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The effects of harvest intensity and seedbed type on germination and early survival of balsam fir and white spruce in the southern boreal forest

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A Thesis

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The Department

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ABSTRACT

The effects of harvest intensity and seedbed type on germination and early survival of balsam fir and white spruce in the southern boreal forest

Catherine Calogeropoulos

The effects of harvest intensities and seedbed type on germination success and early (first summer) survival for balsam fir (*Abies balsamea* (L.) Mill) and white spruce (*Picea glauca* (Moench) Voss) were exmined. The harvest intensities canopies included a 1/3rd and 2/3rd partial cut, a clearcut and a control (full canopy). The seedbeds were mineral, humus (O_h) and organic (O_f). In clearcuts, seedbeds included both slash and non-slash treatments. Germination of both species was negatively affected by an increase in harvest intensity. The reverse effects of harvesting intensity were observed during subsequent survival, where spruce was much more affected than fir by a reduction in canopy cover. Cumulative survivorship analyses showed that clearcuts without slash were the worst areas for early plant establishment. Mineral seedbeds allowed the highest rates of seedling establishment for both species, although survival of fir was highest on O_f seedbeds. Cumulative survivorship showed that mineral soil is the most suitable substrate for establishment. This finding however, was not strong for spruce, suggesting adverse effects of mineral soils with a high clay content. The slash treatment benefited the establishment of fir, but not for spruce. This study showed the strong initial influence of harvesting intensity and seedbed type. The effects of light however, quickly become muted when cumulative survivorship is considered. Conversely, seedbeds have persistent effects on early establishment.

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Introduction

Following harvesting, stand replacement can be by natural or artificial regeneration. The success of natural regeneration depends on (1) the source strength of adjacent or residual uncut stands for sufficient seeds to obtain the next generation of trees, and (2) the quality of the seedbeds. Even with a mast year and a small cut-block the potential to germinate and survive over the next few years will ultimately depend on the microenvironment at the ground surface. This study will focus, then, on the microsite responses of two boreal tree species: white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.).

For the last three decades, throughout Canada, harvest blocks have been conventionally planted. More recently, there has been some interest in the cheaper alternative of careful harvesting, allowing the advanced regeneration that is present constitute the next crop. As such, research has focused on the physiological and morphological responses of different light regimes on naturally established saplings (>1m) and planted or naturally established seedlings (<1m) (e.g. Klinka et al. 1992; Lieffers and Stadt 1994; Pacala et al. 1994; Chen et al. 1996; Chen 1997; Coates 2000). In the literature however, there is very little information on tree seed germination under various light levels.

Recently, partial cut harvesting and mixedwood management techniques have been developed for boreal forests with the aim of maintaining biological diversity (e.g. tree species diversity) and ecological integrity (e.g. species interactions) (Rowe 1992).

Sometimes with partial cuts one relies on advanced regeneration, whereas in other cases one may be expecting post-harvest sexual recruitment (in effect, a shelterwood treatment). A partial harvest system removes only a fraction of the canopy creating a range of small (single tree) to medium and large canopy gaps. Essentially, this alteration of the amount of light transmitted through the forest strata affects the growth responses of both desirable and undesirable species (Constabel and Lieffers 1996). Increased light levels promote the growth of understory shrub and herb layers (Rowe 1955; Cannell and Grace 1993; Lieffers and Stadt 1994; Constabel and Lieffers 1996). The ideal partial cutting scheme would maintain good growing conditions for the species of interest while suppressing competition. While competitive species interactions are not assessed in this study they remain an important aspect of regeneration dynamics.

Generally, germination rates increase as a function of decreasing light intensity (McLaren and Janke 1996; Wright et al. 1998; Duchesneau and Morin 1999). It is assumed that light is simply a proxy for dessication of surface substrates; that is, the key factor in juvenile mortality is water relations (Wright et al. 1998). McLaren and Janke (1996) found that germination for fir was highest on sites with greater than 40% canopy closure. Similarly, Duchesneau and Morin (1999) reported emergence was 4% higher in low light environments than on sites with greater light availability. In Wright et al. (1998) for all six boreal tree species studied, gap positioning strongly affected emergence. The rate of seed germination increased from the sunny north end of gaps (<3%) to the shadier south end of gaps (<33%), with understory environments (i.e. under full canopy) engendering intermediate germination rates. Only one study demonstrated that clearcuts engender higher germination rates than closed canopy sites (Feller 1998).

However, light environments conducive to germination are not necessarily the same as those promoting subsequent survival. Indeed, a minimum percent solar radiation is required to maintain whole seedling carbon balance and this minimum will, of course, differ between shade tolerant and intolerant species (Coates 2000). Duchesneau and Morin (1999) found that, regardless of the higher germination rates observed under reduced light, to obtain 1 seedling/m^2 under low light required 340 seeds/m^2 as opposed to 167 seeds/m^2 for environments receiving more light. However, above 36.5% PPFD (percent photon flux density) mortality increased suggesting (at least for fir) a critical threshold above which mortality begins to increase again (Duchesneau and Morin 1999). Another study showed that while the greatest canopy cover class (>80%) ranked high for germination success (approx. 7%), by the second growing season, mortality in this cover class ranked highest, exceeding the mortality in all other light environments (McLaren and Janke 1996). Indeed, the authors found that intermediate cover classes sponsored the highest cumulative survival rates. Wright et al. (1998) report that mortality was also high in the understory (where germination rates were high) and this was more pronounced for shade intolerants. Post-germination survival then increases with an increase in solar radiation, with a suggested minimum of 20% (Coté and Bélanger 1991; Osawa 1994; McLaren and Janke 1996; Wright et al. 1998; Duchesneau and Morin 1999) and a maximum of 40% for shade-tolerants (McLaren and Janke 1996; Duchesneau and Morin 1999).

Why does an intermediate light environment lead to lower post-germination mortality? Elevated mortality under increasing canopy cover has been attributed to delayed germination with a consequent reduction in growing season length during the critical first summer (McLaren and Janke 1996), or smothering during the leaf abscission period (Gregory 1966). At the other extreme, elevated mortality at fully exposed sites has been attributed to reduced moisture levels and higher temperatures (Day 1964; Eis 1965; Cui and Smith 1991; McLaren and Janke 1996; Wright et al. 1998).

The effects of substrates (i.e. soil type and moisture regimes) are also important in determining suitable niches within a forest community for germination and subsequent survival (Fleming and Mossa 1994; Wright et al. 1998; Duchesneau and Morin 1999; LePage et al. 2000). It is generally agreed that the most common seedbed, O_f (the fibric layer in the Canadian soil classification system), offers the least suitable habitat for the germination and survival of small seeded species because of higher susceptibility to desiccation (Zasada and Gregory 1969; Dobbs 1972; Potts 1985). This fibric layer is typically composed of hardwood litter or, more rarely on aspen-dominated upland sites, feather-mosses. However, species with bigger seeds (i.e. greater food reserves and a longer germinant length) can germinate on a variety of substrates (Seiwa and Kukizawa 1996).

Because the spruce seed is three times smaller than fir (and has a germinant about two times smaller: Charron 1998), it follows that white spruce germination and survival requirements are much more constrained than for fir. Poor root contact with the soil, because of the inability of the root cap to extend deep into the moister soil horizons, results in reduced germination and subsequent survival (Place 1955; Day 1963; Dobbs 1972). Mineral soil, thin humus (<3cm) and rotten logs are ideal environments for spruce establishment (Youngblood 1991; Delong 1997) especially during periods of prolonged droughts (Parker et al. 1997). Elevated microsites (e.g. small hummocks) are also suitable niches for germination (Delong et al. 1997). Both rotten logs and hummocks share a critical characteristic: fallen leaves of hardwoods are blown away by the wind. Mineral soil and humus (rare in intact forests) are created via scarification and they, of course, have few leaves for the first few years.

In order to determine the effects of a cover gradient on germination and survival three harvest intensities were created during the winter of 1999. The study site included an uncut (full canopy) treatment, a 1/3rd and 2/3rd partial cut and a clear cut. The sites were selected prior to harvesting, which enabled the control of a few confounding variables e.g. age, stand composition and canopy openness. This scheme provided an ideal opportunity to investigate regeneration dynamics under varying light levels and substrates. This is the first study where light intensity and seedbed type are examined for germination and early survival for two of the most important boreal tree species, *Picea glauca* and *Abies balsamea*. In relation to the light gradient, the initial expectation is that germination success will be greatest in intact forest (least desiccation) while subsequent survivorship will be greatest in the clearcut (least leaf-fall). It is not clear at the outset, however, which portion of the gradient will have the greatest *cumulative* survivorship.

Objectives

My objectives here are to:

1) Determine the effects of harvest intensity on germination and survival of *A. balsamea* and *P. glauca*.

2) Determine the effects of seedbed type on both germination and survival.

Methods

Study area

This study was conducted in a 1923 forest (dated since last fire) at the Lake Duparquet Research and Teaching Forest (FERLD) in Abitibi-Temiscamingue, approximately 50 km northwest of Rouyn-Noranda (79°W, 48°N). The area is part of the northern Clay Belt of Québec and Ontario, where the soils are derived from clay deposits left from the maximum Holocene extension of the Bartlow- Ojibway proglacial lakes (Vincent and Hardy 1977). The climate is characterized as cold with a mean annual temperature of 0.8°C, and mean annual precipitation of 857mm. Although frost can occur at any time throughout the year, the frost-free period is estimated to be an average of 64 days (Environment Canada 1993).

Harvesting treatments

Three harvesting treatments were created during the winter months of 1999, differing in the proportion of basal area removed. Each was replicated three times once at each different site (referred to as Blocks 1, 2 and 3) within the 1923 forest. Prior to harvesting, the blocks were composed mainly of *Populus tremuloides*. There was a sparse subcanopy of *Pinus banksiana*, *Thuja occidentalis*, *Abies balsamea*, *Picia mariana* and *P. glauca*.. The dominant herbaceous species were *Aralia nudicaulis* and *Aster macrophylus*.

Each block included a 1/3rd partial cut, a 2/3rd partial cut, a clearcut, and a control treatment (where no harvesting was performed) measuring one hectare in size. The 1/3rd partial cut removed 27% of the basal area, where only subdominant stems of lesser quality were removed. In the 2/3rd treatment, 58% of the basal area was removed. The higher grade aspen stems were removed and the lesser quality aspen and other hardwood stems were left on site. The clearcuts removed all of the standing biomass, while protecting the short (1m) advance regeneration and soils. Table 1 shows the pre- and post- harvest stem densities ($m^2 ha^{-1}$) for all three blocks, 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.

Seedbed treatments

Tree seed regeneration of white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*) was studied on three seedbed types under each harvest intensity. The three seedbeds studied were organic soil (O_f), humus (O_h) and mineral soil. The O_f seedbed represents the normal forest floor (LFH) comprised primarily a layer of aspen (*Populus tremuloides*) and less abundantly of mountain maple (*Acer spicatum*) leaf litter. Conifer litter represents a small fraction of the litter layer. The O_h seedbed required manually removing the litter layer (aspen, maple and conifer litter) and all identifiable fibers. Finally, the mineral soil was created by removing the O_f and O_h layers.

Under each of the harvest intensities, 8 permanent plots (2m X 2m) were set up in early May 2000. On each plot, the O_f seedbed occupied the northwest (1m X 1m) sub-quadrat. The O_h and mineral seedbeds occupied the southwest (1m X 1m) and northeast (1m X 1m) sub-plots respectively. The southeast sub-plot was vacant. In total, the control, 1/3rd and 2/3rd treatments had 16 replicates of each seedbed type (8 permanent plots per block). The clearcut treatment had a total of 24 replicates, because of the inclusion of Block 2. Moreover the clearcuts received an additional 8 permanent plots, per bloc, which were then covered with slash debris from the clearcut covering approximately 70% of the plot. These plots are referred to as the clearcuts with slash treatment *(ccs)* to differentiate from the clearcut plots without slash treatment *(ccns).*

Germination analyses

The seeds were provided by the Ministère des Resources Naturelles du Québec. A viability test was performed in the laboratory on wetted filter paper. Based on a sample size of 200 seeds of each species, seed viability was 79% for spruce, and 50% for fir. Table 2 shows the number of spruce and fir seeds sown on each seedbed type.

All of the seeds were sown during the third week of May 2000. The plots were revisited weekly to note if germination had occurred. Germinant emergence began in mid June and the first census was done on June 25th, 2000. The second and third censuses were done on July 20th and September 4th, 2000 respectively where newly emerged individuals and mortality were recorded. The percentage of germinating seeds was calculated as the quotient of the germinable portion of seeds sown by the number of emerged individuals on each sub-quadrat. The mean percent germination value for each seedbed under a given harvest intensity was based on the percent germination rate of 16 replicates (24 for the clearcut treatments).

All statistical analyses involving germination rates were completed using arcsine-transformed data. First, a model I one-way Anova was used to determine differences between harvest intensities. In order to determine if seedbed suitability changes under differing cover classes, a separate Anova was performed for each seedbed type. If a significant difference was found, a post-hoc Tukey test was then performed to determine which treatments differed significantly from one another. Next, the effects of seedbed type were analyzed using a model I one-way Anova, and separated by harvest intensity.

An analysis between species often allows one to infer the probable causes of the observed patterns within a single species especially when a number of species of differing seed sizes (i.e. different germinant sizes, (e.g. Wright et al. 1998; Seiwa and Kikuzawa 1996)) are used. Hence, a pairwise t-test was used to determine differences between the two species. Differences were tested for each seedbed type under all of the harvest intensities. Next, with the effects of seedbed removed (i.e. lumping all seedbed types), the differences between the two species were then determined across all of the harvest intensities. Finally, species differences in germination rates across the three seedbed types were examined, where harvest intensity effects were removed.

First-summer survival analyses

From the July to September censuses mortality rates of emerged germinants were recorded. These data are represented in terms of survival for consistency with the literature. Plots where no germination occurred were removed from the analyses thus reducing the number of replicates.

The same analyses discussed above for mean percent germination were done here with the exception that non-parametric tests were used. The one-way Anova was substituted with the Kruskal-Wallis test, and the post hoc Tukey test with the Bonferroni correction test. The latter reduces the error rate ($\alpha=0.05$) by the number of groups in the pairwise comparison (5%/n, where n in this case was 5 for comparisons between harvest intensities (4 harvesting treatments plus the ccns treatment), and 3 for the comparison between seedbed types). The pairwise t-test comparison was replaced with the non-parametric Wilcoxon paired t-test.

Cumulative survivorship analyses

The cumulative first year survivorship values were obtained as the product of the percent germination and first summer survival values. The statistical analyses were performed on arcsine transformed data in order to conform to the statistical assumptions of normality and homogeneity of variances, and followed the same analyses as discussed for the germination data.

All statistical analyses were performed with SPSS for Windows, 10.1.

Results

The effects of harvest intensity and seedbed type on tree seed regeneration are analyzed below in three separate sections. I begin with the effects on the germination rates for both species, followed by the effects on survival during the first summer, and conclude with the effects on cumulative survivorship. Each section begins with an analysis of the effects of 1) harvest intensity 2) seedbed type, with fir and spruce considered separately. I conclude with a comparison between fir and spruce with respect to the effects of harvest intensity and seedbed type on germination, survival and cumulative survivorship.

Percent germination

i) Effects of harvest intensity

For all three seedbed types harvest intensity significantly affected the mean germination rates of both fir and spruce seeds (Table 3). For fir, the germinability of seeds sown in the clearcut treatment without slash (ccns) treatment was significantly lower than at all other harvest intensities, on all seedbeds (Fig. 1a; Table 4), with the exceptions of seeds sown in the 1/3rd treatment on mineral soil and seeds on O_f in the clearcut with slash (ccs) treatment which did not differ significantly from the germination rates of the ccns treatment.

Spruce seeds sown under full canopy on mineral soil, had significantly higher germination rates than those sown in both clearcut treatments (Fig 1b; Table 4). Seeds on humus at all harvest intensities had significantly higher germination values than those from the ccns treatment. Furthermore, on humus soil, germination rates in the controls were significantly higher than those in the ccs treatment. On O_f, only the control showed a significantly higher germination rate than the ccns treatment ($p= 0.001$). Unlike fir, however, the germination rate of spruce seeds showed a clear decline as a function of increasing cutting intensity (Fig. 1b) for all seedbeds considered.

ii) Effects of seedbed type

With the exception of the 1/3rd partial cut, germination rates for fir seeds were significantly affected by seedbed type under all harvest intensities (Table 5). For spruce seeds, under all harvest intensities, except the 2/3rd treatment, seedbed type had a significant effect on germination rates.

With the exception of the ccs treatment, germination of fir seeds was significantly higher on mineral soil than on humus or O_f (Fig. 1a; Table 6). For fir seeds sown in the ccs treatment, germination was significantly higher on mineral soil than on O_f seedbeds only. Under all harvest intensities except the 2/3rd and ccns treatments germination of spruce seeds was significantly higher on mineral soil and humus than on O_f seedbeds, but there was no significant difference between mineral and humus seedbeds (Fig. 1b; Table 6).

iii) Between species differences and general trends

There were no significant differences in germination rates between species when seeds were sown in the ccns treatment for any of the seedbeds. Under full canopy, germination of fir seeds was significantly higher than spruce but only for seeds sown on mineral soil (p=0.03). For the 1/3rd treatment, germination of fir seeds was higher than that of spruce on O_f (p=0.05). On mineral soil, for seeds sown in the 2/3rd partial cut, germination of fir was significantly higher than for spruce (p<0.001). Finally, for the ccs treatment, germination of fir seeds was higher than for spruce on both mineral and humus soil (p=0.018 and 0.007 respectively).

When seedbed effects are removed, the general effects of harvest intensity can be observed. There is a clear decline in spruce germination as a function of increasing harvest intensity. Conversely, fir is not affected by harvest intensity except in the ccns treatment). Under the 2/3rd and ccs treatments germination of fir seeds were significantly higher than that of spruce seeds (p=0.001 and < 0.001 respectively) (Fig. 2).

When germination rates between the two species on different seedbed types with harvest intensities were lumped, no significant difference was observed on humus soil, but there is a large difference on mineral soil and on O_f seedbeds, where fir performs better than spruce (p=0.001 and 0.002 respectively) (Fig. 3).

Survival during the first summer

i) Effects of harvest intensity

Harvest intensity had a significant effect on the survival of spruce germinants on mineral and O_h seedbeds, where survival was poor on the control sites, whereas germinant survival on O_f seedbeds was not affected by harvest intensity. The same analysis for fir showed to significantly affect survival only for those germinants established on mineral soil (Table 7). However, a post hoc Bonferroni test failed to show a significant difference between any of the harvest intensities on mineral soil. Nevertheless, the control treatment engendered the lowest survival both on mineral and O_f seedbeds (Fig. 4a). The Bonferroni test performed for spruce germinants on mineral soil showed that the control treatment engendered a significantly lower survival rate than all other harvest treatments (Fig. 4b; Table 8). On humus soil, both the control and the 1/3rd treatments were significantly lower than survival rates in the ccns treatment. Moreover, on humus, survival on the control treatment was significantly lower that the 2/3rd partial cut .

ii) Effects of seedbed type

For fir germinants, under any of the harvest intensities, seedbed type had no significant effects on survival rates (Fig. 4a). Conversely, for spruce germinants under the 1/3rd treatments, seedbed type significantly affected survival rates (p=0.02), where germinants on mineral soil had significantly higher survival rates than either those on humus or O_f seedbeds (p=0.01 and 0.002 respectively) (Fig. 4b). In conclusion, once past the germination stage, during the first year, seedbed type has only a minimal effect on survival within a single species.

iii) Between species differences and general trends

Only under the 1/3rd partial cut on O_f soil and on mineral soil in the ccs treatment did we find a significant difference between survival rates of the two species ($p=0.042$ and 0.028 respectively).

However, when we remove the effects of seedbed and allow harvesting intensity to be the only independent variable, we find that under the control and the 1/3rd treatments fir enjoyed a significantly higher survival rate than spruce during the first summer ($p=0.017$ and 0.003 respectively) (Fig. 5).

Next, when the effects of harvesting intensity are removed and the effects of seedbed type are considered alone, fir had higher survival rates on both mineral and O_f seedbeds ($p= 0.002$ and 0.005 respectively) (Fig. 6).

Cumulative survivorship

i) Effects of harvest intensity

Survivorship in the 1/3rd and 2/3rd treatments to be significantly higher than in ccns ($p= 0.042$ and 0.032 respectively) (Fig. 7a). Differences in mean cumulative survivorship values for spruce, between the different harvest intensities, were not observed for any of the seedbeds (Fig. 7b).

ii) Effects of seedbed type

Seedbed type had a significant effect on cumulative survivorship, for both species, under all harvest intensities (Table 9). In fir, the control, 1/3rd and 2/3rd treatments, mineral soil engendered significantly higher survivorship values than either the O_h or O_f (Fig. 7a; Table 10). No significant differences between seedbeds were detected with the Tukey test for the ccs and ccns treatments. In spruce, survivorship on mineral soil was consistently significantly higher than on O_f (Fig. 7b; Table 10). Furthermore, under the 2/3rd treatment, spruce survived better in humus than in organic seedbeds.

iii) Between species differences and general trends

On organic seedbeds, cumulative survivorship was significantly different between spruce and fir under all of the harvest intensities($p<0.032$), except for the ccns treatment. On mineral soil, all but the 1/3rd and ccns treatments showed fir to have significantly higher cumulative survivorship than spruce($p<0.028$). On humus, only under the ccs treatment was the survivorship of fir significantly higher than spruce ($p=0.013$).

When the effects of seedbed were removed fir seedlings showed a significantly higher mean cumulative survivorship than those of spruce (figure 8). Next, when the effects of harvest intensity are removed, all of the seedbeds show a significantly higher receptivity towards fir.

Discussion

Germination

i) Effects of harvest intensity

The presence of a light gradient, created by the different harvest intensities, affected the germination rates of both spruce and fir. Indeed, as shown in previous studies (e.g. McLaren and Janke 1996; Duchesneau and Morin 1999; Wright et al. 1998), emergence increased as a function of decreasing canopy cover. In this study, the affects were more pronounced for spruce, but only for seeds sown on mineral and O_h soil. The organic substrate (O_f) essentially muted any effects of harvest intensity. This was not surprising given the higher susceptibility of this substrate to desiccation under higher light regimes. However, under a reduced light environment moisture levels can remain high, thereby reducing surface drying (Wright et al. 1998). Thus, under such treatments the lower germination rates suggest that poor soil-root contact plays a role in the reduced establishment. Low and intermediate light environments did not significantly affect germination of fir. Only clearcut plots with no slash differed significantly from the other treatments with germination rates being significantly reduced.

Germination of fir seeds in clearcuts was increased by the addition of slash whereas that of spruce was not. This suggests that the amount of light intercepting the soil surface was reduced by the addition of slash on clearcut plots. Light measurements were not taken beneath the slash. Only an estimate of percent cover was made and thus it can not be clearly established whether or not seeds were subjected to greater or less light than that in the 1/3rd or 2/3rd harvest intensities. It is also possible that, in some instances, a number of seeds may have germinated, quickly died, and not been censused. Interspecific differences observed with the slash treatment suggest that the smaller spruce radicle is more prone to desiccation than fir and thus, even under intermediate light levels will experience higher mortality than fir germinants. As such, germination rates were found to be lower but to some degree this finding may be linked to elevated early mortality.

ii) Effects of seedbed type

Under all harvest treatments both species had higher germination rates on mineral soil. Moreover, the receptivity of both humus and mineral soil for spruce decreased as a function of canopy openness, whereas the same did not apply for O_f. Seedbed receptivity for fir remained constant across all harvest intensities until full light conditions were introduced. Seiwa and Kikuzawa (1996) found that larger seeded temperate species (e.g. *Quercus* and *Acer*) have higher germination rates on organic seedbeds than smaller seeded species (e.g. *Betula*, *Alnus*). Similarly, Knapp and Smith (1982) found a greater proportion of *Abies lasiocarpa* germinating on organic substrates than *Picea englemanni* (42% vs. 5% respectively). Similarly my data showed fir, the larger-seeded species, performed better on O_f than spruce.

Contrary to the literature, however, spruce germinated poorly on mineral soil in my study. The mineral soil of the study site is 76.5 % clay, 19.5% silt and 4% sand (S.

Brais, pers. comm.). Although previous studies have not defined the exact composition of the mineral soil horizon, a few studies have noted (mainly anecdotal) the adverse effects of clay soils. Nowhere has there been a study that quantifies the receptivity of mineral seedbeds differing in composition of sand, silt and clay. Interspecific differences in germination rates are most prevalent on mineral soil under all harvest intensities. Previous research has demonstrated that mineral soil confers the most hospitable environments for germination (Timoney and Peterson 1996; Feller 1998). Intuitively then, germination rates of spruce should more closely resemble those of fir (as they do with humus). It appears that clay poses a mechanical obstruction to radicle penetration (Zisa et al. 1980; Béland et al. 1999; Galipeau et al. 1997). Moreover, an increase in light radiation further hardens clay soils (Galipeau et al. 1997). A stand reconstruction study, 68 years following fire, in southern boreal Quebec (Galipeau et al. 1997) found that the basal area of spruce was lower for sites occurring on clay pockets as opposed to till sites. Conversely, basal area of fir was not affected, suggesting that the relatively smaller size of spruce seeds is more detrimental to germination success. The impenetrable character of clay soil becomes of paramount importance when subsequent survival is examined.

Subsequent survival

i) Effects of Harvest intensity

Survival of spruce during the first summer increased as a function of increasing harvest intensity only for germinants established on mineral and humus seedbeds. When the effects of seedbed were removed and harvest were intensity considered alone, the reverse trend from germination was observed. Fir survival was not significantly reduced in full light conditions as would be expected from the literature (e.g. McLaren and Janke 1996; Duchesneau and Morin 1999).

Given that the results of this study are based on survival during the first summer, growth rate measurements would have been premature. From a myriad of leaf level and field experiments, we can expect growth rates to follow one of two patterns. In several studies, growth rates of planted seedlings begin to approach an asymptote at 40% full light (Logan 1969; Lieffers and Stadt 1994; Coates 2000) with annual height increments equal to those in full light conditions. Conversely, other research shows continued growth all the way to full light (Eis 1970; Coates and Burton 1999).

ii) Effects of seedbed type

For humus and organic substrates there was no significant difference in subsequent survival for either species. However, the receptivity for establishment of fir was consistently less for humus than for O_f (although this was not statistically significant), and this was most pronounced in the ccns treatment. Knapp and Smith (1981) reported that *A. lasiocarpa* seedling densities decreased more uniformly than those of *P. engelmanni* as a function of increasing solar radiation. It is possible then that the drop may be an artifact of increased surface desiccation on humus: that is, leaf litter may retard evaporative water loss on O_f seedbeds. It follows then that this same pattern may be expected for spruce, however, this was not observed. One possible explanation is perhaps the inherent inability to develop roots rapidly in spruce.

In this study there was a minimal increase in survival for spruce germinants on mineral soil, under the 1/3rd treatment only. Mineral soil substrates did not significantly increase survival of fir under any harvest intensity. Previous studies, suggest that mineral soil consistently engenders higher rates of first year survival than organic seedbeds (not including rotten logs and sphagnum) (Parker et al 1997; DeLong et al. 1997; Feller 1998; Timoney and Peterson 1996; McLaren and Janke 1996). The mineral soil from this research area consistently became waterlogged following a heavy rainstorm (pers. obs.). This in effect creates anaerobic conditions causing poor aeration of soil resulting in elevated mortality of established seedlings (Galipeau et al. 1997). Eis (1970) found that seedlings planted on clay soils had a weak and poorly formed taproot with a root system mainly concentrated between the organic horizon and the clay horizon. Moreover, the author reports that during periods of prolonged waterlogging, there seemed to be a " continuous dieback of downward penetrating roots" causing seedlings to depend solely on the network of surface roots. Elevated first summer and overwinter mortality rates were attributed to this effect. Germinants established on mineral soil from this study could not form a root system into the organic strata (given that the organic surface was stripped away). As such, overwinter mortality rates are likely to be higher than would be expected for this seedbed type.

Cumulative survivorship

i) Effects of harvest intensity

At the germination stage, increased harvesting intensity diminished the emergence of spruce and fir. Survival, however, was improved by lower harvest rates. Consequently, the dramatic effects of harvest intensity observed on both survival and germination are muted when we look at cumulative survivorship.

Mortality experienced during the first year of establishment is far more severe than at any other stage of development (precluding of course disturbances) (Cayford 1963; Fleming and Mossa 1994). For fir intermediate harvesting levels conferred the highest cumulative survivorship values. The extremes on the control and clearcut without slash treatment impacted negatively on cumulative survivorship, particularly for the clearcut without slash areas. With the addition of slash, seedbeds were likely able to retain higher levels of surface moisture. This retention of water, however, was not sufficient for spruce, which requires a greater reduction in solar radiation at the germination stage and increased light for subsequent survival. In conclusion, the cumulative survivorship of spruce was highest at low light intensities, a trend influenced by the success of establishment observed at the germination stage. In other words, the increase in survival in high light environments was not strong enough to compensate for the low emergence rates under these same conditions.

Clearcut conditions also promote the growth of competitors, which have the potential to out-grow shade tolerant conifers. As such, a partial canopy in subsequent years has been suggested to be an ideal growing environment (Osawa 1994; Cote and Belanger 1991). Subsequent survival is also dependent on humidity levels surrounding the seedling. Reduced humidity levels in cut-blocks will cause stomatal closure to prevent evaporative loss (Marsden et al. 1996). Thus, the retention of at least 30% of the canopy would maintain appreciable levels of humidity during the critical stage of early plant development (Marsden et al. 1996).

ii) Seedbed effects

For both spruce and fir, mineral soil offered the highest cumulative survivorship, followed by O_h and O_f. The patterns observed were mostly influenced by the effects at the germination stage, then subsequent survival. The elevated germination and survival of fir relative to spruce on mineral soil seedbeds results in increased cumulative survivorship. This further supports the notion that clay could be responsible for reduced germination and survival of spruce. Constant swelling and drying of clay during repeated wetting and drying would presumably further damage root systems of the established seedlings during subsequent years of growth.

The negative effects of clay have received very little study, but as observed in this study, clay can have deleterious persistent effects on early survivorship especially for small seeded species. Harvest intensity, as seen here does play a critical role in germination and survival. However, because of the reverse effects of harvesting intensity at the two stages, cumulative survivorship essentially mutes the effects of harvest with the exception of rendering intermediate canopy cover classes as the most hospitable. The practice of delimbing on site (effectively creating slash seedbeds) will benefit larger seedbed species such as fir that can make more efficient use of low light, but will not benefit smaller seeded species, which require low light for germination and high light for successful establishment.

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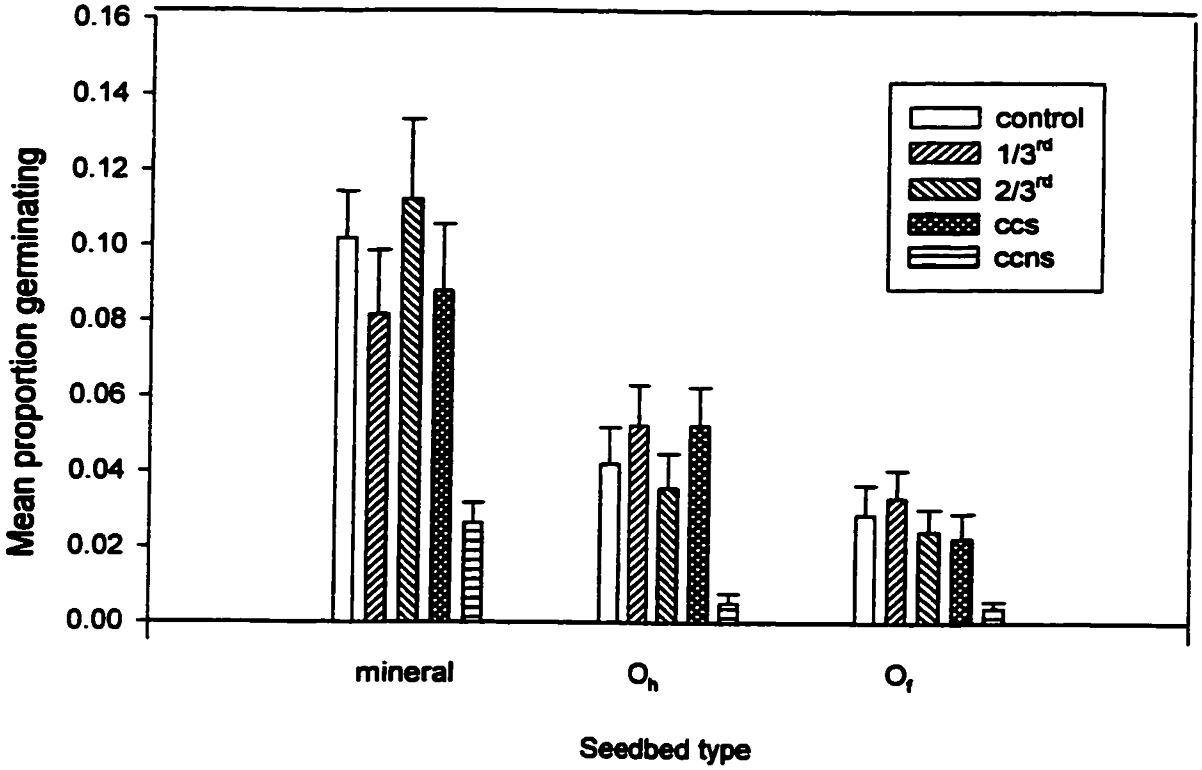
Figure 1(a). Proportion of fir seeds germinating across all harvest intensities for each seedbed type. (Bars represent ± 1 SE of the mean).



(b) Proportion of spruce seeds germinating across all harvest intensities for each seedbed type. (Bars represent ± 1 SE of the mean).

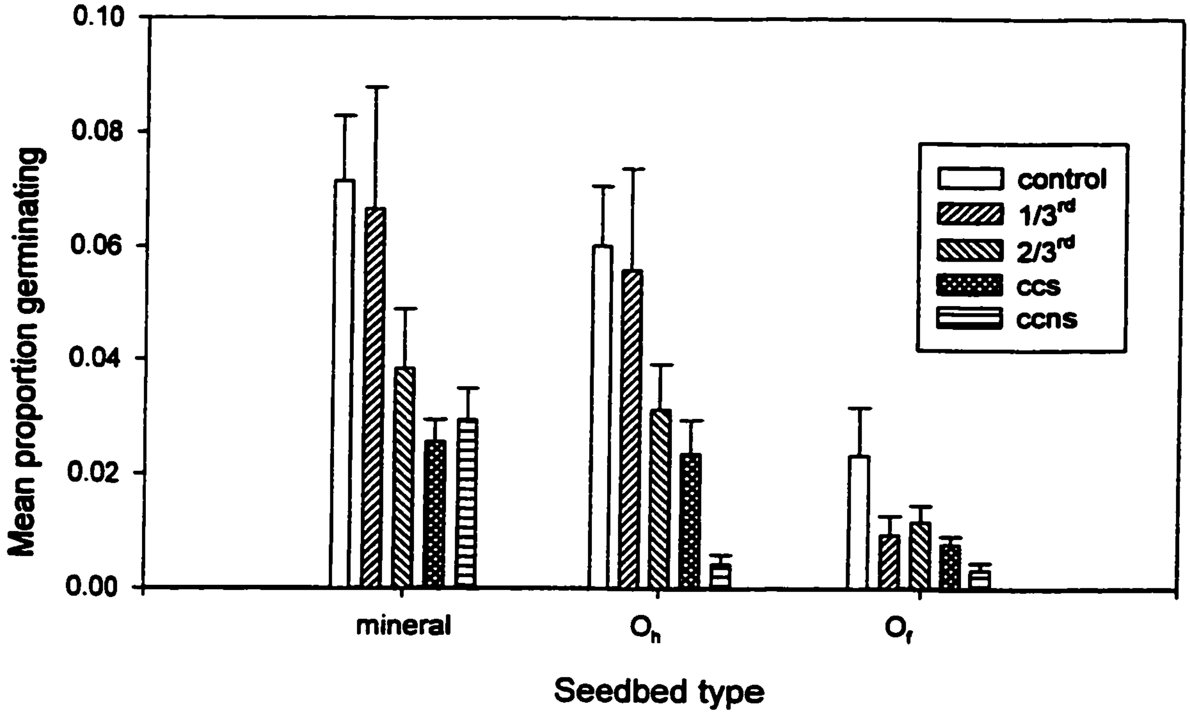
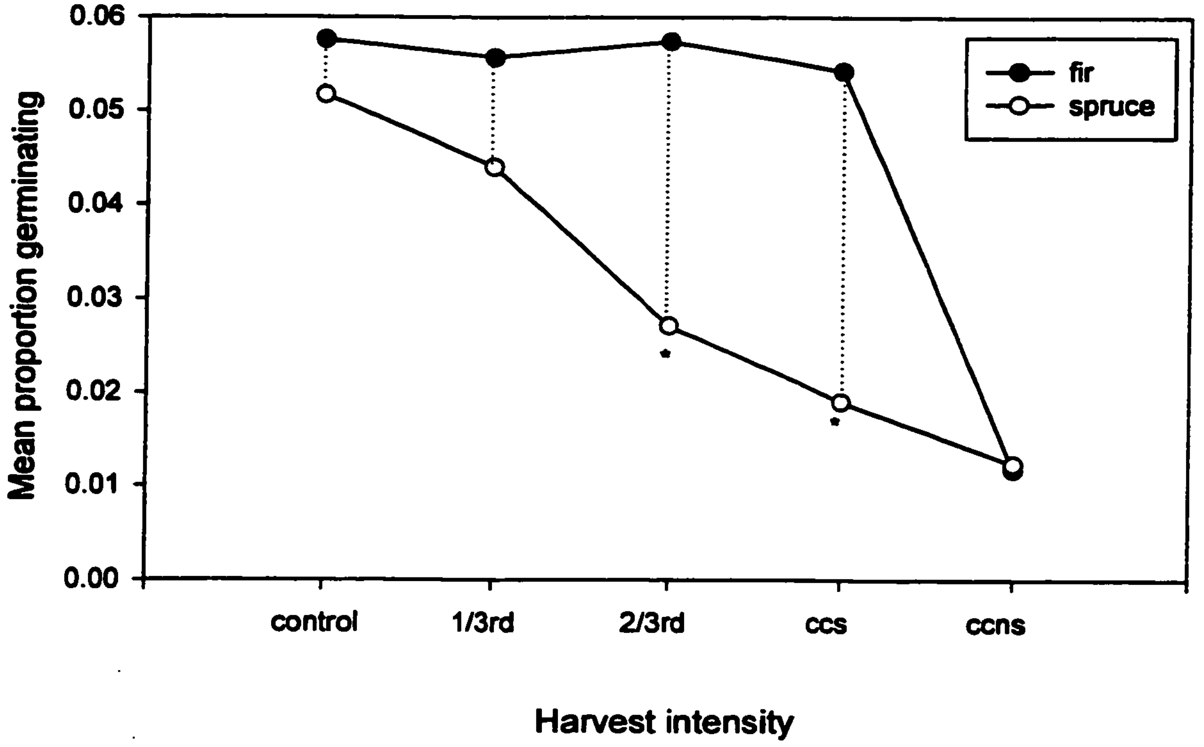
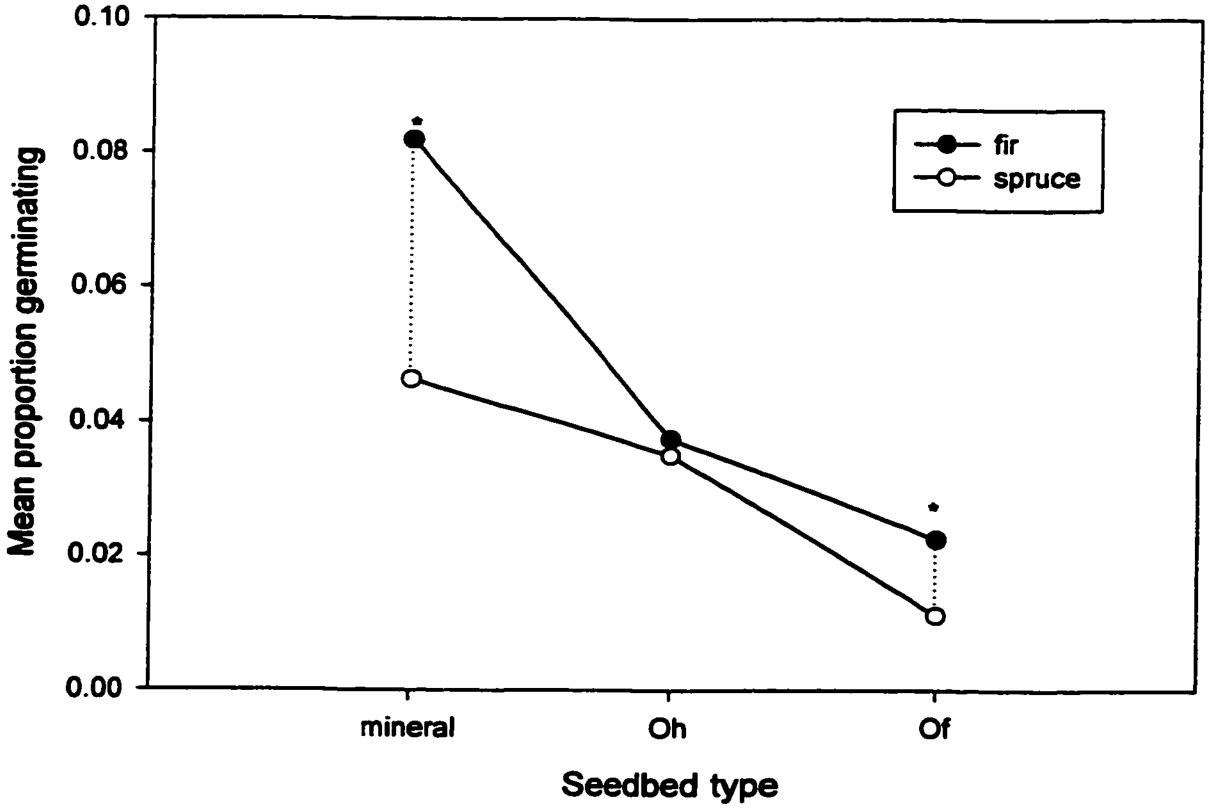


Figure 2. Differences between fir and spruce in the mean proportion of seeds germinating across all harvest intensities with all seedbeds lumped.



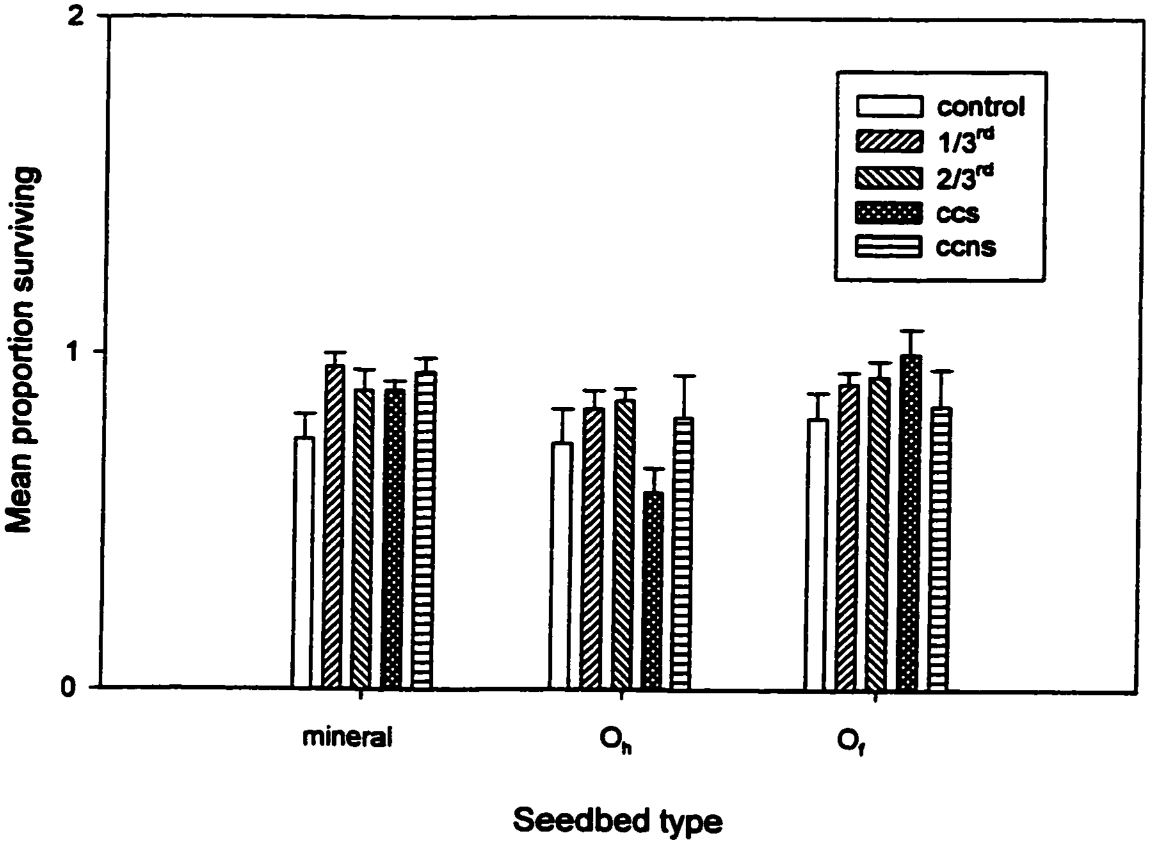
(* indicates a significant difference between species (<0.05))

Figure 3. Differences between fir and spruce in the mean proportion of seeds germinating on each seedbed type with harvest intensities lumped.



(* indicates a significant difference between species (<0.05))

Figure 4(a).Proportion of fir germinants surviving across all harvest intensities for each seedbed type. (Bars represent ±1 SE of the mean)



(b) Proportion of spruce germinants surviving across all harvest intensities for each seedbed type. (Bars represent ±1 SE of the mean)

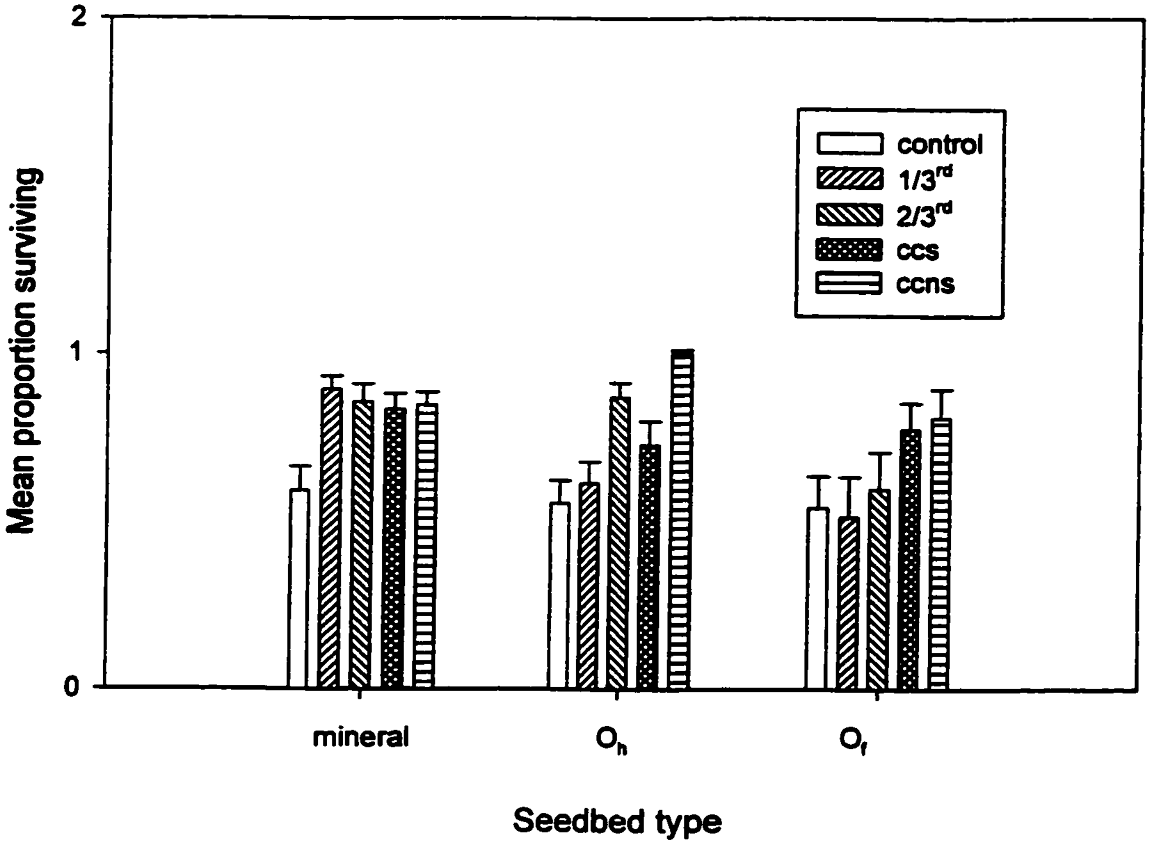
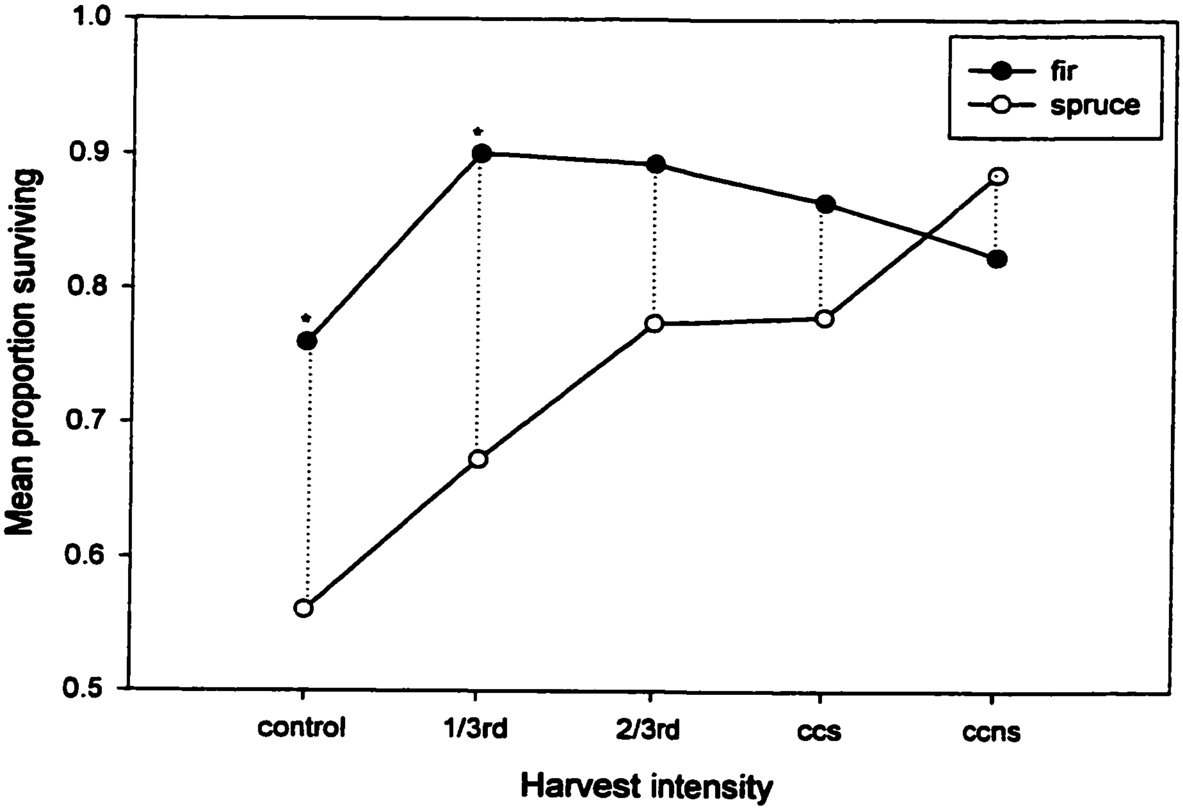
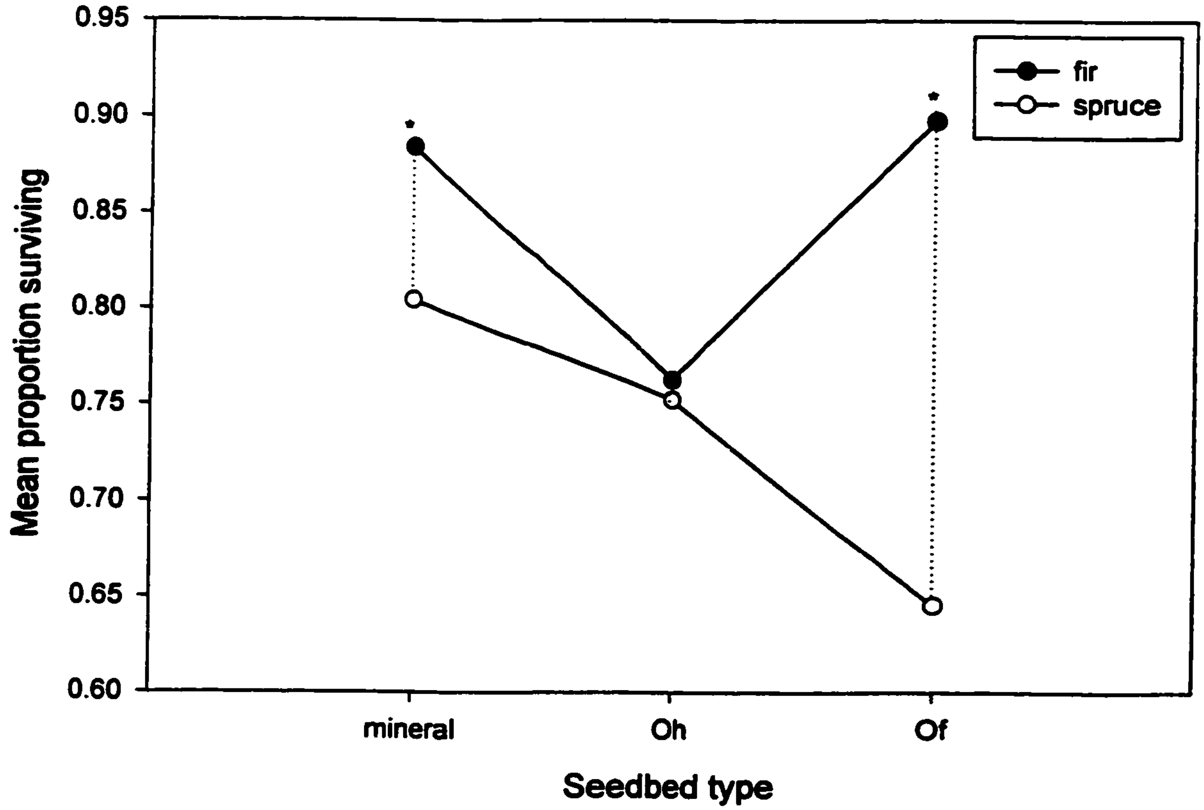


Figure 5. Differences between fir and spruce in the mean proportion of germinants surviving across all harvest intensities, with seedbeds lumped.



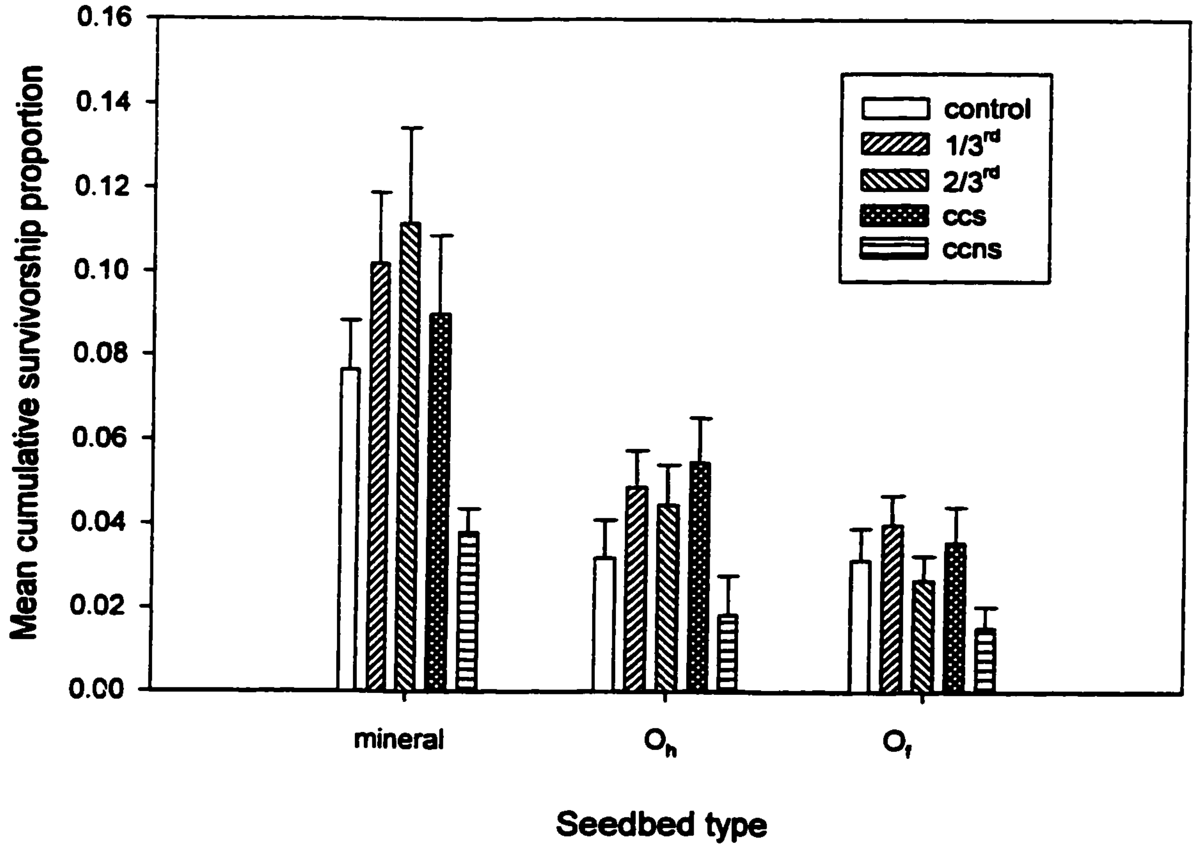
(* indicates a significant difference between species (<0.05))

Figure 6. Differences between fir and spruce in the mean proportion of germinants surviving on each seedbed type with harvest intensities lumped.



(* indicates a significant difference between species (<0.05))

Figure 7(a). Cumulative survivorship proportion of fir across all harvest intensities for each seedbed type.
(Bars represent ±1 SE of the mean).



(b) Cumulative survivorship proportion of spruce across all harvest intensities for each seedbed type. (Bars represent ±1 SE of the mean).

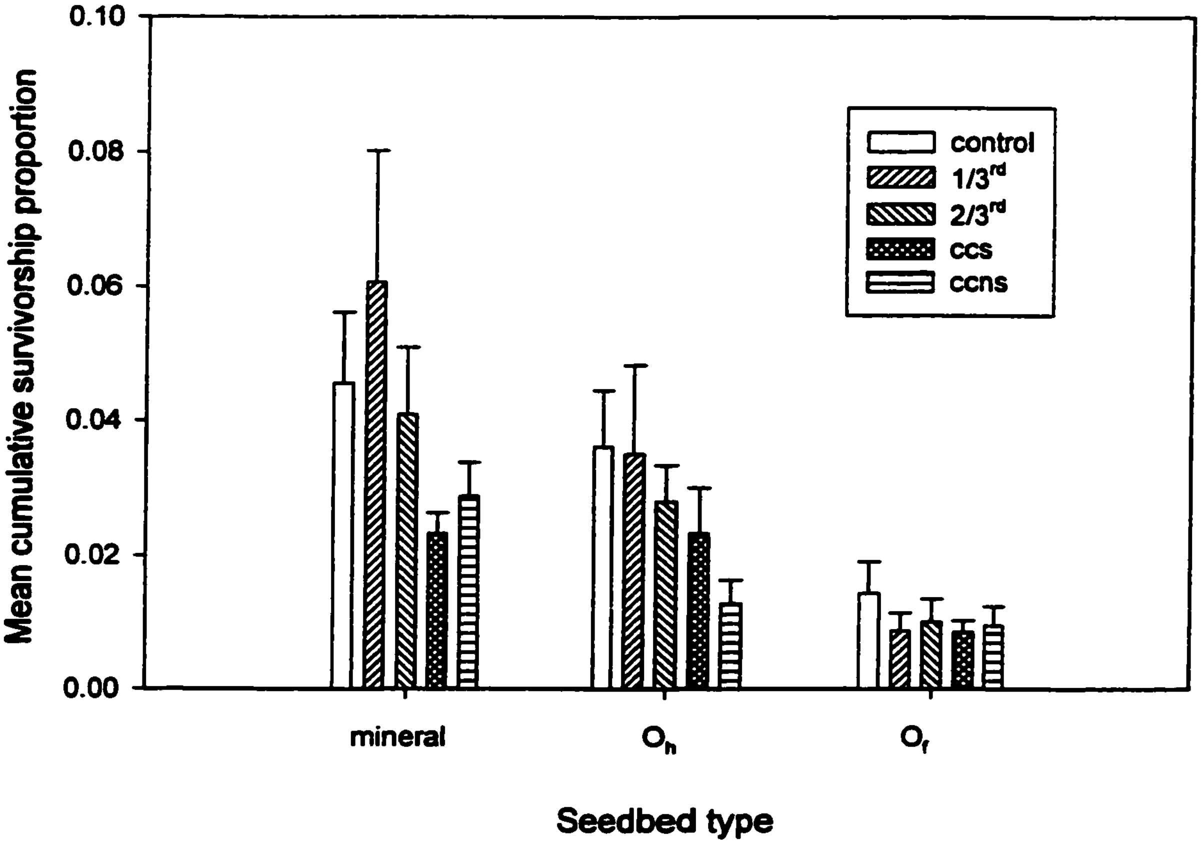
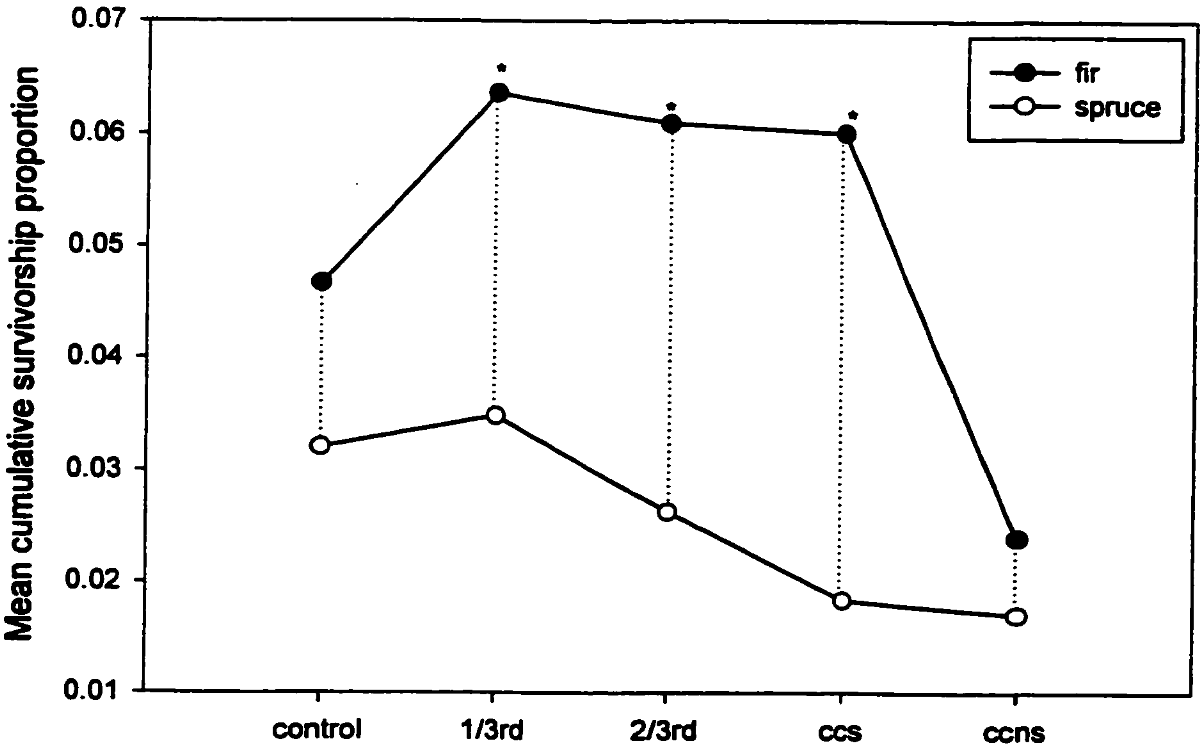
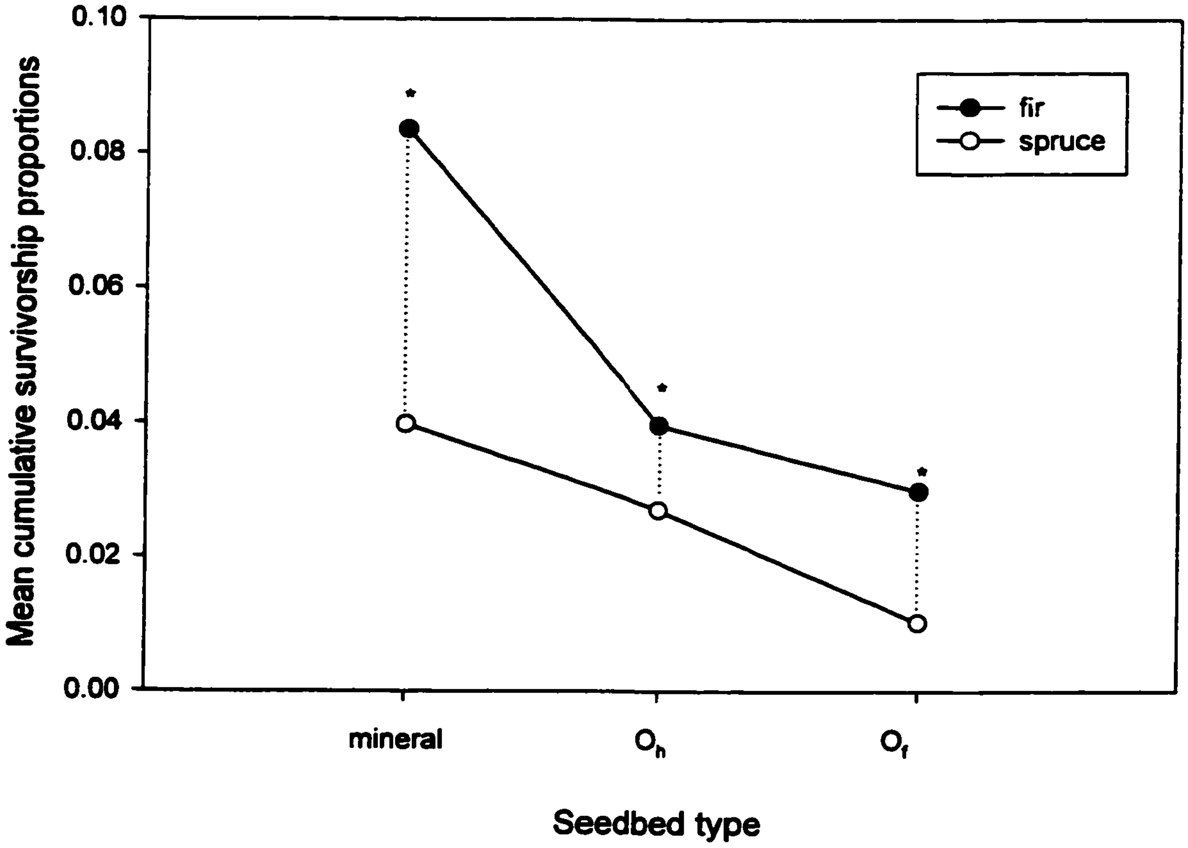


Figure 8. Differences between fir and spruce in the mean cumulative survivorship proportion across all harvest intensities with seedbeds lumped.



(* indicates a significant difference between species (<0.05))

Figure 9. Differences between fir and spruce in the mean cumulative survivorship proportion on each seedbed type with harvest intensities lumped.



(* indicates a significant difference between species (<0.05))

Table 1. Pre- and post-harvest tree densities ($m^2 ha^{-1}$) for Blocks 1,2 and 3.

Block	**Treatment**	**Pre-harvest**	**Post-harvest**
1	Control	45.1	45.1
	1/3rd	43.9	32.2
	2/3rd	39.2	16.5
	Clearcut	46.7	0
2	Clearcut	37.2	0
3	Control	42.4	42.4
	1/3rd	38.5	29.2
	2/3rd	39.7	16.8
	Clearcut	48.2	0

Table 2. Number of fir (F) and spruce (S) seeds sown on mineral, humus (O_h) and organic (O_f) seedbeds under each of the harvest intensities. The seeding rate applies to all three blocs.

	Control		**1/3rd**		**2/3rd**		**ccs**		**ccns**	
	F	S	F	S	F	S	F	S	F	S
mineral	50	200	50	200	50	200	100	200	100	200
O_h	200	200	200	200	200	200	200	200	200	200
O_f	200	200	200	200	200	200	200	200	200	200

Table 3. Results from one-way ANOVA analyses on the effects of harvest intensity on the mean germination values of fir (F) and spruce (S) performed for each seedbed type.

	Df	F	p-value
(F) mineral	4	6.338	<0.001
O_h	4	9.902	<0.001
O_f	4	5.377	0.001
(S) mineral	4	4.383	0.003
O_h	4	13.069	<0.001
O_f	4	4.817	0.001

Table 4. Results obtained from Tukey analyses for comparisons in mean germination values between harvest intensity (presented for each seedbed type) for fir and spruce. Included is the difference in the mean proportion germinating.

Fir	**Difference**	**p-value**	**Spruce**	**difference**	**p-value**
mineral			mineral		
ccns - control	-0.191	0.001	control - ccs	0.111	0.008
2/3rd	-0.189	0.001	ccns	0.107	0.012
ccs	-0.118	0.035	O_h		
O_h			ccns - control	-0.194	<0.001
ccns - control	-0.156	<0.001	1/3rd	-0.168	<0.001
1/3rd	-0.176	<0.001	2/3rd	-0.118	0.002
2/3rd	-0.122	0.006	ccs	-0.093	0.008
ccs	-0.165	<0.001	ccs - control	-0.101	0.011
O_f			O_f		
ccns - control	-0.106	0.01	ccns - control	-0.092	0.001
1/3rd	-0.125	0.001			
2/3rd	-0.104	0.011			

Table 5. Results from one-way ANOVA analyses on the effects of seedbed type on the mean germination values of fir (F) and spruce (S), performed for each harvest intensity.

	df	F	p-value
(F) control	2	14.65	<0.001
1/3rd	2	1.93	0.156
2/3rd	2	10.68	<0.001
ccs	2	6.40	0.003
ccns	2	11.79	<0.001
(S) control	2	8.83	0.001
1/3rd	2	7.78	0.001
2/3rd	2	3.15	0.052
ccs	2	7.28	0.001
ccns	2	25.66	<0.001

Table 6. Results obtained from Tukey analyses for comparisons in mean germination values between seedbed types (presented for each harvest intensity) for fir and spruce. Included is the difference in the mean proportion germinating.

Fir	**Difference**	**p-value**
Control		
min - O_h	0.132	0.001
O_f	0.183	0.001
$2/3^{rd}$		
min - O_h	0.163	0.001
O_f	0.182	<0.001
Ccs		
min - O_f	0.143	0.002
Ccns		
min - O_h	0.097	<0.001
O_f	0.098	<0.001

Spruce	**Difference**	**p-value**
Control		
O_f - min	-0.137	0.001
O_h	-0.108	0.008
$1/3^{rd}$		
O_f - min	-0.156	0.002
O_h	-0.136	0.008
Ccs		
O_f - min	-0.075	0.001
O_h	-0.057	0.02
Ccns		
min - O_h	0.115	<0.001
O_f	0.121	<0.001

Table 7. Results from Kruskal-Wallis analysis on the effects of harvest intensity on the mean survival values of fir and spruce performed for each seedbed type.

	χ^2	**Df**	**p-value**
(Fir) min	13.99	4	0.007
O_h	1.06	4	0.901
O_f	2.71	4	0.608
(Spruce) min	24.96	4	<0.001
O_h	32.44	4	<0.001
O_f	8.43	4	0.07

Table 8. Results obtained from Bonferonni analyses for comparisons in mean survival values between harvest intensity (presented for each seedbed type) for *spruce*. (No significant differences were observed for fir). Included is the difference in the mean proportion surviving.

		difference	**p-value**
Mineral			
control -	1/3rd	-0.304	0.003
	2/3rd	-0.298	0.002
	ccs	-0.256	0.006
	ccns	-0.306	<0.001
O_h			
control -	2/3rd	-0.313	0.007
	ccns	-0.438	<0.001
1/3rd -	ccns	-0.376	0.001

Table 9. Results from one-way ANOVA analyses on the effects of seedbed type on the mean cumulative survivorship values of fir and spruce performed for each harvest intensity.

		df	**F**	**p-value**
(Fir)	control	2	6.19	0.005
	1/3rd	2	8.38	0.001
	2/3rd	2	7.57	0.002
	ccs	2	3.43	0.04
	ccns	2	3.51	0.047
(Spruce)	control	2	3.42	0.042
	1/3rd	2	3.73	0.033
	2/3rd	2	5.34	0.009
	ccs	2	4.55	0.015
	ccns	2	4.71	0.019

Table 10. Post-hoc Tukey results on the effects of seedbed on fir and spruce cumulative survivorship values. Results are separated by harvest intensity.

Fir	Difference	p-value
control		
min - Oh	0.114	0.006
Of	0.097	0.037
1/3rd		
min - O_h	0.104	0.006
O_f	0.122	0.002
2/3rd		
min - O_h	0.109	0.044
O_f	0.158	0.002

Spruce	difference	p-value
control		
min - O_h	0.088	0.041
1/3rd		
min - O_h	0.132	0.026
2/3rd		
min - O_f	0.1	0.01
O_h - O_f	0.081	0.043
ccs		
min - O_f	0.064	0.012
ccns		
min - O_f	0.071	0.031