken the cumulative survivorship values obtained in this study and present it in Table 4, where we calculated the number of seeds per hectare required to obtain adequate stocking. We will assume that adequate stocking is achieved with 20 000 seedlings per hectare at the end of the third summer. Given that seedling mortality levels off after the first few years, we will consider this density to be adequate for all of the harvest units. For example, if the cumulative survivorship was 0.05, it will require 400 000 seeds/ha to obtain 20 000 seedlings at the end of the third

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summer. For comparison, we have also included estimates obtained from other similar studies.

Based on the third year cumulative survivorship from this study, the lowest seed input for adequate spruce regeneration can be obtained on mineral soil under the 2/3 partial harvest (867 000) followed by one million seeds for the same seedbed under the 1/3 harvest. Lees (1970) showed that white spruce regeneration can be achieved with fewer than 400 000 seeds/ha. Given that a significant response to harvest intensity was not observed for spruce, we can conclude that either of the two partial harvests coupled with seedbed manipulation are the most suited for regeneration.

Our results showed that a seedbed response was still observed at the end of the third year. The very poor germination rates on Of seedbeds coupled with poor subsequent survival (not shown) demands a very high seed input. Based on our sowing rate of 200 spruce seeds on Of soil under the 1/3 partial cut, no survivors were present by the end of the third summer. Thus, it is seems that at least for spruce, seeding on Of soil will likely result in a failure to sufficiently regenerate a stand.

The comparisons in Table 4 apply to spruce only. The literature has, to our knowledge, no comparative cumulative data for fir. Several studies have looked at germination of fir on various seedbeds (Duchesneau and Morin 1999; Maclaren and Janke 1996) but failed to tease apart the effects of seedbeds from canopy cover gradient. This is, to our knowledge, the first study to look at the survivorship of fir along a canopy gradient cover and seedbed types until the third year. The suitability of fir regeneration in partial harvests is evident when we look at the number of seeds required to obtain adequate stocking (see Fig. 4). The range of seed input for fir in partial harvests ranges between 270 000 on mineral soil in the 2/3 treatment and 2 222 000 on Of in the 1/3 treatment. Effectively, the suitability of both species under the partial harvest has much to do with high germination rates relative to the clearcuts and high subsequent survival relative to the control. Given that both partial cuts were still significantly higher after the third year for fir, the regenerative capacity of this species can be greatly increased if suitable seedbeds are coupled with partial cuts.

As with the clearcuts, the unharvested stands also resulted in very low cumulative survivorship values for both species investigated. The fifth year cumulative survivorship in Gregory (1966) is even lower. As such, it is recommended that recruitment from seed, under full canopy, should be avoided.

Effects of slash

The very low germination rates of fir in the CCNS treatments (Fig. 1*a*) are largely responsible for the tremendous seed input that is required to adequately regenerate these stands. Because of the significantly higher cumulative survivorship values under the CCS treatment for fir, the input of seeds can be reduced by threefold. The low cumulative survivorship values of spruce in clear-cut environments (CCS and CCNS) require a seed density range between 909 000 to 28 000 000. When we contrast this with the fifth year cumulative survivorship data in Alexander (1984), the numbers now range between 667 000 to infinity (i.e., no survivors). The influence of slash on the cumulative survivorship of spruce seeds on mineral soil in clearcuts is still unclear. The data of Alexander (1984) under these same conditions contrast with the results from this study, suggesting that shade can greatly improve this initial step in establishment.

Second year cumulative survivorship (coh2)

Effects of harvest and seedbed

The effects of harvest and seedbed type on the survivorship of subsequent cohorts are of interest if sowing is to be performed in the years following soil manipulation. In this work, the second germinating cohort of fir was no longer affected by either harvest or seedbed type at the end of the second year. Unlike fir, spruce still responded significantly to seedbed type. The data here are also useful in predicting the recruitment potential for these sites in subsequent years that may result from natural seed input.

Effects of slash

The significantly elevated fir germination rates in the CCNS treatments relative to the previous year (Fig. 1*b*), coupled with high subsequent survival, resulted in high cumulative survivorship values at the end of the second year. Relative to the cumulative survivorship of the first cohort, the optimal sowing density for fir is now 3 and 1.5 times lower in the CCNS and CCS treatments, respectively. Clearcuts without slash can therefore benefit the most from repeated sowings, at least within the first 2 years of harvest and seedbed manipulation. For spruce, the sowing density is halved in the CCS treatment but increased by 1.5 times in the CCNS treatment relative to the first year cumulative survivorship data.

Recently, silvicultural practices that emulate natural forest disturbances have received considerable attention (Bergeron and Harvey 1997; Harvey et al. 2002; Bergeron et al. 2002). This study outlined some of the responses of softwood species to these types of disturbances, but much more work needs to be invested before any conclusions can be made. Most importantly, we need to monitor these cohorts during subsequent years at least until they are recruited into the sapling–juvenile stage. This would allow a highly comprehensive and detailed examination of sexual recruitment under varying canopy gradients and seedbed types.

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